Arch. Molluskenkunde | **144** | (1) | 31–50 | 23 figs, 4 pls | Frankfurt am Main, 30.06.2015

# Resolution of the confused classification of some Miocene Nassariidae, and reappraisal of their paleobiodiversity on the French Atlantic seaboard

### (Gastropoda: Neogastropoda)

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## Abstract

The genus or subgenus *Cyllenina* previously included in the Cylleninae is diagnosed as a member of the subfamily Dorsaninae. *Cyllenina* appears related to the Early Miocene species *Dorsanum aquensis*. A lectotype is designated for *Buccinum ancillariaeformis*, the type species of *Cyllenina*. In addition, the Paratethys group *Buccinum duplicatum* (= *Duplicatula*) appears closely related to *Dorsanum aquensis*. It is also shown that the generic names *Phos* or *Nassarius* are incorrectly used for *Nassa lineolata,* an Early Miocene species *Dorsanum.* On the other hand, the Paleogene clade *Keepingia* is excluded from the Dorsaninae and treated here as an unassigned group of Nassariidae. An overview of the biodiversity (specific richness) is proposed for the Nassariidae of the French Atlantic coasts showing their rapid diversification during the Late Oligocene. For the Nassariinae, the highest richness is encountered during the Middle Miocene and for the Dorsaninae, during the Later Oligocene. The Cylleninae is represented by only one species, and like the Dorsaninae, it has not been recorded in the Late Miocene.

**Key words**: Mollusca, Nassariidae, *Cyllenina*, *Dorsanum*, Taxonomy, Paleogene, Oligocene.

## Introduction

Phylogenetic inferences leads to a new insight of the family Nassariidae, with discoveries of unexpected relationships between the different groups (Allmon 1990, Haasl 2000). A new molecular phylogeny of the Nassariidae leading to a revised generic classification is currently underway (Galindo 2014). This preliminary study revealed the need of redefining the informative characters among the lineage of Nassariidae.

In this setting, the reappraisal of fossil data appears necessary to testify and supplement the results of molecular data and improve the knowledge on the evolution of this family. Otherwise, the major periods of diversification of this family during the Cenozoic may be clarified, at least in the European realm.

We will focus here on the relationship between *Cyllene*, *Cyllenina*, *Dorsanum* (subfamilies Cylleninae and Dorsaninae) and the placement of one common Lower Miocene species whether in *Phos* (Photinae), Nassariinae or *Dorsanum*. Incidentally, we propose an evaluation of the biodiversity (specific richness) of the Nassariidae on the French Atlantic coasts during the Oligocene and the Miocene.

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DOI 10.1127/arch.moll/1869-0963/144/031-050

Abbreviations of collections:

| | |
|---|---|
| MNHN.F. | Muséum national d'Histoire naturelle, Paleontology |
| MNHN-IM | Muséum national d'Histoire naturelle, Malacology |
| SMF | Senckenberg Forschungsinstitut Frankfurt am Main |

## Systematics

Hereafter is the list of genera discussed in this paper and the systematic placement adopted. The systematic position of the Photinae is questionable (HAASL 2000, CERNOHORSKY 1984, VOKES 1969). It is generally accepted that the Photinae are part of the family Buccinidae. However, the results of cladistic analysis of the shell characters by HAASL (2000), the latest general work on the classification of the Nassariidae, led to include the Photinae within the Nassariidae. Since this result is in accordance with the preliminary molecular analysis of GALINDO (2014), we choose to include the Photinae within the Nassariidae.

Class Gastropoda CUVIER 1797

Nassariidae IREDALE 1916 (1835)

Subfamily Cylleninae BELLARDI 1882
**Cyllene** GRAY 1834
Type species: *Cyllene owenii* GRAY 1834 (by monotypy), Recent, West Africa.

Subfamily Dorsaninae COSSMANN 1901 (=Duplicatinae MUSKHELISHVILI 1967)
**Dorsanum** Gray 1847
Type species: *Buccinum politum* LAMARCK 1822 (= *D. miran* BRUGUIÈRE 1789) by original designation, Recent, West Africa.
(= *Duplicatula* KOLESNIKOV 1939; type species: *Buccinum verneuilii* D'ORBIGNY 1844 (by original designation), Middle Miocene (Sarmatian), Paratethys.
**Cyllenina** BELLARDI 1882
Type species: *Buccinum ancillariaeformis* GRATELOUP 1834 (subsequent designation COSSMANN 1901), Lower Miocene (Burdigalian).
***Keepingia*** group
*Keepingia* NUTTALL & COOPER 1973
Type species: *Buccinum gossardi* NYST 1836 (by original designation); Oligocene, Europe.
(= *Colwellia* NUTTALL & COOPER 1973; type species: *Cominella flexuosa* EDWARDS 1866 (by original designation); Eocene, Europe).
(= *Desorinassa* NUTTALL & COOPER 1973; type species: *Buccinum desori* DESHAYES, 1865; (by original designation); Paleocene, Europe).
**Pseudocominella** NUTTALL & COOPER 1973
Type species: *Buccinum desertum* SOLANDER in BRANDER 1766 (by original designation); Eocene, Europe.
**Thanetinassa** NUTTALL & COOPER 1973
Type species: *Buccinum bicorona* MELLEVILLE 1843; (by original designation); Paleocene, Europe.
**Whitecliffia** NUTTALL & COOPER 1973
Type species: *Buccinum suturosum* NYST 1836 (by original designation); Upper Eocene/Lower Oligocene, Europe.

Subfamily Photinae GRAY 1857
**Phos** MONTFORT 1810
Type species: *Murex senticosus* LINNAEUS 1758 (by original designation), Recent, Indo-Pacific.
**Europhos** LANDAU, HARZHAUSER, ISLAMOGLU & SILVA 2014
Type species: *Buccinum polygonum* BROCCHI 1814 (by original designation), Pliocene, Italy.
**Antillophos** WOODRING 1928
Type species: *Cancellaria candeana* D'ORBIGNY 1842 (by original designation), Caribbean.
**Tritiaria** CONRAD 1865
Type species: *Buccinum mississippiensis* CONRAD 1865 (by monotypy), Lower Oligocene, Mississippi (USA).

