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New Cenozoic Muricidae (Mollusca: Gastropoda) from Europe

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ABSTRACT

This paper introduces new European Cenozoic muricids coming mainly from different French basins (Paris, Aquitaine, Loire and Normandy). Firstly, 24 species are described: *Muricopsis pontileviensis* n. sp., *Muricopsis neraudeaui* n. sp., *Favartia jansseni* n. sp., *Dermomurex* (*Gracilimurex*) *ligerianus* n. sp., *Trubatsa ganensis* n. sp., *Trubatsa calviniacensis* n. sp., *Timbellus magnificus* n. sp., *Timbellus occidentalis* n. sp., *Timbellus calciacus* n. sp., *Timbellus longicanalis* n. sp., *Timbellus magnei* n. name (for *Murex trigonus* Rouault, 1850, not Gmelin, 1791), *Timbellus sixi* n. sp., *Timbellus curvispina* n. sp., *Timbellus radulfiensis* n. sp., *Timbellus submicropterus* n. sp., *Ponderia remyi* n. sp., *Pterynotus* (*Pterymarchia*) *gaasensis* n. sp., *P.* (*Pterymarchia*) *pelouatensis* n. sp., *Textiliomurex chodmonensis* n. sp., *Flexopteron constantinense* n. sp., *F. liancurtense* n. sp., *Crassimurex* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp., *Nucellopsis parisiensis* n. sp. and *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp. Secondly, four genera and one subgenus are described: *Paleochicoreus* Merle, n. gen. (type species: *Chicoreus* (*Phyllonotus*) *initialis* Vokes, 1990), *Beyregrex* Merle, n. gen. (type species: *Murex pereger* Beyrich, 1854), *Pseudotrophonopsis* Merle, n. gen. (type species: *Buccinum defossum* Pilkington, 1804), *Pronucellopsis* Merle, n. gen. (type species: *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp.) and *Crassimurex* (*Pliocrassimurex*) n. subgen. (type species: *Crassimurex* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp.). Thirdly, based on a phylogenetic analysis one new subfamily is erected for a clade of fossil genera that are not closely related to extant subfamilies: Nucellopsinae Merle, n. subfam. (type genus: *Nucellopsis* Merle, 2005c) including *Nucellopsis* and *Pronucellopsis* Merle, n. gen. In addition, a neotype for *Murex tripteroides* Lamarck, 1822, *Murex tricarinatus* Lamarck, 1803 and a lectotype for *Murex fusoides* Deshayes, 1865 and *Murex sandbergeri* (Hörnes, 1856) are designated.

KEY WORDS
Muricidae,
Europe,
Cenozoic,
phylogeny,
neotypifications,
lectotypification,
new combinations,
new name,
new subfamily,
new genera,
new subgenus,
new species.

RÉSUMÉ

Muricidae nouveaux (Mollusca: Gastropoda) du Cénozoïque d'Europe.

Cet article présente de nouveaux Muricidae Rafinesque, 1815 du Cénozoïque d'Europe provenant principalement de différents bassins français (bassins de Paris, d'Aquitaine, de la Loire et de Normandie). Premièrement, 24 espèces sont décrites : *Muricopsis pontileviensis* n. sp., *Muricopsis neraudeaui* n. sp., *Favartia jansseni* n. sp., *Dermomurex* (*Gracilimurex*) *ligerianus* n. sp., *Trubatsa ganensis* n. sp., *Trubatsa calviniacensis* n. sp., *Timbellus magnificus* n. sp., *Timbellus occidentalis* n. sp., *Timbellus calciacus* n. sp., *Timbellus longicanalis* n. sp., *Timbellus magnei* n. name (pro *Murex trigonus* Rouault, 1850, non Gmelin, 1791), *Timbellus sixi* n. sp., *Timbellus curvispina* n. sp., *Timbellus radulfiensis* n. sp., *Timbellus submicropterus* n. sp., *Ponderia remyi* n. sp., *Pterynotus* (*Pterymarchia*) *gaasensis* n. sp., *P.* (*Pterymarchia*) *pelouatensis* n. sp., *Textiliomurex chodmonensis* n. sp., *Flexopteron constantinense* n. sp., *F. liancurtense* n. sp., *Crassimurex* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp., *Nucellopsis parisiensis* n. sp. et *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp. Deuxièmement, quatre nouveaux genres et un nouveau sous-genre sont décrits : *Paleochicoreus* Merle, n. gen. (espèce type : *Chicoreus* (*Phyllonotus*) *initialis* Vokes, 1990), *Beyregrex* Merle, n. gen. (espèce type : *Murex pereger* Beyrich, 1854), *Pseudotrophonopsis* Merle, n. gen. (espèce type : *Buccinum defossum* Pilkington, 1804), *Pronucellopsis* Merle, n. gen. (espèce type : *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp.) et *Crassimurex* (*Pliocrassimurex*) n. subgen. (espèce type : *Crassimurex* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp.) sont décrits. Troisièmement, se fondant sur une analyse phylogénétique, une nouvelle sous-famille est érigée pour un clade de genres fossiles : Nucellopsinae Merle, n. subfam. (genre type : *Nucellopsis* Merle, 2005c) incluant *Pronucellopsis* Merle, n. gen. et *Nucellopsis*. Enfin sont désignés un néotype pour *Murex tripteroides* Lamarck, 1822, *Murex tricarinatus* Lamarck, 1803, ainsi qu'un lectotype pour *Murex fusoides* Deshayes, 1865 et *Murex sandbergeri* (Hörnes, 1856).

MOTS CLÉS
Muricidae,
Europe,
Cénozoïque,
phylogénie,
néotypifications,
lectotypification,
combinaisons nouvelles,
nom nouveau,
sous-famille nouvelle,
genres nouveaux,
sous-genres nouveaux,
espèces nouvelles.

INTRODUCTION

Among the Gastropoda, the family Muricidae Rafinesque, 1815 displays a high species richness with around 1 200 extinct species (Vokes 1971) and 1 700 extant species (Houart 2018). This diversity results from a long and spectacular adaptive Cenozoic radiation. The oldest known muricid species is represented by *Flexopteron cretaceum* (Garvie, 1991) from the Maastrichtian (72.1-66 Ma) of Texas (Garvie 1991). During the Paleogene, the number of species increased constantly and about 340 species are recorded for this period (Merle 1999). Based on molecular data Oliverio (2008: 482) estimates that the diversification of muricid subfamilies probably occurred during the Paleocene and Eocene, about 66-40 Mya. Based on biostratigraphic and paleobiogeographic data, Merle *et al.* (2011, 2022: 34) identified four Cenozoic phases of diversification: 1) Danian Explosion (66-61 Myr): whereas one species is known from the Maastrichtian, six species of *Flexopteron* Shuto, 1969, *Poirieria* Jousseaume, 1880 (Pagodulinae Barco *et al.* 2012) and *Timbellus* de Gregorio, 1885 are recorded in North Atlantic; 2) basal diversification (61-37 Myr): this period extends from late Palaeocene to the end of middle Eocene and corresponds to the progressive appearance of oldest members of five subfamilies: Muricinae Rafinesque, 1815, Typhinae Cossmann, 1903, Trophoninae Cossmann, 1903, Ocenebrinae Cossmann, 1903 and Coralliophilinae Chenu, 1859; the distribution of the family is worldwide; 3) switch Phase (37-28 Myr): this phase extends from the late Eocene to the early Oligocene; a dramatic decrease of temperature is observed at the Eocene-Oligocene transition and is named the "Terminal Eocene Event". The Switch Phase corresponds first to the rarefaction or the disappearance of dominant genera of the preceding phase and second to the appearance of genera having living members in almost all subfamilies, mostly tropical taxa (Merle *et al.* 2022: 36); and 4) modern Diversification (28 Myr to present day): the number of species appearing in Pacific, Indian oceans and tropical western Atlantic increases, whereas it decreases in eastern Atlantic and in Tethys which is gradually closing.

Although numerous Cenozoic species were described during the past, recent paleontological investigations allow descriptions of many new species (e.g., Pacaud *et al.* 2017; Pacaud 2018; Kovács 2019; Merle & Pacaud 2019; Landau *et al.* 2019; Merle & Landau 2020; Merle *et al.* 2021, 2022b; Lesport & Garrigues 2022; Lozouet 2023; Ledon *et al.* 2023) and suggest that fossil muricid diversity is far from not completely documented. Therefore, the aim of this paper is to continue to document muricid diversity from the European Cenozoic and particularly the Paleogene series.

GEOLOGICAL INFORMATION

A great part of the material used to describe new species comes from Paris Basin (Paleogene), Aquitaine Basin (Paleogene and Miocene), Normandy (Eocene) and Loire Basin (Eocene and Miocene). As the geological context of each basin is too complex to be explained in detail, so instead, a list of references is provided below for the reader to consult.

Paris Basin

Fritel (1910, location of historical geosites), Abrard (1925, Lutetian stratigraphy), Alimen (1936, Stampian stratigraphy), Morellet & Morellet (1948, Bartonian stratigraphy), Feugueur (1963, Ypresian stratigraphy), Mégnien *et al.* (1980, Paleocene stratigraphy), Bignot *et al.* 1980 (Ypresian stratigraphy), Blondeau *et al.* (1980, middle Eocene stratigraphy), Cavelier *et al.* (1980, late Eocene stratigraphy), Aubry (1983, Paleogene biostratigraphy), Gély & Lorenz (1991, Eocene sequence stratigraphic analysis), Gély (1996, Lutetian sequence stratigraphic analysis), Merle (2008, Lutetian stratotype), Lozouet (2012, Stampian stratotype), Huyghe *et al.* (2015, Eocene stratigraphy and paleoclimate).

Aquitaine Basin

Nolf *et al.* (2002, Cenozoic stratigraphy), Sztrákos & Steurbaut (2017, Oligocene stratigraphy), Parize *et al.* (2008, Burdigalian stratigraphy), Londeix (2014, Aquitanian stratotype).

Loire Basin

Mathelin & Bignot (1989, Eocene stratigraphic correlations), Macaire *et al.* (2020, stratigraphy of the Miocene geosite of Pontlevoy).

Normandy

Bignot *et al.* (1980, Lutetian stratigraphy), Cavelier (1979, late Eocene stratigraphy).

MATERIAL AND METHODS

The studied material was collected by the authors, by private collectors or is based on a reexamination of material already present in the collections. The origin of the material is given for each new species and almost all the type material is housed in the collection of paleontology of the Muséum national d'Histoire naturelle, Paris.

Abbreviations

Repositories

BMNH	Natural History Museum, London (= NHMUK);
MGSH	Mining and Geological Survey of Hungary (= MAFI);
MNHN	Muséum national d'Histoire naturelle, Paris;
MNHN.F	MNHN, collection de Paléontologie;
MNHN.IM	MNHN, collection des Invertébrés marins;
NHMW	Naturhistorisches Museum, Wien;
RGM	National Museum of Natural History (Rijksmuseum van Geologie en Mineralogie), Leiden;
UCBL-EM	École des Mines de Paris in Université Claude Bernard Lyon 1;
UPMC	Sorbonne Université, Campus Pierre et Marie Curie, Paris;
USNM	United States national Museum, Washington.

Shell terminology

The description of the new taxa and the comparisons adopt the terminology suggested by Merle (1999, 2001, 2005a), see below:

Ab	abapical (or abapertural);
abis	abapical infrasutural secondary cord (shoulder);
ABP	abapertural primary cord on the siphonal canal;
abs	abapertural secondary cord on the siphonal canal;
Ad	adapical (or adapertural);
adis	adapical infrasutural secondary cord (shoulder);
ADP	adapertural primary cord on the siphonal canal;
ads	adapertural secondary cord on the siphonal canal;
D1-D7	abapical denticles of the outer lip;
ID	infrasutural denticle (internal denticles of the outer lip);
IP	infrasutural primary cord (primary cord on shoulder);
MP	median primary cord on the siphonal canal;
ms	median secondary cord on the siphonal canal;
P	primary cord;
P1	shoulder cord;
P2-P6	primary cords of the convex part of the teleoconch whorl;
s	secondary cord;
sc	sinusigeral scar;
SP	subsutural cord;
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.);
p	partition;
t	tertiary cord.

Phylogenetic analysis

Objective of the analysis

Although the classification of living muricids is divided into more than 220 genera, fossil genera curiously remain few (Merle 1999) despite a 70-Myr evolutionary history. The main reason of this situation comes from the traditional descriptive method, which was too superficial and resulting in numerous assignments of fossil taxa to extant genera. Precise homologies and the use of cladistic analyses demonstrated that Eocene species of *Jsowerbya* Merle, 2005b and *Nucellopsis* Merle, 2005c are extinct taxa and are not related with the Ocenebrinae, the Trophoninae or the Muricopsinae Radwin & d'Attilio, dec. 1971 (junior synonym of the Aspellinae Keen, apr. 1971) to which they had been attributed in the past (for the details see Merle 2005b, c). However, there are several other European Paleogene species that pose generic attribution problems similar to those posed by species now attributed to *Nucellopsis* or *Jsowerbya*. These species are:

Murex sarroniensis **Carez, 1879 (late Paleocene, France, England).** Considered as ?*Trophon sarroniensis* by Merle (1986), as *Muricopsis sarroniensis* by Le Renard & Pacaud (1995) and as "*Vauxyrytis*" *sarroniensis* by Merle (1999), *Vauxyrytis* being a unpublished genus; proposed herein as *Beyregrex sarroniensis* n. comb.

Murex hantoniensis **Edwards *in* Lowry *et al.*, 1866 (late Eocene, England).** Considered as *Vauxyrytis hantoniensis* by Merle (1999); proposed herein as *Beyregrex hantoniensis* n. comb.

Murex pereger **Beyrich, 1854 (late Eocene to early Oligocene, France, Germany).** Considered as *Murex* (*Trophon*) *pereger* by Cossmann & Lambert (1884), *Muricopsis pereger* by Cossmann (1903), Vokes (1971), Janssen (1978, 1979), as *Murex* (*Muricopsis*) *pereger* by Steuer (1912) and as *Vauxyrytis pereger* by Merle (1999); proposed herein as *Beyregrex pereger* n. comb.

Murex **(*Muricopsis*) *multistriatus*** **(Cossmann, 1889, not Deshayes, 1865) (late Paleocene, France).** Considered as *Jania* (*Muricopsis*) *multistriatus* by (Cossmann (1892), *Muricopsis multistriatus* by Cossmann & Pissarro (1911), *Trophonopsis multistriata* by Le Renard & Pacaud (1995) and *Vauxyrytis multistriatus* by Merle (1986); proposed herein as *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp.

Buccinum defossum **Pilkington, 1804 (late Eocene, France, England).** A species having a junior synonym: *Murex sublamellosus* Deshayes, 1835, considered as *Trophonopsis sublamellosa* by Cossmann & Pissarro (1911) and Le Renard & Pacaud (1995); species proposed herein as *Pseudotrophonopsis defossa* n. comb.

These five species are included in the present analysis with other Paleogene taxa as species of *Nucellopsis* and *Jsowerbya*. Thus, it will enable to propose hypotheses on their phylogenetic relationships with extant genera such as *Muricopsis* or *Trophon*, as well as with extinct genera such as *Nucellopsis* or *Jsowerbya*. It will be also used to define new taxa of supraspecific rank and thus document the Paleogene muricid diversity.

Included taxa

The matrix (Appendix 1) contains 27 taxa including 14 extinct species and 13 extant species that are representative of seven subfamilies. The extinct taxa are *Flexopteron cretaceum* (Garvie, 1991) (Campanian-Maastrichtian, Texas) and *F. foliaceum* (Melleville, 1843) (Ypresian, France), three species of *Nucellopsis* [*N. plicatilis* (Deshayes, 1835), *N. ponsi* Merle, 2005b and *N. parisiensis* n. sp.], three species of *Jsowerbya* [*J. sexdentata* (Sowerby, 1823), *J. auversiensis* (Deshayes, 1865) and *J. depauperata* (Deshayes, 1865)], the five species discussed above: *Beyregrex sarroniensis* n. comb., *B. pereger* n. comb., *B. hantoniensis* n. comb., *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp., *Pseudotrophonopsis defossa* n. comb. and the Lutetian species: *Typhis tubifer* (Bruguière, 1792), type species of the *Typhis* Montfort, 1810, genotype of the Typhinae Cossmann, 1903. The extant representative members of seven other subfamilies are: 1) *Nucella* Röding, 1798, *Ocenebra* Gray, 1847, *Ocinebrina* Jousseaume, 1880 and *Urosalpinx* W. Stimpson, 1865 for the Ocenebrinae Cossmann, 1903; 2) *Trophon* Montfort, 1810 for the Trophoninae Cossmann, 1903; 3) *Ergalatax* Iredale, 1831 and *Orania* Pallary, 1900 for the Ergalataxinae Kuroda, Habe & Oyama, 1971; 4) *Drupa* Röding, 1798, *Drupina* Dall, 1923 and *Stramonita* Schumacher, 1817 for the Rapaninae Gray, 1853; 5) *Muricopsis* for the Muricopsinae Radwin & D'Attilio, 1971 (junior synonym of the Aspellinae Keen, 1971); 6) *Truncularopsis* Cossmann, 1921 for the Muricinae Rafinesque, 1815; and 7) *Pagodula* Monterosato, 1884 for the Pagodulinae Barco, Schiaparelli, Houart & Oliverio, 2012. Each genus is represented in the matrix (Appendix 1) by its type species, except *Ergalatax* which is represented by *E. obscura* Houart, 1996.

Characters and polarity determination

Characters. A difficulty encountered when describing muricids shells is how to accurately characterise their diverse sculptural elements, which are usually counted without being precisely identified (Hylleberg & Nateewathana 1992; Merle 1999). In addressing this problem of comparative morphology, structural homologies have been proposed referring to the construction of the characters (Miller 1999) or to their ontogenetic (homologous order of appearance) and topological correspondences (Merle 2001, 2005a, see abbreviations above in the section Shell terminiology). Therefore, the 37 characters (Appendices 1; 2) defined in the present matrix are based on these homology criteria and come largely from the phylogenetic analysis proposed by Merle (2005c) for the study of Nucellopsis.

Polarity determination. In order to determine the polarity of character transformations, two outgroups are selected: 1) *Flexopteron cretaceum*, the oldest known muricid; and 2) *F. foliaceum* a basal Eocene *Flexopteron*. As observed in Paleocene muricids, they have a poorly developed sculpture (cords and cords spines), the ontogeny of which has been described in detail (Merle & Pacaud 2002). They allow a functional polarity determination of characters, because a high developement of the sculptural elements is observed since the early Eocene and reflects an evolutionary trend favorizing armored shells, particularly in tropical seas.

Statistic treatments

In a first time, the matrix of 27 taxa and 37 characters has been processed by the software WinClada 1.00.08 (Nixon 2002) with the options Search strategy: Multiple TBR+TBR (mult*max*), maximum trees to keep (hold): 100, unconstraint search and all characters are non-additive. In a second time, it has been processed by the software PAUP (version 4.0a of Swofford 2002), option heuristic setting, all characters unordered, with equal weight. Recent molecular-based phylogenetics (Barco *et al.* 2010, 2012; Russini *et al.* 2023) suggest different topologies that those based on shell characters (Merle 1999, 2005b, c). However, no morphologically-based analysis has so far produced similar results mostly because of strong homoplasy in muricid lineages. In order to take into account the molecular phylogenies, we applied a topological constraint (based on the tree provided by Russini *et al.* 2023) to our phylogenetic analysis with a molecular backbone tree of extant species included in this study (see above section Included taxa).

RESULTS

Phylogenetic analysis

Description of the consensus tree of Winclada

Winbclada generated seven equally parsimonious trees (length 107, ci 0.53, ri 0.78) and a strict consensus tree (Fig. 1; Appendices 3; 4). The script with the character matrix, the back bone tree and commands for replicating the analysis

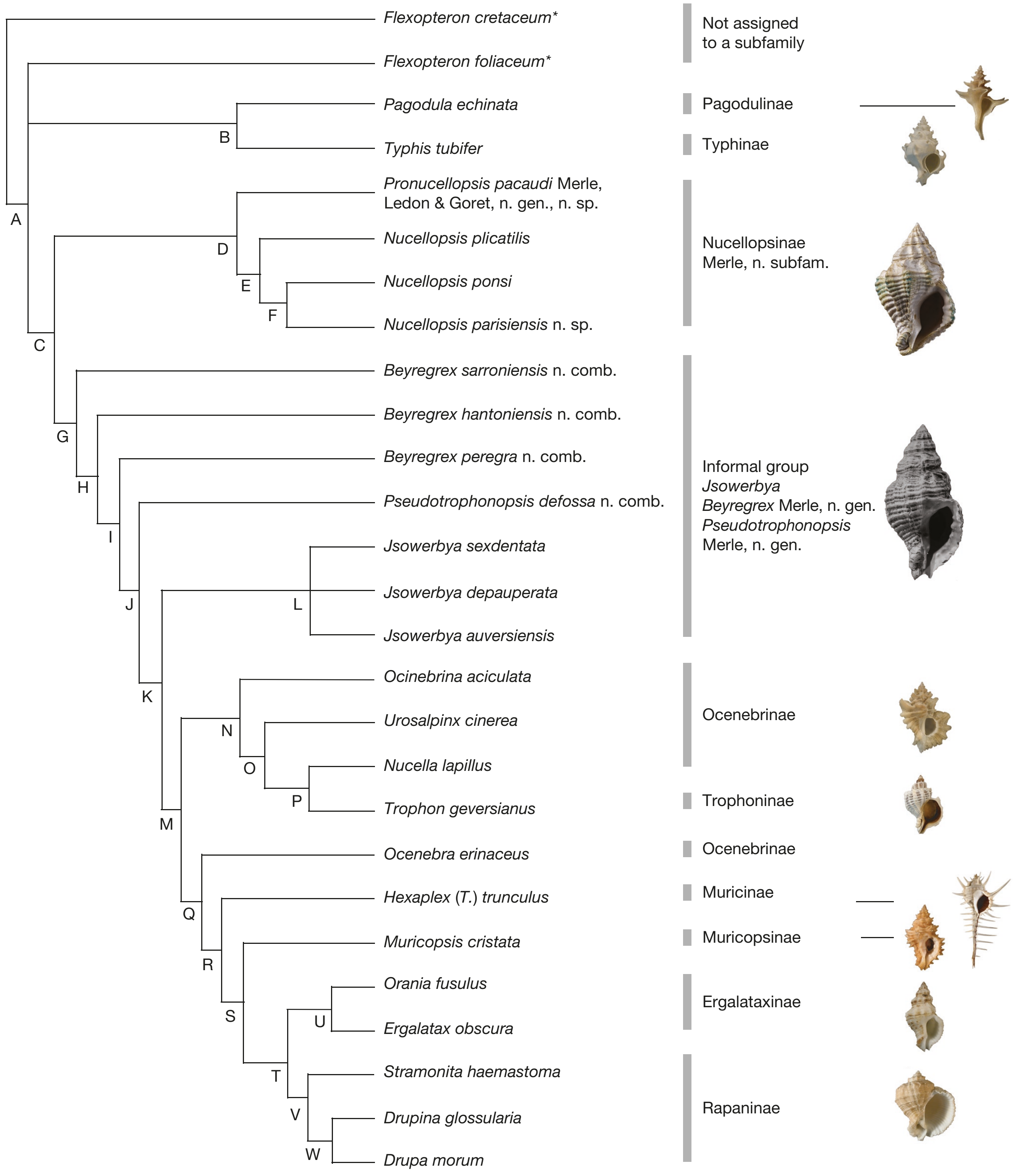

Fig. 1. — Strict Consensus tree of 7 equally parsimonious trees (length 107, ci 0.53, ri 0.78) generated by Winclada and computed using the option Heuristic Analysis (mult* max*), all characters non additive.

is provided in the Appendix 5. The Clade A displays a basal polytomy with *F. foliaceum*, the Clade B (*Pagodula echinata* and *Typhis tubifer*) and the Clade C including the other studied muricids of the ingroup. The Clade B is supported by four ambiguous apomorphies (homoplastic character): 26 (1), 27 (2), 30 (2), 31 (2) indicating a loss of the internal denticles in the outer lip (see Appendix 2 for details). The monophyly of Clade C is supported by four unambiguous synapomorphies: 8 (1) posterior sinus present, 20 (1) P6 present, 21 (1) ADP present, 22 (1) MP present and one ambiguous synapomorphy: 2 (1) subangular whorl. It is divided in two branches (Clades D + G). The Clade D includes *Pronucellopsis* n. gen. and the three species of *Nucellopsis* (Clade E). The Clade D is supported by one ambiguous synapomorphies: 7 (1) rounded shoulder sinus, and the Clade E is supported by two ambiguous synapomorphies: 1 (1) buccinoid shape and 2 (2) rounded spiral whorls. The Clade F (*Nucellopsis ponsi* + *N. parisiensis* n. sp.) is supported by one ambiguous synapomorphy: 4 (2) tubercles on angle of columella. The Clade G (*Beyregrex sarroniensis* n. comb. + Clade H) is supported by one ambiguous synapomorphy: 16 (1) P4 on the two early whorls. The Clade H (*Beyregrex hantoniensis* n. comb. + Clade I) is supported by two unambiguous synapomorphies: 17 (1) P5 on the two early whorls and 23 (1) ABP present. The Clade I (*Beyregrex pereger* n. comb. + Clade J) is supported by two ambiguous synapomorphies: 4 (2) tubercles on angle of columella and 12 (1) IP cord fine. The Clade J (*Pseudotrophonopsis defossa* n. comb. + Clade K) is supported by one ambiguous synapomorphy: 7 (1) rounded shoulder sinus. The Clade K (Clades L + M) is supported is one unambiguous synapomorphy: 25 (1) presence of secondary cords on siphonal canal. The Clade L (clade of *Jsowerbya*) is supported by one ambiguous synapomorphy: 5 (2) tubercle on centre of columella. It is the sister group of the Clade M represented by extant muricids except *Pagodula* and *Typhis* (clade B). The Clade M is divided into two main branches: the Clade N (*Ocinebrina*, *Urosalpinx*, *Nucella* + *Trophon*) supported by three ambuiguous synapomorphy 4 (1) no tubercles at the angle of columella, 8 (0) posterior sinus absent 27 (0 = reversion) ID denticle present and one unambiguous synapomorphy 19 (1) P6 on the two first whorls, and the Clade Q (*Ocenebra erinaceus* + Clade R) containing derived muricine-muricopsine and the Clade T (rapanine/ergalataxine Clades U and V) which take the most apical place. The clade Q is only supported by an ambiguous synapomorphy 15 (1) present of P3 spine. Compared to molecular phylogeny (Barco *et al.* 2010, 2012; Russini *et al.* 2023) this result is no congruent because *Ocenebra*, *Ocinebrina*, *Urosalpinx* and *Nucella* don't belong to the clade of *Trophon*.

Description of the consensus tree of PAUP

PAUP generated 39 equally parsimonious trees (length 114, ci 0.50, ri 0.7522, homoplasy index 0.50) and a strict consensus tree (Appendix 5). The topology is quite similar to that of the strict consensus tree generated by Winclada. Thus, we retrieve the same basal polytomy comprising *F. foliaceum*, the Clade 28 (Clade B of Winclada branching *Pagodula echinata* and *Typhis tubifer*) and the Clade 48 (Clade C of Winclada) including all other muricids of the ingroup. The Clade 47 is also completely similar to the clade D of Winclada linking *Pronucellopsis* Merle, n. gen. and *Nucellopsis*. The Clade 44 resembles the Clade G of Winclada, but differs on two points: 1) the three species of *Jsowerbya* don't form a clade, but form a polytomy at the base of Clade 40; and 2) *Ocenebra* is correctly placed in the ocenebrine clade (Clade 31) with *Ocinebrina*, *Urosalpinx* and *Nucella*, and *Trophon* is separate from this clade as in the tree of Russini *et al.* (2023).

Comparison between shell-based trees and molecular trees

Although new taxa were added to the shell-based matrix computed by Merle (2005c) using the software Hennig86 (Farris 1988), the topology of the consensus trees generated by Winclada and PAUP are fairly similar to the one presented by Merle (2005c: fig 3). A first difference is the Clade *Pronucellopsis* Merle, n. gen. + *Nucellopsis* in which *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp. is the sister species of the subclade of *Nucellopsis*. A second difference results from the addition of species of *Beyregrex* Merle, n. gen. (*B. sarroniensis* n. comb., *B. hantoniensis* n. comb., *B. pereger* n. comb.) and *Pseudotrophonopsis* Merle, n. gen. (*P. defossa* n. comb.) in the matrix, whose order of appearance in the trees of Winclada and PAUP forms grades. In the tree generated by Winclada *Pseudotrophonopsis defossa* n. comb. is the sister taxon of the Clade K and within the clade K, the *Jsowerbya* clade (Clade L) is the sister group of the Clade M including the extant muricids (except *Pagodula* and *Typhis*). Although the shell-based trees display differences with recent molecular trees (Barco *et al.* 2010, 2012; Russini *et al.* 2023), several common points can be observed: monophyly of the Ergalataxinae, the Rapaninae, apical positions of the clade Ergalataxinae ands Rapaninae, close relationships between the Ocenebrinae and the Trophoninae, basal place of the Muricopsinae (synonym of Aspellinae) and the Muricinae. The greatest difference with molecular trees is the basal position of *Pagodula* and *Typhis* found in the shell-based trees. Although *Pagodula* (Pagodulinae) and *Typhis* (Typhinae) belong to the ingroup, they don't share shell synapomorphies with the Clade C of Winclada or the Clade 48 of PAUP (including more derived taxa and extant taxa), they display many plesiomorphic shell characters associated to their poorly developed sculpture, and therefore obtaining a basal polytomy is no surprise. In addition, the differences with molecular trees also come from the choice of the ougroup (*Flexopteron cretaceum*) selected to polarize the characters of Paleogene species, which display a poorly developed sculpture. As a result, these species are placed at the base of the trees and their order of appearance in the trees follows fairly closely their order of appearance in the geological record.

Early Paleogene diversity and taxonomic consequences

As it is widely known, working with shell characters is problematic, but it is the only way to resolve phylogenetic relationships within a family with so many extinct taxa. The studied Paleogene species take a basal position in trees generated by Winclada and PAUP and the results clearly demonstrate that they have not close relationships with living *Muricopsis* or *Trophon*. In addition, the study also suggests that members attributed herein in *Beyregrex* Merle, n. gen. and *Pseudotrophonopsis* Merle, n. gen. don't belong to the clades of *Jsowerbya* or *Nucellopsis*. Moreover, another clade (clade D of Winclada or Clade 47 of PAUP) is distinguished, the clade including *Pronucellopsis* n. gen. and *Nucellopsis* Merle, 2005c. Consequently, the taxonomic attribution of these genera within a subfamily corresponding to derived clades is not possible and a new subfamily is erected: Nucellopsinae Merle, n. subfam.

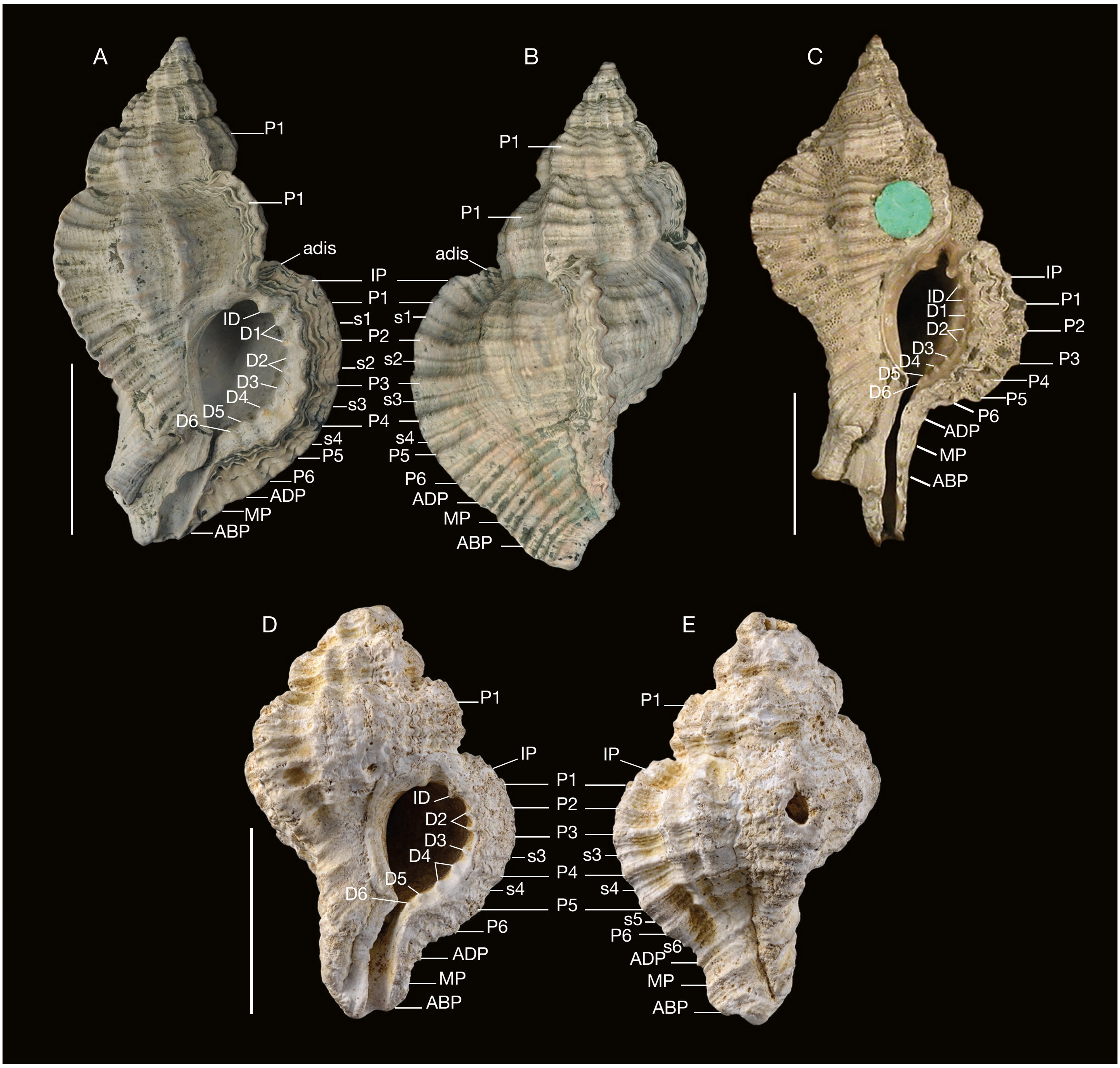

Fig. 2. — Spiral cords and internal denticles of the outer lip in *Paleochicoreus* Merle, n. gen.: **A**, **B**, *Paleoochicoreus initialis* (Vokes, 1990), n. comb., holotype, USNM450376, Nacodoches, Texas (United States), middle Eocene (Lutetian); **C**, *P. newtoni* (Eames, 1957), holotype, BMNH G41982, Ombralla, Nigeria, middle Eocene; **D**, **E**, *P. bicostatus* (Deshayes, 1835), n. comb., holotype, UCBL-EM 33437 (Deshayes coll.), Valmondois, Val d'Oise, Paris Basin, France, middle Eocene (Bartonian). Scale bars: 10 mm. Credits: A, B, Y. Villacampa and J. Jorstad (USNM); C, S. Tracey (NHM); D, E, P. Loubry (MNHN/CNRS).

SYSTEMATICS

Order NEOGASTROPODA Wenz, 1938
Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Muricinae Rafinesque, 1815

Genus *Paleochicoreus* Merle, n. gen.
(Fig. 2)

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Type species. — *Chicoreus* (*Phyllonotus*) *initialis* Vokes, 1990. United States, Texas, middle Eocene (Bartonian) (Fig. 2A, B).

Species included. — *Murex packardi* Dickerson, 1915, Washington (United States), middle Eocene; *Chicoreus* (*Phyllonotus*) *initialis* Vokes, 1990, Texas (United States), middle Eocene (Lutetian); *Pterynoyus newtoni* Eames, 1957 [new name for "*Pteropurpura*" cf. *tricarinatus* Newton, 1922], Nigeria, middle Eocene, Fig. 2C; *Murex diderrichi* Vincent, 1913 [?synonym of *Murex camerunensis* Oppenheim, 1904], Angola, Cameroon, late Paleocene-early Eocene; *Murex bicostatus* Deshayes, 1835, France, middle Eocene (Bartonian) (Fig. 2D, E).

Etymology. — Name formed by *palaiós* (meaning old in ancient Greek) and *Chicoreus*.

Diagnosis. — Biconic and middle-sized shell with *Chicoreus* shape. Well marked primary cords. Spire: IP (infrasutural ramp), P1 to P3 (convex part of whorl). Last whorl: IP, P1 to P6 (convex part of whorl), P6 not atrophied, ADP, MP and ABP (siphonal canal). Nodulose protovarices on early whorls. Three varices with one or two intervarices on succeeding whorls. Varices slightly winged on last whorl. No cord spine even on P1. Shoulder sinus very short. Aperture ovate with strong internal denticles within outer lip: ID, D1 to D6. Columellar lip smooth. Parietal callus and anal notch present. Aragonite microstructure.