### *Cyllene* and *Cyllenina*

The oldest *Cyllene* known (Pl. 1 Figs 1–5; Figs 1–2) is *C. desnoyersi* (BASTEROT 1825) from the Late Oligocene of the Aquitaine Basin (LOZOUET et al. 2001). In fact it is the only species of *Cyllene* recognized in the European Cenozoic although several species or subspecies were described by TOURNOUËR (1875), PEYROT (1903, 1927) and SACCO (1890): Upper Oligocene, *Cyllene degrangei* PEYROT 1927; Lower Miocene *C. desnoyersi aquitanica* TOURNOUËR 1875, *C. desnoyersi bisinuata* TOURNOUËR 1875; Middle Miocene, *C. desnoyersi turonica* PEYROT 1903, C. *desnoyersi taurocrassa* SACCO 1890, C. *desnoyersi taurangusta* SACCO 1890. As indicated by TOURNOUËR (1875), the Recent West-African species *Buccinum lyratum* LAMARCK 1822 (non *B. lyratum* GMELIN 1791) appears to be very close to the fossil one. Consequently, it was considered as a subspecies and renamed *Cyllene desnoyersi lamarcki* by CERNOHORSKY (1975).

The *Cyllenina* species were common in South Europe (including Paratethys) and the Mediterranean Sea from the Burdigalian to the Messinian (Upper Miocene). Its wide distribution diminished in the Pliocene when species occur only in the Iberian Peninsula and in the Mediterranean Sea (Landau & Marquet 1999). *Cyllenina* is considered as extinct after the Pliocene and no record of it is known in the Pleistocene.

Peyrot (1927) indicated seven species (including varieties) of *Cyllenina* from the shallow water Miocene deposits of Gironde (North of Aquitaine) and Middle Miocene of Pyrénées-Atlantiques (Orthez and Salies-de-Béarn):

- Lower Miocene (Burdigalian): *Cyllene (Cyllenina) vulgatissima vulgatissima* Peyrot 1927, var. *stylifera* Peyrot 1927, var. *ovulina* Peyrot 1927, *C. baccata* (Basterot 1825), *Cyllene (Cyllenina) ancillariaeformis* (Grateloup 1834).
- Middle Miocene (Serravallian): *Cyllene (Cyllenina) ignorata* Peyrot 1927, *Cyllene (Cyllenina) ancillariaeformis* var. *helvetica* Peyrot 1927).

There are no clear-cut differences among the species or varieties described by Peyrot and we acknowledge only two species: *Cyllenina ancillariaeformis* (Grateloup 1834) (Lower Miocene) [Pl. 1 Figs 6–17; Pl. 2 Fig. 4–5] and *Cyllenina helvetica* (Peyrot 1927) (Middle Miocene) [Pl. 2 Figs 6–8]. There is another species characterized by an elongate shape occurs in the Middle Miocene (Langhian of Baudignan, Landes). The generic assignation of *B. baccatum* (*Cyllenina* for Peyrot 1927) remains questionable and will be discussed below. Harzhauser & Kowalke (2004) admitted 10 species of *Cyllenina* in the Miocene of Paratethys. At least 9 species or varieties occurred in the Pliocene according to Bellardi (1882), Sacco (1904) and Landau & Marquet (1999).

Since Cossmann (1901), *Cyllenina* is regarded as a subgenus of *Cyllene* (Peyrot 1927; Wenz 1938–1944), included in the Buccinidae (Cossmann 1901; Sacco 1904) or in the Nassariidae (Wenz 1938–1944). In the classification of Cernohorsky (1984), followed by most European palaeontologists ever since (Chirli 2000; Harzhauser & Kowalke 2004, Landau & Marquet 1999; Landau et al. 2009, 2011), *Cyllenina* was, together with *Cyllene,* the only member of the subfamily Cylleninae. Allmon (1990) has suggested that *Cyllenina* is probably not closely related to *Cyllene*, and may be closer to *Dorsanum*. However Allmon says that “The generic names [“*Cyllenina*”] as the systematic status of many of the species to which they have been applied, are of uncertain status”.

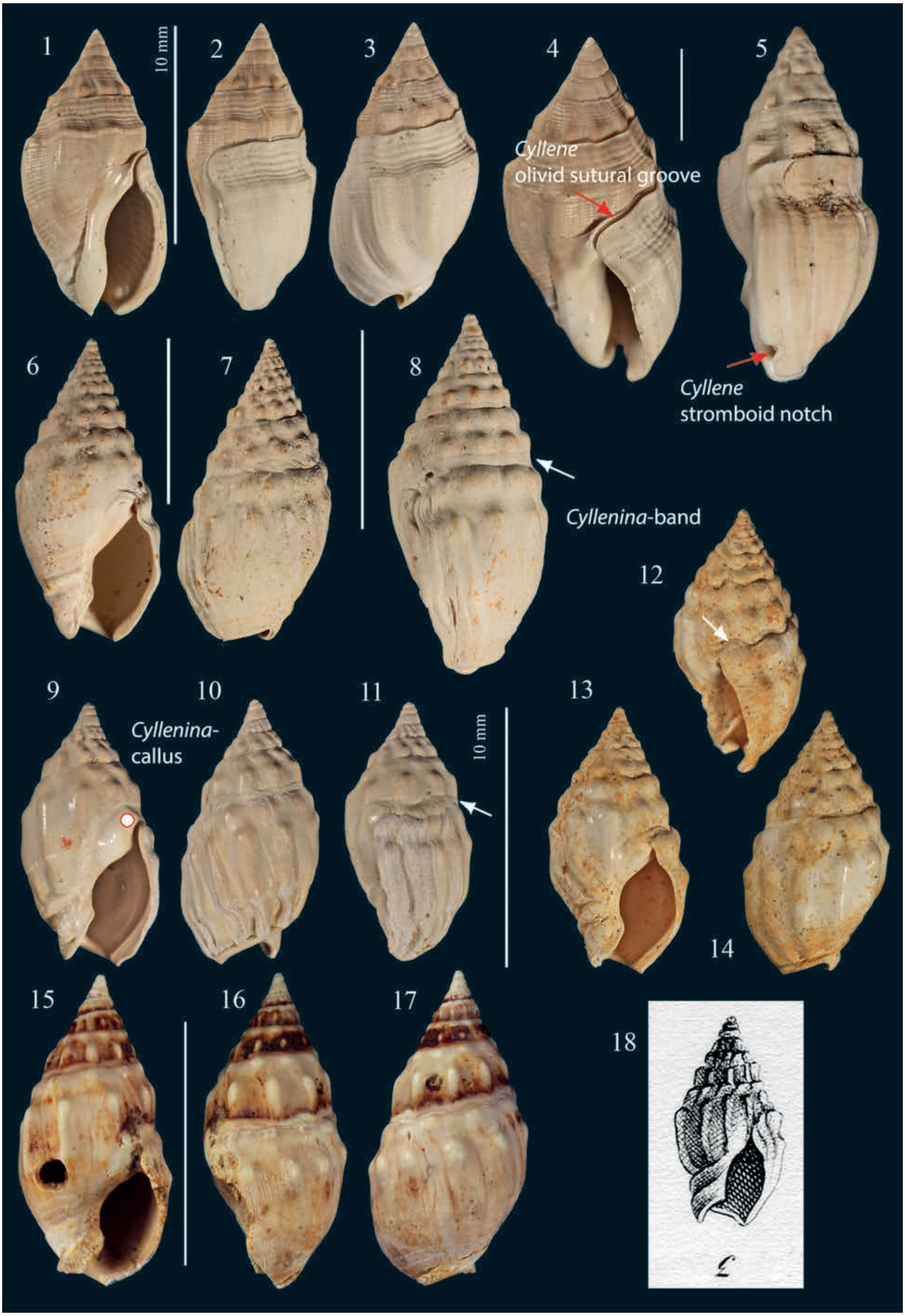
The reason of the placement of *Cyllenina* as subgenus of *Cyllene* or close to *Cyllene* is not well-argued. The major distinctive characters of *Cyllene* are the presence of an olivid-type sutural groove (Pl. 1 Fig. 4), and the obliquely plicate columellar callus (Cernohorsky 1984). We note also on some specimens of *Cyllene desnoyersi* (not on all) a distinct or shallow stromboid notch on the abapical edge of the outer lip (Pl. 1 Fig. 5). Yet, these characters are absent on *Cyllenina,* which is characterized by the presence of a glossy band, more or less developed, above the suture (*Cyllenina*-band: Pl. 1 fig. 8–11, 12; Pl. 2 Fig. 9) and in some species by a thick callus (Pl. 1 Fig. 9; Pl. 2 Fig. 12) in the parietal area (*Cyllenina*-callus). The term *Cyllenina*-band used by Harzhauser & Kowalke (2004) is equivalent to “bourrelet” of Cossmann (1901) or “bourrelet calleux” of Peyrot (1925–1927).

The *Cyllenina*-band is not homologous to the sutural groove of *Cyllene*. It is a distinctive character encountered only in this group. *Cyllenina* have also a relatively pronounced siphonal fasciole in comparison with *Cyllene*. The protoconch morphology of *Cyllene* and *Cyllenina* is also very different. *Cyllene* has a very conical protoconch reflecting a planktotrophic development (Text-figs 1–2) while *Cyllenina* or *Dorsanum* have a globular protoconch (Text-figs 3–10; Text-figs 17–21). Landau et al. (2009, p.69) quoting Cernohorsky (1984) indicate that “*Cyllenina* with multispiral protoconchs… were characterised by protoconch-angles of less than 60° which differentiated them from Nassariinae and Dorsaninae that have protoconch angles of more than 60°”. This is a misquotation, as we could not find in Cernorhorsky (1984) any allusion to the protoconch of *Cyllenina.* However, were find in Harzhauser & Kowalke (2004: 5) a close sentence about the planktotrophic protoconch of Cylleninae (not *Cyllenina*) that refers to an illustration of Cernorhorsky (1984: figs 169–173).

## What is *Cyllenina ancillariaeformis*?

The type species of *Cyllenina*, *Buccinum ancillariaeformis* Grateloup 1834, was described from the Upper Burdigalian at St-Jean-de-Marsacq (Landes, Southern Aquitaine). However, *C. ancillariaeformis* is rare in this locality and Peyrot (1927) indicated that the original specimen of Grateloup is missing. The original figure of *Buccinum ancillariaeformis* Grateloup 1834 (Grateloup 1845–47, pl. 36 fig. 3) shows a specimen with a *Cyllenina*-callus and a poorly developed *Cyllenina*-band (Pl. 1 Fig. 18). The specimen designated here as neotype (MNHN.F.51545, Pl. 1 Figs 15–17; Pl. 2 Fig. 4) originates from the type locality (St-Jean-de-Marsacq) and exhibits the same features.

We note that the specimens identified as *C. ancillariaeformis* by most authors bear a thick *Cyllenina*-callus but they do not originate from the Lower Miocene. Cossmann (1901) and Harzhauser & Kowalke (2004) figured under this name specimens originating respectively from