Remarks

During the Eocene several species of *Paleochicoreus* Merle, n. gen. appeared in Eastern Pacific (North American coast), Western Atlantic (North American coast) and Eastern Atlantic (West Africa and Europe), which have been attributed in the literature to *Pterynotus* Swainson, 1833 or *Chicoreus* Montfort, 1810 (Eames 1957; Vokes 1971, 1990; Merle *et al.* 2011 as ?*Chicoreus*). With *Chicoreus,* they share a biconic shell, medium length of siphonal canal, trivaricate morphology, nodulose protovarices, an anal notch, and a parietal callus. However, these features are also shared with the genera *Naquetia* Jousseaume, 1880, *Phyllonotus* Swainson, 1833 and *Chicomurex* Arakawa, 1964. *Paleochicoreus* Merle, n. gen. differs from these three genera by having a smooth columellar lip. For example, according to Vokes (1990), *Chicoreus* (*Phyllonotus*) *initialis* (herein *Paleochicoreus initialis* n. comb.) (Fig. 2A, B) is most similar to members of *Phyllonotus*, because of developed internal denticles of the outer lip, but it lacks the derived characters of *Phyllonotus* (rugae and expanded parietal shield). *Paleochicoreus newtoni* (Fig. 2C) possesses an expanded varical flange, like that in *Paleochicoreus initialis* n. comb., but this character is lacking in many *Chicoreus* species. Members of *Chicoreus* (*Triplex*) and *C.* (*Rhizophorimurex*) also bear similarities with those of *Paleochicoreus* Merle, n. gen., but they lack an expanded varical flange, their internal denticles are reduced or missing, and they often develop spiny processes. *Chicoreus* (*s.s.*), which is rather similar to *C.* (*Triplex*), differs by having a labral groove spine placed between P4 and P5 (Merle *et al.* 2011: fig. 37A, B), lacking in *Paleochicoreus* Merle, n. gen. Species such as *Paleochicoreus initialis* n. comb. and *P. newtoni* represent ideal ancestral lineages for *Chicoreus*, *Chicomurex* or *Phyllonotus* (Vokes 1990) but cannot readily be assign to one of these branches. This comment is true for other species attributed here to *Paleochicoreus* Merle, n. gen. Here, we figure and give a new description of the holotype of *P. bicostatus* (Deshayes, 1835), n. comb. This very rare species has not been found subsequent to its original description. Information given hereunder is based on the holotype retrieved from the collections of the École des Mines, Lyon.

Paleochicoreus bicostatus (Deshayes, 1835), n. comb.
(Fig. 2D, E)

Murex bicostatus Deshayes, 1835: 602, 603, no. 17, pl. 81, figs 28-30.

Pterynotus bicostatus – Vokes 1971: 23.

?*Chicoreus bicostatus* – Merle *et al.* 2011: 107, text-fig. 41a, b.

Type material. — **Holotype (by monotypy). France** • Paris Basin, Val d'Oise, Valmondois; Sables d'Auvers (biozone NP16); middle Eocene (lower Bartonian); UCBL-EM 33437 (Deshayes coll.); H: 21.5 mm (apex incomplete) (Fig. 2D, E).

Type horizon. — Sables d'Auvers (biozone NP16), see Gély & Lorenz (1991: pl. 1), middle Eocene (lower Bartonian).

Type locality. — France, Paris Basin, Val d'Oise, Valmondois (see Fritel 1910: 315).

Distribution. — Only known from the type locality.

Description

Teleoconch of 21.5 mm in height (apex incomplete), of 13.2 mm in width, biconic in profile, composed of 3.5 preserved whorls. Moderately high spire with convex whorls. Last whorl up to 79% of total length of teleoconch. Apical angle 63°. Spiral sculpture with well-marked primary cords. Spire with P1 and P2 cords. Last whorl: IP, P1 to P6 (P6 placed on top of siphonal canal), ADP, MP and ABP; secondary cords (adis, abis, s3-s6, ads and ms). Axial sculpture not known on early teleoconch whorls. On spire and last whorl, three varices and between them two intervarices. Intervarices strongly developed. Intersection between axial and spiral sculpture displaying small nodules on IP, P1 to P5, ADP and MP. Intervarical nodules, present and more developed on P1 and P2. Ovate aperture of 24% of diameter, up to 64% of length of last whorl. Parietal lip smooth, adherent. Columellar lip smooth, slightly erect. Anal notch deep. Parietal callus well developed. Outer lip showing internal denticles: ID stronger than D1, D2 and D3, D4, D5 and D6 stronger than D1 to D3, D6 split. Siphonal canal of 50% of apertural length. Pseudoumbilicus narrow.

Comparisons

No new specimens of this species have been found since its original description by Deshayes (1835). Cossmann & Pissarro (1911: pl. 36, fig. 170bis-1) attributed an eroded specimen (MNHN.F.J02588 refigured in Merle *et al.* 2022: pl. 147, fig. 4a, b) to this species under the name *Ocenebra* (*Ocinebrina*) *bicostata* (Deshayes, 1835). However, re-examination of this specimen (Merle 1999) reveals that it represents *Eofavartia subrudis* (d'Orbigny, 1850). *Paleochicoreus bicostatus* (Deshayes, 1835), n. comb. shares with *P. newtoni* (Eames, 1957) and *P. initialis* (Vokes, 1990), n. comb. an aperture with developed internal denticles, a strong parietal callus, and a deep anal notch. *P. newtoni* differs in having a slenderer shape and lower, less coarse intervarices. In *P. initialis* n. comb., the intervarices are also lower than in *P. bicostatus* (Deshayes, 1835), n. comb. *Paleochicoreus packardi* (Dickerson, 1915) is poorly preserved (see Merle *et al.* 2011), but it bears slightly winged varices as do *P. newtoni* and *P. initialis* n. comb. *Paleochicoreus diderrichi* (Vincent, 1913) displays well developed denticulation within the outer lip (see Merle *et al.* 2011: fig. 41.3). *Paleochicoreus bicostatus* (Deshayes, 1835), n. comb. differs from these species in lacking winged varices. However, the holotype is eroded and in the early Bartonian (Auversian) from the Paris Basin, many species tend to lose their delicate ornaments (wings, spines) and thicken their shell, as is the case in another muricid, *Eofavartia subrudis* (Deshayes, 1835).

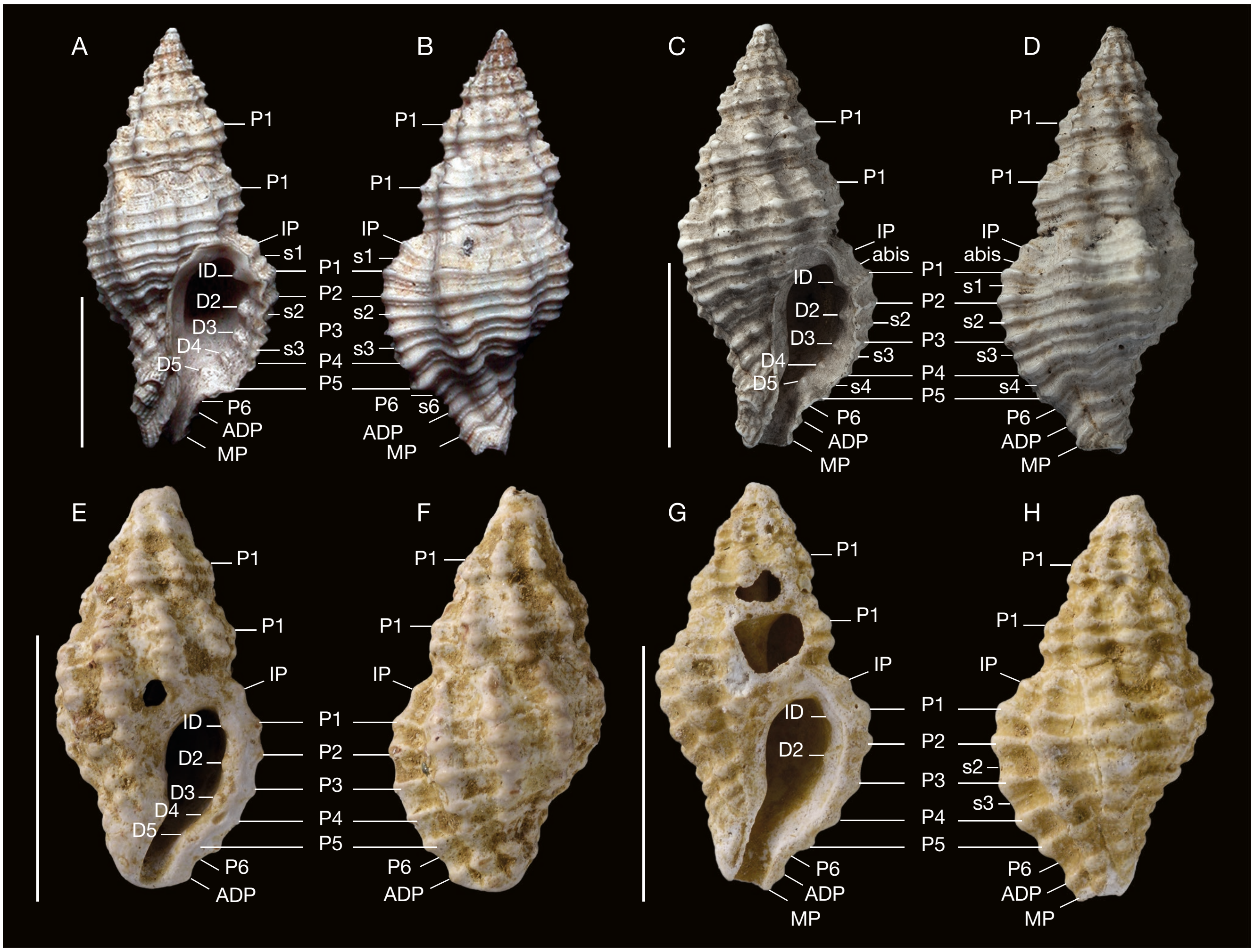

Fig. 3. — Spiral cords and internal denticles of the outer lip in *Muricopsis pontileviensis* n. sp. (**A**-**D**) and *M. neraudeaui* n. sp. (**E**-**H**): **A**, **B**, holotype, MNHN.F.A71120 (Dollfus coll.), Pontlevoy, Loire-et-Cher, Loire Basin, France, Middle Miocene (Langhian); **C**, **D**, paratype, MNHN.F.A77743, (Dollfus coll.), Pontlevoy; **E**, **F**, holotype, MNHN.F.A77746 (Néraudeau sample), Saint-Jacques-de-la-Lande (Ille-et-Vilaine), Rennes basin, France, Late Miocene (Messinian); **G**, **H**, paratype, MNHN.F.A77747 (Néraudeau sample), Saint-Jacques-de-la-Lande. Scale bars: 5 mm. Credits: A-D, D. Lamy; G, H, P. Loubry (MNHN/CNRS).

Subfamily ASPELLINAE Keen, apr. 1971

Muricopsinae Radwin & d'Attilio, dec. 1971: 64.

Tripterotyphinae d'Attilio & Hertz, 1988: 6.

Subclade Muricopsis (Russini *et al.* 2023)

Genus *Muricopsis* Bucquoy & Dautzenberg, 1882

Muricopsis Bucquoy & Dautzenberg *in* Bucquoy *et al.,* 1882: 19.

Type species. — *Murex blainvillii* Payraudeau, 1826 (junior synonym of *Muricopsis cristata* (Brocchi, 1814)) by original designation.

Muricopsis pontileviensis n. sp.
(Figs 3A-D; 25A, B)

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Muricopsis dujardini – Merle 1999: pl. 12, fig. D, pl. 13, fig. D, pl. IX, figs 5, 6 [*non Murex dujardini* Peyrot, 1938].

Muricopsis sp. 2 – Merle *et al.* 2022: 63, 70, fig. 29D; pl. 3, figs 4-6.

Type material. — **Holotype. France** • Loire Basin, Loir-et-Cher, Pontlevoy; Faluns du Blésois (mammal biozone MN5b); Middle Miocene (base of the Langhian); MNHN.F.A71120 (Dollfus coll.), figured specimen in Merle *et al.* (2022: pl. 3, fig. 4), H: 14 mm (Figs 3A, B; 25A).

Paratypes. France • 1 spm; same data as for the holotype; MNHN.F.A71122, figured specimen in Merle *et al.* (2022: pl. 3, fig. 5) • 11 spm; idem;MNHN.F.A77742 (Dollfus coll.) • 1 spm; idem; MNHN.F.A77743 (Dollfus coll., Figs 3C, D; 25B) • spm; idem; MNHN.F.B26846 (MNHN coll.) • 5 spm; idem; MNHN.F.A77744 (Lhomme coll.); • 2 spm; Loire Basin, Indre-et-Loire, Paulmy (Pauvrelay); idem; MNHN.F.A77745 (Faullummel coll.).

Etymology. — The name *pontileviensis* refers to the type locality: Pontlevoy.

Type horizon. — Faluns du Blésois (mammal biozone MN5b), see Ginsburg (2000), Middle Miocene (base of the Langhian).

Type locality. — France, Loire Basin, Loir-et-Cher, Pontlevoy (see Macaire *et al.* 2020).

Distribution. — Loire Basin (France), Faluns du Blésois, Middle Miocene (Langhian).

Description

Paucispiral and rounded protoconch of 1.5 whorls. Teleoconch up to 14 mm in height, up to 6.5 mm in width, biconic in profile, composed of six whorls. Moderately high spire with subcarinate whorls. Last whorl up to 67.7% of total length. Apical angle 42°. Spiral sculpture with marked primary cords. First whorl: appearance of P1 and P2 (P2 more developed than P1) at beginning of whorl and appearance of IP on second half of whorl; second to fifth-sixth whorl: no change, but sometimes s3 placed slightly above suture. Sixth whorl: IP (sutural ramp), P1 to P5 (convex part of whorl, P6 atrophied (on siphonal canal), ADP and MP well developed, ABP poorly developed. Secondary cords s1, s4, s5 and s6 appear between end of fourth whorl and fifth whorl; s2 and s3 appear earlier. On first whorl: 14 varices; from second to fourth whorl: 10-12 varices; from fifth to sixth whorl: 10-11 varices. On spire axial ornamentation forming small nodules placed on IP, P1 and P2. P1 and P2 nodules more developed than IP. On convex part of last whorl, P1 to P4 nodules more or less equally developed; P5 slightly more developed; on siphonal canal, P6 not atrophied, ADP and MP more developed than ABP when present. Ovate aperture up to 42% of diameter and up to 70% of length of last whorl (including siphonal canal). Columellar lip narrow, entirely adherent, bearing two weak tubercles anteriorly. No anal sulcus, no parietal callus. Outer lip with strong internal denticles. Series of denticles including: ID, D2 to D5. D1 missing. D2 stronger than other denticles. Outer lip not crenulate. Siphonal canal open, up to 33% of apertural length and slightly dorsally recurved. Pseudo-umbilicus narrow.

Comparisons

This species is comparable to *Muricopsis crassicostata* (Benoist, 1880) from the late Oligocene/Early Miocene of Aquitaine Basin (France) and *M. dujardini* Peyrot, 1938 from the Middle Miocene of Loire Basin (France). *Muricopsis crassicostata* clearly differs from *M. pontileviensis* n. sp. in being larger (19-23 mm for 6-7 whorls vs 12-14 for 5.5-6 whorls) and having a multispiral protoconch of three convex whorls (for more comparative details, see Merle 1999: 348, fig. 115). *Muricopsis dujardini* and *M. pontileviensis* n. sp. both occur at Pontlevoy. Specimens of *M. dujardini* are larger (19-24 mm for 6-6.5 whorls), but they are mainly distinguishing from *M. pontileviensis* n. sp. by having short spines on P1 to P5 in which P3 is atrophied and by having stronger denticles within the outer lip. *Muricopsis pontileviensis* n. sp. never bears spines. Merle (1999) wrongly attributed studied specimens of *M. pontileviensis* n. sp. to *M. dujardini*, however, he demonstrated that they display a paedomorphic shape (particularly because of the post-displacement of the secondary cords s1, s4 and s6) compared to larger shells as *M. crassicostata*.

Muricopsis neraudeaui n. sp.
(Figs 3E-H; 25C, D)

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Type material. — **Holotype. France** • Rennes Basin, Ille-et-Vilaine, Saint-Jacques-de-la-Lande; Yellow bed of the quarry; Late Miocene (lower Messinian); MNHN.F.A77746 (Néraudeau's sample), H: 8.5 mm (Figs 3E, F; 25C).
Paratypes. France • 1 spm; same as for the holotype; MNHN.F.A77747 (Néraudeau sample, Figs 3G, H; 25D) • 12 spm; idem; MNHN.F.A90516 (Néraudeau's sample).

Etymology. — Dedicated to Didier Néraudeau who collected and provided the material.

Type horizon. — Yellow bed of the quarry, Late Miocene (lower Messinian), see Néraudeau *et al.* (2002).

Type locality. — France, Rennes Basin, Ille-et-Vilaine, Saint-Jacques-de-la-Lande (Lilion sand pit).

Distribution. — Only known from the type locality.

Description

Protoconch not preserved. Teleoconch up to 8.5 mm in height, up to 4 mm in width, biconic in profile, composed of five whorls. Moderately high spire with subcarinate whorls. Last whorl up to 69.6% of total length. Apical angle 50°. Spiral sculpture with coarse primary cords. First whorl eroded; second whorl appearance of IP; P2 more developed than P1; second to fourth whorl: no change (IP, P1 and P2). Fifth whorl (last whorl): IP, P1 to P5, P6 atrophied (on siphonal canal), ADP and MP well developed, ABP poorly developed. Secondary cords s2 and s3. On second whorl: 12-13 varices; on fourth whorl: 10-11; on fifth whorl: 9-10 varices. On spire, axial ornamentation forming marked nodules on IP, P1 and P2. P1 and P2 nodules more developed than IP nodule. On convex part of last whorl, P1 to P5 acute nodules more or less equally developed; on siphonal canal, only ADP and MP displaying nodules. Ovate aperture up to 44% of diameter and up to 72% of length of last whorl (including siphonal canal). Columellar lip narrow, entirely adherent, bearing two tubercles anteriorly. No anal sulcus; no parietal callus. Outer lip with strong internal denticles. Series of denticles including ID, D2 to D5. D1 missing. D2 stronger. Outer lip not crenulate. Siphonal canal open, up to 32% of apertural length, slightly dorsally recurved. Pseudo-umbilicus narrow.

Comparisons

Like *Muricopsis pontileviensis* n. sp., *M. neraudeaui* n. sp. is another very small species for the genus and is comparable to the Langhian *M. pontileviensis* n. sp. in size. However, *M. neraudeaui* n. sp. is even smaller (8.5 mm for 5 whorls instead 12-14 mm for 5.5-6 whorls). *Muricopsis neraudeaui* n. sp. displays a stronger sculpture formed by acute nodules on IP, P1 to P5 and ADP, MP), whereas *M. pontileviensis* n. sp. bears only a swelling on the varices.

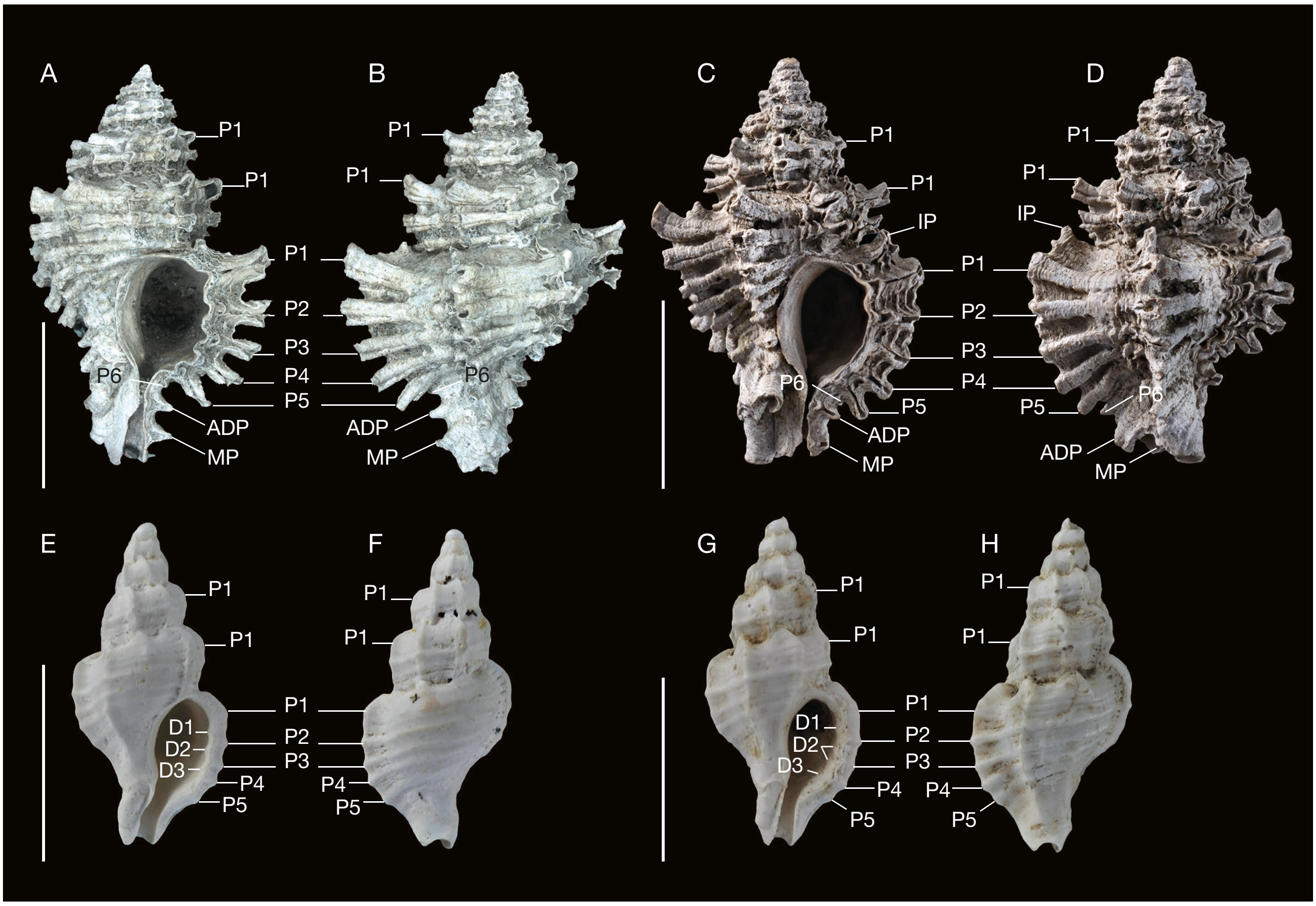

FIG. 4. — Spiral cords and internal denticles of the outer lip in *Favartia jansseni* n. sp. (**A**-**D**) and *Dermomurex* (*Gracilimurex*) *ligerianus* n. sp. (**E**-**H**): **A**, **B**, holotype, RGM.225979, Winterswijk, North Sea Basin, The Netherlands, Middle Miocene (Langhian); **C**, **D**, paratype, MNHN.F.A77748 (Ledon coll.), Winterswijk; **E**, **F**, holotype, MNHN.F.A33456 (Dollfus coll.), Pontlevoy, Loire Basin, France, Middle Miocene; **G**, **H**, paratype, MNHN.F.A33457 (Dollfus coll.), Pontlevoy. Scale bars: 5 mm. Credits: A, B, R. Pouwer and E. de Vogel (Naturalis Biodiversity Center); C, D, L. Cazes (MNHN/CNRS); E-H, P. Loubry (MNHN/CNRS).

In addition, the secondary cords are less numerous in *M. neraudeaui* n. sp. (only s2 and s3 instead s1, s2, s3, s4, s5 and s6 in *M. pontileviensis* n. sp.). In spite of its very small size, *M. neraudeaui* n. sp. bears strong columellar denticles. This is the first record of very small *Muricopsis* species in fossil record. Assemblages containing very small species of *Muricopsis* are only documented in the Recent faunas. The best examples come from the islands of São Tomé and Martinique which contain several very small *Muricopsis* species (Houart 1996; Garrigues & Lamy 2019 respectively).

Subclade Favartia (Russini *et al.* 2023)

Genus *Favartia* Jousseaume, 1880

Favartia Jousseaume, 1880: 335.

Murexiella Clench & Pérez Farfante, 1945: 49. — Type species: *Murex hidalgoi* Crosse, 1869 by original designation.

Minnimurex Woolacott, 1957: 115. — Type species: *Minnimurex phantom* Woolacott, 1957 by original designation.

Caribiella Perrilliat, 1972: 82. — Type species: *Murex intermedius* C.B. Adams, 1850 (synonym of *Murex alveatus* Kiener, 1842) by original designation.

TYPE SPECIES. — *Murex breviculus* G. B. Sowerby II, 1834 by original designation. Recent: Indo-Pacific.

Favartia jansseni n. sp.
(Figs 4A-D; 25E, F)

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Favartia collega – Janssen 1984: 214, pl. 59, fig. 7 [*non* Boettger, 1906].

Favartia sp. 2 – Merle *et al.* 2022: pl. 58, figs 3, 4.

TYPE MATERIAL. — **Holotype. The Netherlands** • North Sea Basin, Miste, Winterswijk; Miste bed; Middle Miocene (middle Langhian); RGM.225979 (figured specimen in Janssen [1984: pl. 59, fig. 7]), H: 12.5 mm (Figs 4A, B; 25E).

Paratype. The Netherlands • 1 spm; same as for the holotype; MNHN.F.A77748 (Ledon coll., Figs 4C, D; 25F).

Etymology. — Dedicated to Arie W. Janssen for his paleontogical and malacological work.

Type horizon. — Miste bed, Middle Miocene (middle Langhian), see Janssen (1984) and Schneider & Heissig (2005).

Type locality. — The Netherlands, North Sea Basin, Miste, Winterswijk (see Janssen 1984).

Distribution. — Only known from the type locality.

Description

Protoconch not preserved. Delicate teleoconch up to 12.5 mm in height, up to 7.5 mm in width, composed of five whorls. Moderately high spire with subangular whorls. Last whorl up to 72% of total length. Apical angle 72° (including spines) and 48° (excluding spines). Spiral sculpture with strong primary cords. From first to fourth whorl: P1 and P2; on fourth whorl, appearance of IP. Fifth whorl: IP and abis, P1 to P5, P6 atrophied (on siphonal canal), ADP and MP present, ABP missing. Surface of P1, P2 and P3 bearing deep spiral grooves. Second whorl: 8-9 varices; from third to fourth whorl: 8 varices; fifth whorl: 6-7 varices. Adapertural face of varices with some imbricated growth lamellae. Axial ornamentation forming short spines on P1 to P5, ADP and MP. Axial microsculpture with small erect lamellae. Suboval aperture up to 29% of diameter and up to 71% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, erect anteriorly. Outer lip lacking denticles. Siphonal canal open, up to 42% of apertural length and slightly dorsally recurved. Pseudo-umbilicus rather wide.

Comparisons

This rare species from the Langhian of Miste (North Sea) was identified as *Favartia collega* (Boettger, 1906) by Janssen (1984). The holotype of *F. collega* (SMF XII2258a, figured in Merle *et al.* 2022: pl. 58, fig. 2) comes from the Langhian of Costeiu de Sus (Romania, Paratethys Sea). It differs from *F. jansseni* n. sp. by having a slenderer shell, a rounded shoulder sinus in the aperture, and weak internal denticles within the outer lip (D1 to D5). Secondary cords are poorly developed, but the holotype of *F. collega* is a juvenile specimen of only 7.5 mm height. *Favartia collega* and *F. czjzeki* (Hoërnes & Auinger, 1885) from the Langhian of Austria (Paratethys Sea) and Hungary (Kovács *et al.* 2018) share a slender shell, a rounded shoulder sinus, and a multispiral protoconch (Kovács *et al.* 2018). The shells of *F. collega* and *F. czjzeki* are very similar, and therefore, *F. collega* is considered to be a junior synonym of *F. czjzeki* herein. The syntype of *F. czjzeki* (NHMW 1855/0045/008 figured in Merle *et al.* 2022: pl. 58, fig. 1) and other adult specimens of this species display the secondary cords (s1, s2, s3 and s5) and weak internal denticles missing in *F. jansseni* n. sp.

Subclade Dermomurex (Russini *et al.* 2023)

Genus *Dermomurex* Monterosato, 1890

Type species. — *Murex scalarinus* Bivona-Bernardi, 1832 (synonym of *Murex scalaroides* Blainville, 1829) by typification of replaced name (nom. n. for *Poweria* Monterosato, 1884, *non* Bonaparte, 1840 [Pisces]). Early Pliocene: Mediterranean Sea to Recent: Mediterranean Sea, Senegal.

Subgenus *Gracilimurex* Thiele, 1929

Type species. — *Murex bicolor* Thiele, 1929 (synonym of *Aspella bakeri* Hertlein & Strong, 1951) by monotypy. Recent: Southern Gulf of California.

Dermomurex **(*Gracilimurex*)** ***ligerianus*** n. sp.
(Figs 4E-H; 25G, H)

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Dermomurex (*Gracilimurex*) sp. – Merle *et al.* 2011: pl. 173, fig. 1-2.

Type material. — **Holotype. France** • Loire Basin, Loir-et-Cher, Pontlevoy; Faluns du Blésois (mammal biozone MN5b); Middle Miocene (base of the Langhian); MNHN.F.A33456 (Dollfus coll.) figured specimen in Merle *et al.* (2011: pl. 173, fig. 1a-b), H: 8 mm (Figs 4E, F; 25G).
Paratype. France • 1 spm; same as for the holotype; MNHN.F.A33457 (Dollfus coll.) figured specimen in Merle *et al.* (2011: pl. 173, fig. 2a, b) (Figs 4G, H; 25H).

Etymology. — From the Latin adjective *ligerianus* meaning Loire.

Type horizon. — Faluns du Blésois (mammal biozone MN5b), see Ginsburg (2000), Middle Miocene (base of the Langhian).

Type locality. — France, Loire Basin, Loir-et-Cher, Pontlevoy (see Macaire *et al.* 2020).

Distribution. — Only known from the type locality.

Description

Bulbous protoconch of 1.5 whorls. Teleoconch of up to 8-9 mm in height, up to 4 mm in width, composed of five elongated whorls. Spire high, weakly convex whorls. Last whorl up to 67% of total height. Apical angle 45°. Spiral sculpture with moderately marked primary cords. First to second whorl: no cord. Third whorl: appearance of P2 on base of whorl. Fourth whorl: appearance of IP and P1 (weak), presence of P2 and P3. Fifth whorl: IP, P1 to P5 on convex part of whorl, siphonal canal smooth. From first to second whorl, six lamellose protovarices extending between sutures. On third whorl, 6-7 protovarices. From fourth to fifth whorl, two thickened varices placed at periphery, 180° to each other, with two intervarices intercalated. Bivaricate morphology giving shell laterally compressed appearance. No cord spine, but only flat nodules at intersection between axial sculpture and major cords (P1 to P5). Aperture ovate, up 35% of diameter, up to 67% of height of last whorl (including siphonal canal). Columellar lip smooth

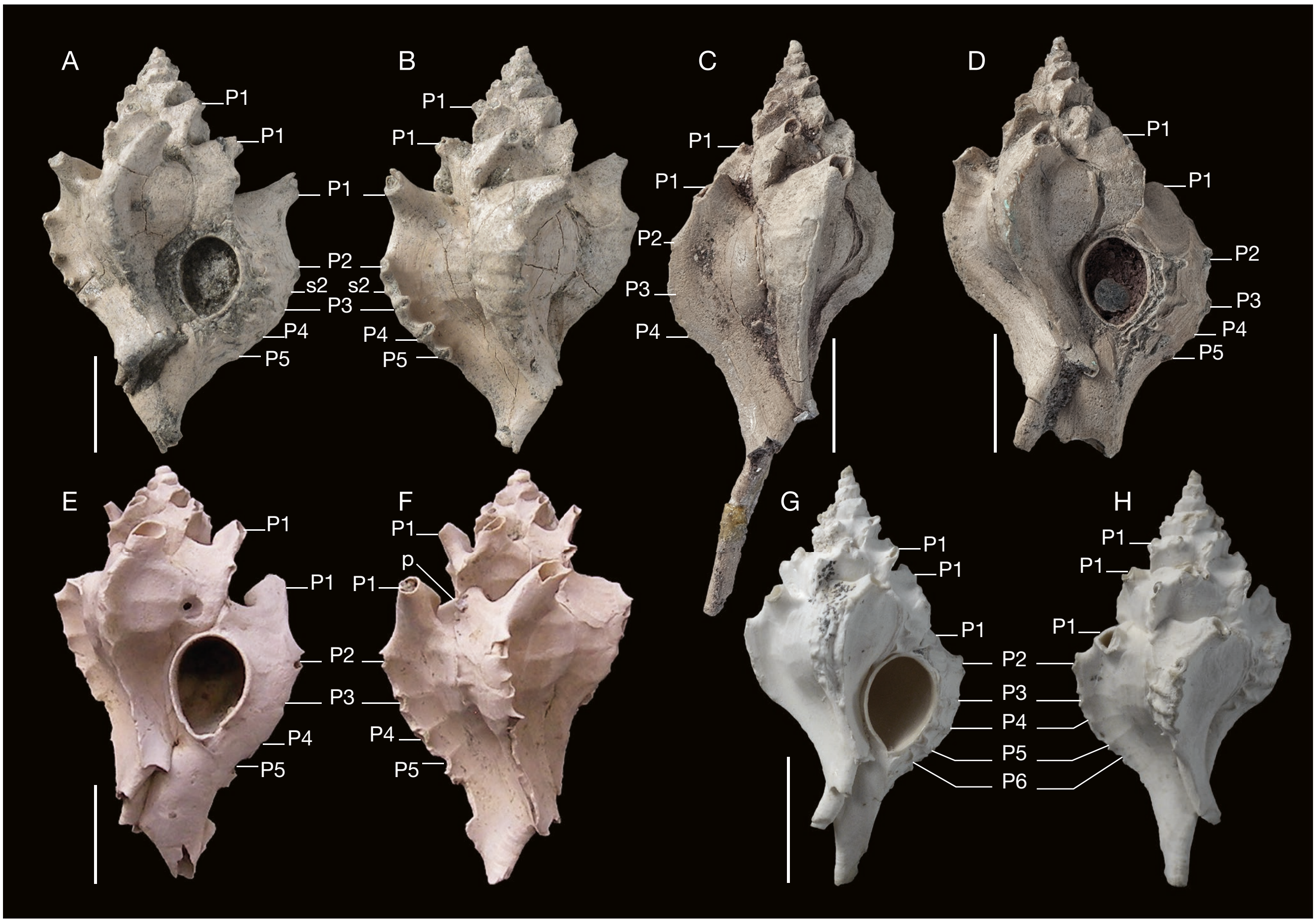

Fig. 5. — Spiral cords in *Trubatsa ganensis* n. sp. (**A**-**D**), *T. parisiensis* (d'Orbigny, 1850) (**E**, **F**) and *T. calviniacensis* n. sp. (**G**, **H**): **A**, **B**, holotype, MNHN.F.A90520 (Varone coll.), Gan (Tuilerie), Pyrénées-Atlantiques, Aquitaine Basin, France, early Eocene (Ypresian); **C**, paratype, MNHN.F.A90518 (Merle coll.), Gan (Tuilerie); **D**, paratype, MNHN.F.A90517 (Merle coll.), Gan (Tuilerie); **E**, **F**, Alan Morton coll., Upper Barton Bed H, Barton-Highcliff, United Kingdom, middle Eocene (Bartonian); **G**, **H**, holotype, MNHN.F.A25590 (Pacaud coll.) Cauvigny (Châteaurouge), Oise, Paris Basin, France, middle Eocene (Lutetian). Scale bars: 5 mm. Credits: A-D, G, H, P. Loubry (MNHN/CNRS); E, F, A. Morton.

poorly erect anteriorly. Outer lip with very weak internal denticles. Series of internal denticles including ID, D1 to D4. D5 and D6 not developed. Pseudo-umbilicus narrow. Siphonal canal up to 35% of apertural lenght. Remains of intritacalx near varices.

COMPARISONS

All other members of the subgenera of *Dermomurex* [*Dermomurex* (*s.s.*), *Takia* Kuroda, 1953 and *Viator* E. H. Vokes, 1974] are characterized by a series of internal denticles containing ID, D1 to D5 or D6, whilst D5 and D6 are missing in the two known species of this subgenus: *D.* (*Gracilimurex*) *bakeri* (Hertlein & Strong, 1951), Recent, Eastern Pacific (Gulf of California) and *D.* (*G.*) *elisabethae* (McGinty, 1940), Pleistocene to Recent, Western Atlantic (Florida, Mexico). Nevertheless, only *D.* (*Gracilimurex*) *ligerianus* n. sp. bears a poorly developed D5, but this character state, restricted in this old species of *D.* (*Gracilimurex*), could be interpreted as the retention of the primitive state, the derived state being the loss of this denticle. The bivaricate morphology found in *D.* (*Gracilimurex*) is unique in *Dermomurex* and can be compared to *Aspella*. However, it appears early during ontogeny in *Aspella*, whereas it appears later (on the penultimate or the last whorl) in *D.* (*Gracilimurex*). According to Vokes (1992: 72), the shell ornamentation of *D.* (*Gracilimurex*) is more closely akin to that of *Dermomurex* (*s.s.*), especially the group of the type species. The oldest record of *D.* (*Gracilimurex*) was *D.* (*Gracilimurex*) *elisabethae*, found in the Pleistocene (Calabrian, Bermont Formation) of Florida. Therefore, this new species from the Middle Miocene of Loire Basin predates the previous oldest record by 12 million years and expand the geographic range of the subgenus to the Eastern Atlantic.

Subfamily TYPHINAE Keen, 1971

Genus *Trubatsa* Dall, 1889

TYPE SPECIES. — *Typhis longicornis* Dall, 1888 by subsequent designation (Keen 1944: 52, 57). Recent: Florida Straits.

Trubatsa ganensis n. sp.
(Figs 5A-D; 25I-K)

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Trubasta [*sic*] *parisiensis* – Merle 1990: 169, pl. 3, figs 13-15, pl. 4, fig. 12 [*non* d'Orbigny, 1850].

TYPE MATERIAL. — **Holotype. France** • Aquitaine Basin, Pyrénées-Atlantiques, Gan (Tuilerie); Uppermost part of the Marnes de Gan only (top biozone N12/base biozone NP13); Early Eocene (Ypresian); MNHN.F.A90520 (Varone coll.), H: 17 mm (Figs 5A, B; 25I).
Paratype. France • 1 spm; same as for the holotype; MNHN.F.R61441 (Merle coll., figured specimen of Merle (1990: pl. 3, fig. 13) • 1 spm; idem; MNHN.F.A90518 (Merle coll., with complete siphonal canal, Figs 5C; 25J) • 1 spm; idem; MNHN.F.A90517 (Merle coll. with incomplete siphonal canal; Figs 5D; 25K) • 12 spm; idem; MNHN.F.A90519 (Merle coll.) • 17 spm; idem; MNHN.F.A72383 (Varone coll.).