1
10 mm
2
3
4
5
Cyllene
olivid sutural groove
Cyllene
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6
7
8
Cyllenina-band
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10
11
Cyllenina-
callus
10 mm
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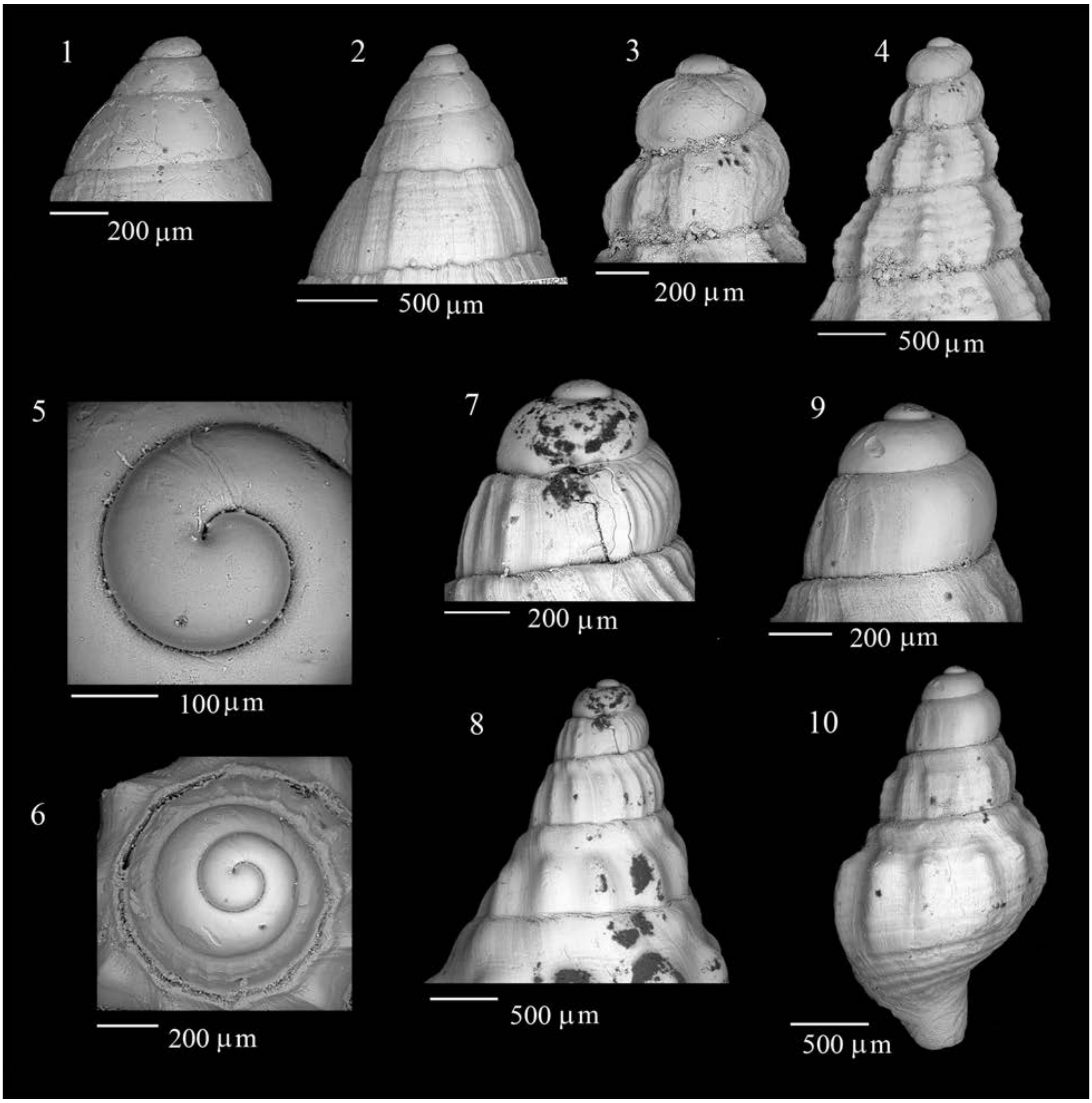

Text-figs 1–10 Protoconchs of *Cyllene*, *Dorsanum* and *Cyllenina*. Figs 1–2: *Cyllene desnoyersi* (Basterot 1825), Lower Miocene, Aquitanian, France, Landes, Meilhan, Carrière Vives, MNHN.F.51541. Figs 3–4: *Dorsanum lineolatum* (Grateloup 1834), Lower Miocene, Burdigalian, France, Landes, St-Paul-lès-Dax, Cabanes, MNHN.F.51548. Figs 5–8: *Cyllenina ancillariaeformis* (Grateloup 1834), Lower Miocene, Burdigalian, France, Gironde, Saucats "Pont-Pourquey", 5–6 (MNHN.F.51554), 7–8 (MNHN.F.51553). Figs 9–10: *Cyllenina baccata* (Basterot 1825), Lower Miocene, Aquitanian, France, Gironde, Saucats, Pont-Pourquey, MNHN.F.51555.

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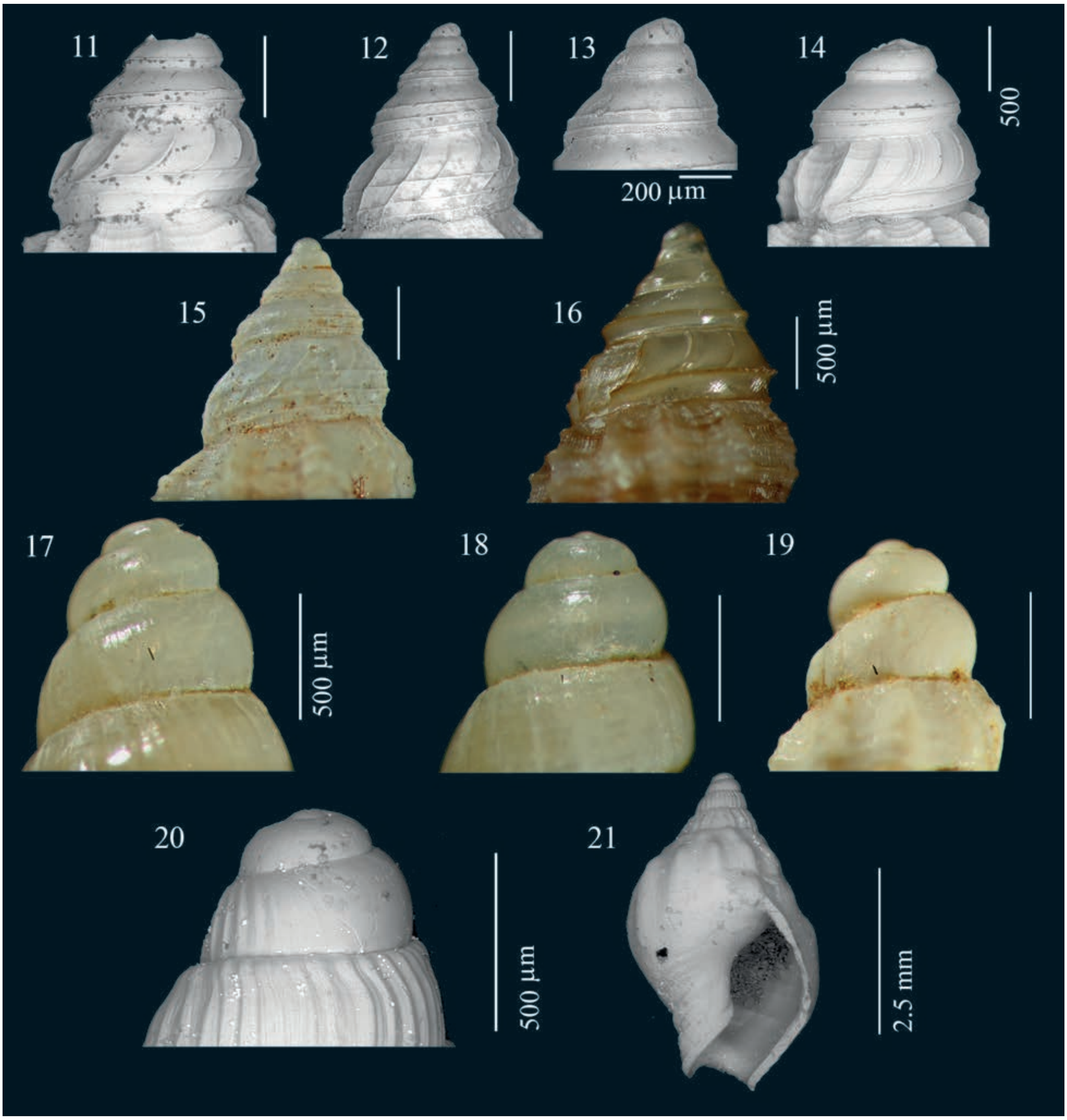
**Plate 1**. Figs 1–5. *Cyllene desnoyersi* (Basterot 1825), Lower Miocene, Aquitanian, France, Landes, Meilhan, Carrière Vives, (1–3: SMF 345995), (4–5: MNHN.F.51540). — Figs 6–18. *Cyllenina ancillariaeformis* (Grateloup 1834). Figs 6–8, 12–14, Lower Miocene, Burdigalian, France, Gironde, Saucats "Pont-Pourquey", (6–8: MNHN.F.51542), (12–14: MNHN.F.51543), Figs 9–11, Lower Miocene, Burdigalian, France, Gironde, Cestas (MNHN.F.51554). — Figs 15–17, *Cyllenina ancillariaeformis* (Grateloup 1834), neotype designated, Lower Miocene, Burdigalian, France, Landes, St-Jean-de-Marsacq (MNHN.F.51545). — Fig. 18 *Buccinum ancillariaeformis* Grateloup 1834, original figure from Grateloup 1845 (pl. 36 fig. 3), St-Jean-de-Marsacq. — Scale bars correspond to 10 mm.



Text-figs 11–21 Protoconchs of Indo-Pacific, Caraibbean, European Miocene *Phos*, *Cyllenina* and *Dorsanum*. Fig. 11 *Europhos* sp.1: New Caledonia (Banc Durand), EXBODI, St. DW3846, 22°04'S 168°38'E, 396 m (MNHN-IM-2009-20630). Figs 12–13, 15 *Europhos subpolygonum* (d'Orbigny 1852): Middle Miocene, Langhian, France, Landes, Saubrigues "Tauziets" (MNHN.F.51552). Figs 14 *Europhos* sp.2: New Britain (Jacquinot Bay), BIOPAPUA, St. DW3770, 05°34'S 151°32'E, 220–294 m (MNHN-IM-2009-13112). Fig. 16 *Antillophos* aff. *chazaliei* (Dautzenberg 1900): Guadeloupe (Vieux-Bourg, Les Abymes), KARUBENTHOS 2012, St. GD37, 16°22.8'N–61°33.44'W, 60 m (MNHN-IM-2013-9286). Figs. 17–18 *Dorsanum miran* (Bruguière 1789): Dakar, Gorée (MNHN-IM-2012-31935). Fig. 19 *Dorsanum lineolatum* (Grateloup 1834): Lower Miocene, Burdigalian, France, Landes, St-Paul-lès-Dax, Cabanes (MNHN.F.51548). Figs 20–21: *Cyllenina ancillariaeformis* (Grateloup 1834), Lower Miocene, Burdigalian, France, Landes, St-Jean-de-Marsacq, Pinot (MNHN.F.A5271)

the Italian Upper Miocene and from the Middle Miocene of the Paratethys. These specimens are referred to *Cyllenina miocenica* (Michelotti 1847) [Pl. 2 Figs. 12–14] originally described from the Upper Miocene of Italy (Michelotti 1847, p. 205 pl. 17 fig. 1).

*Cyllenina* is common in some outcrops (Cestas, Saucats "Pont-Pourquey") in the Burdigalian shallow water deposits of Gironde (North of Aquitaine). The observed specimens did not bear a heavy *Cyllenina*-callus (Pl. 1 Fig. 6–17). In fact the hypertrophy of the callus appears in this group after the Lower Miocene and all specimens identified as *Cyllenina ancillariaeformis* (Grateloup) with very thick callus are from the Middle or the Upper Miocene (Pl. 2 Figs 12–14). In one of the last members of *Cyllenina*, the Pliocene species *Cyllenina lucinensis* (Landau & Marquet 1999) (Pl. 2 Figs 15–17), the callus covers completely the spire giving to the shell an unusual Olividae shape. At first glance, the close relationship between *Cyllenina ancillariaeformis* and *C. lucinensis* is not obvious.

Landau & Marquet (1999) suggested that several elongated Pliocene species included in *Cyllenina*, but bearing a thin *Cyllenina*-callus, could belong to the genus *Dorsanum*. It is the case of *Cyllenina paulucciana* (De Stefani & Pantanelli 1879) and its three varieties. This is also true for *Cyllenina sismondai* Bellardi 1882 (see Chirli 2000, pl. 41 figs. 3–8 and 9–10). However the presence of large *Cyllenina*-band on those species indicates their placement in *Cyllenina* (Pl. 2 Figs 9–11). Harzhauser & Kowalke (2004, pl. 4 figs 8, 11–14) include also in this genus some species from the Miocene of Paratethys with a thin *Cyllenina*-callus (but with a large *Cyllenina*-band): *C. suessi* (Hoernes & Auinger 1882), *C. neumayri* (Hoernes & Auinger 1882), and *C. echinata* (Hörnes 1852).