ADDITIONAL MATERIAL. — 4 spm; idem; MNHN.F.A90521 (Combault coll.).

ETYMOLOGY. — From the type locality, Gan (Pyrénées-Atlantiques).

TYPE HORIZON. — Uppermost part of the Marnes de Gan only (top biozone N12/base biozone NP13), see Nolf *et al.* (2002: 173, fig. 4), Early Eocene (Ypresian).

TYPE LOCALITY. — France, Aquitaine Basin, Pyrénées-Atlantiques, Gan (Tuilerie) (Merle 1986: 8; Nolf *et al.* 2002: 185, 186).

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Bulbous protoconch of 1.5-2 whorls (see Merle 1990: pl. 4, fig. 12). Teleoconch up to 17 mm (canal siphonal not complete) in height, up to 11 mm in width, biconic in profile, composed of five whorls. Moderately high spire. Last whorl representing 72% of total height. Spiral angle 56°. Suture weakly impressed. Axial sculpture consisting in four slightly foliate varices per whorl. On spire, anal tube (P1) and very short spine (P2). Anal tube forming angle of approximately 60-65° with axis of shell. Anal tube (P1) totally integrated within varices, eliminating shoulder. Small callus at base of anal tube. On convex part of last whorl and abapically to anal tube four spinelets (P2, s2, P3, P4 and P5). Intervarical spaces usually smooth, but with P3-P5 cords on holotype. Rounded aperture up to 25% of diameter, up to 74% of height of last whorl (including siphonal canal). Edge, erect, smooth, peristome complete. Siphonal canal closed, usually broken, occupying 60% of apertural lenght (complete siphonal canal longer, see Fig. 5C).

COMPARISONS

Merle (1990: 169) attributed this material collected at Gan to *Typhis parisiensis* d'Orbigny, 1850 and to the genus *Trubatsa* Dall, 1889. The generic attribution is correct and the distinction between *Siphonochelus* Jousseaume, 1880 and *Trubatsa* is now validated by molecular data (Houart *et al.* 2021). Nevertheless, after further comparison, specific attribution of the Gan material to this species incorrect. Firstly, the protoconchs are different, that of *T. ganensis* n. sp. is paucispiral (Merle 1990: pl. 4, fig. 12) and that of *T. parisiensis* is multispiral (see juvenile specimen from Barton illustrated by A. Morton (2023; www.dmap.co.uk/fossils). In addition, the Bartonian specimens are more sculptured than the specimens from Gan (Fig. 5E, F). They display stronger spines (P2 to P5) and P6, spiral cords (P2 to P5) in the intervarical spaces and a partition recalling that of *T. gaasensis* (Tournouër in Benoist, 1880) from the Rupelian of Aquitaine Basin. *Trubatsa parisiensis* occur in the Bartonian from England and in the Priabonian from Germany (von Koenen 1889). Merle (1985) also suggested that *Typhis sinuosus* Cossmann, 1902 from the Bartonian of Bois-Gouët (France, Loire-Atlantique) was a junior subjective synonym of *T. parisiensis*. According to Merle (1985), the shape of the varices of the type specimen (Dumas coll.) of *T. sinuosus* recalls that of *Trubatsa*. However, it is a juvenile (H: 8 mm) and the varices of the juveniles of *Typhina rutoti* Cossmann, 1882 are also similar. Moreover, the type specimen of *T. sinuosus* is worn, lacks a protoconch and finally lacks diagnostic characters. Thus, we consider *T. sinuosus* as a *nomen dubium*.

Trubatsa calviniacensis n. sp.
(Figs 5G, H; 25L)

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Trubatsa parisiensis – Merle & Pacaud 2019: 16, 17, text-fig 3.5 [*non* d'Orbigny, 1850].

TYPE MATERIAL. — **Holotype. France** • Paris Basin, Oise, Cauvigny (Châteaurouge); Calcaire grossier moyen (biozone NP15); middle Eocene (middle Lutetian); MNHN.F.A25590 (Pacaud coll.), H: 17 mm (Figs 5G, H; 25L).

ETYMOLOGY. — From *Calviniacus*, the Latin name of the type locality Cauvigny (Oise, France).

TYPE HORIZON. — Calcaire grossier moyen (biozone NP15), see Gély & Lorenz (1991: pl. 1); middle Eocene (middle Lutetian).

TYPE LOCALITY. — France, Paris Basin, Oise, Cauvigny (Châteaurouge), see Fritel 1910: 85).

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Bulbous protoconch of two whorls; pointed apex. Teleoconch up to 17.8 mm in height, up to 9.2 mm in width, biconic in profile, composed of six whorls. High spire. Last whorl representing up to 70% total height. Spiral angle 62°. Suture weakly impressed. Axial sculpture consisting of four slightly spiny varices per whorl. On spire, anal tube (P1) and short spine (P2). Anal tube forming angle of approximately 45° with shell axis. Anal tube (P1) totally integrated in varices eliminating shoulder. Short P2 spine on first whorls. No callus at base of anal tube. On convex part of last whorl and abapically to anal tube, five spinelets (P2, P3, P4, P5 and P6). Intervarical spaces with weak P2 to P5 cords. Ovate

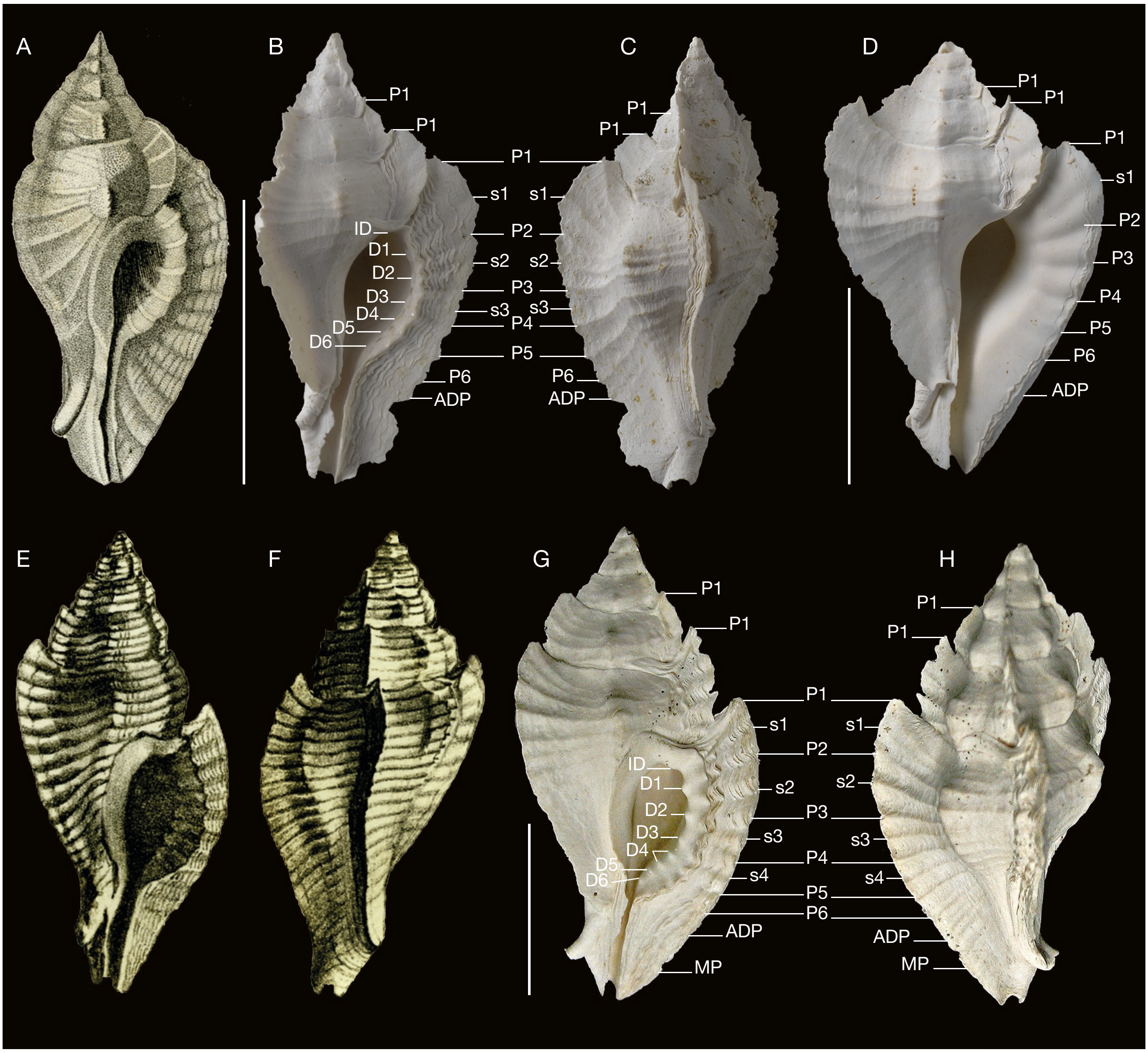

Fig. 6. — Neotype, historical figures, spiral cords and denticles of the outer lip in *T. tripteroides* (Lamarck, 1822): **A**-**D**, morphotype with rounded varices and poorly distinguishable P1 spine; **E**-**H**, morphotype with easily distinguishable P1 spine: **A**, original figure of Lamarck (1805: pl. 3, fig. 4); **B**, **C**, neotype designated herein, MNHN.F.A90546 (Club géologique d'Île-de-France leg.), Thiverval-Grignon (Falunière), Yvelines, Paris Basin, France, middle Eocene (Lutetian); **D**, MNHN.F.A90552 (Pacaud coll.), Chaussy (Les Garennes), Paris Basin, France, middle Eocene (Lutetian); **E**, **F**, figured specimen of Deshayes (1835: pl. 82, fig. 1-2); **G**, **H**, figured specimen of Cossmann & Pissarro (1911: pl. 35, fig. 169-1; MNHN.F.J10350 (Cossmann coll.), Chaussy (Les Garennes). Scale bars: 20 mm. Credits: B-D, P. Loubry MNHN/CNRS; G, H, J. Mouchart.

aperture up to 30% of diameter, up to 74% of height of last whorl (including siphonal canal). Edge, erect, smooth. peristome complete. Siphonal canal closed, occupying 47% of apertural lenght.

Comparisons

Merle & Pacaud (2019: pl. 3, fig. 4) attributed a specimen (MNHN.F.A25590) from the middle Lutetian of Cauvigny (Paris Basin) to *T. parisiensis* (d'Orbigny, 1850). Like *T. ganensis* n. sp. it has a paucispiral protoconch and lacks partition. Therefore, it can easily be distinguished from *T. parisiensis* from the Hampshire Basin which has a multispiral protoconch. *Trubatsa calviniacensis* n. sp. differs from *T. ganensis* n. sp. in being higher spired, the primary cord P6 on the last whorl, weak primary cords P2 to P4 in the intervarical spaces, and by having a more ovate aperture. P2 spine is also more marked on the first teleoconch whorls. Although we have only one specimen, the number of shell differences with the Gan specimens and its occurrence in a strongly different paleoenvironment (deep water at Gan (Merle 1985; Merle & Roux 2018) in Aquitaine Basin, versus shallow water in the Paris Basin (Gély 2008) and also quite different age, highly suggest that it represents a different species.

Subfamily *incertae sedis*

Genus *Timbellus* de Gregorio, 1885

Type species. — *Murex latifolius* Bellardi, 1873, by subsequent designation (Vokes 1964: 14). Middle Miocene: Italy.

Comments on the subfamilial placement

Historically, fossil and Recent members of *Timbellus* have usually been attributed to the genus *Pterynotus* Swainson, 1833 (e.g., Cossmann 1889; Cossmann & Pissarro 1911; Glibert 1963; Vokes 1970) in the subfamily Muricinae. Based on molecular data, Barco *et al.* (2010, 2012) studied the phylogenetic relationships of *Pterynotus* Swainson, 1833 represented by *P. elongatus* (Lightfoot, 1786) and *P. fulgens* Houart, 1988 and *Pterymarchia* Houart, 1995 represented by *P. martinetana* (Röding, 1798). These authors demonstrated firstly, that *Pterynotus* and *Pterymarchia* are not phylogenetically close to *P. fulgens* Houart, 1988 and secondly, none of these taxa are included within the clade of the Muricinae. According to Merle *et al.* (2011), *Pterynotus fulgens* is closely related to the type species of *Timbellus* and is now attributed to that genus. Thus, Merle *et al.* (2011) and Houart (2018) excluded *Timbellus* from the Muricinae, but did not give a subfamilial attribution. Russini *et al.* (2023: 866) place *Timbellus* in *incertae sedis* and considered it likely to represent an independent lineage worthy of subfamilial rank.

Species group of *T. tripteroides* (Lamarck, 1822)

In order to delineate different lineages included in *Pterynotus* (*s.s.*), Harasewych & Jensen (1979) and more recently Vokes (1992) defined five "species groups" for the Western Atlantic Region. With the exception of the typical group of *Pterynotus* [species group of *Pterynotus pinnatus* (Swainson, 1822)], the four other species groups are members of the genus *Timbellus* (Merle *et al.* 2011). Merle *et al.* (2011: 130) added a fifth group to *Timbellus*: the species group of *T. tripteroides* (Lamarck, 1822). Members of that group display a strong development of the internal denticles within the outer lip and their shell shape is narrower than those belonging to the group of *T. crenulatus* (Röding, 1798). Fine growing lamellae forming a scabrous surface are usually missing and only reported in *T. capitaneus* Pacaud, Ledon & Goret, 2017. The following new species described herein, *T. magnificus* n. sp., *T. occidentalis* n. sp., *T. calciacus* n. sp., *T. longicanalis* n. sp. and *T. magnei* n. name (for *Murex trigonus* Rouault, 1850, *non Murex trigonus* Gmelin, 1791) display features allowing a placement in this species group. Several of these new species (*T. occidentalis* n. sp., *T. calciacus* n. sp., *T. longicanalis* n. sp. and *T. magnei* n. name) are superficially similar to, and mistaken for, *T. tripteroides* in the past. Moreover, the type material of *T. tripteroides* is lost, as it is missing in the Lamarck's collections in Geneva and Paris. In order to avoid future taxonomic mistakes, we designate a neotype herein (MNHN.F.A90546, coll. of the Club géologique d'Île-de-France, Fig. 6B, C). The type material of Lamarck was collected at Grignon (middle Lutetian) and the neotype is selected from the same type locality (precisely Falunière of Grignon; Calcaire à Orbitolites complanatus Formation, biozone NP15, see Gély & Lorenz 1991). The neotype was chosen to closely represent the specimen illustrated by Lamarck (1805: pl. 3, fig. 4; Fig. 6A). It displays rounded wings, P1 spine is included in the wings and is not protruding. This morphology of the anterior part of the wings (Fig. 6D) differs from that of the *Murex tripteroides* illustrated by Deshayes (1835: pl. 82, figs 1, 2; Fig. 6E, F) and Cossmann & Pissarro (1911: pl. 34, 169-1), which display a well individualized P1 spine (Fig. 6G, H). We examined numerous specimens from different localities in the Paris Basin and found transitional forms between the two morphotypes. Thus, we consider this difference to fall within the intraspecific variation.

Timbellus magnificus n. sp.
(Figs 7A-F; 25M-O)

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Type material. — **Holotype. France** • Paris Basin, Oise, Baron (Sablière Heudebert); Sables d'Auvers (biozone NP16); middle Eocene (lower Bartonian, Auversian); MNHN.F.A90522 (Pacaud coll.), H: 58.5 mm (Figs 7A, B; 25M).
Paratypes. France • 1 spm; same as for the holotype; early Bartonian; MNHN.F.A90523 (Pacaud coll.) (Figs 7E, F; 25O) • 3 spm; idem; MNHN.F.A90524 (Faullummel coll.) • 1 spm Paris Basin, Oise, Saint-Vaast-lès-Mello (Barisseuse); idem; MNHN.F.A90525 (Schtrock coll.) (Figs 7C, D; 25N) • 1 spm; Paris Basin, Aisne, Montreuil-aux-Lions; idem; MNHN.F.A73852 (Pons coll.) • 1 spm; Paris Basin, Seine-et-Marne, Isle-les-Meldeuses; idem; MNHN.F.A90526 (Faullummel coll.) • 1 spm; Paris Basin, Val d'Oise, Auvers-sur-Oise (Bois-le-Roi); idem; MNHN.F.A90527 (ex galerie de Zoologie coll.).

Additional material. — **France** • 1 spm; Paris Basin, Aisne, Bézu-le-Guéry; Sables d'Auvers (biozone NP16); early Bartonian; MNHN.F.A90528 (Faullummel coll.) • 1 spm; Paris Basin, Aisne, Baron (Sablière Heudebert); idem; MNHN.F.A90529 (Merle coll.) • 1 spm; Paris Basin, Seine-et-Marne, Le Limon; idem; MNHN.F.A90530 (Pacaud coll.).

Etymology. — From the Latin *magnificus* meaning magnificent.

Type horizon. — Sables d'Auvers (biozone NP16), see Gély & Lorenz (1991, pl. 1), middle Eocene (lower Bartonian, Auversian).

Type locality. — France, Paris Basin, Oise, Baron (Sablière Heudebert), see Wyns (1980).

Distribution. — Paris Basin (France), Sables d'Auvers, middle Eocene (lower Bartonian, Auversian).

Description

Unknown not preserved. Teleoconch up to 58.5 mm in height, up to 33 mm in width, subfusiform in profile, composed of seven whorls. Moderately high spire. Last whorl up to 85% of total length. Apical angle 71°. Spiral sculpture with moderately marked primary cords on varices. From first to fourth whorl, no spiral sculpture. Fifth whorl: appearance of weak cords corresponding to P1, P2, P3, s1 and s2; primary and secondary cords of same thickness. Sixth whorl: increase of

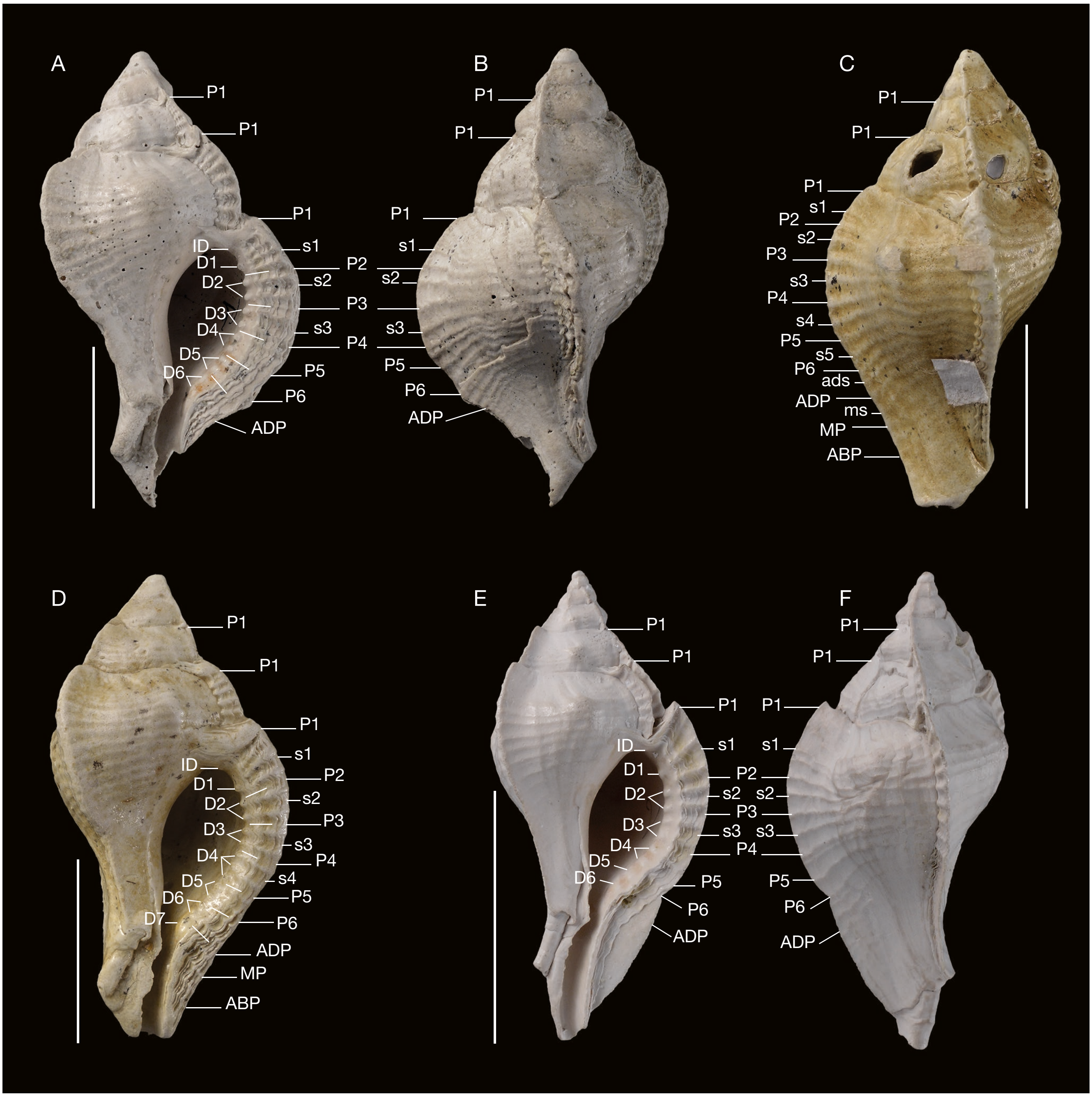

FIG. 7. — Spiral cords and internal denticles of the outer lip in *Timbellus magnificus* n. sp.: **A**, **B**, holotype, MNHN.F.A90522 (Pacaud coll.), Baron (Sablière Heudebert), Oise, Paris Basin, France middle Eocene (Bartonian); **C**, **D**, paratype, MNHN.F.A90525 (Schtrock coll.), Saint-Vaast-lès-Mello (Barisseuse), Oise, middle Eocene (Bartonian); **E**, **F**, paratype, MNHN.F.A90523 (Pacaud coll.), Baron (Sablière Heudebert). Scale bars: 20 mm. Credits: P. Loubry (MNHN/CNRS).

thickness of cords. Seventh whorl: P1 to P6, s1 to s5, P6 weak; ADP, MP and ABP on siphonal canal. Axial sculpture eroded on first whorl. On second whorl, eight protovarices. On third whorl: appearance of varices; three varices and one intervarix between. From fourth to last whorl no change; intervarices low. Higher relief intervarices around on P2. Varices sublamellose on early whorls, thickened on last whorls. Appearance of short P1 spine on fourth whorl. On last whorl, short P1 spine oriented adapically; no other cord spine. Ovate aperture up to 36% of diameter and up to 70% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, slightly erect anteriorly and forming very flat curved inductura at base. Parietal lip slightly adherent. Outer lip with small denticles, ID, D1, D7 simple, D2-D6 bifid or trifid for D4. Siphonal canal narrow, open, bent, slightly dorsally recurved, up to 43% of apertural length. Pseudoumbilicus narrow.

COMPARISONS

With a length exceeding 55 mm, it is one of the largest Eocene *Timbellus* with *T. capitaneus* Pacaud, Goret & Ledon,

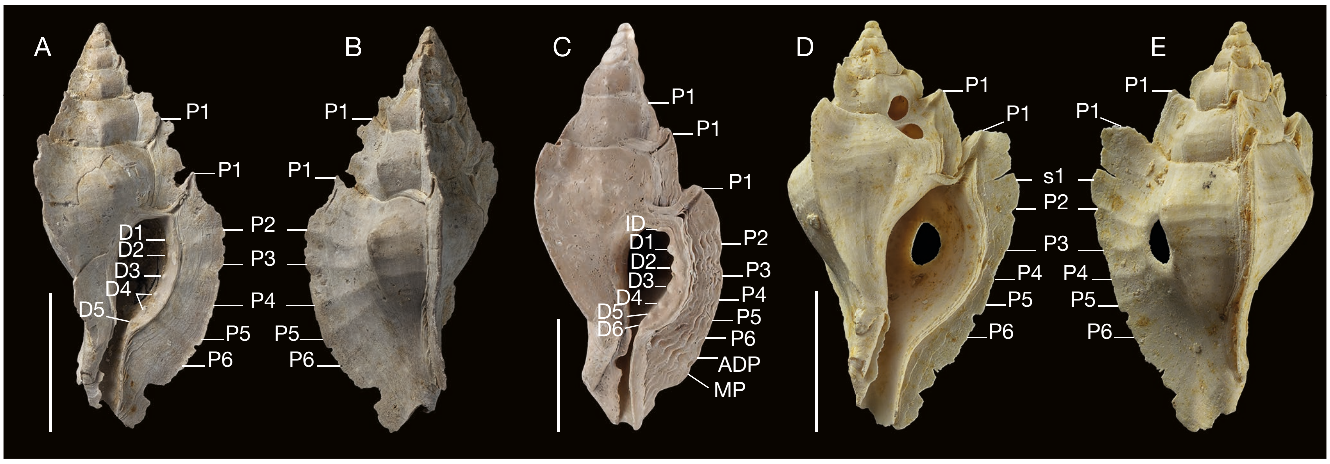

Fig. 8. — Spiral cords and internal denticles of the outer lip in *Timbellus occidentalis* n. sp. (**A**-**C**) and *T. tripteroides* (Lamarck, 1822) for comparison (**D**-**E**): **A**, **B**, holotype, MNHN.F.A90533 (Le Marchand coll.), Fresville, Manche, Normandy, France, middle Eocene (upper Lutetian); **C**, paratype, MNHN.F.A24031 (Vasseur coll.), Saffré (Bois-Gouët), Loire-Atlantique, Loire Basin, France, middle Eocene (Bartonian); **D**, **E**, MNHN.F.A90540 (Merle coll.), Beynes (Ferme de l'Orme), Yvelines, Paris Basin, France, middle Eocene (Lutetian). Scale bars: 5 mm. Credits: A-C, P. Loubry; D, E, L. Cazes.

2017 which can exceeed a length of 65 mm. The spiral cords of *T. magnificus* n. sp. are weak in juvenile specimens of four whorls, whereas they are already well developed and well marked in juvenile specimens of *T. capitaneus* at the same growth stage. In addition, *T. magnificus* n. sp. bears a small and very short P1 spine oriented adapically, whereas that of *T. capitaneus* is strong and abaxially oriented. Moreover, *T. capitaneus* and *T. magnificus* n. sp. share a series of internal denticles including D1 to D6, but all internal denticles of *T. magnificus* n. sp. are bifid and more or less of the same size.

Timbellus occidentalis n. sp.
(Figs 8A-C; 26A, B)

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Murex (*Pterymurex*) *tripteroides* – Cossmann & Pissarro 1901: 78, pl. 13, fig. 29 [*non* Lamarck, 1822].

Timbellus cf. *tripteroides* – Merle *et al.* 2011: 446, pl. 101, figs 1, 2.

Type material. — **Holotype. France** • Normandy, Manche, Fresville; Calcaire de Fresville; middle Eocene (uppermost Lutetian); MNHN.F.A90533 (ex A24100 ex galerie de zoologie coll., Le Marchand coll.), H: 20 mm (Figs 8A, B; 26A).
Paratypes. France • 1 spm; same as for the holotype; MNHN.F.A90534 (ex A24100 ex galerie de zoologie coll., Le Marchand coll.) • 4 spm; idem; MNHN.F.B63570 (de Morgan coll.) • 1 spm, MNHN.F.A90532 (de Morgan coll.) • 1 spm; Normandy, Manche, Hautteville-Bocage; middle Eocene (upper Lutetian); MNHN.F.A90531 (ex B63609, de Morgan coll.) • 1 spm; idem; MNHN.F.B63609 (de Morgan coll.) • 35 spm; idem; MNHN.F.B63610 (de Morgan coll.) – Gourbesville, Manche, middle Eocene (upper Lutetian) • 3 spm; idem; MNHN.F.A24128 (Munier-Chalmas coll.) • 10 spm; Loire Basin, Loire-Atlantique, Saffré (Bois-Gouët); middle Eocene (lower Bartonian); MNHN.F.A29658 (Pacaud coll.) • 1 spm; idem; MNHN.F.A24031 (Vasseur coll.), figured in Merle *et al.* (2011: pl. 101, fig 1) as *Timbellus* cf. *tripteroides* (Lamarck, 1822) (Figs 8C; 26B) • 1 spm; idem; MNHN.F.J06383 (Vasseur coll.), figured in Merle *et al.* (2011: pl. 101, fig 2) as *Timbellus* cf. *tripteroides* (Lamarck, 1822).

Etymology. — From the Latin *occidentalis* meaning west, considering the geographic range of this species in Normandy and in the Loire Basin.

Type horizon. — Calcaire de Fresville, middle Eocene (uppermost Lutetian), see Bignot *et al.* 1968).

Type locality. — France, Normandy, Manche, Fresville, see APGN (2024).

Distribution. — Normandy (Calcaire de Fresville and Faluns de Hautteville) middle Eocene (uppermost Lutetian) and Loire Basin (Sables du Bois-Gouët), lowermost Bartonian see Mathelin & Bignot (1989).

Description

Smooth, bulbous protoconch of 1.25 whorls. Teleoconch up to 26.6 mm in height, up to 15.3 mm in width, biconic in profile, composed of five whorls. Moderately high spire. Last whorl up to 85% total length. Apical angle 64° excluding spines, 91° including spines. Spiral sculpture with weak primary cords in adult specimens. First to fourth whorl, no cord. Fifth whorl: P1 to P3. Sixth whorl: P1 to P6 weak, s2 and no other cord below, ADP and MP occasional. On first whorl, eight protovarices. From second to last whorl, three varices and one intervarix intercalated Higher relief of intervarices on P2-P3. Varices lamellose, winged on last whorls. Appearance of short, straight P1 spine on third whorl. Sinus of P1 spine narrow and pointing adapically. On last whorl alate varices. Ovate aperture up to 9% of diameter and up to 80% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, slightly erect anteriorly, forming curved inductura at base. Parietal lip slightly adherent. Outer lip with denticles ID (occasional), D1 to D6, D1 and D2 more strongly developed. Outer lip not crenulate. Siphonal canal narrow, open, up to 49% of apertural length. Pseudo-umbilicus narrow.

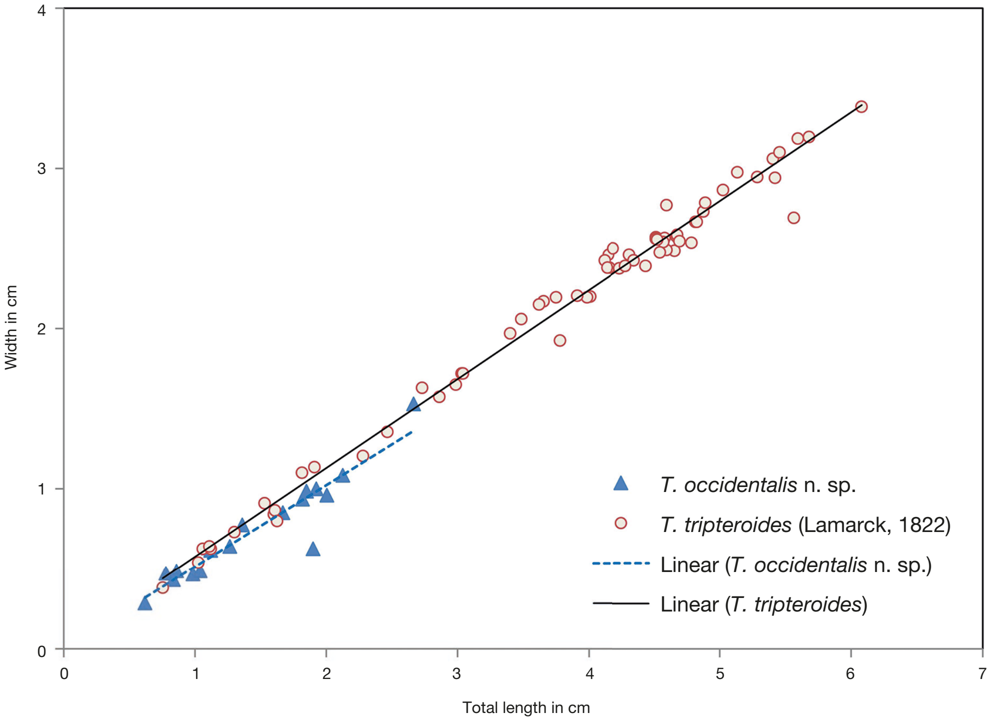

Fig. 9. — Bivariate plot of total length against width comparing *Timbellus tripteroides* (Lamarck, 1822) from the middle Lutetian of Paris Basin (65 complete specimens) and *T. occidentalis* n. sp. from the upper Lutetian of Normandy (18 complete specimens).

Comparisons

This species was previously attributed to *Murex tripteroides* Lamarck, 1822 by Cossmann & Pissarro (1901) and later with some doubts by Merle *et al.* (2011). According to those authors, there are apparently strong similarities with *T. tripteroides* such as: a bulbous protoconch, an elongate shape, developed internal denticles, and few and weak cords. However, *T. occidentalis* n. sp. is smaller and does not exceed 26 mm for five teleoconch whorls. At the same size and same number of whorls *T. tripteroides* is still juvenile, does not bear internal denticles, and their axial wings are only developed on the last whorl (Fig. 8D, E). Adults of *T. tripteroides* can reach more than 60 mm height at 7-8 whorls. A bivariate diagram (Fig. 9) illustrates the differences in size between *T. occidentalis* n. sp. from Normandy and *T. tripteroides* from the Paris Basin. In addition, the spiral cords of *T. tripteroides* (Figs 6; 8D, E) are usually more marked than those of *T. occidentalis* n. sp. (Fig. 8A-C) Finally, *T. occidentalis* n. sp. could be regarded as a progenetic species of *Timbellus*, because it associates a small size with adult characters comparable to *T. tripteroides.* Moreover, the two species never co-occur. *Timbellus occidentalis* n. sp. ranges between the uppermost Lutetian (Normandy) and the lowermost the Bartonian (Loire-Atlantique), whereas *T. tripteroides* ranges from the lower to the middle Lutetian in the Paris Basin and in the Hampshire Basin during the Bartonian.

Timbellus calciacus n. sp.
(Figs 10A-D; 26C, D)

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Pterynotus tripteroides – Merle 1990: 185, pl. 4, fig. 3 only [*non* Lamarck, 1822].

Type material. — **Holotype. France** • Paris Basin, Val d'Oise, Chaussy (Les Garennes); Falun de Chaussy (biozone NP15); middle Eocene (middle Lutetian); MNHN.F.A90536 (Merle coll.), H: 8 mm (Figs 10A, B; 26C).
Paratypes. France • 3 spm; same as for the holotype; MNHN.F.A90537 (Figs 10C, D; 26D, H: 12 mm), MNHN.F.A90538, MNHN.F.A90539 (Merle coll.) • 1 spm; idem; MNHN.F.R61443 (Merle coll.), figured specimen of Merle (1990: pl. 4, fig. 3) • 1 spm; Paris Basin, Yvelines, Beynes (Ferme de l'Orme); middle Lutetian; MNHN.F.A90535 (Merle coll.).

Etymology. — *Calciacus* (Latin adjective): from the ancient name of the village of Chaussy given in 690. Name given in apposition.

Type horizon. — Falun de Chaussy (biozone NP15), see Gély & Lorenz (1991: pl. 1), middle Eocene (middle Lutetian).

Type locality. — France, Paris Basin, Val d'Oise, Chaussy (Les Garennes), see Fritel (1910: 88).

Distribution. — Faluns de Chaussy and Calcaire à Orbitolites at La Ferme de l'Orme (biozone NP15), Paris Basin (France), middle Eocene (middle Lutetian only).

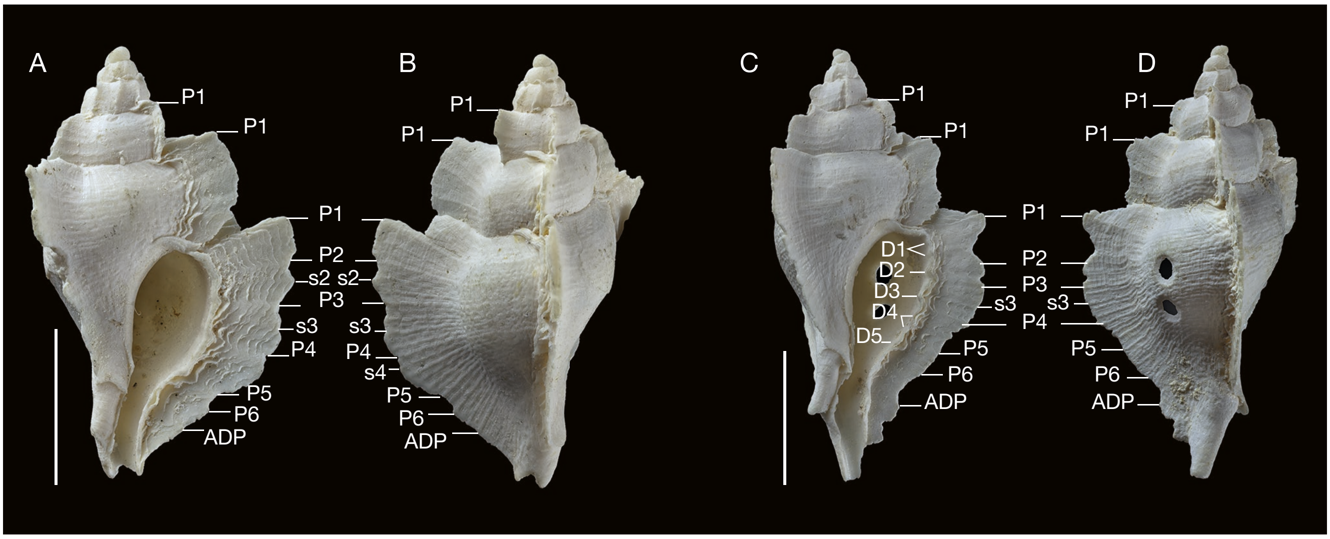

Fig. 10. — Spiral cords and internal denticles of the outer lip in *Timbellus calciacus* n. sp.: **A**, **B**, holotype, MNHN.F.A90536 (Merle coll.), Chaussy (Les Garennes), Val d'Oise, Paris Basin, France, middle Eocene (Lutetian); **C**, **D**, paratype, MNHN.F.A90537 (Merle coll.), Chaussy (Les Garennes). Scale bars: 3 mm. Credits: L. Cazes.