### *Cyllenina* and *Dorsanum*

In the Aquitaine Basin, the Lower Miocene species *Buccinum baccatum* Basterot 1825 [including the species *D. aquensis* (Grateloup 1845)] was considered by Lozouet et al. (2001) as a *Dorsanum* (Pl. 3 Figs 1–12). However Peyrot (1925–1927) classified *B. baccatum* in the genus *Cyllene (Cyllenina)* and *D. aquensis* in the genus *Dorsanum*. For Peyrot (1925), *D. aquensis* comprises also several varieties “var. *gracilis*”, “mut. *pertinax*”. For Lozouet et al. (2001) these names express only the variability of *D. aquensis*. Apart from the well-developed row of nodes, *B. baccatum* from the Middle Burdigalian of the Gironde (Saucats “Pt-Pourquey”) shows an inconspicuous *Cyllenina*-band (the reason of the placement of *B. baccatum* by Peyrot in *Cyllenina*) unknown on *D. aquensis* or on other *Dorsanum* species. The *Cyllenina*-band is very inconspicuous on the specimens from Saucats “Lagus”, a Burdigalian deposit a little older than Pt-Pourquey (Pl. 3 Figs 13–16). In the Upper Aquitanian of Meilhan (Vives) some specimens of *Dorsanum aquensis* show an erratic *Cyllenina*-band (Pl. 3 Figs 7–9). They also have a lirate outer lip in the same way as some specimens of *D. aquensis* from the Burdigalian of St-Paul-lès-Dax. Finally we agree with Peyrot to consider *D. aquensis* as a distinct species (with several morphotypes) but the generic affiliation of *B. baccatum* is questionable. The characters of *B. baccatum* indicate that this species was related to the common ancestor of *Dorsanum* and *Cyllenina*. However, to be consistent, we consider *B. baccatum* (Pl. 3 Figs 13–19) as an elongate *Cyllenina* with weak *Cyllenina*-band. *D. aquensis* occurs in the Aquitanian stage and in the Lower Burdigalian, *C. baccata* occurs in the Burdigalian.

These examples show that the acquisition of a *Cyllenina*-band appears in the lineage of *Dorsanum aquensis*. In fact, the uncertainty of the generic affiliation of *Buccinum baccatum* Basterot 1825 reflects the close relationship between *Dorsanum* and *Cyllenina*.

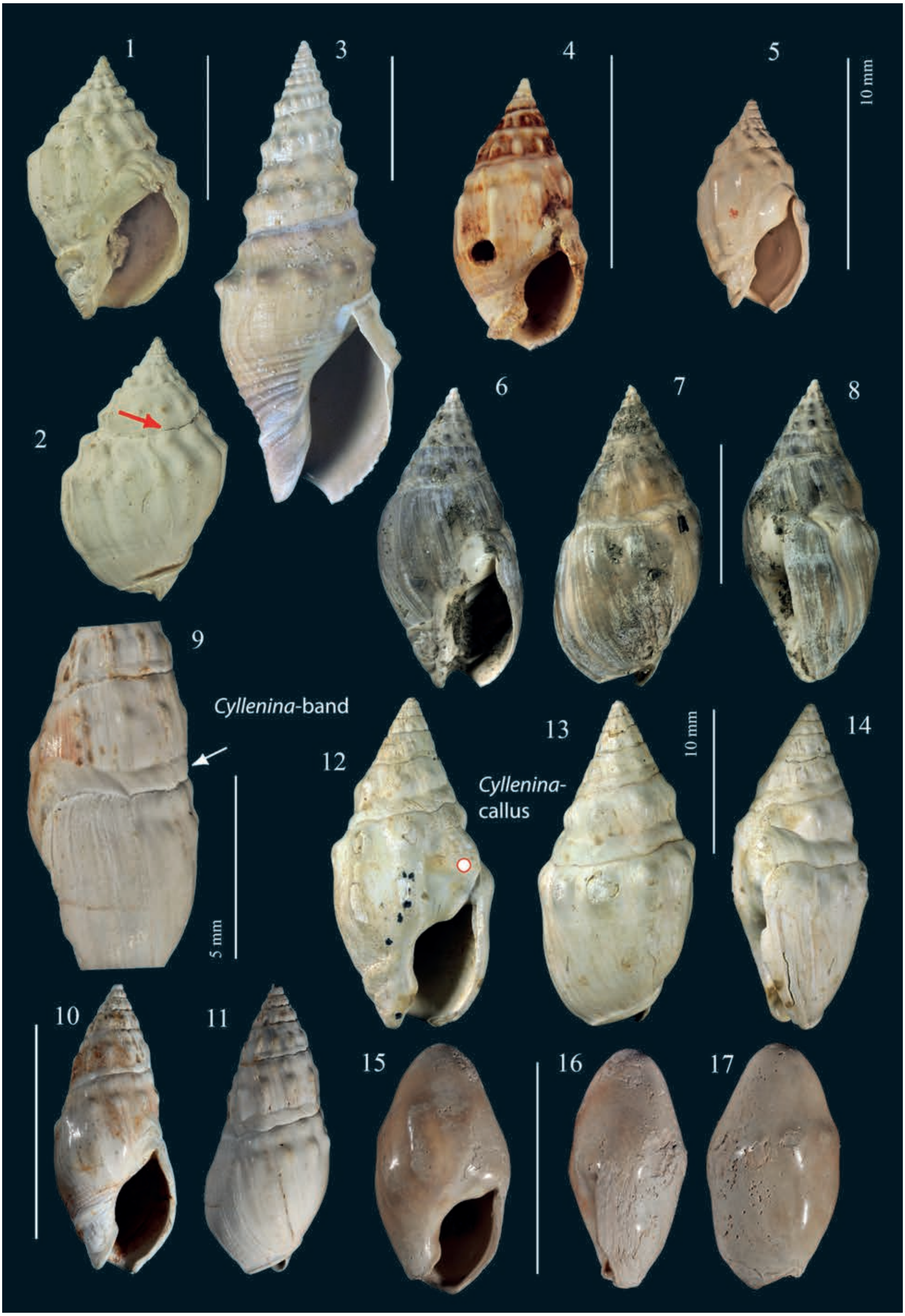
### Duplicatulinae Muskhelishvili 1967

Harzhauser & Kowalke (2004) include in the genus *Duplicata* Zhizhchenko in Kolesnikov 1939 several species apparently close to *Dorsanum aquensis or Cyllenina baccata*. Among them, we note *Buccinum duplicatum* Sowerby, 1832 or *Buccinum haueri* Michelotti 1847 from the Eggenburgian (Lower Miocene). Allmon (1990) included *Buccinum baccatum* and *B. duplicatum* is an informal group “*Cyllenina* 1” placed in the genus *Dorsanum*.