Description

Bulbous protoconch of 1.2 whorls. Teleoconch up to 12 mm in height, up to 5.5 mm in width, biconic in profile, composed of four whorls. Moderately high spire. Last whorl up to 76% of total length. Apical angle 71° including winged varices, up to 55° excluding them. Spiral sculpture with poorly marked primary cords. First whorl: appearance of very weak P1, P2 and P3. Second whorl: weak P1 to P3. Third whorl: appearance of weak s1, s2 and threads covering base of whorl. Fourth whorl: P1 to P6 weak, ADP on siphonal canal, secondary cords undistinguishable from threads; threads covering entire surface of shell. On first whorl, axial sculpture with 8-9 lamellose protovarices. On second whorl: appearance of varices (three varices and one low intervarix between two varices). From third to last whorl, numerous growing microlamellae covering surface of shell and forming delicate, reticulate sculpture covering surface of shell. Intervarical relief very low, but slightly higher on P1-P2. Varices well winged on last two whorls. Appearance of short P1 spine on second whorl. On last whorls, axial ornamentation forming winged varices, rounded in outline, without evidence of spines, even on P1. Subtriangular aperture up to 33% of diameter and up to 74% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, slightly erect anteriorly and forming a curved inductura at base. Parietal lip slightly adherent. Outer lip with very weak denticles including D1 to D5. Siphonal canal open, up to 45% of apertural length. Pseudo-umbilicus narrow.

Comparisons

This small species was never distinguished from its congeners in the Paris Basin, probably mistaken for juveniles of *T. tripteroides* (Lamarck, 1822), with which it co-occurs at two localities: Chaussy and La Ferme de l'Orme. With a maximum height of 12 mm, *T. calciacus* n. sp. is a very small *Timbellus*. *Timbellus calciacus* n. sp. differs from juveniles of *T. tripteroides* in having the aperture completely formed and by having a peculiar reticulate microsculpture (see Fig. 6C, D). This last character lacks in specimens of *T. tripteroides* at any growth stage. Specimens of *T. occidentalis* n. sp. from the upper Lutetian of Normandy and the early Bartonian of Loire-Atlantique share with *T. calciacus* n. sp. a small size, but *T. occidentalis* n. sp. is double the size (H: 26.6 mm vs 12 mm). As with *T. tripteroides*, *T. occidentalis* n. sp. lacks the peculiar microsculpture found in *T. calciacus* n. sp.

Timbellus longicanalis n. sp.
(Figs 11A-D; 26E, F)

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Timbellus fusoides – Merle *et al.* 2011: 446, pl. 101 fig. 5a, b only [*non* Deshayes, 1865].

Type material. — **Holotype. France** • Normandy, Manche, Fresville; Calcaire de Fresville; middle Eocene (uppermost Lutetian); MNHN.F.A24101 (Le Marchand coll.), H: 35 mm (Figs 11A, B; 26E). **Paratype. France** • 1 spm; same as for the holotype; MNHN.F.A24100 (Le Marchand coll.) (Figs 11C, D; 26F).

Etymology. — From the Latin adjective *longus* meaning elongated and *canalis* meaning canal, refecting the elongated siphonal canal of this species.

Type horizon. — Calcaire de Fresville, middle Eocene (uppermost Lutetian), see Bignot *et al.* (1968).

Type locality. — France, Normandy, Manche, Fresville, see APGN (2024).

Distribution. — Normandy (Calcaire de Fresville); middle Eocene (uppermost Lutetian).

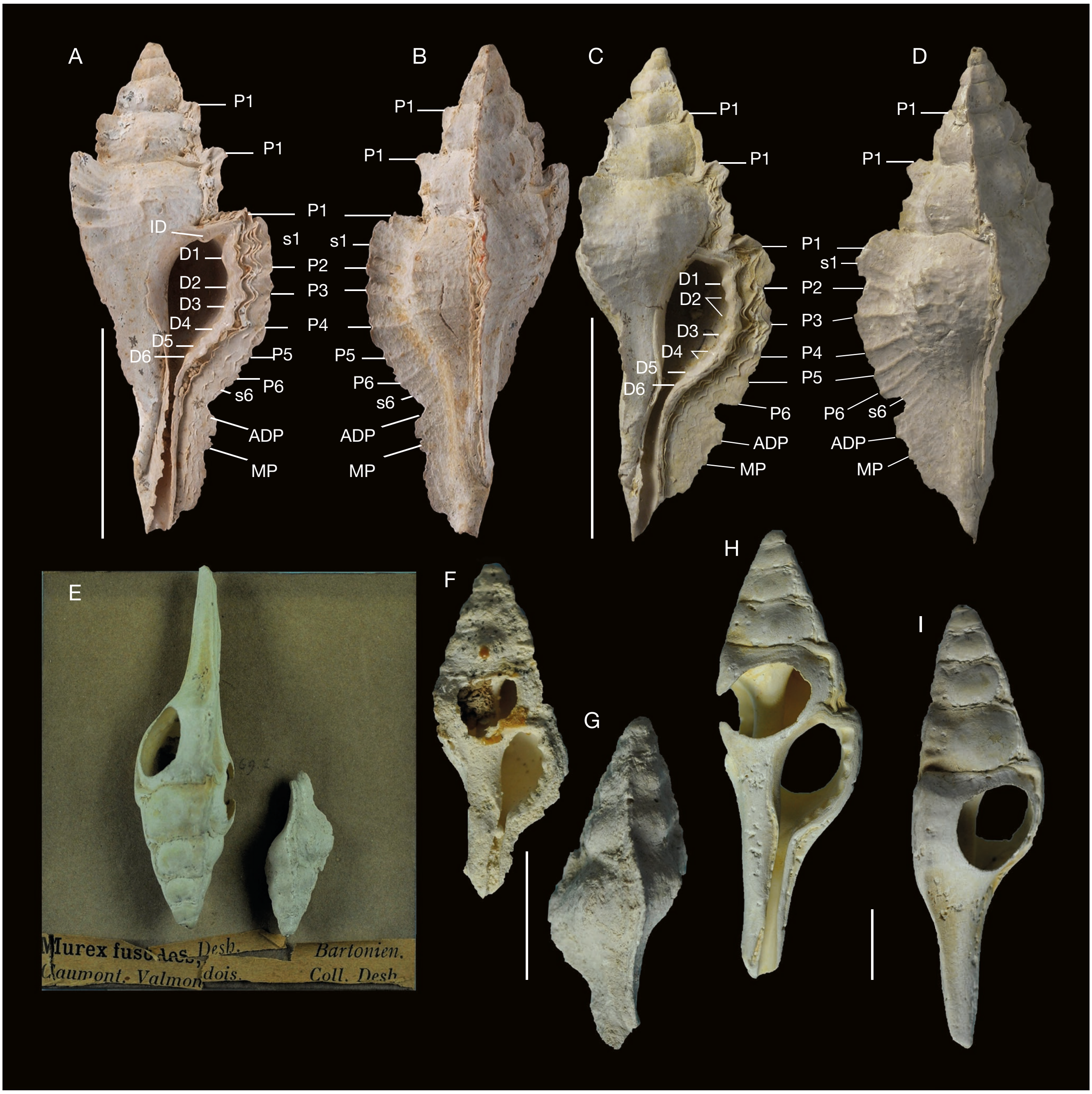

Fig. 11. — Spiral cords and internal denticles of the outer lip in *Timbellus longicanalis* n. sp. (**A**-**D**) and type material of *Murex fusoides* (Deshayes, 1865) (**E**-**I**): **A**, **B**, holotype, MNHN.F.A24101 (Le Marchand coll.), Fresville, Manche, Normandy, France, middle Eocene (upper Lutetian); **C**, **D**, paratype, MNHN.F.A24100, Fresville; **E**, type material of *M. fusoides* in the Deshayes's collection corresponding to two eroded *T. tripteroides*; **F**, **G**, lectotype designated herein, UCBL-EM 33384, Valmondois, Val d'Oise, Paris Basin, France, middle Eocene (Bartonian); **H**, **I**, paralectotype, UCBL-EM 33383, Sainte-Aulde (Caumont), Seine-et-Marne, Paris Basin, France, middle Eocene (Bartonian). Scale bars: 10 mm. Credits: A-D, P. Loubry (MNHN/CNRS); E-I, E. Robert (UCBL).

Description

Protoconch not preserved. Teleoconch up to 35 mm in height, up to 14 mm in width, fusiform in profile, composed of six whorls. Moderately high spire. Last whorl up to 77% of total length. Apical angle 41° excluding spine and 61° including spines. Spiral sculpture with moderately marked primary cords on varices. First and second whorl eroded. Third whorl: appearance of weak s1 and P2 on intervarices. Fourth whorl: appearance of weak P1 cord. Fifth whorl: no change. Sixth whorl: P1-P4 marked, P5-P6 weak, s1, s2, s6, P6 not atrophied, s1-s2, s6 weak; ADP, MP and ABP weak. Axial sculpture eroded on two early whorls. From third last whorl: three varices and one intervarix intercalated. Higher relief of intervarices on P2. Varices lamellose, slightly winged. Appearance of P1 spine on third whorl, no other spines adapically. On last whorl P1 spine short, straight, slightly bent adaxially. On last whorl growth lamellae erect giving scabrous aspect to shell surface. Ovate aperture up to 29% of diameter and up to 78% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, slightly erect anteriorly, forming very slightly curved inductura at base. Parietal lip adherent. Outer lip with simple, weak denticles including ID, D1 to D6. Siphonal canal narrow, open, straight, up to 59% of apertural length. Pseudoumbilicus narrow.

COMPARISONS

This species was previously identified as *Timbellus fusoides* (Deshayes, 1865) by Merle *et al.* (2011: pl. 101, fig. 5a, b). Nevertheless, attribution to *Murex fusoides* is problematic, as the type material on which that Bartonian species is based is poorly preserved. It corresponds to two syntypes housed in the collection of the University Lyon (no. UCBL-EM 33383-84; Fig. 11E). The largest is a strongly eroded specimen with most of its axial sculpture, particularly its winged varices lost. This loss of sculpture gives the shell an artificially fusiform shape. The second specimen is smaller and also strongly eroded, but P1 spine is rather turned adapically as in some *Timbellus tripteroides* (Lamarck, 1822) and its aperture resembles that of *T. tripteroides*. We designate herein this smaller specimen (UCBL-EM 33384; Fig. 11F, G) as the lectotype of *M. fusoides*. Therefore, *M. fusoides* can be regarded as a possible junior synonym of *T. tripteroides* or a *nomen dubium* as it is impossible to clearly identify a species based on the type material. Moreover, Bartonian specimens from the Paris Basin identified as *T. fusoides* are present in several collections housed in the MNHN (e.g., Faullummel, Pons and Schtrock colls). Examination of these specimens shows them to represent eroded *T. tripteroides* (probably reworked from the Lutetian) or to large and eroded *Pterochelus contabulatus* (Lamarck, 1803). The type material of *T. longicanalis* n. sp. comes exclusively from the upper Lutetian of Normandy. It is very well preserved and its delicate and winged varices are not eroded. Thus, its fusoid shape is not due to a post-mortem alteration. The species differs from *T. tripteroides* by having more staged and more quadrate whorls, more adaxially oriented P1 spines, a straighter siphonal canal, a less rounded aperture, and by having weaker internal denticles and spiral cords.

Timbellus magnei n. name
(Figs 12A-F; 26G-I)

Murex trigonus Rouault, 1850: 204, pl. XVII, fig. 17a [*non Murex trigonus* Gmelin, 1791].

Pterynotus trigonus – Glibert 1963: 11 [*non Murex trigonus* Gmelin, 1791].

Pterynotus tricarinatus trigonus – Merle 1990: 158, pl. 2, figs 13, 14 only [*non Murex trigonus* Gmelin, 1791].

Pterynotus tripteroides – Merle 1990: 156, pl. 3, fig. 1 only [*non* Lamarck, 1822].

Timbellus tripteroides – Merle *et al.* 2011: 44, pl. 100 figs 3, 4 only [*non* Lamarck, 1822].

Timbellus crenulatus palensis – Merle *et al.* 2011: 440, pl. 98, fig. 1 only [*non* Magne, 1941].

TYPE MATERIAL. — **Neotype. France** • Aquitaine Basin, Pyrénées-Atlantiques, Bos d'Arros; uppermost part of the Marnes de Gan only (top biozone N12/base biozone NP13); Early Eocene (Ypresian); BMNH 69802 (Seaman coll.) designated by Merle (1990: 158, pl. 2, fig. 14) (Fig. 12A).

ADDITIONAL MATERIAL. — **France** • 1 spm Aquitaine Basin, Pyrénées-Atlantiques, Gan (Tuilerie); uppermost part of the Marnes de Gan only (top biozone N12/base biozone NP13); Early Eocene (Ypresian, uppermost part of the Marnes de Gan); MNHN.F.A32506 (Merle coll.), figured specimen of Merle *et al.* (2011: pl. 100, fig. 3) • 1 spm; idem; MNHN.F.A32508 (Merle coll.), figured specimen of Merle *et al.* (2011: pl. 100, fig. 1) (Figs 12C, D; 26G) • 1 spm; idem; MNHN.F.R61437, Merle coll., figured specimen of Merle (1990: pl. 3, fig. 1) • 1 spm; idem; MNHN.F.A24115 (Merle coll.) • 2 spm; idem; MNHN.F.A72443 (Varone coll.) (Figs 12E, F; 26I) • 35 spm; idem; MNHN.F.A24114 (Merle coll.) • 1 spm (juvenile with protoconch); idem; MNHN.F.A90545 (Merle coll.) (Figs 12B; 26H).

TYPE HORIZON. — Uppermost part of the Marnes de Gan only (top biozone N12/base biozone NP13), see Nolf *et al.* (2002: 173, fig. 4), Early Eocene (Ypresian).

TYPE LOCALITY. — France, Aquitaine Basin, Pyrénées-Atlantiques, Bos d'Arros (Nolf *et al.* 2002: 185).

DISTRIBUTION. — Known from the type locality and Gan (tuilerie), Aquitaine Basin (France), early Eocene (Ypresian).

DESCRIPTION

Smooth, multispiral protoconch of 3.5 whorls (Figs 12B; 26H). Sinusigeral scar well marked. Teleoconch up to 46 mm in height, up to 39 mm in width, subfusiform in profile, composed of eight whorls. Moderately high spire. Last whorl up to 70% of total length. Apical angle 53° excluding wings, 70° including wings. Spiral sculpture with marked primary cords on varices and intevarices. First whorl: no cord. Second whorl: appearance of weak P1, P2 and s1. Third whorl: P1, P2, s1 well marked; appearance of s2 weak. Fourth whorl: s2 well marked. From fifth to seventh whorl: no change or appearance of threads. Eighth whorl: P1 to P6, s1, s2, s3 (well developed), P6; ADP, MP weak or missing on siphonal canal. First whorl: around ten protovarices. Second whorl: appearance of varices, three varices and two intervarices between. From third to last whorl, three to five low intervarices. Higher relief of intervarices on P2. Varices lamellose and strongly winged. Appearance of short P1 spine on second whorl. P1 spine short, almost included in wing. No other cord spines. Ovate aperture up to 22% of diameter and up to 71% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, erect anteriorly, forming curved inductura at base. Parietal lip slightly adherent. Outer lip with well developed internal denticles including ID, D1 to D6. D1 and D2 bifid. Outer lip not crenulate. Siphonal canal narrow, open, straight, up to 57% of apertural length. Pseudoumbilicus narrow.

COMPARISONS

Rouault (1850) described from Bos d'Arros (a locality very close to Gan), *Murex trigonus* based on juvenile specimens. Unfortunately, *Murex trigonus* Rouault, 1850 is a junior homonym of *Murex trigonus* Gmelin, 1791 and Magne

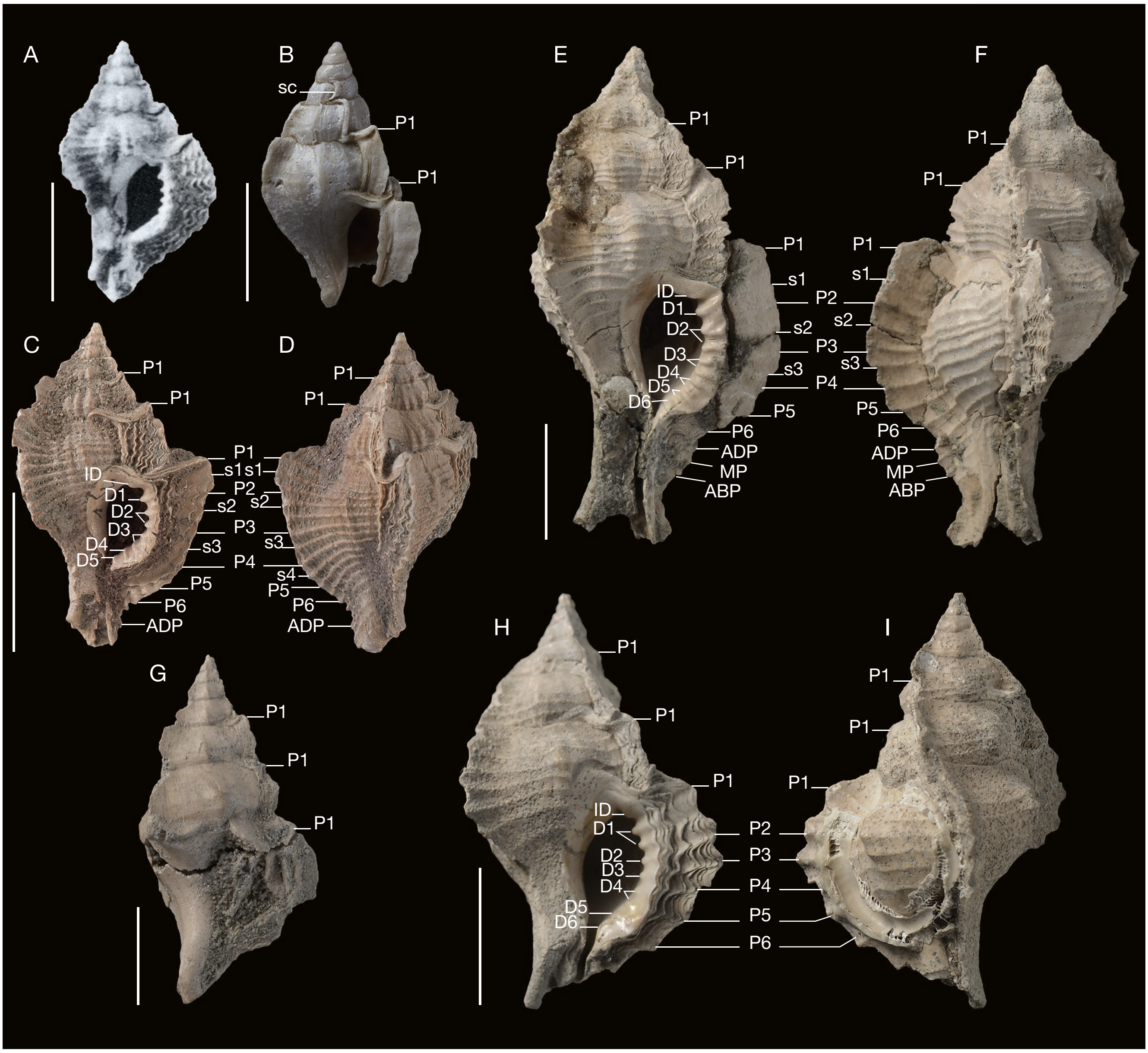

Fig. 12. — Spiral cords and internal denticles of the outer lip in *Timbellus magnei* n. name (**A**-**F**) and *T. palensis* (Magne, 1941) (**G**-**I**): **A**, neotype, BMNH 69802 (Seaman coll.), Bos d'Arros, Pyrénées-Atlantiques, Aquitaine Basin, France, early Eocene (Ypresian); **B**, MNHN.F.A90545 (Merle coll.), juvenile specimen and protoconch, Gan (Tuilerie), Pyrénées-Atlantiques, early Eocene (Ypresian); **C**, **D**, MNHN.F.A32508 (Merle coll.), juvenile specimen, Gan (Tuilerie); **E**, **F**, MNHN.F.A72443 (Varone coll.), Gan (Tuilerie); **G**, MNHN.F.A90553 (Merle coll.), juvenile specimen, Gan (Tuilerie); **H**, **I**, MNHN.F.A32509 (Merle coll.), Gan (Tuilerie). Scale bars: A, G, 5 mm; B, 2 mm; C-F, H, I, 10 mm. Credits: A, D. Serrette (MNHN); B, L. Cazes; E-I, P. Loubry (MNHN/CNRS).

(1941), a homonymy as yet uncorrected. Therefore, we propose the new name *Timbellus magnei* n. name herein. The juvenile specimens illustrated by Rouault (1850) are characterized by low intervarices varying from three to five (compare Fig. 12C, D and G). This character is present on the early whorls of the adults of *T. tripteroides sensu* Merle (1990: pl. 2, figs 13, 14 only). Thus, one can accept that these large *T. tripteroides sensu* Merle (1990) correspond to adult specimens of *T. magnei* n. name. *Timbellus magnei* n. name is easily separated from typical *T. tripteroides* by having a multispiral protoconch (Fig. 12B), whilst typical *tripteroides* has a paucipiral protoconch (see Fig. 8D, E) and by having more and lower intervarices.

Cossmann & O'Gorman (1923) misinterpreted *Murex trigonus sensu* Rouault and illustrated a specimen typical of the genus *Ponderia*: *P. daguini* (Magne, 1941). In addition, Cossmann & O'Gorman (1923) described and figured an adult specimen of *Timbellus* that Cosmann named *Murex* cf. *tricarinatus* Lamarck, 1803. Magne (1941) gave the name *Murex* (*Pteropurpura*) *palensis* to *Murex* cf. *tricarinatus* Lamarck, 1803 (*sensu* Cossmann 1923) and demonstrated that the juvenile specimens illustrated by Rouault (1850) as *Murex trigonus* were not juveniles of *Murex* (*Pteropurpura*) *palensis*. We discovered a young specimen from Gan differing from the juveniles of *T. magnei* n. name. It displays one high intervarix between each varix (Fig. 12G), a character also present

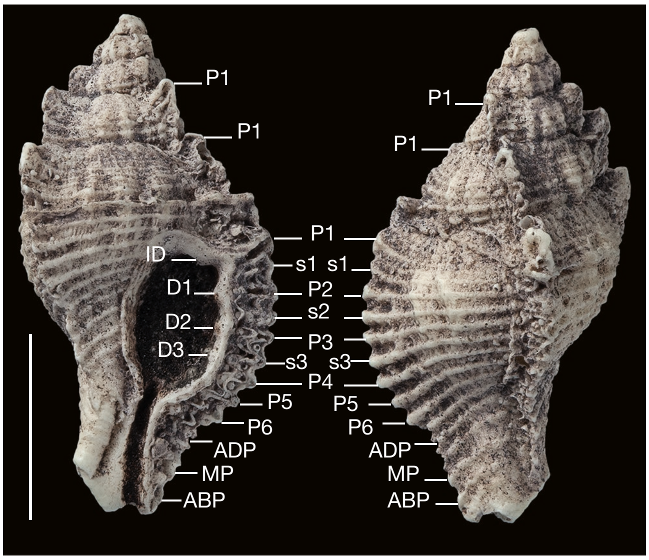

Fig. 13. — Spiral cords and internal denticles of the outer lip in *Timbellus sixi* n. sp. holotype, MNHN.F.A90544 (Six coll.), Trosly-Breuil (Fond Couturier), Oise, Paris Basin (France), early Eocene (Ypresian). Scale bar: 5 mm. Credits: P. Loubry.

on the early teleoconch whorls of well preserved adults of *T. palensis* (Fig. 12H, I). Douvillé & O'Gorman (1929: pl. 29, fig. 1) figured a specimen from the early Eocene of Biron (near Orthez) and called it *Murex tripteroides*. That specimen bears one high intervarix between each varix and possibly represents *T. palensis*.

Timbellus sixi n. sp.
(Figs 13; 26M)

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Type material. — **Holotype. France** • Paris Basin, Oise, Trosly-Breuil (Fond Couturier); Sables de Cuise, (biozone NP12); early Eocene (Ypresian, lower Cuisian); MNHN.F.A90544 (Six coll.), H: 14 mm (Figs 13; 26M).

Etymology. — Dedicated to Didier Six who collected this rare species.

Type horizon. — Sables de Cuise, (biozone NP12), see Gély & Lorenz (1991: pl. 1), early Eocene (Ypresian, lower Cuisian).

Type locality. — France, Paris Basin, Oise, Trosly-Breuil (Fond Couturier).

Distribution. — Only known from the type locality.

Description

Unknow protoconch. Teleoconch up to 14 mm in height, up to 7.6 mm in width, biconic in profile, composed of five whorls. Moderately high spire. Last whorl 74% of total length. Apical angle 74° including spines, 66° excluding spines. Spiral sculpture with fine, narrow, well developed primary cords. First whorl, no spiral sculpture. Second whorl, appearance of weak P1 and P2. Third whorl, P1 and P2 well marked, appearance of s1. Fourth whorl, appearance of threads on infrasutural ramp. Fifth whorl: P1 to P6, s1 to s3; primary and secondary cords almost same relief; ADP to ABP on siphonal canal. On first whorl, nine protovarices. On second whorl, appearance of varices with two intervarices intercalated. On third whorl: three varices and three intervarices intercalated. From fourth to fifth whorl, three varices and two or three intervarices intercalated. Intevarices low. Higher relief of the intervarices on P2. Varices sublamellose on early whorls, rather thick on last whorls. Appearance of short P1 spine on second whorl. On last whorl, short P1 spine oriented adapically; no other cord spines. Ovate aperture up to 34% of diameter and up to 68% of length of last whorl (including the siphonal canal). Columellar lip smooth, narrow, slightly erect anteriorly, forming flat curved inductura at base. Parietal lip adherent. Outer lip with well developed denticles including ID, D1 to D3 (D4-D5 probably not formed); all denticles simple. Siphonal canal open, slightly dorsally recurved, up to 43% of apertural length. Pseudoumbilicus narrow.

Comparisons

This shell represents the oldest known *Timbellus* from the Paris Basin, as no *Timbellus* has been recorded from the Early Cuisian (biozone NP12, Ypresian) despite intensive fieldwork. It is easily distinguishable from the middle Eocene Paris Basin *Timbellus* species: *T. tripteroides* (Lamarck, 1822), *T. crenulatus tricarinatus* (Lamarck, 1803), *T. micropterus* (Deshayes, 1835) and *T. capitaneus* Pacaud, Ledon & Goret, 2017. Juveniles of *T. tripteroides* and *T. capitaneus* have weak spiral sculpture; *Timbellus crenulatus tricarinatus* lacks internal denticles, and juveniles of *T. micropterus* have coarser spiral sculpture. *Timbellus sixi* n. sp. resembles juveniles of *T. magnei* n. name from Bos d'Arros and Gan (Fig. 12C, D) in sharing a similar shape of its cords (fine, narrow, but well marked) and by having flat intervarices between the varices. However, *T. sixi* n. sp. differs from *T. magnei* n. name in having less foliated varices, having less numerous intervarices (usually 2-3 instead 4-5 in *T. magnei* n. name), and by having MP and ABP on the siphonal canal.

Species group of *T. crenulatus* (Röding, 1798)

In this species group, the last whorl is generally broader than in the species group of *T. tripteroides* and the shoulder spine (P1) is more strongly developed. The spiral sculpture corresponds to fine primary cords, as in the *T. tripteroides* species group. Two species have an acute open shoulder spine, similar to that seen in the genus *Pterochelus* Jousseaume, 1880: the Eocene species *T. crenulatus* (Röding, 1798) and the Miocene species *T. valdintortus* (Cossmann & Peyrot, 1924). In the *T. crenulatus* species group the rounded aperture bears poorly developed denticles or lirae within the outer lip, except in the oldest known member (*T. palensis* [Magne, 1941]) from the early Eocene of Aquitaine Basin of Gan (Fig. 12G-I). However, according Cossmann & O'Gorman (1923), the short shape and the rounded aperture

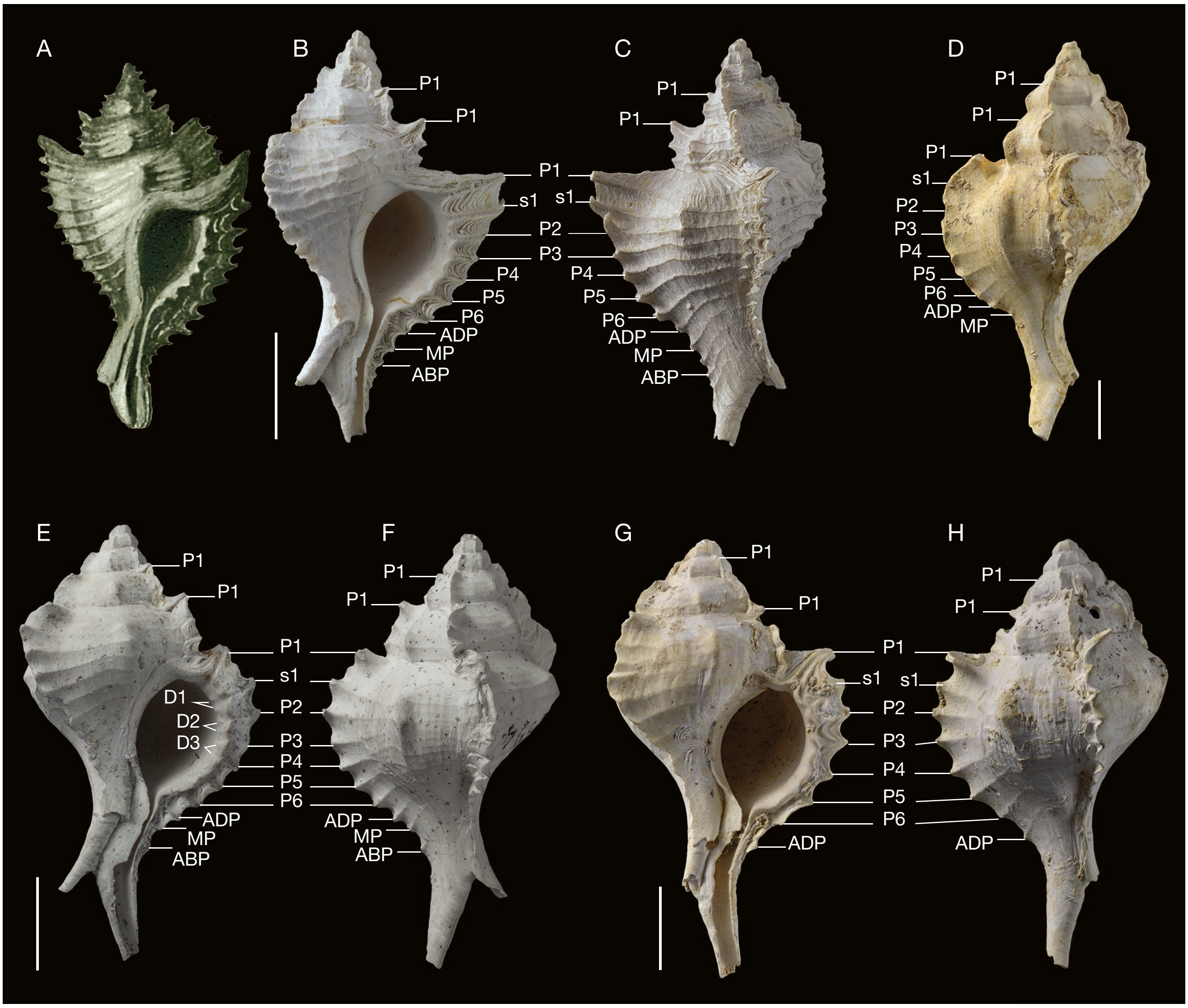

Fig. 14. — Spiral cords and internal denticles of the outer lip in *Timbellus crenulatus tricarinatus* (Lamarck, 1803) (**A**-**C**) and *T. curvispina* n. sp. (**D**-**H**): **A**, original figure of Lamarck (1816: pl. 418, fig. 5a), Thiverval-Grignon, Yvelines, Paris Basin, France, middle Eocene (Lutetian); **B**, **C**, neotype designated herein, MNHN.F.A90547 (MNHN coll.), Thiverval-Grignon (Falunière); **D**, paratype, MNHN.F.A73848 (Pons coll.), Fontenay-en-Vexin (Bois-du-But), Eure, Paris Basin, France, middle Eocene (Lutetian); **E**, **F**, holotype, MNHN.F.A90541 (MNHN coll.), Parnes, Oise, middle Eocene (Lutetian); **G**, **H**, paratype, MNHN.F.A90543 (Pons coll.), Fontenay-en-Vexin. Scale bars: B-H, 10 mm. Credits: P. Loubry.

of shells of this species resemble more closely *T. crenulatus tricarinatus* (Lamarck, 1803) than *T. tripteroides*. Probably, the presence of internal denticles in *T. palensis* represents a plesiomorphic character state and its loss in younger species of this group (e.g., *T. crenulatus tricarinatus* and *T. crenulatus crenulatus*) represents a derived state. For this group, we describe a new species: *T. curvispina* n. sp. from the Lutetian of the Paris Basin. As for *T. tripteroides*, the type material of *Murex tricarinatus* Lamarck, 1803 is lost, as it is also missing in the collections of Geneva and Paris. In order to avoid future taxonomic mistakes, we designate a neotype herein (MNHN.F.A90547, Fig. 14B, C) from the original type locality of Grignon (precisely Falunière of Grignon; Calcaire à Orbitolites complanatus Formation, biozone NP15, see Gély & Lorenz [1991: pl. 1], middle Lutetian).

Timbellus curvispina n. sp.
(Figs 14D-H; 26J-L)

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Murex tricarinatus – Deshayes 1835: 597, pl. 82, figs 9, 10 [*non* Lamarck, 1803].

Timbellus crenulatus tricarinatus – Merle *et al.* 2011: 440, pl. 98, figs 6, 7 only [*non* Lamarck, 1803].

Type material. — **Holotype. France** • Paris Basin, Oise, Parnes (Les Bôves); Falun de Parnes (biozone NP15); middle Eocene (middle Lutetian); MNHN.F.A90541 (ex B63594), H: 51.8 mm (Figs 14E, F; 26J).
Paratypes. France • 3 spm Paris Basin; Eure; Fontenay-en-Vexin (Bois du but); Falun de Parnes (biozone NP15); middle Eocene (Lutetian); MNHN.F.A73848 (Figs 14D; 26L), MNHN.F.A90542,

MNHN.F.A90543 (Pons coll.) (Figs 14G, H, 26K)• 1 spm; idem; MNHN.F.A32514 (Pacaud coll.), figured *in* Merle *et al.* (2011: 440, pl. 98, fig. 7) • 1 spm; Paris Basin, Yvelines, Villiers-Saint-Frédéric (Butte Saint-Léonard); Falun de Parnes (biozone NP15); Lutetian; MNHN.F.A32516 (Schtrock coll.), figured *in* Merle *et al.* (2011: 440 pl. 98, fig. 6)• 1 spm; Paris Basin, Yvelines, Parnes; Falun de Parnes (biozone NP15); Lutetian; MNHN.F.A90544 (ex Galerie de Zoologie coll.).

ETYMOLOGY. — Name derived from Latin *curv-* (meaning curved) and *spina* (meaning spine) and refers to the P1 spine dorsally curved; gender female.

TYPE HORIZON. — Falun de Parnes (biozone NP15), see Gély & Lorenz (1991: pl. 1), middle Eocene (middle Lutetian).

TYPE LOCALITY. — France, Paris Basin, Oise, Parnes (Les Bôves), see Fritel (1910: 221).

DISTRIBUTION. — Calcaire grossier moyen, biozone NP15, Paris Basin (France), middle Eocene (middle Lutetian).

DESCRIPTION

Protoconch not preserved. Teleoconch up to 51.8 mm in height, up to 30 mm in width, subfusiform in profile, composed of six whorls. Moderately high spire. Last whorl up to 85% of total length. Apical angle 63°. Spiral sculpture with marked primary cords on varices, but weaker on intervarices. First and second whorls eroded. From third: appearance of weak P1 and P2. Third word: no change. Fourth whorl: appearance of s1. Fifth whorl: occasional appearance of s2. Sixth whorl: P1 to P6, s1, s2, P6 not atrophied, s1 well developed; ADP developed, MP, ABP weak or missing on siphonal canal. Axial sculpture eroded on two early whorls. On second whorl, eight protovarices. Third whorl: appearance of varices; three varices and one intervarix between. From fourth to last whorl, no change. Higher relief of intervarices on P2. Varices sublamellose. Appearance of short straight P1 spine on fourth whorl. On last whorl, axial ornamentation forming very short spinelets, dorsally recurved on P1 to P6. P1 spine more strongly developed than other cord spines. Rounded aperture up to 34% of diameter and up to 74% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, slightly erect anteriorly, forming curved inductura at base. Parietal lip slightly adherent. Outer lip with very weak denticles including D1 to D6. Small crenulations at edge of outer lip. Siphonal canal narrow, open, bent, slightly dorsally recurved, up to 81% of apertural length. Pseudoumbilicus narrow

COMPARISONS

This species can be included in the group of *T. crenulatus* defined by Harasewych & Jensen (1979), Vokes (1992), and updated by Merle *et al.* (2011: 15). In this group the last whorl is generally wider than in species of the *T. tripteroides* group, the shoulder spine (P1) is more delineated and the internal denticles within the outer lip are weaker. The spiral sculpture corresponds to fine primary cords, as in the *T. tripteroides* group. *Timbellus curvispina* n. sp. was mistaken for the Lutetian species *T. crenulatus tricarinatus* (Lamarck, 1803) but it differs by the construction of the P1 spine. This spine is straight, long and oriented abaperturally in *T. crenulatus tricarinatus*, whereas it is shorter, curved and dorsally oriented in *T. curvispina* n. sp. (see Fig. 14). *Timbellus curvispina* n. sp. also bears cord spines that are always more developed than in *T. crenulatus tricarinatus*. Moreover, the spiral cords of *T. curvispina* n. sp. are weak in the intervarical spaces, whereas those of *T. crenulatus tricarinatus* are well marked. Pacaud *et al.* (2017) recently designated the lectotype of *Murex tricarinoides* Deshayes, 1835 demonstrating that authors confused this species with another: *T. capitaneus* Pacaud, Ledon & Goret, 2017. In addition, they synonymised *T. tricarinoides* with *T. crenulatus tricarinatus*. However, *T. tricarinoides* differs from *T. crenulatus tricarinatus* in lacking true P1 spines and in displaying a rounded outer lip. *T. crenulatus crenulatus* (Röding, 1798) from the Bartonian is easily distinguishable from *T. curvispina* n. sp. by its acute and long P1 spine pointing abaperturally.

SPECIES GROUP OF *T. PHYLLOPTERUS* (LAMARCK, 1822)

Members of this group are usually large sized and share a strong development of the internal denticles within the outer lip and strong primary cords; secondary cords are poorly developed. All species lack columellar denticles, except in the holotype of *T. xenos* (Harasewych, 1982), which is presumably a pathological specimen (Vokes 1992: 18). In the middle Eocene from Europe, *Timbellus submicropterus* n. sp. (upper Lutetian) and the Bartonian *T. micropterus* (Deshayes, 1835) represent the oldest members of this species group. It becomes more diversified in the late Eocene/early Oligocene with *T. lamarckii* (Grateloup, 1845), *T. detritus* (von Koenen, 1890), *T. arenarius* (Steuer, 1912), *T. danapris* Pacaud, 2018 and *T. radulfiensis* n. sp. It contains three Miocene species: *T. perlongus* (Bellardi, 1872), *T. rosavendae* (Bellardi, 1872) and *T. pseudolamarcki* (Magne, 1941), and becomes extinct before the Pliocene.

Timbellus radulfiensis n. sp.
(Figs 15; 26N-P)

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TYPE MATERIAL. — **Holotype. France** • Normandy, Manche, Rauville-la-Place; Argiles à Corbules Formation; late Eocene (Priabonian); MNHN.F.A77754 (MNHN coll.), H: 13.5 mm (Figs 15A, B; 26N). **Paratypes. France** • 1 spm; same as for the holotype; MNHN.F.A77755 (MNHN coll.) (Figs 15C; 26O) • 3 spm; idem; MNHN.F.A77756 (MNHN coll.) • 3 spm; idem; MNHN.F.A24118 (Vasseur coll.) • 1 spm; idem; MNHN.F.A90559 (Vasseur coll.) (Figs 15D; 26P).

ETYMOLOGY. — From the ancient name of the type locality *Radulfi villa* around 1083.

TYPE HORIZON. — Argiles à Corbules Formation, late Eocene (Priabonian), stratigraphic data given by Cavelier (1979) and Chateauneuf (1980).

TYPE LOCALITY. — France, Normandy, Manche, Rauville-la-Place (Cauvin), Cavelier (1979).

DISTRIBUTION. — Only know from the type locality.

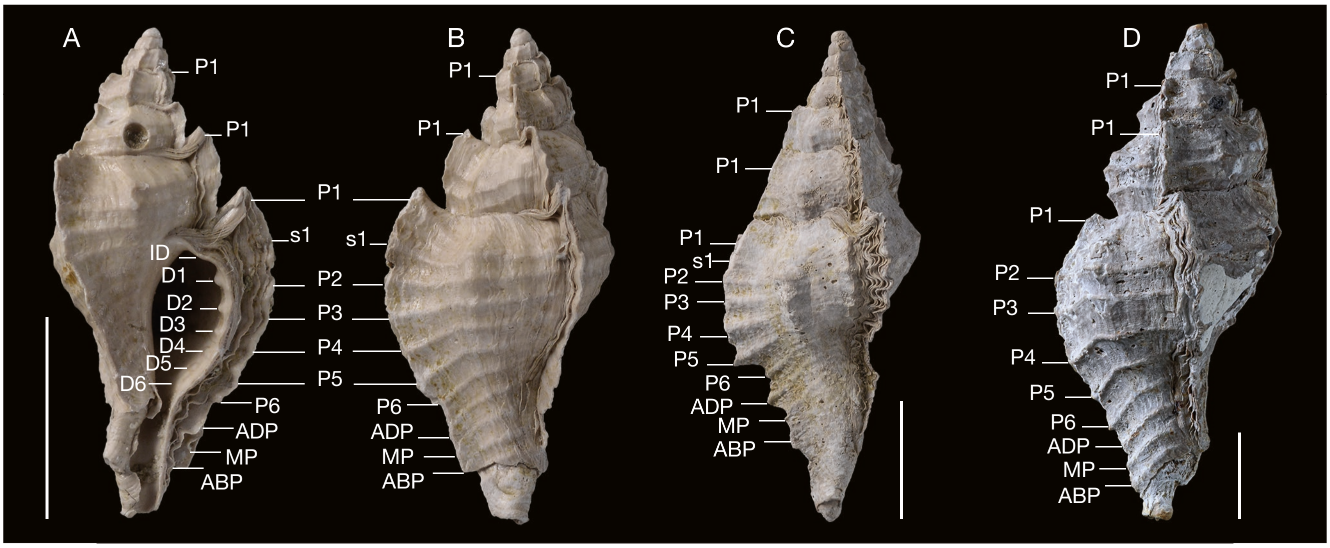

Fig. 15. — Spiral cords and internal denticles of the outer lip in *Timbellus radulfiensis* n. sp.: **A**, **B**, holotype, MNHN.F.A77754 (MNHN. coll.), Rauville-la-Place, Manche, Normandy, France, late Eocene (Priabonian); **C**, paratype, MNHN.F.A77755 (MNHN coll.), Rauville-la-Place; **D**, paratype, MNHN.F.A90559 (Vasseur coll.), Rauville-la-Place. Scale bars: 5 mm. Credits: A-C, P. Loubry (MNHN/CNRS); D, L. Cazes (MNHN/CNRS).

Description

Bulbous protoconch of one whorl. Teleoconch up to 20.5 mm in height, up to 7.5 mm in width, subfusiform in profile, composed of six whorls. Moderately high spire. Last whorl up to 74% of total length. Apical angle 61°. Spiral sculpture with moderately marked primary cords. First whorl: no cord. Second whorl: appearance of P2. Third whorl: appearance of P1 (weaker than P2) and s2. Fourth and fifth whorl: no change. Sixth whorl: P1 to P6, s1; P6 not atrophied; ADP, MP and ABP on siphonal canal. From first whorl to second whorl: ten protovarices. On third whorl: seven protovarices. Fourth whorl: appearance of varices; three varices and one intervarix intercalated. From fifth to sixth whorl: no change. Higher relief of intervarices on P2. Varices sublamellose. Appearance of short P1 spine on third whorl. Abapically spinelets from P1 to P6 and ADP. Ovate aperture up to 34% of diameter and up to 74% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, poorly erect anteriorly, forming curved inductura at base. Parietal lip slightly adherent. Outer lip with developed denticles including ID, D1 to D6. Outer lip not crenulate. Siphonal canal open, straight, up to 47% of aperture length. Pseudoumbilicus narrow.

Comparisons

This species can be compared to other Priabonian and Rupelian species from Northern Europe (Germany) and Eastern Europe (Ukraine) with which it shares a narrow shape. It differs from *T detritus* (von Koenen, 1890), *T. arenarius* (Steuer, 1912) and *T. danapris* Pacaud (2018) in having finer spiral cords. The spiral sculpture resembles more that of *T. priabonicus* Pacaud, 2018 (nom. n. for *Murex trialatus* von Koenen, 1889, *non* G. B. Sowerby (II), 1834), but *T. priabonicus* bears strongly developed P1 and P2 spines, whereas only P1 spine is developed in *T. radulfiensis* n. sp.

Timbellus submicropterus n. sp.
(Figs 16A-H, K; 27A-D)

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Murex (*Pterymurex*) *tricarinatus* – Cossmann & Pissarro 1901: 128, pl. 14, fig. 1 [*non* Lamarck, 1803].

Timbellus micropterus – Merle *et al.* 2011: 448, pl. 102, fig. 4a, b only [*non* Deshayes, 1865].

Type material. — **Holotype. France** • Normandy, Manche, Fresville; Calcaire de Fresville; middle Eocene (uppermost Lutetian); MNHN.F.A24111 (MNHN coll.), H: 23.6 mm (Figs 16A, B; 27A).
Paratypes. France • 1 spm; same as for the holotype; UCBL-EM 33438 (Bourdot coll., figured specimen of Cossmann & Pissarro 1901) (Figs 16E, F; 27C) • 1 spm; idem; MNHN.F.A90556 (MNHN coll.) (Fig. 16K) • 1 spm; idem; MNHN.F.B63700 (de Morgan coll.) • 1 spm; Normandy, Manche, Gourbesville; Calcaire de Fresville; upper Lutetian; MNHN.F.A24126 (Munier-Chalmas coll.), figured specimen of Merle *et al.* (2011: 135, pl. 102, fig. 4a, b) (Figs 16C, D; 27B).

Additional material (material referring to *Timbellus* cf. *submicropterus* n. sp.). — **France** • 3 spm; Loire-Atlantique, Loire Basin, Saffré (Bois Gouët); middle Eocene (lower Bartonian); MNHN.F.A29660 (Pacaud coll.) • 2 spm; Saint-Aignan-Grand-Lieu (Pierre-Aiguë), Loire-Atlantique; idem; MNHN.F.A29662, (Brébion coll.), MNHN.F.A90557 (Brébion coll. (Figs 16G, H; 27D).

Etymology. — Name formed by the prefix *sub-* and *micropterus* for this species older than Bartonian *Timbellus micropterus* (Deshayes, 1835).

Type horizon. — Calcaire de Fresville, middle Eocene (uppermost Lutetian), see Bignot *et al.* (1968).

Type locality. — France, Normandy, Manche, Fresville, see APGN (2024).

Distribution. — Normandy (Calcaire de Fresville) middle Eocene (uppermost Lutetian) and ? Loire Basin (Sables du Bois-Gouët), lowermost Bartonian, see Mathelin & Bignot (1989).

Description

Bulbous protoconch of one whorl (Fig. 16K). Teleoconch up to 23.6 mm in height, up to 11.6 mm in width, biconic in profile, composed of six whorls. Moderately high spire. Last whorl up to 70% of total length. Apical angle 59°. Spiral sculpture with coarse primary cords. First to third whorl: no cord. Fourth whorl: appearance of weak P1, s1 and P2. Fifth whorl: P1, s2 and P2 coarser. Sixth whorl: P1 to P6, s1; P6 not atrophied on convex part of whorl; ADP, MP and ABP on siphonal canal. From first whorl to second whorl: 6-7 protovarices. On third whorl: appearance of varices; three varices and one intervarix intercalated. From third to sixth whorl: no change. Higher relief of intervarices on P2. Varices rather thick. Appearance of short P1 spine on third whorl. Ovate aperture up to 27% of diameter and up to 71% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, poorly erect anteriorly, forming curved inductura at base. Parietal lip slightly adherent. Outer lip with developed denticles including ID, D1 to D6. D6 in some specimens. Outer lip not crenulate. Siphonal canal open, straight, up to 40% of apertural length. Pseudoumbilicus narrow.

Comparisons

A specimen of this species (Figs 16E, F; 27C) was identified as *Murex* (*Pterymurex*) *tricarinatus* Lamarck, 1803 (synonym of *Timbellus crenulatus tricarinatus*) by Cossmann & Pissarro (1901). *Timbellus crenulatus tricarinatus* differs greatly by apertural (with weak internal denticles within the outer lip), sculptural and shape characters, and belongs to another group species (see above Fig. 14). In fact, this specimen illustrated by Cossmann & Pissarro (1901) more closely resembles *T. micropterus* from the Bartonian Paris Basin. Merle *et al.* (2011) attributed another Norman specimen (pl. 102, fig. 4a, b) to *T. micropterus* (Figs 16C, D; 27B). It is true that these two specimens are superficially similar to *T. micropterus*, but further comparison reveals some differences, such as only one intervarice (instead two in typical *T. micropterus*) and finer secondary cords on the last whorl. The bivariate plot of total length against width (Fig. 17) does not suggest strong differences Normandy and Paris Basin populations. Finally, it is tempting to conclude that the observed teleoconch differences in *T. submicropterus* n. sp. fall within the intraspecific variation of *T. micropterus*. However, *T. submicropterus* n. sp. has a paucispiral protoconch, whereas *T. micropterus* has a multispiral (Fig. 16K, L), suggesting two separate species with different modes of larval development. In the Bartonian from Loire-Atlantique, there are specimens showing coarse spiral cords like those of typical *T. submicropterus* n. sp., but they bear a more pronounced shoulder (Fig. 16G, H). Their protoconch is not preserved. We therefore attribute these specimens to *T. submicropterus* n. sp. with hesitation.

Genus *Pterynotus* Swainson, 1833

Type species. — *Murex pinnatus* Swainson, 1822, by monotypy. Recent: Indo-Pacific.

Comments on the subfamilial place

As seen above, fossil and Recent members of the genus *Timbellus* de Gregorio, 1885 were usually attributed to *Pterynotus* Swainson, 1833 (e.g., Cossmann 1889; Cossmann & Pissarro 1911; Glibert 1963; Vokes 1970) in the subfamily Muricinae. Based on molecular data, Barco *et al.* (2010, 2012) studied the phylogenetic relationships of *Pterynotus* represented by *P. elongatus* (Lightfoot, 1786) and *P. fulgens* Houart, 1988 and *Pterymarchia* Houart, 1995 represented by *P. martinetana* (Röding, 1798). These authors demonstrated firstly, that *Pterynotus* and *Pterymarchia* are not phylogenetically close to *P. fulgens* Houart, 1988 and secondly, none of these taxa are included within the clade of the Muricinae. According to Merle *et al.* (2011), *Pterynotus fulgens* is closely related to the type species of *Timbellus* and is now attributed to that genus. Thus, Merle *et al.* (2011) and Houart (2018) rejected *Pterynotus* and *Pterymarchia* from the Muricinae. Russini *et al.* (2023: 866) place *Pterynotus* in *incertae sedis* and consider that it likely represented an independent lineage, worthy of subfamilial rank.

Subgenus *Pterymarchia* Houart, 1995

Type species. — *Murex tripterus* Born, 1778, by original designation. Recent: Indo-Pacific.

Comments on the subgenus

According to Houart (1995), *Pterymarchia* can be distinguished from *Pterynotus* (*s.s.*) by having more numerous axial varices on the early teleoconch whorls (9-11 vs 6-8), later appearance in ontogeny of the trivaricate sculpture, when present, sometimes more varices on the last whorls (3-5 vs 3), and more strongly developed denticles. Houart (1995, 2018) proposed full generic status for *Pterymarchia*. However, we prefer to maintain it at subgeneric rank because: 1) based on molecular data, *Pterynotus* and *Pterymarchia* are very close (Barco *et al.* 2010); and 2) based on shell characters, *Pterymarchia* shares with *Pterynotus* a scabrous surface appearing early in ontogeny, generally fine to moderately fine primary cords (from IP to ABP), and a series of internal denticles from ID to D6. Furthermore, several other characters are occasionally shared by both genera, such as the trivaricate sculpture, columellar tubercles [e.g., *P.* (*s.s.*) *patagiatus* (Hedley, 1912), *P.* (*s.s.*) *praepatagiatus* Vokes, 1992 and *P.* (*s.s.*) *granuliferus* (Grateloup, 1833)], and even developed denticles in some *P.* (*s.s.*) *albobruneus* Bertsch & D'Attilio, 1980.

***Pterynotus* (*Pterymarchia*) *gaasensis* n. sp.**
(Figs 18A-D; 27E, F)

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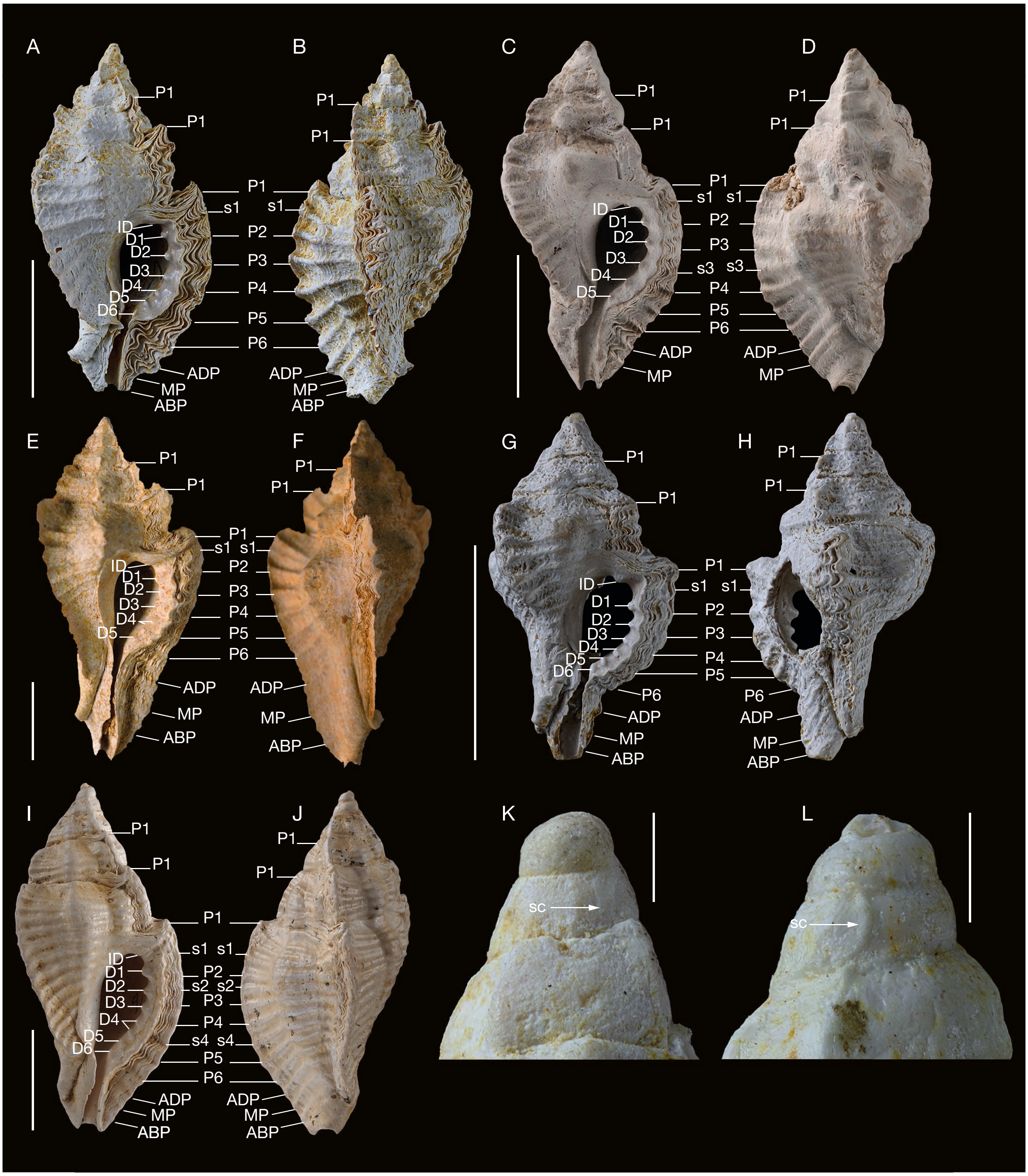

FIG. 16. — Spiral cords and internal denticles of the outer lip in *Timbellus submicropterus* n. sp. (**A**-**H**, **K**) and *T. micropterus* (Deshayes, 1835) (**I**, **J**, **L**): **A**, **B**, holotype, MNHN.F.A24111 (MNHN coll.), Fresville, Manche, Normandy, France, middle Eocene (Lutetian); **C**, **D**, paratype, MNHN.F.A24126 (Munier-Chalmas coll.), Gourbesville, Manche, middle Eocene (Lutetian); **E**, **F**, paratype, UCBL-EM 33438 (Bourdot coll.), Fresville; **G**, **H**, MNHN.F.A90557 (Brébion coll.), Saint-Aignan-Grand-Lieu (Pierre-Aiguë), Loire-Atlantique, Loire Basin, France, middle Eocene (Bartonian); **I**, **J**, MNHN.F.A32522 (Faullummel coll.), Le Limon, Seine-et-Marne, Paris Basin, France, middle Eocene (Bartonian); **K**, paratype (protoconch), MNHN.F.A90556 (MNHN coll.), Fresville; **L**, MNHN.F.A90558 (Faullummel coll., protoconch), Chavençon (Carrière Tuyttens), Oise, Paris Basin, France, middle Eocene (Bartonian). Scale bars: A-J, 10 mm; K, L, 0.5 mm. Credits: A-D, I, J, P. Loubry (MNHN/CNRS); E, F, E. Robert (UCBL); G, H, K, L, L. Cazes (MNHN/CNRS).

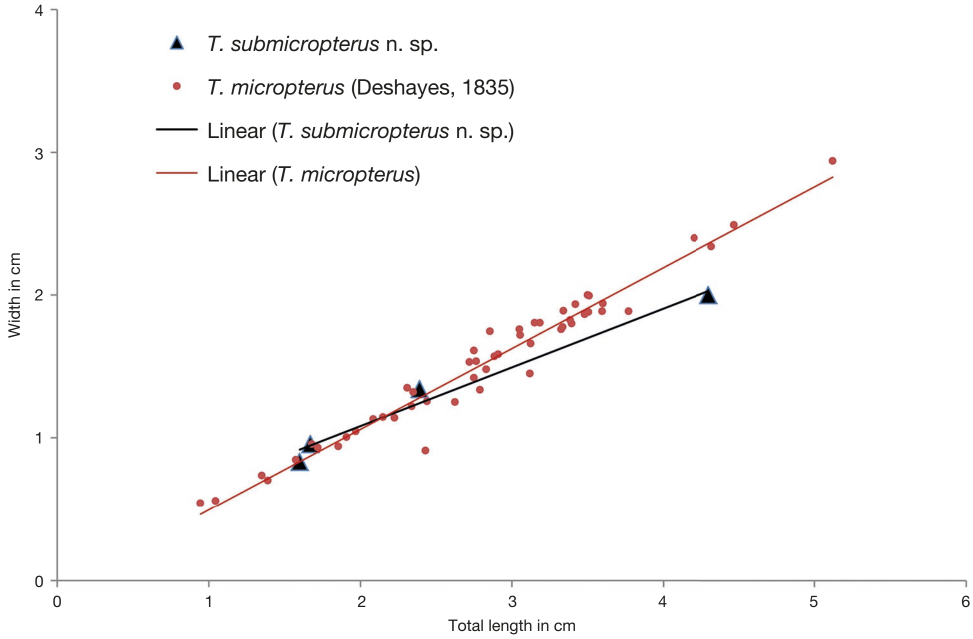

FIG. 17. — Bivariate plot of total length against width comparing *T. micropterus* (Deshayes, 1835) from the lower Bartonian of the Paris Basin (50 complete specimens) and *T. submicropterus* n. sp. from the uppper Lutetian of Normandy (five complete specimens).

Murex quadrifrons – Grateloup 1845: pl. 3 [pl. 31], fig. 10 [*non Murex quadrifrons* Lamarck, 1822].

Pterynotus (*Pterymarchia*) cf. *subquadrifrons* – Merle *et al.* 2011 (*partim*): pl. 90, figs 3-74 only.

Pterynotus cf. *subquadrifrons* – Lozouet 2023: 21, pl. 17, figs 1-9, text-fig. 10E.

TYPE MATERIAL. — **Holotype. France** • Aquitaine Basin, Landes, Gaas (Espibos); Gaas Formation (biozone NP23); early Oligocene (Rupelian); MNHN.F.A32492 (Merle coll.), figured specimen in Merle *et al.* (2011: pl. 90, fig. 3), H: 27 mm (Figs 18A, B; 27E).
Paratypes. France • 6 spm; same as for the holotype; MNHN.F.A77749 (Merle coll.) • 1 spm; idem; MNHN.F.A90554 (Merle coll.) (Figs 18C, D; 27F) • 1 spm; idem; MNHN.F.A86913 (Lozouet coll.), figured in Lozouet (2023: text-fig. 10a, b).

ADDITIONAL MATERIAL. — **France** • 1 spm; Aquitaine Basin, Landes, Gaas (La Gouarde); same as for the holotype; Aucoin coll., figured *in* Merle *et al.* (2011: pl. 90, fig. 4a, b).

ETYMOLOGY. — From the type locality, Gaas (Landes), France.

TYPE HORIZON. — Gaas Formation (biozone NP23), see Sztrákos & Steurbaut (2017: 752), early Oligocene (Rupelian).

TYPE LOCALITY. — France, Aquitaine Basin, Landes, Gaas (Espibos), see Sztrákos & Steurbaut (2017: 752).

DISTRIBUTION. — Aquitaine Basin (France), early Oligocene (Rupelian).

DESCRIPTION

Paucispiral protoconch (*fide* Lozouet 2023: text-fig. 10e). Teleoconch up to 27 mm in height, up to 12 mm in width, biconic in profile, composed of six whorls. Moderately high spire, first two whorls subcarinate; next whorls rounded. Last whorl up to 75% of total length. Apical angle 56°. Spiral sculpture with marked primary cords. First whorl: appearance of primary cords P1 and P2; second whorl: P1 and P2; third whorl: appearance of s1. Fourth whorl: appearance of abis, adis and s2. Fifth whorl: no change or appearance of threads. Sixth whorl: IP, adis and abis, P1 to P6, s1 to s6; s2 and s3 well developed; P6 on base on convex part of whorl; ADP, MP and ABP slightly more developed than ads and ms. Surface of shell with numerous threads appearing on fourth whorl. Axial sculpture with thick varices. On first whorl: nine lamellose varices. From the second to fifth whorl: 9-10 thick varices. On sixth: appearance of three or four varices and one intervarices intercalated. Varices and intervarices thick. From the third to last whorl, numerous, fine microlamellae covering entire surface forming scabrous microsculpture. Ovate aperture up to 25% of diameter and up to 66% of length of last whorl (including siphonal canal). Columellar lip, adherent posteriorly, becoming progressively more erect anteriorly. One or two small columellar tubercles. Parietal lip adherent. Outer lip bearing strong internal denticles: ID, D2 to D6 present, D1 missing. Pseudoumbilicus moderately large. Siphonal canal open, up to 48% of apertural length, slightly dorsally recurved.

COMPARISONS

Merle *et al.* (2011: pl. 90, figs 3-4) attributed with hesitation two specimens from Gaas to *Murex subquadrifrons* d'Orbigny, 1852, originally described as *Murex quadrifrons* by Grateloup (1845) from this same Rupelian locality. The Grateloup's collection is housed in the University of Talence, but the type material of *M. quadrifrons* was not found and is likely lost (personal observation of the first author). Therefore, only the drawing of Grateloup (1845: pl. 3 [pl. 31], fig. 10, refigured in Merle *et al.* 2011: pl. 90, fig. 2) can be used to identify the

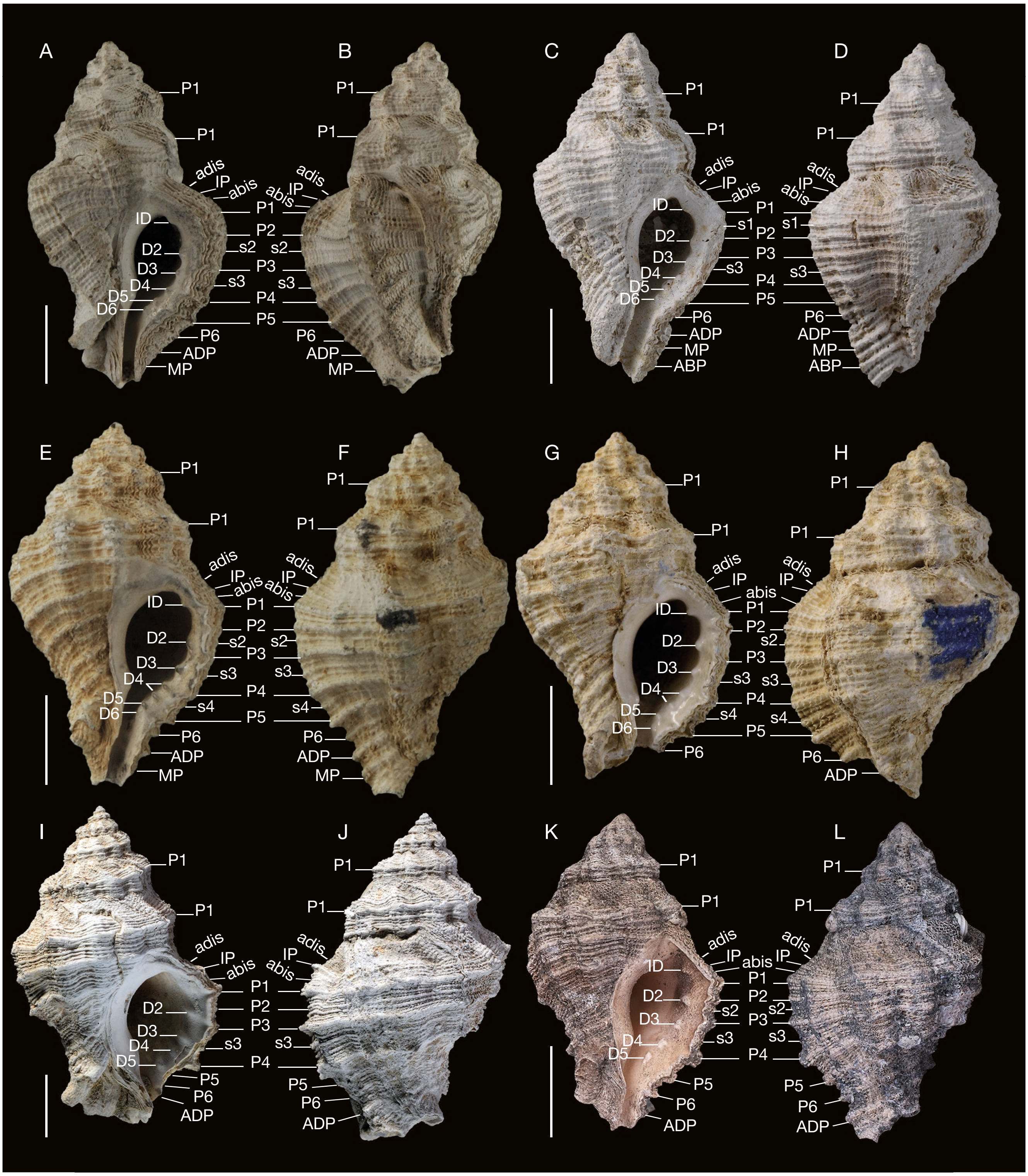

Fig. 18. — Spiral cords and internal denticles of the outer lip in *Pterynotus* (*Pterymarchia*) *gaasensis* n. sp. (**A**-**D**), *P.* (*P.*) *pelouatensis* n. sp. (**E**-**H**) and *P.* (*P*) *sandbergeri* (Hörnes, 1856) (**I**-**L**): **A**, **B**, holotype, MNHN.F.A32492 (Merle coll.), Gaas (Espibos), Landes, Aquitaine Basin, France, early Oligocene (Rupelian); **C**, **D**, paratype, MNHN.F.A90554 (Merle coll.), Gaas (Espibos); **E**, **F**, holotype, MNHN.F.J09945, Saucats (Peloua), Gironde, Aquitaine Basin, Early Miocene (Burdigalian); **G**, **H**, paratype, MNHN.F.J17632, Saucats (Peloua); **I**, **J**, lectotype designated herein, NHMW1855/0045/0435, Gainfarn, Baden, Austria, Middle Miocene (Langhian); **K**, **L**, Landau coll., Bad Vöslau, Baden. Scale bars: A-H, 5 mm; I-L, 10 mm. Credits: A-H, P. Loubry (MNHN/CNRS); I, J, M. Harzhauser (NHMW); K, L, B. Landau.

species. According to Merle *et al.* (2011), the drawing shows a shell with a textiliose surface and a biconic shape, as in the Gaas material at hand. Moreover, to our knowledge, no other muricid from Gaas except *P.* (*Pterymarchia*) is comparable to the specimen illustrated by Grateloup (1845). However, the shell illustrated by Grateloup (1845) lacks internal denticles within the outer lip, lacks columellar denticles, shows more numerous varices (six on the ventral face vs four in the specimens at hand), has a narrower siphonal canal, and is more likely to represent a specimen of *Favartia*. These numerous differences between Grateloup's (1845) figure and the studied material suggest that it obviously corresponds to a species other than *M. subquadrifrons*. *Murex subquadrifrons* is therefore not recognizable using the figure of Grateloup, lacks type material and it should be considered a *nomen dubium*.

Eocene *Pterynotus* (*Pterymarchia*), such as *P.* (*P.*) *antiquus* (Merle 1990), *P.* (*P.*) *denudatus* (Deshayes, 1835) and *P.* (*P.*) *defensus* (Fuchs, 1870) strongly differ from the *P.* (*P.*) *gaasensis* n. sp. in having trivaricate sculpture. *Pterynotus* (*P.*) *fascistria* (von Koenen, 1889) from the Priabonian of North Germany is more similar shape, as it lacks trivaricate sculpture and because their primary cords are poorly distinguishable from the secondary cords on the last whorls. *Pterynotus* (*P.*) *fascistria* is distinguished from *P.* (*P.*) *gaasensis* n. sp. in having a lower spire and by lacking intervarices, D1 and ID denticles. *Pterynotus* (*P.*) *gaasensis* n. sp. can be compared to two other Neogene species: *P.* (*P.*) *pelouatensis* n. sp. from the Burdigalian of Aquitaine Basin (Figs 18E-H; 27G, H) and *P.* (*P.*) *sandbergeri* (Hörnes, 1856) from the Langhian of the Paratethys. Both species differs from *P.* (*P.*) *gaasensis* n. sp. in having more angular whorls with a shoulder delimited by a subspiny P1 and by other primary cords more distinguishable from the secondary cords on the last whorl. Lozouet (2023) followed Merle *et al.* (2011) and adopted the name *Pterynotus* cf. *subquadrifrons* for the Rupelian material from Gaas, but he did not include Chattian and Aquitanian specimens figured in Merle *et al.* (2011: pl. 90, figs 5, 6), because Rupelian shells have a paucispiral protoconch, whereas the Chattian/Aquitanian species has a multispiral protoconch, and is therefore a separate species. Thus, we consider for instance that *P.* (*P.*) *gaasensis* n. sp. to be present only in the Rupelian.

***Pterynotus* (*Pterymarchia*) *pelouatensis* n. sp.**
(Figs 18E-H; 27G, H)

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Pterynotus (*Pterymarchia*) sp. – Merle *et al.* 2011: 424, pl. 90, fig. 7a, b.

TYPE MATERIAL. — **Holotype. France** • Aquitaine Basin, Gironde, Saucats (Peloua); Faluns de Saucats; Early Miocene (lower Burdigalian); MNHN.F.J09945 (Neuville coll.), figured specimen in Merle *et al.* (2011: 424, pl. 90, fig. 7), H: 21 mm (Figs 18E, F; 27G). **Paratype. France** • 1 spm; same as for the holotype; MNHN.F.J17632 (Neuville coll.) (Figs 18G, H; 27H).

ETYMOLOGY. — From the type locality, Peloua, Gironde, France.

TYPE HORIZON. — Faluns de Saucats, Early Miocene (lower Burdigalian), see Parize *et al.* (2008: 396).

TYPE LOCALITY. — France, Aquitaine Basin, Gironde, Saucats (Peloua), see Parize *et al.* (2008: fig. 1).

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Two smooth protoconch whorls preserved delimited by sinusigera scar (protoconch tip not preserved) (see Merle *et al.* 2011: 122, text-fig. 46E). Teleoconch up to 21 mm in height, up to 12.5 mm in width, biconic in profile, composed of five whorls. Moderately high spire with subcarinate whorls. Last whorl up to 73% of total length. Apical angle 64°. Spiral sculpture with marked primary cords. First whorl: appearance of P1 and P2; second whorl: appearance of IP; third whorl: appearance of abis, adis and s2. Fourth whorl: no change or appearance of threads. Fifth whorl: IP, adis and abis, P1 to P6, s1 to s6; s3 and s4 more developed than other secondary cords; P6 slightly atrophied, on base of convex part of whorl; ADP, MP, ads and ms; ABP missing. Surface of shell with numerous threads appearing on fourth whorl. Axial sculpture with thick varices. On first whorl: 10-11 lamellose varices; on second whorl: 10-12 varices; on third whorl: 11-12 varices; on fourth whorl: 10-12 varices; on fifth whorl 8-10 varices. From second whorl to fifth whorl: thick varices. No evidence of intervarices on last whorl. From third to last whorl numerous, fine microlamellae forming scabrous microsculpture covering entire surface. Ovate aperture up to 31% of diameter and up to 72% of length of last whorl (including siphonal canal). Columellar lip adherent posteriorly, becoming progressively more erect anteriorly. One or two weak columellar tubercles. Parietal lip adherent. Outer lip with strong internal denticles: ID, D2 to D6 present, D1 missing; D4 split, D6 poorly developed. Pseudoumbilicus moderately large. Siphonal canal open, up to 43% of aperture length, slightly dorsally recurved.