It should be noted that the proposal of the genus name *Duplicata* (in Kolesnikov 1939) is not accompanied by a description, or an assignation of a type species; subsequently, in application of ICZN rules (Art. 13 & Art. 68), the name is not available. However in the same paper Kolesnikov introduced the genus *Duplicatula* (and three other genera for the same group) with a diagnosis and designation of type species (*Buccinum verneuilii* d’Orbigny 1844 close to *Buccinum duplicatum* Sowerby 1832). Thus we adopt, for this discussion on *Buccinum duplicatum* group, the name *Duplicatula*.

Harzhauser & Kowalke (2004) pointed out the close relationship between *Dorsanum* and *Duplicatula* (=*Duplicata*). In fact, the major distinctive character of *Duplicatula*, compared to the West African species *Dorsanum miran* (Bruguière 1789) (type species of *Dorsanum*), is the presence of a pronounced spiral sculpture. *D. miran* displays a glossy shell with strongly reduced axial sculpture on early spire whorls and a smooth body whorl (Pl. 4 Figs 12–13, 18–20). Nevertheless several fossil species of *Dorsanum* show a pronounced axial and spiral sculpture, or have a reduced sculpture (Pl. 4 Figs 4–17). Other features encountered in *Duplicatula*, but considered missing in *Dorsanum*, are the shouldered whorls with a sutural ramp and a row of nodes. In fact, these characters are also encountered in the lineages of *C. baccata* and *D. aquensis* (Pl. 3) although not so pronounced. Otherwise for Harzhauser & Kowalke (2004), *Duplicatula* (=*Duplicata*) differs from *Cyllenina* by the inconspicuous parietal callus and the lack of the *Cyllenina*-band. It is a right observation, although some specimens of *Duplicatula* show a very inconspicuous *Cyllenina*-band as in the example of the lineage of *B. baccatum* (Pl. 2 Figs 1–2) but this seems to be exceptional.

Finally the distinction *Cyllenina baccata/Duplicatula/ Dorsanum* is not so clear-cut and that is the reason which


1
3
4
5
10 mm
2
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7
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9
*Cyllenina*-band
12
13
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*Cyllenina*-
callus
5 mm
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17

led Allmonn (1990) to include *Buccinum baccatum* and *B. duplicatum* in the same genus (*Dorsanum*). Incidentally, and undoubtedly, the subfamily Duplicatulinae Muskhelishvili 1967 is a junior synonym of Dorsaninae as indicated by Bouchet & Rocroi (2005).

### *Cyllenina*, *Dorsanum* and *Duplicatula*

After reviewing these genera it appears that one relevant character, the *Cyllenina*-band, allows to recognise the genus *Cyllenina* as a useful generic subdivision within the european Nassariidae (Dorsaninae). The *Cyllenina*-callus is an interesting character but it can be used only at a specific level.

Otherwise we don't find any unquestionable character to differentiate the group of *Duplicatula* from the other species of *Dorsanum*. Following Harzhauser & Kowalke (2004), *Duplicatula* unifies the Paratethys Dorsaninae with strong axial sculptures, two rows of nodes, and shouldered whorls with a large sutural ramp. However, the two rows of nodes is a character encountered also in the *Dorsanum* of the lineage of *D. aquensis* (see Pl. 3) and in several species of *Cyllenina*.

The lack of *Cyllenina*-band (or only an exceptional fine spiral ridge) separates clearly *Dorsanum* and *Duplicatula* from *Cyllenina* but we have not found a good enough character to separate *Dorsanum* from *Duplicatula*. Also we would like to point out the close relationship between *Duplicatula* and the Early Miocene species *Dorsanum aquensis*. A revision of the *Duplicatula* (=*Duplicata*, = *Omnivaga* = *Corbiana*, = *Dissita*) concept is beyond the scope of this work and it must be accompanied by a general review of European Dorsaninae. So, pending new studies, we retain only the genera *Dorsanum* and *Cyllenina* for the European Oligocene and Miocene species. The *Buccinum duplicatum* group (= *Duplicatula*) can designate this specific diversification of the Paratethyan *Dorsanum*.

### *Phos* and Dorsaninae

Because the Photinae were classified in the Buccinidae or in the Nassariidae some species are tossed between the subfamilies Photinae, Nassariinae, or Dorsaninae. It is the case for *Nassa lineolata* Grateloup 1834 (Pl. 4 Figs 4–11). Peyrot (1925) and Harzhauser & Kowalke (2004) consider it as a Nassariinae (*Nassa* Lamarck 1799 non Röding 1798 or *Nassarius*) and Lozouet et al. (2001) attributed it to *Dorsanum* (Dorsaninae). More recently, Harzhauser & Cernohorsky (2011) included *N. lineolata* in the Photinae (*Phos*).

*D. lineolatum* is an elongated species encountered in the Early Miocene (Aquitanian and Burdigalian) of the Aquitaine Basin (Lozouet et al. 2001) known also in the Late Oligocene of the same area. Grateloup (1834) described *Nassa lineolata* from the Burdigalian or the Aquitanian of St-Paul-lès-Dax where it is very common (Pl. 4 Fig. 6). *D. lineolatum* and the West-African *D. miran* have a close shape and both exhibit the same type of protoconch (Text-figs 17–19) and the same basal fasciole. Otherwise, the last whorl of *D. miran* is smooth, whereas the one of *D. lineolatum* is sculptured. Considering the range variation of the sculpture of the *Dorsanum* (see the "smooth" *D. estotensis* [Pl. 4 Figs 16–17] and *D. plicatum* [Pl. 4 Figs 14–15] from the Lower Miocene or *D. baccatum*) the difference between *D. miran* and *D. lineolatum* is at the specific level. In fact Harzhauser & Cernohorsky (2011) do not discuss any precise shell character to argue the placement of *Nassa lineolata* into the genus *Phos*. They only state that it is "based on comparison with extant Indo-Pacific representatives of *Phos*, such as *Phos naucratoros* Watson 1882, we consider Grateloup's shell a slender *Phos*". No comments are offered on the major features observed in *D. lineolatum*: the pronounced fasciole, characteristic of *Dorsanum* (for Allmon 1990, the most distinct conchological character of *D. miran* is a relatively deep, reflexed dorsal siphonal channel bordered by two distinct oblique spiral ridges), the relatively sharp columellar end and the whorls not shouldered compared to *Phos*. Besides, the protoconch morphology encountered in most species of Photinae is also completely distinct. This can be illustrated by *Buccinum subpolygonum* d'Orbigny 1852 from the Burdigalian. This species has a multispiral protoconch with two cords (Text-figs 12–13, 15), classic of the Indo-Pacific *Photinae* included by Fraussen & Poppe (2005) in the genus *Antillophos* Woodring 1928 (Figs. 11, 14), while all the Dorsaninae have a globular protoconch (Text-figs 17–19).