COMPARISONS

The European Neogene contains two species of *Pterynotus* (*Pterymarchia*): *P.* (*P.*) *pelouatensis* n. sp. and *P.* (*P.*) *sandbergeri* (Hörnes, 1856) n. comb. from the Langhian of Paratethys (Austria, Hungary, Romania, Poland) and the Serravallian of Turkey. The type material of *P.* (*P.*) *sandbergeri* is housed in Naturhistorisches Museum of Wien and contains the figured syntype of the species (Hörnes 1856: pl. 51, fig. 5a, b, NHMW 1855/0045/0435). Here, we designate this specimen as the lectotype (Fig. 18I, J). *Pterynotus* (*P.*) *sandbergeri* was often attributed to *Murexsul* Iredale, 1915 (Landau *et al.* 2013; Kovács *et al.* 2018; Kovács 2019). Although they share several similarities (biconic shells, internal denticles, columellar denticles), members of *Murexsul* have a more rounded aperture, their internal denticles are close together, ID is weaker and their siphonal canal is narrower. The spires of *P.* (*P.*) *pelouatensis* n. sp. and the lectotype of *P.* (*P.*) *sandbergeri* are very similar, but their last whorls are very different. The lectotype of *P.* (*P.*) *sandbergeri* has a larger aperture, a surface covered by numerous threads and atrophy of P2, P5 and P6; P4 is more developed and D6 is missing. The differences between the primary cords are great, but in other specimens attributed from *P.* (*P.*) *sandbergeri* (Fig. 18K, L), the atrophy of P2, P5 and P6 is less strong than in the lectotype from Austria (see

Landau *et al.* 2013; Kovács *et al.* 2018; Kovács 2019). Compared to extant *P.* (*Pterymarchia*), *P.* (*P.*) *pelouatensis* n. sp. and *P.* (*P.*) *sandbergeri* share greatest morphological similarities with *P.* (*P.*) *martinetana* (Röding, 1798) and particularly with specimens from the Red Sea (Merle *et al.* 2011: pl. 92, figs 11, 12), but *P.* (*P.*) *sandbergeri* differs by having develop cord spines on P1, P2, P4, P5, ADP and MP.

Genus *Textiliomurex* Merle, 2011

Type species. — *Murex textiliosus* Lamarck, 1803 by original designation. Middle Eocene: Paris basin, France and Hampshire Basin, England.

Comments on the genus

Textiliomurex shares similarities with *Pterynotus* (*s.s.*) and *Pterynotus* (*Pterymarchia*) such as a scabrous surface, columellar denticles and a series of internal denticles including ID, D1 to D6. *Textiliomurex* does not display trivaricate axial sculpture and lacks intervarices, usually found in *Pterynotus* (*s.s.*). The number of varices on the last whorls of *Textiliomurex* is higher (9-11) than in *Pterymarchia* (3-5, see Houart 1995). As with *Pterynotus*, we cannot give a subfamilial placement to this genus. Merle *et al.* (2011: 127) included six species in the genus. Recently, Lozouet (2023) added (with some doubt) one species from the Chattian of the Aquitaine Basin (*Textiliomurex*? *problematicus* Lozouet, 2023), and we add a new species from the Lutetian of the Paris Basin herein.

Textiliomurex chodmonensis n. sp.

(Figs 19A-D; 27I, J)

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Type material. — **Holotype. France** • Paris Basin, Oise, Chaumont-en-Vexin (Carrière Darcy); Calcaire Grossier inférieur (biozone NP14); middle Eocene (lower Lutetian); MNHN.F.A81144 (Pacaud coll.), H: 28 mm (Figs 19A, B; 27I).
Paratype. France • 1 spm; same as for the holotype; MNHN.F.A81145 (Pons coll.) (Figs 19C, D; 27J).

Etymology. — Name from the type locality Chaumont-en-Vexin. This place name comes from the Celtic words Chod "wood" and Mon "montain".

Type horizon. — Calcaire Grossier inférieur (biozone NP14), see Gély & Lorenz (1991: pl. 1), middle Eocene (lower Lutetian).

Type locality. — France, Paris Basin, Oise, Chaumont-en-Vexin (Carrière Darcy), see Ott d'Estevou *et al.* (2014).

Distribution. — Only known from the type locality.

Description

Protoconch not preserved. Fusiform teleoconch up to 28 mm in height, up to 21 mm in width. High spire, up to seven rounded whorls. Last whorl (seventh whorl) up to 65% of total length. Apical angle 55°. Spiral sculpture with fine, narrow, well marked primary and secondary cords. First to third whorl not preserved. Fourth whorl: IP, s1 and P2. Fifth whorl: appearance of the secondary cord adis (sutural ramp). Sixth whorl: addition of tertiary cords on sutural ramp and convex part of whorl. Seventh and last whorl: IP, adis and abis (sutural ramp), P1 to P6 (convex part of the whorl); P6 placed on base on convex part of whorl; ADP, MP, ABP (siphonal canal), MP, ABP poorly distinct from secondary cords; primary and secondary cords of same thickness. Surface of shell with numerous threads. Axial sculpture with nine varices on fourth whorl, seven on fifth whorls, six on sixth whorls and five on seventh and last whorl. Nodulose varices. No intervarices. No varical spine. Numerous, fine microlamellae covering entire surface forming scabrous microsculpture. Ovate aperture up to 36% of diameter and up to 70% of length of last whorl (including siphonal canal). Columellar lip adherent, smooth. Parietal lip adherent. Short anal sulcus. No shoulder channel. Outer lip with subobsolete internal denticles. Outer lip finely crenulated. Pseudoumbilicus wide. Siphonal canal open, up to 38% of apertural length, slightly dorsally recurved.

Comparisons

Textiliomurex chodmonensis n. sp. can be compared to two other species from the middle Lutetian: *T. textiliosus* (Lamarck, 1803) and *T. bernayi* (Deshayes, 1865). *Textiliomurex textiliosus* differs in having a shorter spire, a more inflated last whorl, a wider aperture, and a longer siphonal canal bearing a narrower pseudoumbilicus. *Textiliomurex bernayi* has angular teleoconch whorls with a marked P1 shoulder, bears well developed internal denticles within the outer lip and cannot be confused with *T. chodmonensis* n. sp. (see Merle *et al.* 2011: 126, text. fig. 47 and pl. 94 about *Textiliomurex*).

Genus *Ponderia* Houart, 1986

Type species. — *Typhis zealandica* Hutton, 1873 by original designation. Pleistocene to Recent: New Zealand.

Comments on the subfamilial placement

Subfamilial placement of the genus *Ponderia* Houart, 1986 has varied in the literature. D'Attilio & Hertz (1988) placed it in the subfamily Tripterotyphinae D'Attilio & Hertz, 1988, whereas Vokes (1996) preferred placement it in the subfamily Muricinae. More recently, Merle *et al.* (2011) included *Ponderia* in a basal muricid group (without subfamilial assignment) and excluded it from the typical Muricinae. Houart (2018) included five genera in the Tripterotyphinae: *Cinclidotyphis* DuShane, 1969, *Prototyphis* Ponder, 1972, *Pterotyphis* Jousseaume, 1880, *Tripterotyphis* Pilsbry & Lowe, 1932 and *Ponderia*. All these genera share trivarical morphology, but the construction of the anal tube in *Cynclidotyphis* and *Pterotyphis* differs from that of *Prototyphis*, *Ponderia* and *Tripterotyphis*. In *Cynclidotyphis* and *Pterotyphis,* the anal tube is built just below the suture probably not with P1, whereas in *Prototyphis*, *Ponderia* and *Tripterotyphis* it is clearly built with P1. *Tripterotyphis* also differs from *Ponderia* and *Prototyphis* in having more strongly developed spiral sculpture. Thus, this group of five genera is likely to be polyphyletic. In their molecular phylogenetic work, Russini *et al.* (2023) confirm this hypothesis showing that: 1) *Tripterotyphis* belongs to a clade containing *Muricopsis*; and 2) *Ponderia* may represent a plesiomorphic lineage at the base of the pagoduline-haustrine diversification. Thus, those authors (p. 866) placed *Ponderia* in *incertae sedis*, and considered it likely to represent an independent lineage worthy of subfamilial rank.

Ponderia remyi n. sp.

(Figs 19E-H; 27K, L)

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TYPE MATERIAL. — **Holotype. France** • Normandy, Manche, Fresville; Calcaire de Fresville; middle Eocene (uppermost Lutetian); MNHN.F.A90548 (Remy coll.), H: 26 mm (Figs 19E, F; 27K).
Paratypes. France • 5 spm; same as for the holotype; MNHN.F.A90549 (Remy coll.) • 1 spm; idem; MNHN.F.A90555 (Remy coll.) (Fig. 19G, H; 27L) • 3 spm, MNHN.F.A90550 (MNHN coll.) • 1 spm; Normandy, Manche, Fresville (coteau de Vauville); idem; MNHN.F.A27328 (MNHN coll.) • 2 spm; idem; MNHN.F.B63590 (de Morgan coll.).

ETYMOLOGY. — Dedicated to Nicolas Remy who collected the material of this species.

TYPE HORIZON. — Calcaire de Fresville, middle Eocene (uppermost Lutetian), see Bignot *et al.* (1968).

TYPE LOCALITY. — France, Normandy, Manche, Fresville, see APGN (2024).

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Bulbous, paucispiral protoconch of 1.5 whorls. Slender, fusiform teleoconch up to 21 mm in height, up to 9 mm in width. High spire, up to six subcarinate whorls. Last whorl (sixth whorl) up to 69% of total length. Apical angle 35° excluding P1 spine and up to 55° including P1 spine. Spiral sculpture with strongly marked primary cords. First and second whorl: no primary cord. Third whorl: appearance of weak P2. Fourth whorl: P2 strongly marked and appearance of weak P1. Fifth whorl: strongly marked P1 and P2. Sixth and last whorl: P1 to P3 well marked, P4 weak (convex part of whorl); secondary cords occasionally s1 and s2. Axial sculpture with 8-9 lamellose protovarices per whorl from first to fourth whorl to four lamellose protovarices. From fifth whorl to sixth whorl, three major varices and two or three nodulose intervarices intercalated. Varices with three major cord spines (P1 to P3). P1 spine appearing at beginning of first whorl and forming open tube at end of first whorl. From second to last whorl P1 spine well developed, open. Intervarical nodules spirally aligned and present on P1 and P2. Ovate aperture up 32% of diameter (including wings) and up to 76% of length of last whorl (including siphonal canal). Columellar lip smooth, poorly erect. Parietal lip adherent. Shoulder channel of P1 open. Outer lip lacking denticle. Outer lip not crenulate. Pseudoumbilicus narrow. Siphonal canal open, up to 55% of apertural length.

COMPARISONS

Amongst European Eocene species, *Ponderia remyi* n. sp. can be compared to *P. daguini* (Magne, 1941) from the Early Eocene of Gan (Aquitaine and Paris Basins) and to *P. bispinosa* (Sowerby, 1823) from the Middle Eocene of the Paris Basin and Hampshire (England) and from the Late Eocene of Lattorf Basin (Germany). *Ponderia daguini* is easily distinguished from *P. remyi* n. sp. in having a broader shape, more numerous cords (with P5, P6 and ADP) and nodulose cords. *Ponderia bispinosa* usually bears more foliaceus varices. The cord spines of *P. bispinosa* varies from two (P1 and P3) to five (P1 to P5). The morphotypes with five cords spines are common in the Lutetian and in the Bartonian of the Paris Basin, where those with two cord spines are common in the Bartonian of Hampshire and in the Priabonian of Lattorf (von Koenen 1889; Merle *et al.* 2011). The varices of *P. bispinosa* are more winged than those of *P. remyi* n. sp. In addition, *P. bispinosa* clearly differs in having a multispiral protoconch and a microsculpture formed of small elongated granules (see Merle 1990).

Genus *Flexopteron* Shuto, 1969

TYPE SPECIES. — *Flexopteron philippinense* Shuto, 1969, by original designation. Late Miocene: Philippines.

COMMENTS

The genus *Flexopteron* Shuto, 1969 was previously included in the subfamily Muricinae (e.g., Vokes 1992, 1996; *inter alia*). According to Merle *et al.* (2011), it displays plesiomorphic shells, differing greatly from the derived shells found in typical Muricinae that are close to the genus *Murex* Linnaeus, 1758. Merle *et al.* (2011: 54) defined an informal group called Basal muricid group including *Flexopteron*, *Paziella*, *Poirieria*, *Timbellus*, and several other genera. In a molecular phylogenetic work, Houart *et al.* (2021) found a clade including *Flexopteron* and *Timbellus*. This result could suggest close relationship between *Flexopteron* and *Timbellus* and confirms that they are not phylogenetically related to the derived clade of typical Muricinae. However, this relationship is not retrieved in the latest molecular phylogenetics of Russini *et al.* (2023), and those authors do not give subfamilial attribution to *Flexopteron* (*incertae sedis* position). *Flexopteron* has been considered in the past as a subgenus of *Poirieria* (e.g., Vokes 1992) or *Paziella* (e.g., Merle *et al.* 2011). As there is no evidence of a close phylogenetic relationship between these two genera based on molecular analyses, we give *Flexopteron* full generic status.

Flexopteron constantinense n. sp.

(Figs 20A-D; 27M, N)

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TYPE MATERIAL. — **Holotype**. **France** • Normandy, Manche, Rauville-la-Place (Cauvin); Argiles à Corbules Formation; late Eocene

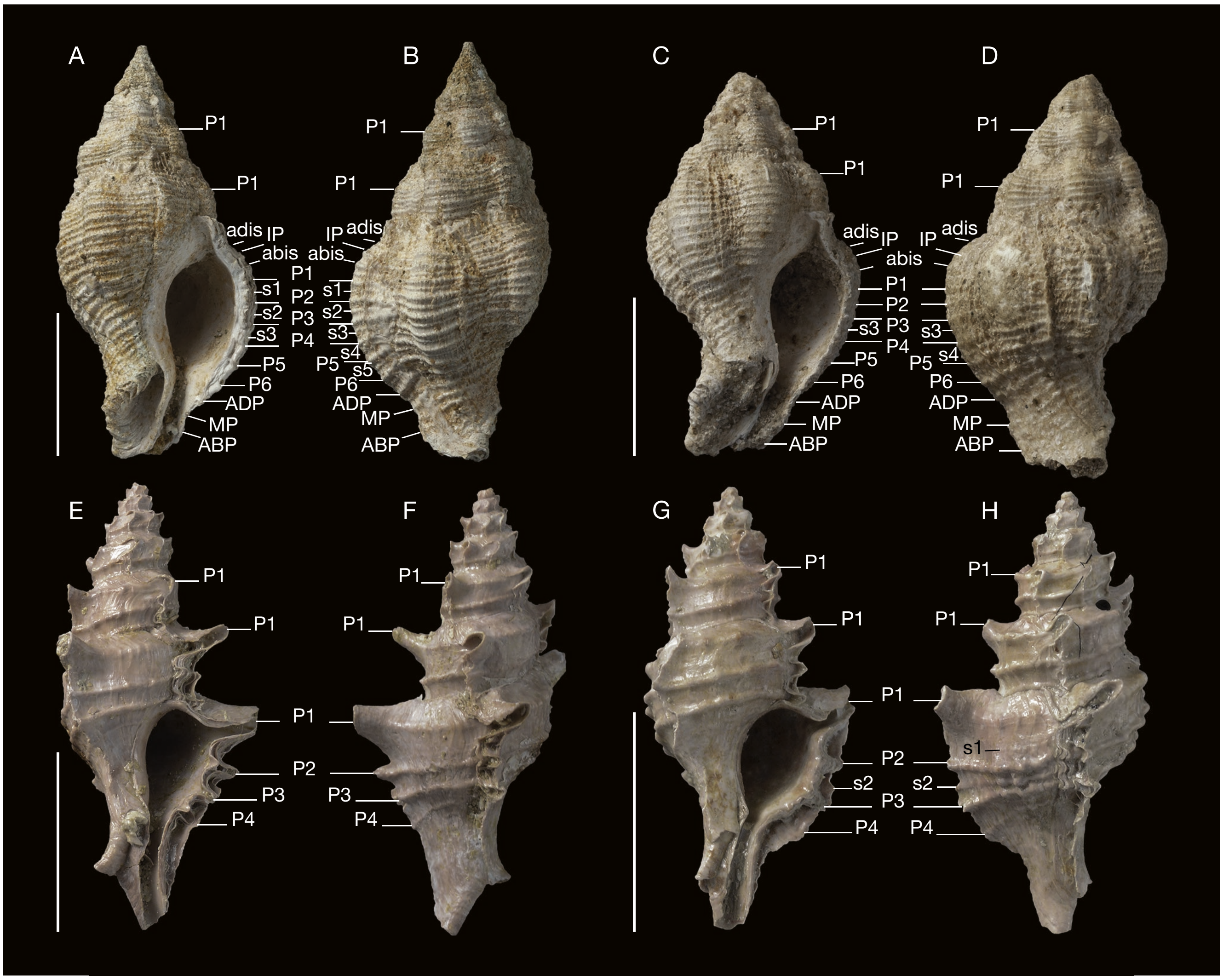

Fig. 19. — Spiral cords and internal denticles of the outer lip in *Textiliomurex chodmonensis* n. sp. (**A**-**D**) and *Ponderia remyi* n. sp. (**E**, **H**): **A**, **B**, holotype, MNHN.F.A81144 (Pacaud coll.), Chaumont-en-Vexin (Carrière Darcy), Oise, Paris Basin, France, middle Eocene (Lutetian); **C**, **D**, paratype, MNHN.F.A81145 (Pons coll.), Chaumont-en-Vexin (Carrière Darcy); **E**, **F**, holotype, MNHN.F.A90548 (Remy coll.), Fresville, Manche, Normandy, France, middle Eocene (Lutetian); **G**, **H**, MNHN.F.A90555, Fresville (Remy coll.). Scale bars: 10 mm. Credits: P. Loubry (MNHN/CNRS).

(Priabonian); MNHN.F.A77760 (MNHN coll.), H: 9.2 mm (fragment of last whorl) (Figs 20C, D; 27N).

Paratypes. France • 1 spm (juvenile); same as for the holotype; MNHN.F.A77761 (MNHN coll.), juvenile (Figs 20A, B; 27M) • 10 spm (juveniles); idem; MNHN.F.A90551 (MNHN coll.).

Etymology. — From the Latin adjective *Constantinus* in reference to the type region of the species (*pagus constantinus* of the Gallo-Roman), the Cotentin (Manche).

Type horizon. — Argiles à Corbules Formation, late Eocene (Priabonian), stratigraphic data given by Cavelier (1979) and Chateauneuf (1980).

Type locality. — France, Normandy, Manche, Rauville-la-Place (Cauvin), Cavelier (1979).

Distribution. — Normandy (France), late Eocene (Priabonian).

Description

Smooth, paucispiral protoconch of 1.5 whorls. Teleoconch probably biconic (spire broken in most adult specimen), last whorl (holotype) up to 9 mm in height, up to 7 mm in width. Moderately high spire in juveniles. Rounded to subcarinate whorls. First whorl to fourth whorl: no cord. Fifth whorl: weak P1 to P5. P1 spine poorly developed. Axial sculpture with five sublamellose varices on first whorl, seven on second whorl, eight on third and fourth whorls. Ten varices on holotype. Ovate aperture, siphonal canal short. Columellar lip smooth, adherent posteriorly. No anal sulcus, no parietal callus. Outer lip with denticles D1, D2 and D3. Shoulder sinus of P1 spine shallow. Pseudo-umbilicus narrow. Siphonal canal short, open.

Comparisons

Although the material is composed of juvenile specimens (paratypes) and a last whorl of an adult specimen (holotype), it differs clearly from all Bartonian and Priabonian species from Northern Europe. The early whorls of *Flexopteron albionis* (Wrigley, 1930) from Barton beds, *F. subplicatilis*

(Wrigley, 1930) from the Bartonian of Southampton Dock and *F. spinulosum* (Deshayes, 1835) from the Bartonian of the Paris Basin differ from those of *F. constantinense* n. sp. by having a more ornamented spiral sculpture with well developed P1 to P3. *Flexopteron elatior* (von Koenen, 1889), found in the Bartonian of the Paris Basin and in the Priabonian of Lattorf (Germany) is another species bearing strong spiral ornamentation.

Flexopteron liancurtense n. sp.
(Figs 20E-H; 28A, B)

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Murex (*Poirieria*) *foliaceus* – Cossmann & Pissarro 1911: pl. 36, fig. 169-17 [*non* Melleville, 1843].

Poirieria (*Flexopteron*) *foliacea* – Le Renard & Pacaud 1995: 114, Ref. GA169-17 [*non* Melleville, 1843].

Vauxyrytis liancurtensis – Merle 1999: 459, pl. 68 (unpublished thesis) (*nomen nudum*).

TYPE MATERIAL. — **Holotype. France** • Paris Basin, Oise, Liancourt-Saint-Pierre; Sables d'Hérouval (biozone NP12); early Eocene (Ypresian); MNHN.F.J02578 (Cossmann coll.), figured specimen in Cossmann & Pissarro (1911: pl. 39, fig. 169-17), H: 7.7 mm (Figs 20E, F; 28A).
Paratypes. France • 1 spm; same as for the holotype; MNHN.F.A77758 (Merle coll.) (Figs 20G, H; 28B) • 17 spm; idem; MNHN.F.A77759 (Merle coll.) • 9 spm; idem; MNHN.F.J17633 (Cossmann coll.); • 1 spm; Paris Basin, Oise, Hérouval; Sables d'Hérouval (biozone NP12); early Eocene (Ypresian); MNHN.F.B63662 (Morlet coll.) • 29 spm; idem; MNHN.F.A90913 (Pacaud coll.).

ETYMOLOGY. — From the Latin adjective *liancurtense* in reference to the type locality, Liancourt-Saint-Pierre (Oise).

TYPE HORIZON. — Sables d'Hérouval (biozone NP12), see Gély & Lorenz (1991: pl. 1), early Eocene (Ypresian).

TYPE LOCALITY. — France, Paris Basin, Oise, Liancourt-Saint-Pierre, see Fritel (1910: 190).

DISTRIBUTION. — Paris Basin (France), early Eocene (Ypresian, Hérouval Formation only).

DESCRIPTION

Smooth, conical multispiral protoconch of around three whorls. Sinusigeral scar well marked. Biconic teleoconch up to 7 mm in height, up to 4 mm in width (including cord spines). Moderately high spire, up to four subcarinate whorls. Last whorl (fourth whorl) up to 68% of total length. Apical angle 54° including P1 spine. Spiral sculpture with marked primary cords. First whorl: no cord; second whorl: appearance of P2 weak; third whorl: development of P1 spine and appearance of P3 above suture line. Fourth and last whorl: no primary cord on sutural ramp, P1 to P5, s1 and s2 moderately marked, P6 and ADP weak on siphonal canal. Axial sculpture with 11 lamellose varices on first whorl, 13 on second, and 14 on third and fourth. Varices axially aligned in a zig-zag fashion. Ovate aperture up to 36% of diameter and up to 77% of length of the last whorl (including siphonal canal). Columellar lip slightly erect anteriorly, adherent posteriorly, usually smooth or occasionnally with one tubercle. No anal sulcus, no parietal callus. Outer lip with small denticles. D1 to D5 simple, D1 more developed than other denticles. Outer lip not crenulate. Shoulder sinus of P1 spine widely open, shallow. Pseudoumbilicus narrow. Siphonal canal open, up to 36% of the apertural length and slightly dorsally recurved.

COMPARISONS

Melleville (1843) described *Murex foliaceous* for a small Ypresian *Flexopteron* displaying axially zizgaging lamellae and a short P1 spine. Later, Cossmann (1889) described *Murex dyscritus* which bears less marked primary cords than *Murex foliaceous*. However, numerous specimens housed in the MNHN show many transitional forms suggesting these differences represent intraspecific variation. Thus, the older binome *Murex foliaceous* takes nomenclatural priority. Moreover, Cossmann & Pissarro (1911) illustrated an atypic specimen from the Ypresian of Liancourt-Saint-Pierre (Hérouval Formation), squatter than usual for *F. foliaceum*, with a bent siphonal canal, poorly developed P1 spines, more marked primary cords and occasionally a tubercle on the columellar lip. This specimen from Liancourt is not a pathological specimen and all specimens from this locality and Hérouval display similar morphology. They differ from *F. foliaceum* (also found at Liancourt-Saint-Pierre) by having spiral cords P1 and P2 appearing earlier in ontogeny. Merle (1999, unpublished thesis) illustrated several other specimens and the ontogenetic changes in their spiral sculpture. He considered this population as a different species and named it *Vauxyrytis liancurtensis*. However, Merle (1999) is an unpublished thesis and the name is a *nomen nudum* made available herein. Placement of this species in the genus *Vauxyrytis* Merle, 1999 (*nomen nudum*), an unpublished genus corresponding to *Beyregrex* Merle, n. gen. (see below), was based on the shape of the varices, which are not spiny, and the occasional presence of a columellar tubercle. Nevertheless, we found some specimens of *F. liancurtense* n. sp. with P1 spines and several species of *Flexopteron* can have a columellar tubercle [e.g., *F. ogormani* (Cossmann, 1923)]. In addition, *F. liancurtense* n. sp. clearly resembles a Tortonian species from NW France: *F. gallicum* (Landau, Merle, Ceulemans & Van Dingenen, 2019), see Landau *et al.* (2019: pl. 11). Thus, we attribute this species to *Flexopteron*.

Genus *Crassimurex* Merle, 1990

TYPE SPECIES. — *Murex calcitrapoides* Lamarck, 1822 by original designation (synonym of *Murex calcitrapa* Lamarck, 1803). Middle Eocene (Lutetian and Bartonian): Paris and Loire basins, France.

COMMENTS ON SUBFAMILIAL PLACEMENT

Members of this genus display a biconic shell with a moderately high spire, spiny varices on P1, internal denticles

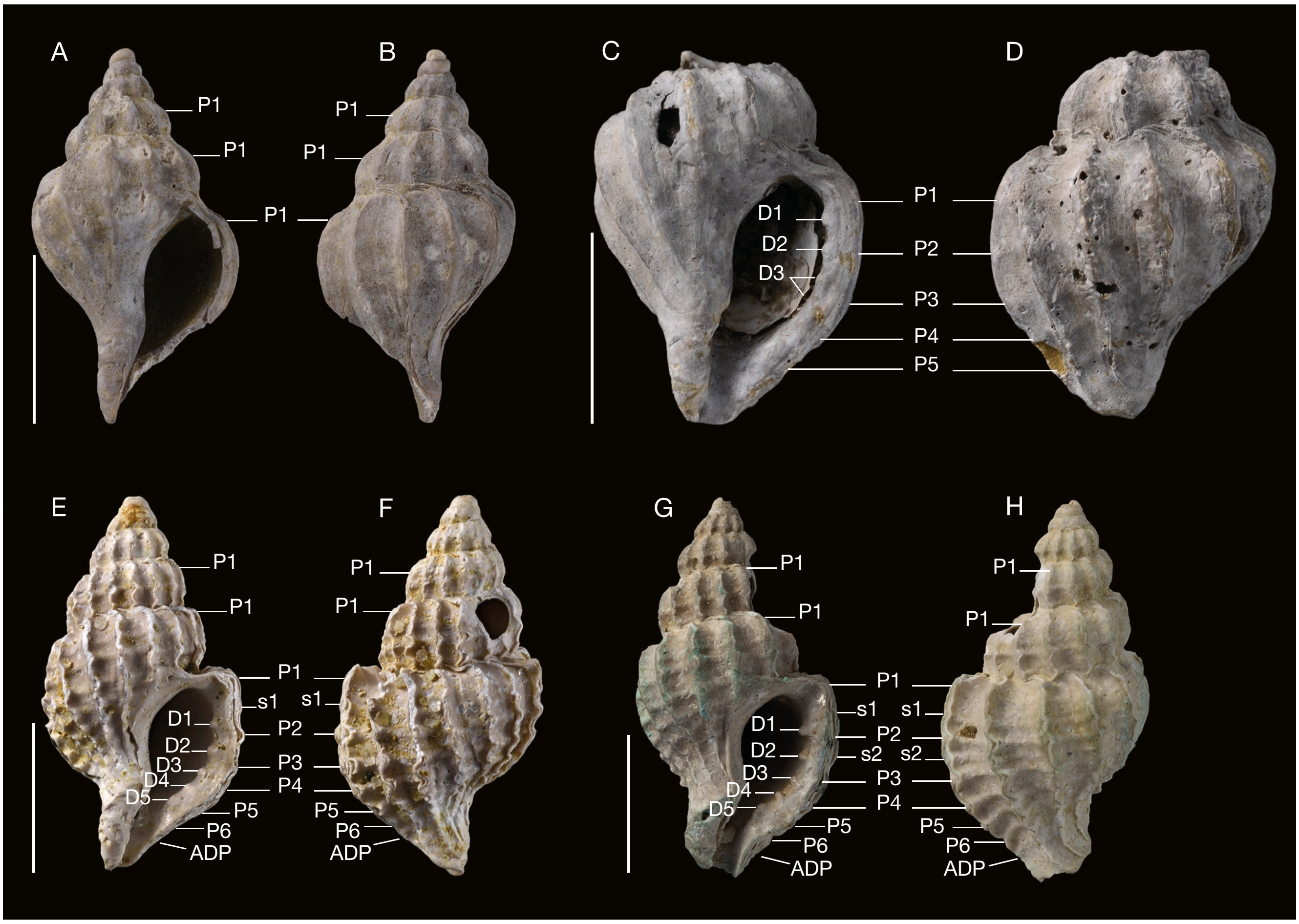

Fig. 20. — Spiral cords and internal denticles of the outer lip in *Flexopteron constantinense* n. sp. (**A**-**D**) and *F. liancurtense* n. sp. (**E**-**H**): **A**, **B**, paratype: MNHN.F. A77761 (MNHN coll.), Carentan-les-Marais (Cauvin), Manche, France, late Eocene (Priabonian); **C**, **D**, holotype: MNHN.F.A77760 (MNHN coll.), Carentan-les-Marais (Cauvin); **E**, **F**, holotype: MNHN.F.J02578 (Cossmann coll.), Liancourt-Saint-Pierre, Oise Paris Basin, France, early Eocene (Ypresian); **G**, **H**, paratype: MNHN.F.A77758 (Merle coll.), Liancourt-Saint-Pierre. Scale bars: A, B, E-H, 3 mm; C, D, 5 mm. Credits: P. Loubry (MNHN/CNRS).

(D1 to D6), a broad and open siphonal canal, a sinus of P1, around 8-10 varices, and complex spiral sculpture including the primary cords P1 to P6 (convex part of the whorl) and ADP-MP (siphonal canal). In addition, their shape is similar to that of *Poirieria* Jousseaume, 1880 or *Flexopteron* (see Merle *et al.* 2011). For these reasons, Merle *et al.* (2011) placed *Crassimurex* (*s. s.*) and *Crassimurex* (*Eopaziella*) Gürs, 2001 in an informal group named basal muricids. It is still impossible to place this genus within a subfamily using shell characters. Obervations on *Crassimurex* (*s. s.*) *calcitrapa* Lamarck, 1803 at La Ferme de l'Orme (Lutetian, Paris Basin) suggest this species was a drilling predator (Merle *et al.* 2024), but this ability occurs in different subfamilies (e.g., Muricinae and Ocenebrinae) and does not help in subfamilial attribution.

Subgenus *Pliocrassimurex* n. subgen.

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Type species. — *Crassimurex* (*Pliocrassimurex*) *hirtus* n. sp., Early Pliocene (Zanclean): Spain.

Etymology. — Name formed by the beginning of Pliocene (*Plio-*) and *Crassimurex*.

Species included in the subgenus. — Type species only.

Diagnosis. — Biconic, mid-sized teleoconch. Well marked primary cords. On spire P1 to P2 (convex part of whorl). On last whorl IP (infrasutural ramp), P1 to P5 (convex part of whorl), P6, ADP, MP and ABP (siphonal canal). P2 delimiting shell periphery. Varices lamellose on infrasutural ramp, spiny from shoulder (P1) to siphonal canal. Varices aligned axially with varices on preceding whorl. Short cord spines from IP to MP. Sinus of P1 very short. Aperture ovate. Columellar lip smooth, adherent. No parietal callus; no anal notch. Aragonitic microstructure.

Crassimurex (***Pliocrassimurex***) ***hirtus*** n. subgen., n. sp.
(Figs 21A-F; 28C-E)

urn:lsid:zoobank.org:act:D443EA04-13CB-4AC7-8082-87A2DD4CF2D2

Type material. — **Holotype. Spain** • Llobregat Basin, Molins del Rei; Yellow and grey clays of Molins del Rei (quarry Anna); Pliocene (Zanclean); MNHN.F.A77751 (MNHN coll.), H: 28 mm (Figs 21A, B; 28E).

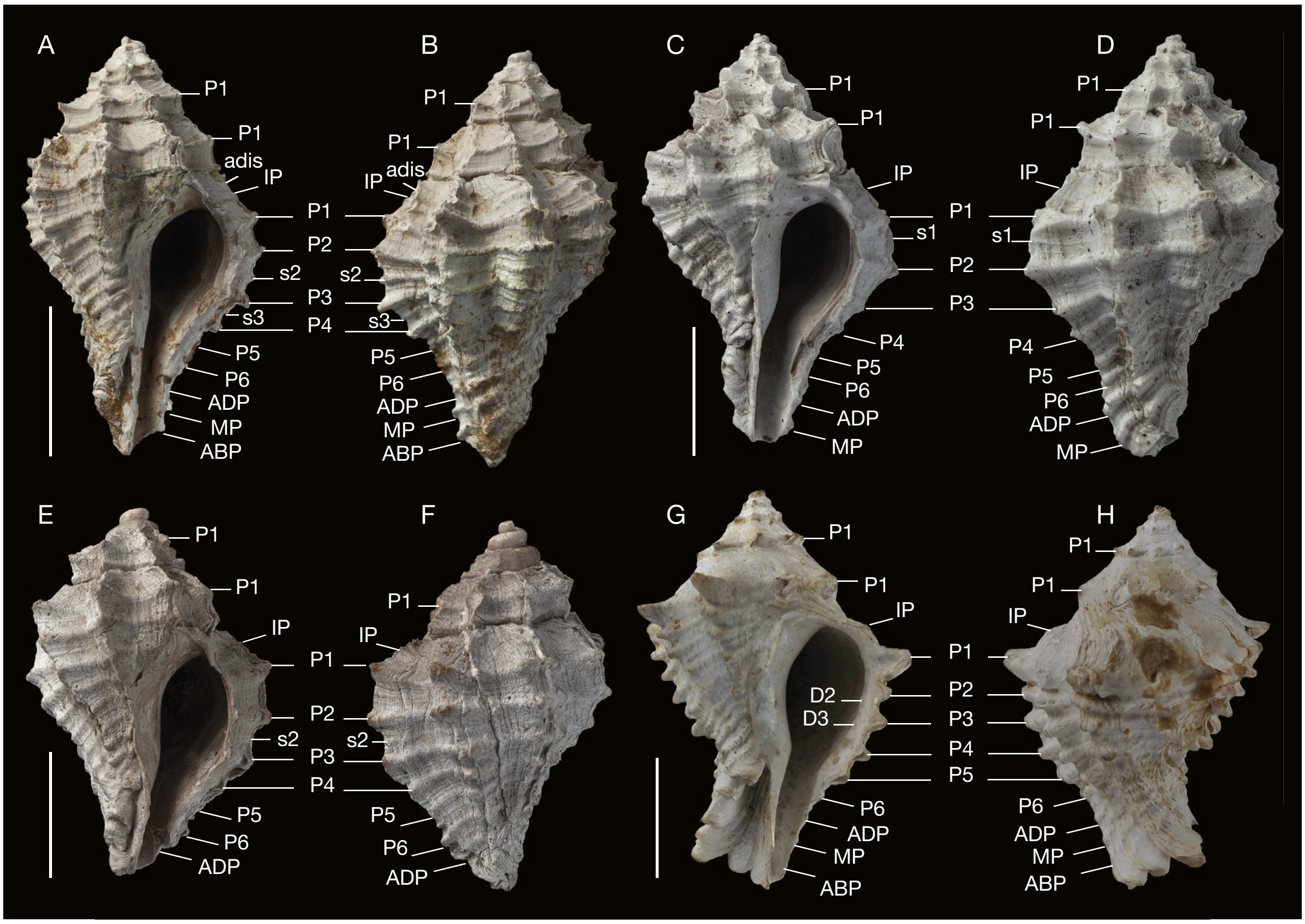

FIG. 21. — Spiral cords and internal denticles of the outer lip in *Crassimurex* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp. (**A**-**F**) and *Crassimurex* (*s.s.*) *calcitrapa* (Lamarck, 1803) (**G**, **H**) for comparison: **A**, **B**, holotype, MNHN.F.A77751 (MNHN coll.), Molins del Rei, Llobregat Basin, Spain, Early Pliocene (Zanclean); **C**, **D**, paratype, MNHN.F.A77752, Molins del Rei; **E**, **F**, paratype (juvenile), MNHN.F.A77753 (MNHN coll.), Molins del Rei; **G**, **H**, MNHN.F.A32445 (Morlet coll.), Beynes (Ferme de l'Orme), Paris Basin, France, middle Eocene (Lutetian). Scale bars: A, B, G, H, 10 mm; C-F, 5 mm. Credits: A-F, P. Loubry (MNHN/CNRS); G, H, C. Lemzaouda (MNHN/CNRS).

Paratypes. Spain • 2 spm; same as for the holotype; MNHN.F.A77752 (MNHN coll.) (Figs 21C, D; 28D, MNHN.F.A77753 (MNHN coll.) (Figs 21E, F; 28C).

ETYMOLOGY. — From the Latin adjective *hirtus* meaning bristly, because of the cord spines of the species; gender masculine.

TYPE HORIZON. — Yellow and grey clays of Molins del Rei (quarry Anna).

TYPE LOCALITY. — Spain, Llobregat Basin, Pliocene (Zanclean; see Salvany & Aguirre 2020), Molins del Rei (quarry Anna).

DISTRIBUTION. — Only known from the type locality.

DESCRIPTION

Protoconch not preserved. Teleoconch up to 28 mm in height (holotype), up to 7.6 mm in width, biconic in profile, composed of six whorls. Moderately low spire with carinate whorls. Last whorl up to 76% of total length. Apical angle 68°. Spiral sculpture with marked primary cords. First whorl: not preserved; from second to fourth whorl: presence of P1 and P2, P2 close to abapical suture; fifth whorl: appearance of IP; sixth whorl: appearance of abis infrasutural ramp. P1 to P5 and s1 to s3 on convex part of whorl; P6, ADP, MP and ABP on siphonal canal. Axial sculpture with high, sublamellose varices. On second whorl: 9-10 varices; on third whorl: ten varices; from fourth whorl to fifth whorl: 8-10 varices; on sixth whorl: eight varices. On spire, short cord spines on P1-P2; P1 delimiting periphery. On last whorl, short cord spines on IP, P1-P6, ADP, MP, ABP, but more developed on P1, P2 and P3; P2 delimiting periphery. Ovate aperture up to 31% of diameter and up to 74% of length of last whorl (including siphonal canal). Columellar lip, smooth, adherent. Parietal lip smooth, adherent. Outer lip lacking internal denticles. Pseudoumbilicus moderately large. Siphonal canal open, up to 41% of aperture length, slightly dorsally recurved. Aragonitic microstructure.

COMMENTS

By its shape and its sculpture, *C.* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp. resembles members of *Crassimurex* Merle, 1990. However, until now, *Crassimurex* was not known in the Pliocene and seemed extinct after the Middle Miocene. *Crassimurex* is currently represented by two subgenera, *Cras-*

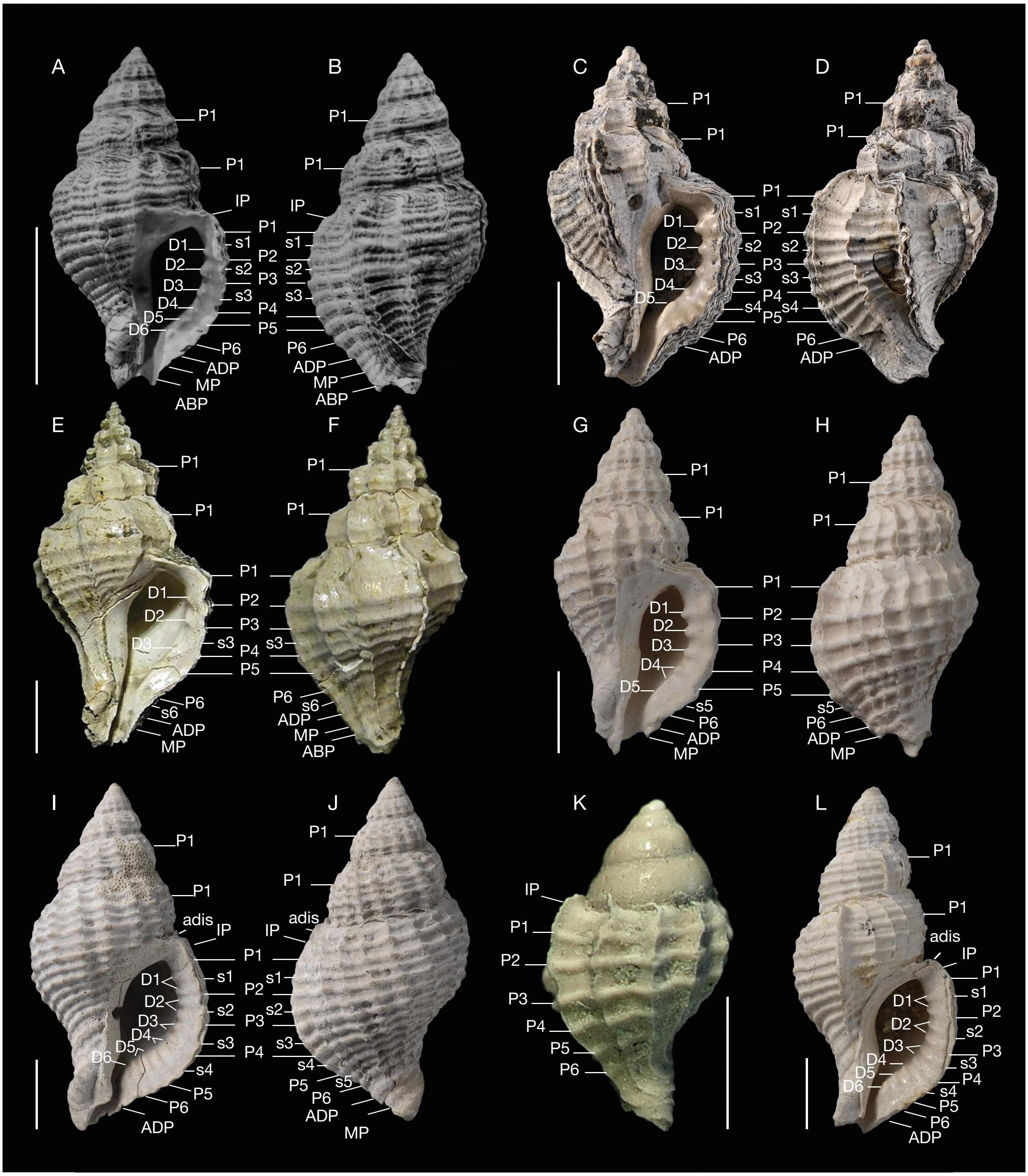

FIG. 22. — Species of the informal group *Jsowerbyia-Beyregrex* n. gen.-*Pseudotrophonopsis* n. gen.: **A**, **B**, *Jsowerbya sexdentata* (Sowerby, 1823), BMNH GG22673 (Burton coll.), Colwell Bay, Wight Island, England, late Eocene (Priabonian); **C**, **D**, *Beyregrex sarroniensis* (Carez, 1870), n. comb., MNHN.F.J02576 (figured specimen of Cossmann & Pissarro 1911: pl. 35, fig.169-14), Sarron, Oise, Paris Basin, France, early Eocene (Ypresian); **E**, **F**, *B. hantoniensis* (Edwards, 1866), n. comb., Morton coll., Middle Headon Brockenhurst bed, Whitecliff Bay, Wight Island, England, late Eocene (Priabonian); **G**, **H**, *B. pereger* (Beyrich, 1854), n. comb., MNHN.F.A90561 (Lozouet & Maestrati coll.), Auvers-Saint-Georges, Essonne, Paris Basin, France, early Oligocene (Rupelian); **I**-**L**, *Pseudotrophonopsis defossa* (Pilkington, 1804), n. comb.: **I**, **J**, MNHN.F.J17634 (Cossmann coll.), Barton-on-Sea, Hampshire, England, middle Eocene (Bartonian); **K**, A. Smith coll. (juvenile specimen), upper Barton bed H, Barton Highcliffe; **L**, MNHN.F.A90560 (Munier-Chalmas coll.), Le Vouast, Oise, late Eocene (Priabonian). Scale bars: A-J, L, 5 mm; K, 1 mm. Credits: A, B, D. Serrette (MNHN); C, D, G-J, L, P. Loubry (MNHN/CNRS); E-F, K, A. Morton.

simurex (*s.s.*): early Eocene to middle Eocene, France, and *Crassimurex* (*Eopaziella*): late Eocene to Middle Miocene (Europe). Therefore, the discovery of a species of *Crassimurex* in the Early Pliocene of Spain is surprising and extends the stratigraphic range of the genus. *Crassimurex* (*Pliocrassimurex*) differs from *Crassimurex* (*s.s.*) and *C.* (*Eopaziella*) by having a more obtuse shoulder angle. In *C.* (*Pliocrassimurex*), P2 delimits the periphery on the last whorl, whereas in *Crassimurex* (*s.s.*) and *C.* (*Eopaziella*), P1 delimits the periphery. *Crassimurex* (*s.s.*) 1990 can share cord spines with *C.* (*Pliocrassimurex*), as seen in the type species *C.* (*s.s.*) *calcitrapa* (Lamarck, 1803) (Fig. 21G, H), but it differs by having varices which are not axially aligned. *Crassimurex* (*Eopaziella*) resembles *C.* (*Pliocrassimurex*) by having varices axially aligned but differs in lacking cord spines (see Merle *et al.* 2011: 178, fig. 62, pl. 144).

Informal group *Jsowerbya*, *Beyregrex* Merle, n. gen, *Pseudotrophonopsis* Merle, n. gen.

Diagnosis. — Shell medium sized for family, biconic. P6 not atrophied. IP, ADP, MP and ABP present. Poorly developed axial sculpture formed by slightly lamellose varices. Posterior sinus of sutural ramp shallow. Shoulder sinus of P1 reduced or missing. ID missing, D1 to D6 present. Columellar lip occasionally ornamented by 1-3 tubercles. Microstructure of three aragonite layers.

Included genera. — *Jsowerbya* Merle, 2005b, *Beyregrex* Merle, n. gen. and *Pseudotrophonopsis* Merle, n. gen.

Discussion

This informal group includes basal taxa often erroneously attributed to the Muricopsinae (synonym of Aspellinae) because of their biconic shape and the presence of 1-3 columellar tubercles or attributed to the Trophoninae, because of the more or less lamellose varices. In the phylogenetic analysis, they represent basal taxa (Clades G, H, I, J, L of Winclada [Fig. 1; Appendix 3] and Clades 44, 43, 42, 41, 40 of PAUP [Appendix 5]). They essentially differ from members from the other subfamilies by having a combination of characters including a posterior sinus, a D6 denticle, occasional columellar tubercles, and by lacking the ID denticle. The primary cords appear late in ontogeny and IP is missing in the most basal species of this group (e.g., *Beyregrex sarroniensis* (Carez, 1879), n. comb.) from the Thanetian, whereas in the derived members (e.g., members of *Jsowerbya* Merle, 2005b) they appear earlier, and the primary cord IP is often present. From an evolutionary point of view, members of this group are diversified from the late Paleocene to the middle Eocene with *Beyregrex* Merle, n. gen. and *Jsowerbya*. The decline of the group begins at the Priabonian in which only *Beyregrex* Merle, n. gen. and *Pseudotrophonopsis* Merle, n. gen. are recorded. *Beyregrex* Merle, n. gen. survives after the Eocene/Oligocene climatic crisis and is known in the Early Miocene (Burdigalian) with *Beyregrex cedillatus* (Cossmann & Peyrot, 1924), n. comb..

Genus *Beyregrex* Merle, n. gen.
(Fig. 22E-H)

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Type species. — *Murex pereger* Beyrich, 1854, late Eocene to late Oligocene: Paris Basin, Belgium, Mainz Basin and north Germany (Fig. 22G, H).

Etymology. — Name based on the type species *Murex pereger* Beyrich, 1854 and using Bey (from Beyrich), the letters reg (from *pereger*) and rex (from *Murex*).

Included species. — *Murex sarroniensis* Carez, 1879 [synonym: *Murex abbatiae* Wrigley, 1930], London and Paris Basins, Paleocene (Thanetian) to Early Eocene (Ypresian) (Fig. 22C, D); *Murex hantoniensis* Edwards *in* Lowry *et al.*, 1866, Hampshire Basin, England, late Eocene (Priabonian) (Fig. 22E, F); *M. pereger* Beyrich, 1854 [synonym: *Murex areolifer* Sandberger, 1861], Paris Basin, Belgium, Mainz Basin and north Germany, late Eocene (Priabonian) to late Oligocene (Chattian) (Fig. 22G, H); *Hexaplex brevaculeatus* Janssen, 1978, Paris basin, early Oligocene (Rupelian), Mainz basins, early Oliogocene and North Germany, late Oligocene; *Murex* (*Poirieria*) *cedillatus* Cossmann & Peyrot, 1924, Aquitaine Basin, France, Early Miocene (Burdigalian).

Diagnosis. — Biconic teleoconch with subangular whorls. D1 well developed. P6 not atrophied. IP weak, ADP, MP present. Varices formed by 1-3 lamellae abaxially turned on the early whorls, occasionally reinforced by several lamellae on the succeeding whorls. P1 spine short. Shoulder sinus widely open, short, moderately deep. Posterior sinus on sutural ramp shallow. Columellar lip usually smooth.

Comments

Members of *Beyregrex* Merle, n. gen. differ from those of *Jsowerbya* in having a deeper shoulder sinus, more lamellose varices, and a smooth columellar lip. *Pseudotrophonopsis* Merle, n. gen. is also distinguishing from *Beyregrex* Merle, n. gen. in having rounded whorls, strong secondary cords of equal strength to the primary cords, and numerous split internal denticles within the outer lip (D1 to D5). Represented by five species, *Beyregrex* Merle, n. gen. is the most diverse genus of the group. It extends from the Anglo-Parisian late Paleocene/early Eocene with *B. sarroniensis* (Carez, 1879), n. comb. to the Early Miocene (Burdigalian) from the Aquitaine Basin with *B. cedillatus* (Cossmann & Peyrot, 1924). *Beyregrex sarroniensis* n. comb. displays several primitive characters, such as missing IP, MP and ABP. During the middle Eocene, no *Beyregrex* Merle, n. gen. species are known, but the genus re-emerges in the late Eocene of Hampshire with *B. hantoniensis* (Edwards *in* Lowry *et al.*, 1866), n. comb.. That species is closely related to *B. pereger* (Beyrich, 1854), n. comb. occurring in the Paris Basin and in Germany (Mainz Basin and north Germany) during the Oligocene. According to Janssen (1978), *B. brevaculeatus* (Janssen, 1978) is another species. It was originally described from the Chattian of Germany (at Glimmerode) but is also recorded in the Rupelian of the Paris Basin (Merle 1999; Lozouet 2012). For the Neogene, *B. cedillatus* (Cossmann & Peyrot, 1924) from the Burdigalian of the Aquitaine Basin demonstrates that the genus was not restricted to northern Europe.

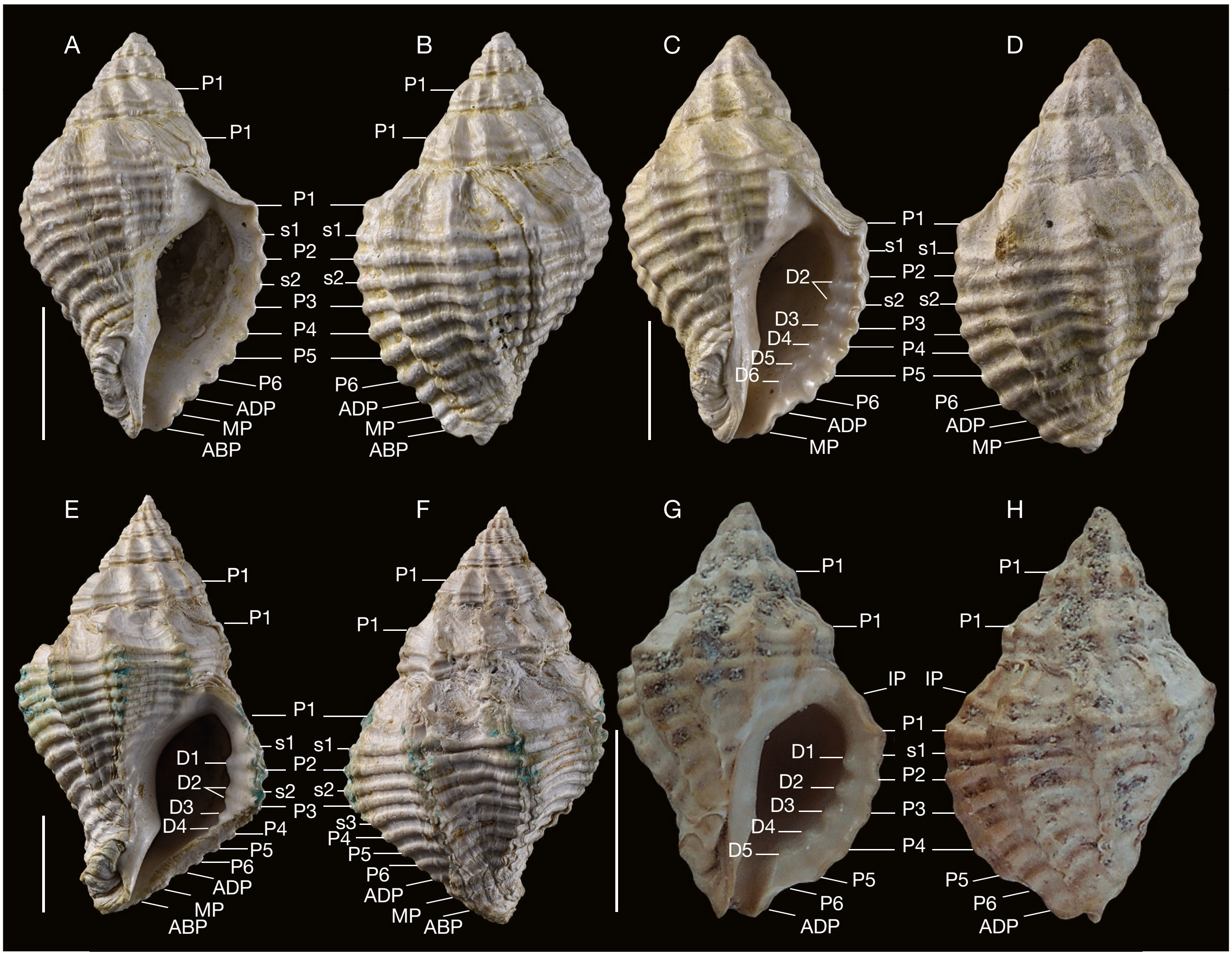

Fig. 23. — Spiral cords and internal denticles of the outer lip in *Nucellopsis parisiensis* n. sp. (**A**-**F**) and *N. dudariensis* (Strauzs, 1966) (**G**, **H**): **A**, **B**, paratype, MNHN.F.A90964 (Faullummel coll.), Saint-Witz (Le Guépelle), Val d'Oise, Paris Basin, France, middle Eocene (Bartonian); **C**, **D**, paratype, MNHN.F.A90963 (Faullummel coll.), Saint-Witz (Le Guépelle); **E**, **F**, holotype, MNHN.F.R64955 (Merle coll.), Saint-Witz (Le Guépelle); **G**, **H**, holotype of *Cantharus* (*Pollia*) *dudariensis*, MGSH E.467, Dudar, Hungary, middle Eocene (upper Lutetian). Scale bars: 5 mm. Credits: A-D, P. Loubry (MNHN/CNRS); E, F, D. Serrette (MNHN); G, H, courtesy of Z. Kovács.

Genus *Pseudotrophonopsis* Merle, n. gen.
(Fig. 22I-L)

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Type species. — *Buccinum defossum* Pilkington, 1804, middle Eocene (Bartonian) of England (Hampshire) (Fig. 22I-K), and late Eocene (Priabonian) of France (Paris Basin) (Fig. 22L).

Etymology. — Name based on the Greek prefix *pseudo* (false), because the superficial resemblance of the type species with members of the genus *Trophonopsis* Bucquoy & Dautzenberg, 1882.

Included species. — *Buccinum defossum* Pilkington, 1804 [synomym: *Fusus sublamellosus* Deshayes, 1835], England, Hampshire Basin, middle Eocene (Bartonian) and France, Paris Basin, late Eocene (Priabonian).

Diagnosis. — Smooth multispiral protoconch (Fig. 22K). Biconic teleoconch with rounded whorls. P6 not atrophied. IP, ADP, MP, ADP present. Primary P1 to P6 present on first whorl (Fig. 22K). Coarse secondary cords equal in strength to primary cords. Varices low, formed by one short abaxial lamella. No P1 spine. No shoulder sinus. Posterior sinus shallow. Columellar lip smooth. Internal denticles D1 to D6 split. ID missing.

Comments

This strange species differs from members of *Jsowerbya* Merle, 2005b and *Beyregrex* Merle, n. gen. by having rounded whorls, no shoulder sinus and by having strongly developed secondary cords. Because of its rounded whorls, it resembles members of *Nucellopsis*, but they are distinguishing by their buccinoid shape and by a later appearance of the primary cords. The phylogenetic analysis (Winclada tree, Fig. 1) suggests that it could represent a stem group of *Jsowerbya*. We therefore propose the new genus *Pseudotrophonopsis* Merle, n. gen. as *P. defossa* (Pilkington, 1804), n. comb. cannot be attributed to *Jsowerbya* or *Beyregrex* Merle, n. gen. *Pseudotrophonopsis defossa* n. comb. occurs in the Bartonian from Hampshire (England) and is known in the Priabonian from the Paris Basin, where it was identified as *Fusus sublamellosus* Deshayes, 1835. The protoconch of the English and French populations (Fig. 22K)

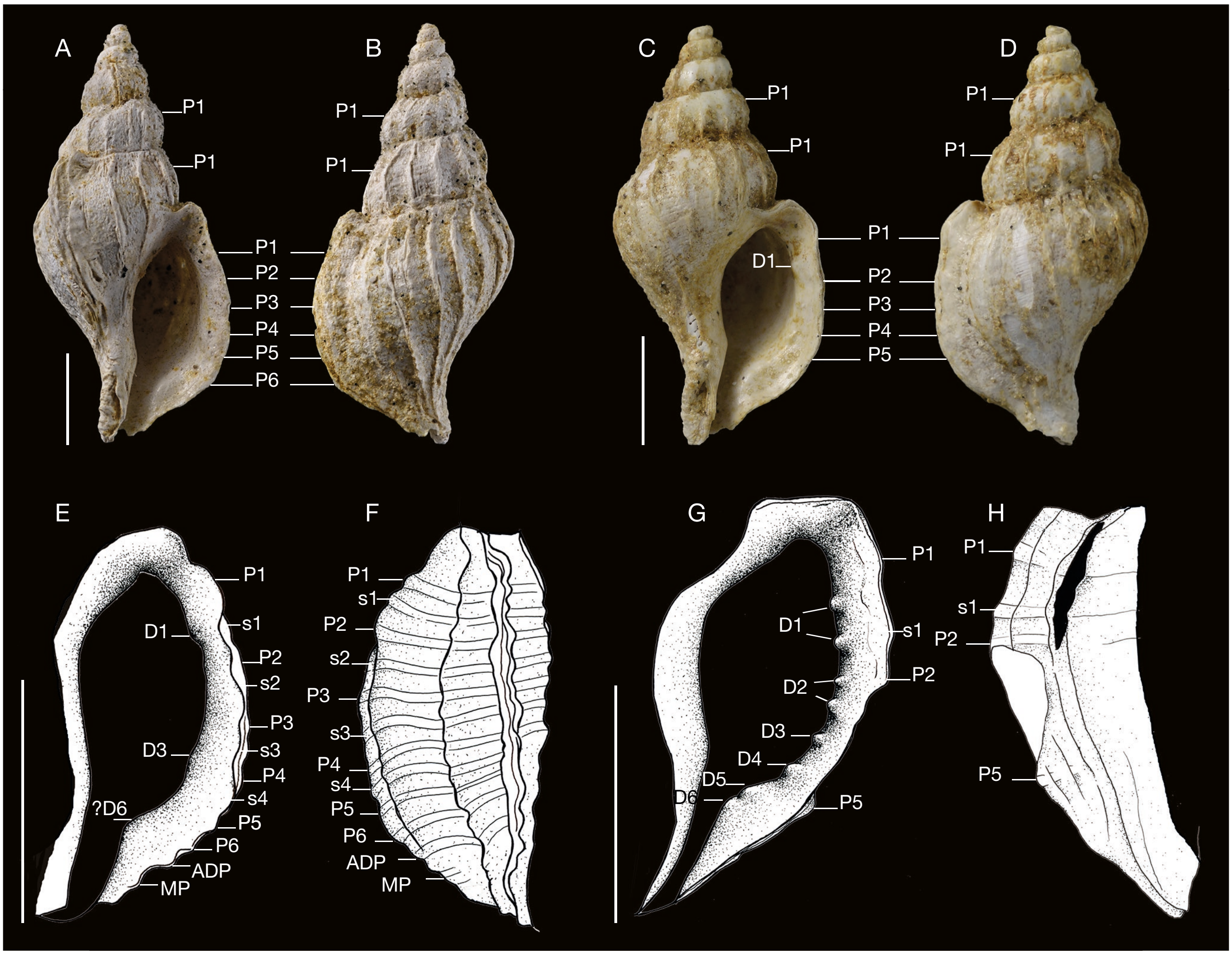

FIG. 24. — Spiral cords and internal denticles of the outer lip in *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen, n. sp.: **A**, **B**, holotype, MNHN.F.J02587 (Cossmann coll.), Châlons-sur-Vesle, Marne, Paris Basin, France, late Paleocene (Thanetian), France; **C**, **D**, paratype, MNHN.F.A90829 (Pacaud coll.), Jonchery-sur-Vesle, Marne, late Paleocene (Thanetian); **E**, **F**, specimen UPMC (Munier-Chlamas coll.), from a drawing of Merle (1999: pl. 66, b-d), Châlons-sur-Vesle; **G**, **H**, specimen MNHN-IM (Staadt coll.), from a drawing of Merle (1999: pl. 66, c-e), Châlons-sur-Vesle. Scale bars: 5 mm. Credits: A-D, P. Loubry (MNHN/CNRS).

is similar and the teleoconch of the French population is only less thick (personal observation DM). Therefore, we believe that they belong to the same species. Glibert (1963) recorded this species in the Bartonian from the Paris Basin, but we cannot confirm this record based on material in the examined collections (MNHN and private collections). It is possible that this species was mistaken for *Jsowerbya depauperata* (Deshayes, 1865).

Subfamily NUCELLOPSINAE Merle, n. subfam.

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TYPE GENUS. — *Nucellopsis* Merle, 2005 by present designation.

INCLUDED GENERA. — *Nucellopsis* Merle, 2005 and *Pronucellopsis* n. gen.

DIAGNOSIS. — Shell medium sized for family. Bucciniform shape with rounded whorls. P6 not atrophied. ADP, MP present; ABP and IP present in some species of *Nucellopsis*. Poorly developed axial sculpture formed by weakly lamellose varices. Posterior sinus on sutural ramp deep. D1 to D6 present. ID missing. Columellar lip usually smooth. Microstructure of three aragonite layers.

DISCUSSION

The Nucellopsinae Merle, n. subfam. includes basal taxa often erroneously attributed to the Muricopsinae (synonym of Aspellinae) because of their biconic shape or attributed to the Trophoninae because of their weakly lamellose varices. The Nucellopsinae Merle, n. subfam. (Clade D of Winclada or Clade 47 of PAUP) includes Paleocene and Eocene species that usually share a late appearance of the primary cords (P1 to MP), rounded whorls and buccinoid shape in *Nucellopsis*.

Genus *Nucellopsis* Merle, 2005

TYPE SPECIES. — *Murex plicatilis* Deshayes, 1835 by original designation. Early Eocene: Paris Basin (France) and London Basin (England).

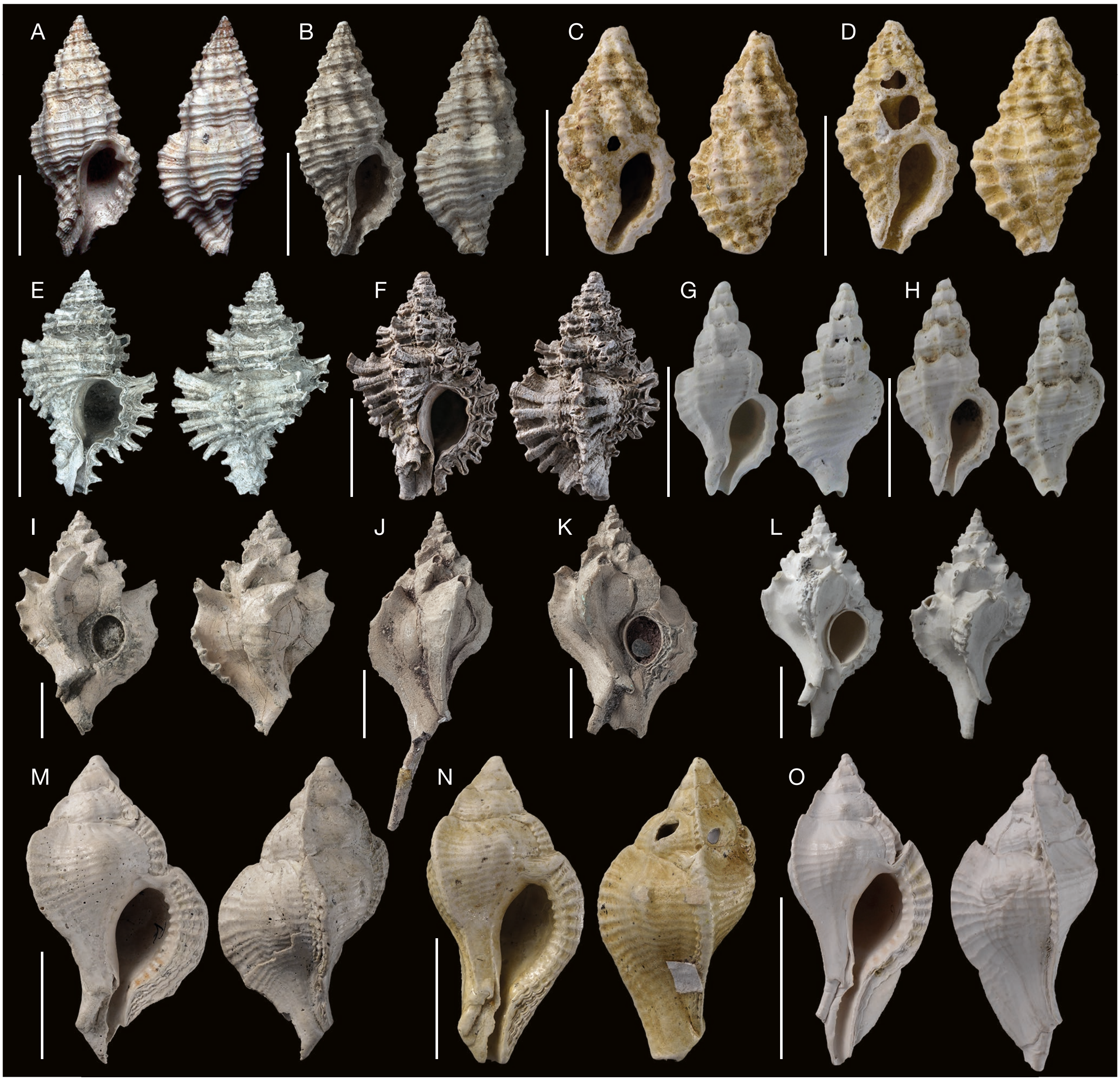

Fig. 25. — New species of *Muricopsis* Bucquoy & Dautzenberg, 1882, *Favartia* Jousseaume, 1880, *Dermomurex* Monterosato, 1890, *Trubatsa* Dall, 1889 and *Timbellus* De Gregorio, 1885: **A**, **B**, *Muricopsis pontileviensis* n. sp.: **A**, holotype, MNHN.F.A71120 (Dollfus coll.), Pontlevoy, France, Langhian; **B**, paratype, MNHN.F.A77743, (Dollfus coll.), Pontlevoy; **C**, **D**, *M. neraudeaui* n. sp.: **C**, holotype, MNHN.F.A77746 (Néraudeau sample), Saint-Jacques-de-la-Lande, France, Messinian; **D**, paratype, MNHN.F.A77747 (Néraudeau sample), Saint-Jacques-de-la-Lande; **E**, **F**, *Favartia jansseni* n. sp.: **E**, holotype, RGM.225979, Winterswijk, The Netherlands, Langhian; **F**, paratype, MNHN.F.A77748 (Ledon coll.), Winterswijk; **G**, **H**, *Dermomurex* (*Gracilimurex*) *ligerianus* n. sp.: **G**, holotype, MNHN.F.A33456 (Dollfus coll.), Pontlevoy; **H**, paratype, MNHN.F.A33457 (Dollfus coll.); **I**-**K**, *Trubatsa ganensis* n. sp.: **I**, holotype, MNHN.A90520 (Varone coll.), Gan (Tuilerie), France, Ypresian; **J**, paratype, MNHN.F.A90518 (Merle coll.), Gan (Tuilerie); **K**, paratype, MNHN.F.A90517 (Merle coll.), Gan (Tuilerie); **L**, *T. calviniacensis* n. sp., holotype, MNHN.F.A25590 (Pacaud coll.), Cauvigny (Châteaurouge), France, Lutetian; **M**-**O**, *Timbellus magnificus* n. sp.: **M**, holotype, MNHN.F.A90522 (Pacaud coll.), Baron (Sablière Heudebert), France, Bartonian; **N**, paratype, MNHN.F.A90525 (Schtrock coll.), Saint-Vaast-lès-Mello (Barisseuse), France, Bartonian; **O**, paratype, MNHN.F.A90523 (Pacaud coll.), Baron (Sablière Heudebert). Scale bars: A-L, 5 mm; M-O, 20 mm.

Nucellopsis parisiensis n. sp.
(Figs 23A-F; 28F, G)

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Muricopsis depauperatus – Cossmann & Pissarro 1911: fig. 169bis-2 [*non* Deshayes, 1865].

Muricopsis sp. *non depauperata* – Merle *in* Le Renard & Pacaud 1995: 114, réf.: GA 169bis-2.

Nucellopsis dudariensis – Merle 2005c [*non* Strausz, 1966].

Type material. — **Holotype. France** • Paris Basin, Val d'Oise, Saint-Witz (Le Guépelle); Sable du Guépelle (biozone NP16); middle Eocene (early Bartonian, Auversian); MNHN.F.R64955 (Merle coll.), figured specimen in Merle (2005c: fig. 2H), H: 21.5 mm (Figs 23E, F; 28F).

Fig. 26. — New species of *Timbellus* De Gregorio, 1885: **A**, **B**, *Timbellus occidentalis* n. sp.: **A**, holotype, MNHN.F.A90533 (Le Marchand coll.), Fresville, France, upper Lutetian; **B**, paratype, MNHN.F.A24031 (Vasseur coll.), Saffré (Bois-Gouët), France, Bartonian; **C**, **D**, *T. calciacus* n. sp.: **C**, holotype, MNHN.F.A90536 (Merle coll.), Chaussy (Les Garennes), France, Lutetian; **D**, paratype, MNHN.F.A90537 (Merle coll.), Chaussy (Les Garennes); **E**, **F**, *T. longicanalis* n. sp.: **E**, holotype, MNHN.F.A24101 (Le Marchand coll.), Fresville, France, upper Lutetian; **F**, paratype, MNHN.F.A24100, Fresville; **G**-**I**, *T. magnei* n. name: **G**, MNHN.F.A32508 (Merle coll.), juvenile specimen, Gan (Tuilerie), France; **H**, MNHN.F.A90545 (Merle coll.), juvenile specimen with protoconch, Gan (Tuilerie); **I**, MNHN.F.A72443 (Varone coll.), Gan (Tuilerie); **J**-**L**, *T. curvispina* n. sp.: **J**, holotype, MNHN.F.A90541 (MNHN coll.), Parnes, France, Lutetian; **K**, paratype, MNHN.F.A90543 (Pons coll.), Fontenay-en-Vexin, France, Lutetian; **L**, paratype, MNHN.F.A73848 (Pons coll.), Fontenay-en-Vexin; **M**, *T. sixi* n. sp., holotype, MNHN.F.A90544 (Six coll.), Trosly-Breuil (Fond Couturier), France, Ypresian; **N**-**P**, *T. radulfiensis* n. sp.: **N**, holotype, MNHN.F.A77754 (MNHN coll.), Rauville-la-Place, France, Priabonian; **O**, paratype, MNHN.F.A77755 (MNHN coll.), Rauville-la-Place; **P**, paratype, MNHN.F.A90559 (Vasseur coll.), Rauville-la-Place. Scale bars: A,B, N-P, 5 mm; C, D, 3 mm; E-G, I-L, 10 mm; H, 2 mm.

Paratypes. France • 1 spm; same as for the holotype; MNHN.F.A71797 (Pons coll.), figured specimen in Merle (2005c: fig. 1G) • 1 spm; idem; MNHN.F.A71798 (Pons coll.), figured specimen in Merle (2005c: fig. 1H, I) • 1 spm; idem; MNHN.F.J02585 (Cossmann coll.); figured in Cossmann & Pissarro (1911: pl. 36 fig. 169bis-2) • 1 spm; idem; MNHN.F.A90963 (Faullummel coll.) (Figs 23C, D; 28G) • 1 spm; idem; MNHN.F.A90964 (Faullummel coll.) (Fig. 23A, B) • 6 spm; idem; MNHN.F.A90962 (Faullummel coll.).

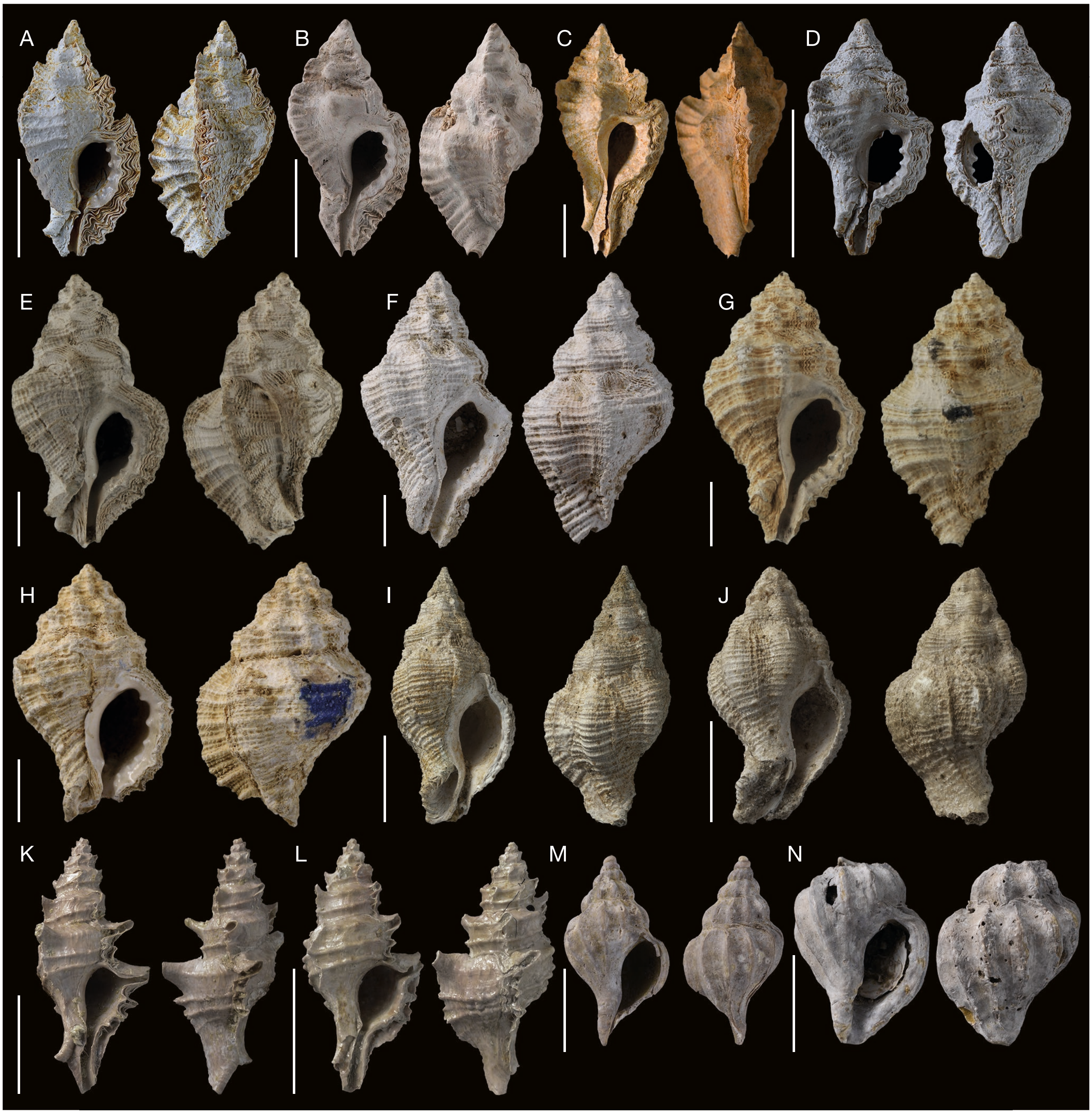

Fig. 27. — New species of *Timbellus* De Gregorio, 1885, *Pterynotus* Swainson, 1833 (*Pterymarchia* Houart, 1995), *Textiliomurex* Merle, 2011, *Ponderia* Houart, 1986 and *Flexopteron* Shuto, 1969: **A**-**C**, *Timbellus submicropterus* n. sp.: **A**, holotype, MNHN.F.A24111 (MNHN coll.), Fresville, France, Lutetian; **B**, paratype, MNHN.F.A24126 (Munier-Chalmas coll.), Gourbesville, France, Lutetian; **C**, paratype, UCBL-EM 33438 (Bourdot coll.), Fresville; **D**, *T.* cf. *submicropterus* n. sp., MNHN.F.A90557 (Brébion coll.), Saint-Aignan-Grand-Lieu (Pierre-Aiguë), France, Bartonian; **E**, **F**, *Pterynotus* (*Pterymarchia*) *gaasensis* n. sp.: **E**, holotype, MNHN.F.A32492 (Merle coll.), Gaas (Espibos), France, Rupelian; **F**, paratype, MNHN.F.A90554 (Merle coll.), Gaas (Espibos); **G**, **H**, *P.* (*P.*) *pelouatensis* n. sp.: **G**, holotype, MNHN.F.J09945, Saucats (Peloua), France, Burdigalian; **H**, paratype, MNHN.F.J17632, Saucats (Peloua); **I**, **J**, *Textiliomurex chodmonensis* n. sp.: **I**, holotype, MNHN.F.A81144 (Pacaud coll.), Chaumont-en-Vexin (Carrière Darcy), France, Lutetian; **J**, paratype, MNHN.F.A81145 (Pons coll.), Chaumont-en-Vexin (Carrière Darcy); **K**, **L**, *Ponderia remyi* n. sp.: **K**, holotype, MNHN.F.A90548 (Remy coll.), Fresville, Lutetian; **L**, paratype, MNHN.F.A90555, Fresville (Remy coll.); **M**, **N**, *Flexopteron constantinense* n. sp.: **M**, paratype, MNHN.F.A77761 (MNHN coll.), Carentan-les-Marais (Cauvin), France, Priabonian; **N**, holotype, MNHN.F.A77760 (MNHN coll.), Carentan-les-Marais (Cauvin). Scale bars: A-D, I-L, 10 mm; E-H, N, 5 mm; M, 3 mm. Credits: A, B, D-F, N, P. Loubry (MNHN/CNRS); C, E. Robert (UCBL).

Additional material. — **France** • 1 spm; Paris Basin, Val d'Oise, Saint-Witz (Le Guépelle); Sable du Guépelle (biozone NP16); early Bartonian; MNHN.F.A27771 (Pacaud coll.) • 1 spm; Paris Basin, Val d'Oise, Auvers-sur-Oise (Bois-le-Roi); idem; MNHN.F.A27770 (Pacaud coll.) • 1 spm; Paris Basin, Aisne, Nogent-l'Artaud; idem; MNHN.F.A90565 (Margerie coll.) • 1 spm; Paris Basin, Aisne, Bézu-le-Guéry; idem; MNHN.F.A90825 (Faullummel coll.) • 1 spm; Paris Basin, Aisne, Mont-Saint-Martin; idem; MNHN.F.J07787

(UMPC coll.) • 1 spm; Paris Basin, Seine-et-Marne, Sainte-Aulde (Caumont); idem; MNHN.F.A90826 – (Faullummel coll.) • 1 spm; Paris Basin, Seine-et-Marne, Luzancy; idem; MNHN.F.A90827 (Faullummel coll.) • Paris Basin, Oise, Loisy; idem; MNHN.F.A90828 (Faullummel coll.).

ETYMOLOGY. — From the Latin adjective *parisiensis*, the geographic origin of this species being the Paris Basin.

TYPE HORIZON. — Sable du Guépelle (biozone NP16, see Gély & Lorenz (1991: pl. 1), middle Eocene (early Bartonian, Auversian).

TYPE LOCALITY. — France, Paris Basin, Val d'Oise, Saint-Witz (Le Guépelle), INPN (2024).

DISTRIBUTION. — Paris Basin (France), middle Eocene (early Bartonian , Auversian).

DESCRIPTION

Smooth, multispiral protoconch of up to 2.5 whorls (see Merle 1999: pl. 23, fig. 5, holotype). Biconic teleoconch, up to 21.5 mm in height, up to 14 mm in width, biconic in profile and composed of six whorls. Moderately high spire with rounded or subcarinate whorls. Last whorl up to 73% of total length. Apical angle 64°. Spiral sculpture with strongly marked primary cords. First whorl: appearance of P1, s1, P2; P1 less marked than s1-P2; from second to third whorl, no addition of cord, P1 of equal strength to s1-P2; on fourth whorl, appearance of IP poorly marked. Fifth whorl: no addition of cord. Last whorl: IP (weak), P1 to P6, P6 not atrophied (on convex part of whorl), ADP, MP and ABP; s1 to s3 dominant, equal in strength to primary cords. First to second whorl: twelve varices. Third to fourth whorl: eleven varices. Fifth whorl: ten varices. Sixth whorl: nine varices. Varices more or less sublamellose. No true spine except angular point on P1. Suboval aperture up to 31% of diameter and up to 66% of length of last whorl (including siphonal canal). Columella slightly angular. Columellar lip narrow, adherent, smooth or with one tubercle. Outer lip with five or six denticles including D1 to D6. D1 appearing late in ontogeny. D6 occasional. ID missing. Siphonal canal, short, open, up to 31% of aperture length, slightly dorsally recurved. Pseudo-umbilicus deep, rather wide.

COMPARISONS

Nucellopsis ponsi Merle, 2005c differs from *N. parisiensis* n. sp., *N. plicatilis* (Deshayes, 1835) and *N. dudariensis* (Strauzs, 1966) by having a deeper posterior sinus and weaker spiral cords. Its columellar lip is occasionally ornamented by a weak denticle mid-columella, whereas it is usually smooth in the other three species. *Nucellopsis parisiensis* n. sp., *N. plicatilis* and *N. dudariensis* bear more numerous cords on the siphonal canal (MP and ABP) and more secondary cords than *N. ponsi*. *Nucellopsis parisiensis* n. sp. differs from *N. plicatilis* by the appearance of P1 and s1 on the first teleoconch whorls, by having more angular teleoconch whorls, and by usually lacking D6. Both species share a multispiral protoconch. *Nucellopsis parisiensis* n. sp. was erroneously identified as *Jsowerbya depauperata* (Deshayes, 1865) by Cossmann & Pissarro (1911) in spite of numerous differences, such as a narrower shell shape, IP on the sutural ramp and a deeper anal sulcus (Merle 2005b). Merle (1999, 2005c) identified *N. parisiensis* n. sp. as *N. dudariensis* due to several similarities with the holotype of *Cantharus* (*Pollia*) *dudariensis* (Fig. 23G, H) from the upper Lutetian of Hungary [apical angle near 64°, subangular whorls, thick varices, poorly developed shoulder sinus, five internal denticles (D1 to D5, D6 missing), angular columella with one small tubercle]. These similarities suggest that *N. parisiensis* n. sp. and *N. dudariensis* are closely related. However, close examinaton of the holotype of *N. dudariensis* (Fig. 23G, H) reveals several differences with the Parisian species, such as the late appearance of s1 on the last whorl, s1 less coarse than the primary cords P1 and P2, fewer secondary cords (only s1 instead s1 to s3), and the stronger development of IP.

Genus *Pronucellopsis* Merle, n. gen.

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TYPE SPECIES. — *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. sp. by present designation.

INCLUDED SPECIES. — *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp., Paris Basin, France; Paleocene (Thanetian).

DIAGNOSIS. — Subfusiform teleoconch with rounded whorls. Poorly marked cords. No IP. P6 weak, not atrophied. ADP, MP weak. Secondary cords (s1, s2, s3, s4) appearing late in ontogeny. Primary cords P3 to P6 appearing after third whorl. Varices formed by one or two abaxial lamellae on early whorls, occasionally reinforced by several lamellae on succeeding whorls. Number of varices: between 13 and 15. Weak, rounded shoulder sinus. Posterior sinus on sutural ramp deep. Internal denticles usually weak: ID missing. D1 stronger than D2. D6 present. Columellar lip smooth. Siphonal canal narrow. Microstructure of three aragonite layers.

COMMENTS

Pronucellopsis Merle, n. gen. is the sister taxon of *Nucellopsis* (clade E, Fig. 1). Both taxa share a weak or missing shoulder sinus. *Pronucellopsis* Merle, n. gen. is easily differentiated in having a more elongated shape and poorly developed internal denticles. It also displays poor development of the spiral cords which always remain weak and appear late in ontogeny. This feature is present in early muricids from the Paleocene (e.g., *Poirieria* or *Flexopteron*) and seems a plesiomorphic character.

Pronucellopsis pacaudi
Merle, Ledon & Goret, n. gen., n sp.
(Figs 24; 28H, I)

urn:lsid:zoobank.org:act:A1CD0282-7026-43EB-9992-5C106808B8CA

Murex (*Muricopsis*) *multistriatus* – Cossmann 1889: 129 [*non* Deshayes, 1865].

Jania (*Muricopsis*) *multistriatus* – Cossmann 1892: 69 [*non* Deshayes, 1865].

Muricopsis multistriatus – Cossmann & Pissarro 1911: pl. 36, fig. 169bis-5 [*non* Deshayes, 1865].

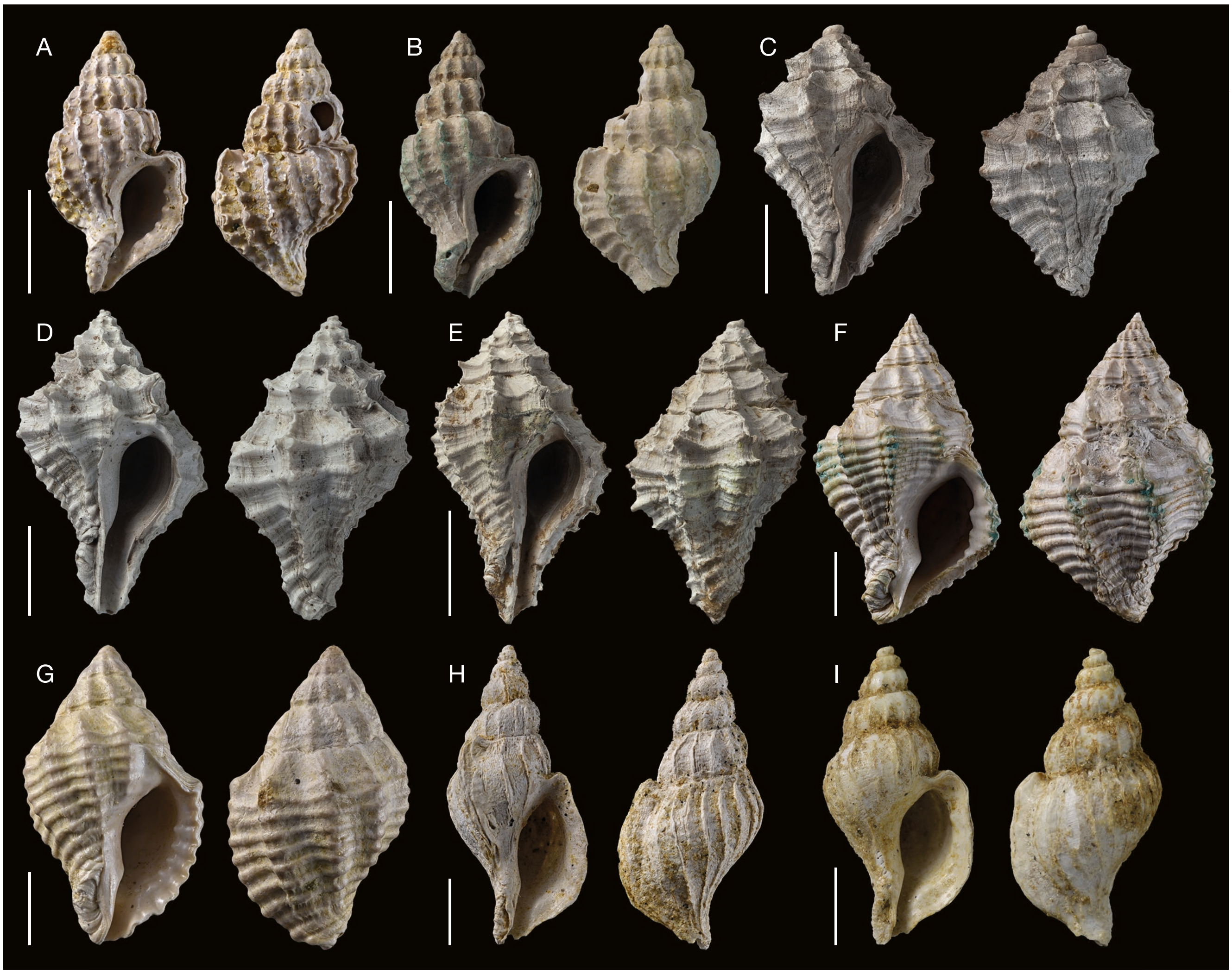

Fig. 28. — New species of *Flexopteron* Shuto, 1969, *Crassimurex* (*Pliocrassimurex*) n. subgen., *Nucellopsis* Merle, 2005 and *Pronucellopsis* Merle, n. gen.: **A**, **B**, *Flexopteron liancurtense* n. sp.: **A**, holotype, MNHN.F.J02578 (Cossmann coll.), Liancourt-Saint-Pierre, France, Ypresian; **B**, paratype: MNHN.F.A77758 (Merle coll.), Liancourt-Saint-Pierre; **C**-**E**, *Crassimurex* (*Pliocrassimurex*) *hirtus* n. subgen., n. sp.: **C**, paratype (juvenile), MNHN.F.A77753, Molins del Rei, Spain, Zanclean; **D**, paratype, MNHN.F.A77752, Molins del Rei; **E**, holotype, MNHN.F.A77751 (MNHN coll.), Molins del Rei; **F**, **G**, *Nucellopsis parisiensis* n. sp.: **F**, holotype, MNHN.F.R64955 (Merle coll.), Saint-Witz (Le Guépelle), France, Bartonian; **G**, paratype, MNHN.F.A90963 (Faullummel coll.), Saint-Witz (Le Guépelle); **H**, **I**, *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp.: **H**, holotype, MNHN.F.J02587 (Cossmann coll.), Châlons-sur-Vesle, France, Thanetian; **I**, paratype, MNHN.F.A90829 (Pacaud coll.), Jonchery-sur-Vesle, France, Thanetian. Scale bars: 5 mm. Scale bar: A, B, 3 mm; C, D, F-I, 5 mm; E, 10 mm. Credits: P. Loubry (MNHN/CNRS).

"*Murex*" *multistriatus* – Glibert 1963: 30, no. 8 [*non* Deshayes, 1865].

Trophonopsis multistriata – Le Renard & Pacaud 1995: 114, Ref. GA-169bis-5 [*non* Deshayes, 1865].

Type material. — **Holotype. France** • Paris Basin, Marne, Châlons-sur-Vesle; Sables de Châlons-sur-Vesle, biozone NP9; Paleocene (Thanetian); MNHN.F.J02587 (Cossmann coll.), figured specimen in Cossmann & Pissarro (1911: pl. 36, fig. 169bis-5), H: 22 mm (Figs 24A, B; 28H).

Paratypes. France • 3 spm; same as for the holotype; MNHN.F.A90831 (Pacaud coll.) • 2 spm; idem; MNHN.F.A90832 (MNHN coll.) • 7 spm; Paris Basin, Marne, Jonchery-sur-Vesle; Paleocene (Thanetian); MNHN.F.A90833 (Staadt coll.) • 1 spm; idem; MNHN.F.A90829 (Pacaud coll.) (Figs 24C, D; 28I) • 8 spm; idem; MNHN.F.A90830 (Pacaud coll.) • 6 spm; Paris Basin, Oise, Abbecourt (Bois-des-Godins), Paleocene (Thanetian); MNHN.F.A90834 (Pacaud coll.).

Additional material. — 1 spm; Paris Basin, Marne, Jonchery-sur-Vesle; Paleocene (Thanetian); UPMC (Munier-Chlamas coll.), figured specimen of Merle (1999: pl. 66, b-d) (Fig. 24E, F) • 1 spm; idem; MNHN-IM (Staadt coll.), figured specimen of Merle (1999: pl. 66, c-e) (Fig. 24G, H) • 5 spm; idem; MNHN.F.A91007 (Staadt coll.).

Etymology. — Dedicated to Jean-Michel Pacaud (MNHN) who has for a long time observed that *Murex multistriatus* Deshayes, 1865 is a junior synonym of *Fusus angusticostatus* Melleville, 1843 (now *Lyrofusus angusticostatus*).

Type horizon. — Sables de Châlons-sur-Vesle, biozone NP9, see Huyghe *et al.* (2015: fig. 2), Paleocene (Thanetian).

Type locality. — France, Paris Basin, Marne, Châlons-sur-Vesles, see Fritel (1910: 77).

Distribution. — Paris Basin (France), Paleocene (Thanetian), Sables de Bracheux and Sables de Châlons-sur-Vesle.

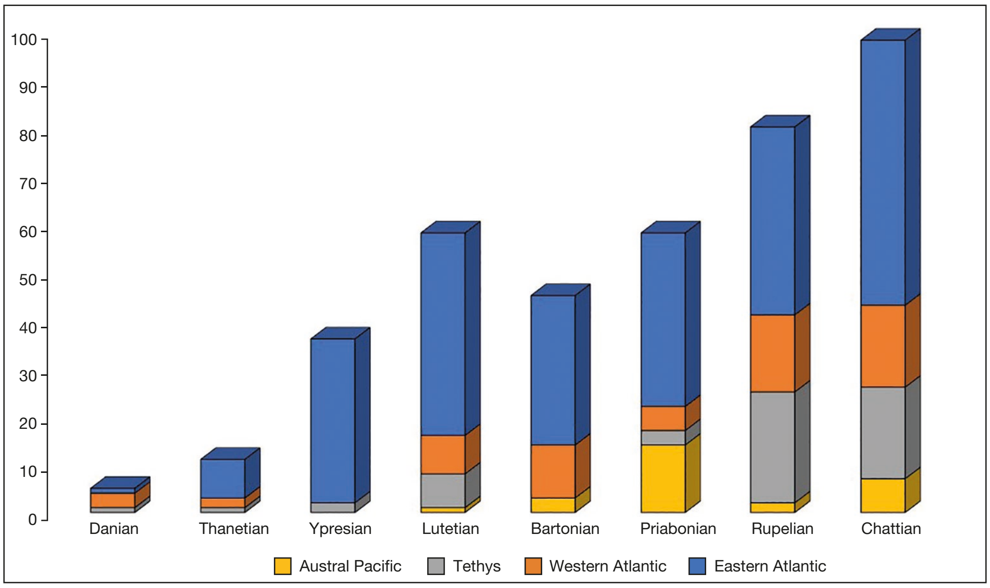

FIG. 29. — Histogram showing the evolution of the species richness during the Paleogene in Western and Eastern Atlantic, Tethys and Austral Pacific (original histogram of Merle *et al.* (2011: 38, fig. 11B) updated from this paper, Pacaud 2018; Pacaud *et al.* 2017; Merle & Pacaud 2019; Kovács & Vicián 2019; Merle & Landau 2020; Ledon *et al.* 2023; Lozouet 2023). It illustrates the Switch phase with the increase of the proportion of the Tethysian and Pacific species.

DESCRIPTION

Unknown protoconch. Teleoconch, up to 22 mm in height, up to 12.5 mm in width, subfusiform in profile, composed of seven whorls. High spire with rounded whorls. Last whorl up to 67% of total length. Apical angle 45°. Spiral sculpture with weak primary cords. First and second whorls: no spiral scultpure; third and fourth whorls, P1 weak. Fifth whorl: appearance of P2. Sixth whorl: appearance of s1. Last whorl and seventh whorl: P1 to P6, s1, s2, s3 and s4 (convex part of whorls), ADP, MP (siphonal canal). Axial sculpture on first to second whorl: not observed; third whorl: nine varices; fourth whorl: 14 varices; fifth whorl: 14-16 varices; sixth whorl: 11-19 varices; seventh whorl: 12-23. Varices finely lamellose. No spine on P1. Wide, ovate aperture up to 45% of diameter and up to 84% of length of last whorl (including siphonal canal). Posterior sinus deep, no shoulder sinus. Columella slightly angular. Columellar lip smooth, narrow and adherent. Outer lip with occasional denticles. D1 to D6 small, poorly developed, ID missing. Siphonal canal, short, open, up to 23% of aperture length, slightly dorsally recurved. Pseudoumbilicus narrow.

COMPARISONS

Deshayes (1865) described *Murex multistriatus* and illustrated a specimen bearing a buccinid shape (pl. 88, fig. 810). In fact, this species is a junior synonym of *Fusus angusticostatus* Melleville, 1843 (now *Lyrofusus angusticostatus*). However, Cossmann (1889) and Cossmann & Pissarro (1911) confused this buccinoid species with a Thanetian Muricidae, which they mistakenly called *Murex multistriatus*. We described this species as *Pronucellopsis pacaudi* Merle, Ledon & Goret, n. gen., n. sp. It can be compared to *Nucellopsis ponsi* Merle, 2005c or *N. plicatilis* (Deshayes, 1835) from the late Paleocene-early Eocene of the Paris Basin. Juveniles of *P. pacaudi* Merle, Ledon & Goret, n. gen., n. sp. share with these *Nucellopsis* a buccinid shape, but at the end of its growth *P. pacaudi* Merle, Ledon & Goret, n. gen., n. sp. displays a subfusiform shape with a high spire. The sculptures (both axial and spiral) of *P. pacaudi* Merle, Ledon & Goret, n. gen., n. sp. and the internal denticles of outer lip are also less developed. Because of its high spire, *P. pacaudi* Merle, Ledon & Goret, n. gen., n. sp. resembles some elongated *Beyregrex sarroniensis* (Carez, 1879), n. comb. but in *B. sarroniensis* n. comb. the spiral sculpture and the internal denticles are always more strongly developed. In addition, P1 spine is present in *B. sarroniensis* n. comb., whereas it is missing in *P. pacaudi* Merle, Ledon & Goret, n. gen., n. sp.

CONCLUSION

Based on new field material and a re-examination of collection material, this paper presents 24 new species, four new genera, one new subgenus and one new subfamily and therefore it deeply increases the knowledge of muricid paleobiodiversity. At species level, this paper highlights the strong diversity of the Eocene *Timbellus* which was underestimated. In addition, with 19 new species, this paper highlights the species richness of European Paleogene muricids and allows updating the diagram showing its evolution given by Merle *et al.* (2011: 36, fig. 21b). This update (Fig. 29) illustrates the high muricid species richness in the Lutetian and confirms the Switch phase (Oligocene) which displays an increase of the proportion of Tethysian and Pacific species after the Eocene.

At supraspecific level, this paper improves the understanding of European Eocene-Oligocene basal muricids (*Pronucellopsis* n. gen, *Beyregrex* Merle, n. gen, *Pseudotrophonopsis* Merle, n. gen., Nucellopsinae Merle, n. subfam.), that have, until now, been shoehorned uncomfortably into extant genera and subfamilies. Supraspecific taxonomy today relies heavily on molecular data, but this paper illustrates the value of using precise homologies basing data gathered on the careful observation of shell characters with which one can construct fossil phylogenies of groups that have no living descendants (see also Merle 2002, 2005b, c).

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APPENDICES

Appendix 1. — Matrix taxa/characters and list of the taxa. Available on MorphoBank: http://morphobank.org/permalink/?P5543.

MATRIX TAXA/CHARACTERS

```
                              10         20         30      37
Flex. cretaceum       0000000000 0100000000 0000000000 0000000
Flex. foliaceum       0001100000 0001000000 0000001000 0000000
Pagodula echinata     0001100000 0000000000 000?012?02 2000000
Typhis tubifer        0011100000 0011110000 000012???2 2000000
Ocinebrina acic.      0221101000 0101011011 1111100000 0100300
Ocenebra erinac.      0021101000 0101111011 1110100000 1001211
Urosalpinx cine.      0201101000 1101011011 1111100000 0100311
Nucella lapillus      1201101000 1101011011 1111100000 0100311
Trophon gevers.       1201101000 1101011011 110112???2 2000011
Muricopsis crist.     0002202000 1211111011 2210100110 1200100
Truncular. trunc.     0001102010 111111?011 2210100000 0001100
Orania fusulus        0102201021 1111111102 0000000001 1210300
Ergalatax obscura     0102201021 1111111102 0000000001 1210300
Drupina glossul.      1101011032 1111110102 0000000201 1210300
Drupa morum           1101011032 11?1110102 0000000201 1210300
Stramonita haem.      1101011021 1111010102 0000000001 1210312
Jsowerbya sexd.       0102201100 0101011001 1110101000 0000000
Jsowerbya depaup.     0102201100 0101011001 1110101000 0000000
Jsowerbya auv.        0102201100 0101011001 1110101000 0000000
Nucellopsis plic.     1201101100 0100000001 1101001000 0000000
Nucellopsis ponsi     1202101100 0000000001 1000001000 0000000
Nucellopsis par.      1202101100 0001010001 1100001000 0000000
Beyregrex sarro.      0101100100 0001010001 1100001000 0000000
Beyregrex pereg.      0102100100 0101011001 1110001000 0000000
Beyregrex hant.       0101000100 0001011001 1110001000 0000000
Pronucellop.pac.      0101101100 0000000001 1100001000 0000000
Pseudotro. defos.     0102101100 0101011001 1111001000 0000000
```

LIST OF THE TAXA

Outgroup (extinct taxa)
Flexopteron cretaceum (Garvie, 1991);
F. foliaceum (Melleville, 1843).

Ingroup (extant taxa)
Pagodula echinata (Kiener, 1839);
Ocinebrina aciculata (Lamarck, 1822);
Ocenebra erinaceus (Linnaeus, 1758);
Urosalpinx cinerea (Say, 1822);
Nucella lapillus (Linnaeus, 1758);
Trophon geversianus (Pallas, 1774);
Muricopsis cristata (Brocchi, 1814);
Trunculariopsis trunculus (Linnaeus, 1758);
Orania fusulus (Brocchi, 1814);
Ergalatax obscura Houart, 1996;
Drupina glossularia (Röding, 1798);
Drupa morum Röding, 1798;
Stramonita haemastoma (Linnaeus, 1767).

Ingroup (extinct taxa):
Typhis tubifer (Bruguière, 1792);
Jsowerbya sexdentata (Sowerby, 1823);
J. depauperata (Deshayes, 1865);
J. auversiensis (Deshayes, 1865);
Nucellopsis plicatilis (Deshayes, 1835);
N. ponsi Merle, 2005;
N. parisiensis n. sp.;
Beyregrex sarroniensis (Carez, 1879), n. comb.;
B. pereger (Beyrich, 1854), n. comb.;
B. hantoniensis (Edwards in Lowry *et al.*, 1866), n. comb.;
Pronucellopsis pacaudi n. gen., n. sp.;
Pseudotrophonopsis defossa (Pilkington, 1804), n. comb.

APPENDIX 2. — List of the characters. Available on MorphoBank: http://morphobank.org/permalink/?P5543.

1. **Shape:**
   0. Biconic
   1. Buccinoid
2. **Shape of the spiral whorls:**
   0. Angular
   1. Subangular
   2. Rounded
3. **Siphonal canal:**
   0. Open
   1. Close (*Typhis* type)
   2. Close (*Ocenebra* type)
4. **Columellar ornamentation (angle):**
   0. Supercifial fold
   1. Absent
   2. Tubercles
5. **Columellar ornamentation (centre):**
   0. Superficial fold
   1. Absent
   2. Tubercles
6. **Basal columellar folds:**
   0. Absent
   1. Present
7. **Shoulder sinus:**
   0. Deep (open)
   1. not developed
   2. Deep (close)
8. **Posterior sinus:**
   0. Absent
   1. Present
9. **Anal sulcus:**
   0. Absent
   1. Present (short, *Hexaplex* type)
   2. Present (short *Orania* type)
   3. Present (long *Drupa* type)
10. **SP cord:**
    0. Absent
    1. Fine
    2. Strong (*Drupa* type)
11. **IP cord on the two first whorls:**
    0. Absent
    1. Present
12. **IP cord (adult):**
    0. Absent
    1. Fine
    2. Strong
13. **P2 spine:**
    0. Absent
    1. Present
14. **P3 on the two first whorls:**
    0. Absent
    1. Present
15. **P3 spine:**
    0. Absent
    1. Present
16. **Ontogeny of the cord P4 on the two early whorls:**
    0. Absent
    1. Present
17. **Ontogeny of the cord P5 on the two early whorls:**
    0. Absent
    1. Present
18. **Position of P5 cord (adult):**
    0. On the convex part of the whorl
    1. On the siphonal canal
19. **P6 on the two first whorls:**
    0. Absent
    1. Present
20. **P6 cord adult:**
    0. Absent (long siphonal canal)
    1. Present
    2. Absent (short siphonal canal)
21. **ADP cord:**
    0. Absent
    1. Present poorly developed
    2. Present strongly developed
22. **MP cord:**
    0. Absent
    1. Present poorly developed
    2. Present strongly developed
23. **ABP cord:**
    0. Absent
    1. Present
24. **Aspect of the secondary cords on convex part of the last whorl:**
    0. Distinct from the primary cords in the adult (lower relief)
    1. Not distinct from primary cords in the adult (same relief)
25. **Secondary cords of the siphonal canal:**
    0. Absent
    1. Present
26. **Internal denticles of the outer lip:**
    0. Present
    1. Absent
27. **ID denticle:**
    0. Present
    1. Absent with a series containing denticles (*Flexopteron foliaceum* Type)
    2. Absent among an aperture lacking denticles (*Typhis* type)
28. **D1 denticle:**
    0. D1 and D2 of the same size
    1. D1 reduced
    2. D1 dominant
29. **D2 denticle:**
    0. Not dominant
    1. Dominant
30. **D5 denticle:**
    0. Present
    1. Absent with a series containing denticles
    2. Absent among a series lacking denticles (*Typhis* type)
31. **D6 denticle:**
    0. Present
    1. Absent with a series of denticles
    2. Absent among a series lacking denticles (*Typhis* type)
32. **Type of axial sculpure (juvenile):**
    0. Lamellose varices
    1. No varices
    2. Varical nodules
33. **Type of axial sculpture (adult):**
    0. Lamellose varices
    1. Varical nodules
34. **Intervarices:**
    0. Absent
    1. Present

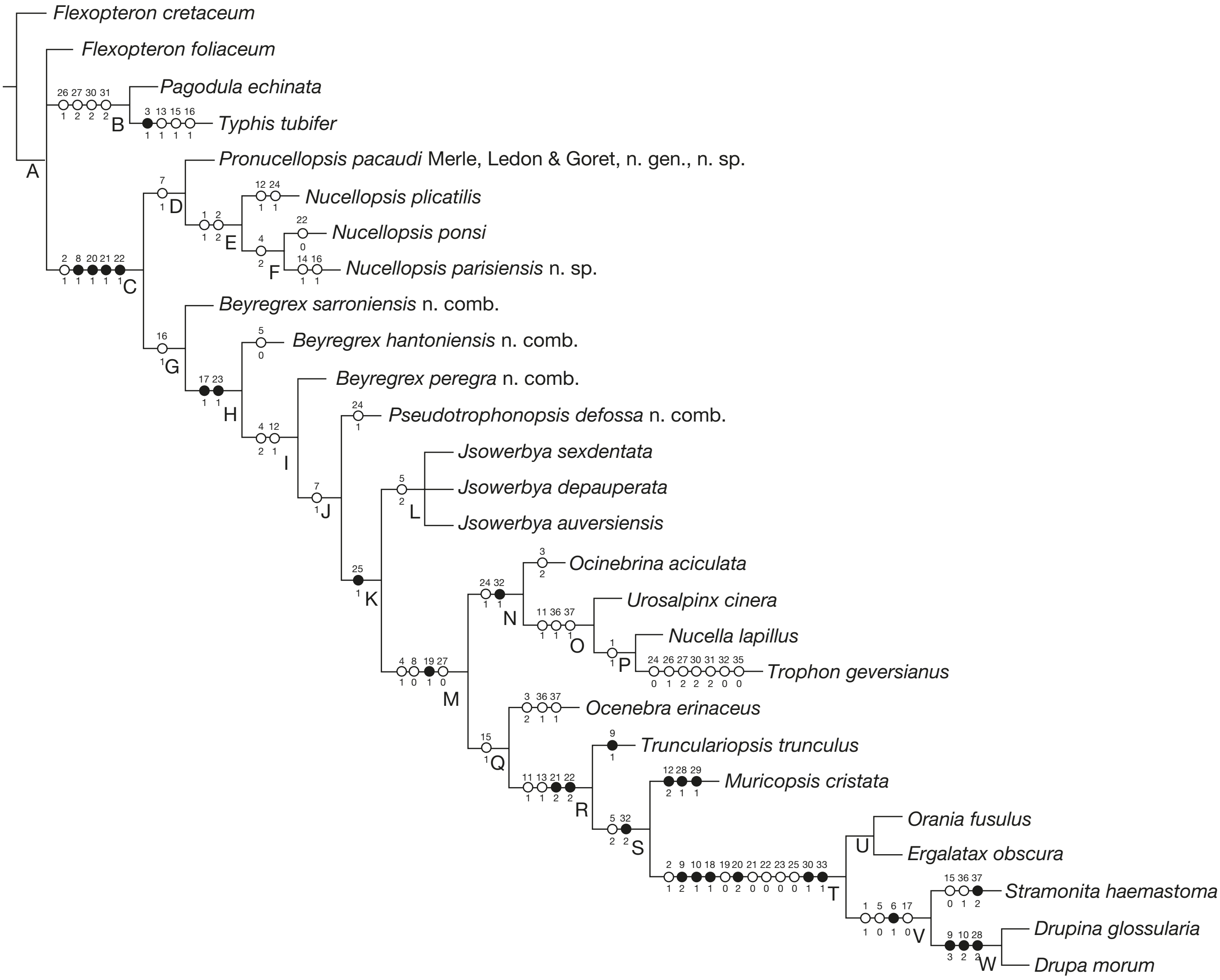
APPENDIX 2. — Continuation.

35. Axial lamellae on the outer lip:
0. simple accretion (*Flexopteron* type)
1. Oriented in the growing direction (*Muricopsis* type)
2. Imbricate (*Ocenebra* type)
3. No accretion

36. Calcite layer:
0. Absent
1. Present

37. Junction Aragonite/Calcite layers:
0. No calcite layer
1. Straigth junction
2. Undulated junction

APPENDIX 3. — Strict consensus tree and apomorphies generated by Winclada: 7 equally parsimonious trees (length 107, ci 0.53, ri 0.78), option Heuristic Analysis (mult* max*), all characters non additive. **Black circles**, unambiguous apomorphies; **white circles**, ambiguous apomorphies. Available on MorphoBank: http://morphobank.org/permalink/?P5543.



APPENDIX 4. — List of the synapomorphies by clade based on the strict consensus tree generated by Winclada. Available on MorphoBank: http://morphobank.org/permalink/?P5543.

Clades	Unambiguous synapomorphies	Ambiguous synapomorphies
Clade A	–	–
Clade B	–	26 (1), 27 (2), 30 (2), 31 (2)
Clade C	8 (1), 20 (1), 21 (1), 22 (1)	2 (1)
Clade D	–	7 (1)
Clade E	–	1 (1), 2 (2)
Clade F	–	4 (2)
Clade G	–	16 (1)
Clade H	17 (1), 23 (1)	–
Clade I	–	4 (2), 12 (1)
Clade J	–	7 (1)
Clade K	25 (1)	–
Clade L	–	5 (2)
Clade M	19 (1)	4 (1), 8 (0), 27 (0)
Clade N	32 (1)	24 (1)
Clade O	–	11 (1), 36 (1), 37 (1)
Clade P	–	1 (1)
Clade Q	–	15 (1)
Clade R	21 (1), 22 (2)	11 (1), 13 (1)
Clade S	32 (2)	5 (2)
Clade T	9 (2), 10 (1), 18 (1), 20 (2), 30 (1), 33 (1)	2 (1), 19 (0), 21 (0), 22 (0), 23 (0), 25 (0)
Clade U	–	–
Clade V	6 (1)	1 (1), 5 (0), 17 (0)
Clade W	9 (3), 10 (2), 28 (2)	–

APPENDIX 5. — Phylogenetic analysis using PAUP. Script with the character matrix, the back bone tree and commands for replicating the analysis. Available on MorphoBank: http://morphobank.org/permalink/?P5543.