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**Plate 2**. *Dorsanum duplicatum* and overview of *Cyllenina.* Figs 1–2. *Dorsanum duplicatum* (d'Orbigny 1832), Middle Miocene, Sarmatian (coll. Staadt), labelled "Sarmatian of Russian, Alexandrousk" (MNHN.F.51562). Red arrow showing an inconspicuous *Cyllenina*-band. — Fig. 3. *Cyllenina baccata* (Basterot 1825), Lower Miocene, Burdigalian, France, Gironde, Saucats, Pont-Pourquey (MNHN.F.51560). — Figs 4–5. *Cyllenina ancillariaeformis* (Grateloup 1834) from the Lower Miocene, Burdigalian, France; Fig. 4, designated Neotype, Landes, St-Jean-de-Marsacq (MNHN.F.51545); Fig. 5, Gironde, Cestas (MNHN.F.51544). — Figs 6–8, *Cyllenina helvetica* (Peyrot 1927), Middle Miocene, Serravallian, France, Landes, Orthez (MNHN.F.51563). — Figs 9–11, *Cyllenina paulucciana* (De Stefani & Pantanelli 1879), Pliocene, Italy, Marcialla (leg M. Taviani), (MNHN.F.51565). — Figs 12–14, *Cyllenina miocenica* (Michelotti 1847), Upper Miocene, Northern Italy (coll. Staadt), Montegibbio, (MNHN.F.51564). — Figs 15–17, *Cyllenina lucinensis* (Landau & Marquet 1999), Pliocene (leg B. Landau), Huelva Formation, Spain, Lucena del Puerto "Santa Catalina", (MNHN.F.51549). — Scale bars correspond to 10 mm.

Landau et al. (2013) reviewed the systematics of the European species attributed to *Phos*. In their paper, they do not mention the species "*Phos lineolatus*" but include all the European *Phos* in a new genus called *Europhos*. Landau et al. (2013) consider *Europhos* restricted to European deposits. *Europhos* is characterized by its protoconch bearing 2–3 spiral cords from the second protoconch whorl and axial riblets on at least a part of the last protoconch whorl. As indicated above, most of the Indo-Pacific classified in the genus *Antillophos* has the same protoconch (Fraussen & Poppe 2005). This is confirmed by Indo-Pacific Photinae examinated:

*"Antillophos"* sp. 1, New Caledonia, Banc Durand [EXBODI, DW3846, 22°04'S 168°38'E, 396 m], MNHN-IM-2009-20630, (Text-fig. 11);

*"Antillophos"* sp. 2, New Britain, Jacquinot Bay, [BIOPAPUA, DW3770, 05°34'S 151°32'E, 220–294 m], MNHN-IM-2009-13112, (Text-fig. 14);

*Antillophos brigitteae* Stahlschmidt & Fraussen 2009, Philippines, 50–150 m, MNHN-IM-2000-22063, paratype;

*Antillophos usquamaris* Fraussen 2005 Saya de Malha Bank, Western Indian Ocean, 60 m, MNHN-IM-2009-9332, Holotype;

*Antillophos boucheti* Fraussen 2003, Coral Sea, New Caledonia, [Campagne CHALCAL 1: stn DC64, 22°11'S 159°15'E, 305 m, Iles Chesterfield], MNHN-IM-2000-6581, Holotype.

Anyhow, the type species of *Antillophos* originates from the Caribbean and up to now we lack detailed information on the anatomy and molecular characters to confirm the close relationship with the Indo-Pacific Photinae reported to *Antillophos* (Zhang & Zhang 2014). From what we observe, the Caribbean *Antillophos* are characterized by a unique keeled multispiral protoconch (Text-fig. 16). If we admit that *Antillophos* with a unique keeled protoconch is restricted to tropical american provinces (Caribbean and Panamanian), the Photinae with protoconch sculptured by two spiral cords (*Europhos*) are largely widespread in the Indo-Pacific [*Antillophos* sensu Fraussen & Poppe 2005], in the European Cenozoic (Miocene to Pliocene (*Europhos* of Landau et al 2013) and also in West-Africa (*Phos grateloupianus* Petit de la Saussaye 1853; syntype examined from Senegal coasts, MNHN-IM-2000-6571). So the use of *Europhos* depends on the molecular clarification but also on the examination of others genera or subgenera included in the Photinae. For the time being we adopt the genus *Europhos* for European and Indo-Pacific species and we restrict the use of *Antillophos* to the American species (according also to Landau et al in review process). *Phos* (s.s.) characterized by a smooth multispiral protoconch, shares this character with the American genus *Tritiaria* (Paleogene of North America) considered as a the most "ancestral" *Phos* by MacNeil & Dockery (1984).

## Biodiversity of the Nassariidae

The geographical area taken into account includes the Paris Basin, the Aquitaine Basin and the Loire, Brittany, and Cotentin (Normandy) in France. The Lower Oligocene fauna is well represented by shallow water deposits in the Paris Basin, Brittany and the Aquitaine Basin. The Upper Oligocene deposits are restricted in the Southern part of the Aquitaine Basin (Adour sub-basin) comprising shallow and deeper water deposits (circalittoral to upper Bathyal). The Lower Miocene deposits are encountered in the Aquitaine Basin. These are sandy shallow-water deposits and circalittoral marly facies. Shallow-water deposits are well represented in the Middle Miocene of the Loire Basin ("Faluns de Touraine") and in the Aquitaine Basin but the deeper circalittoral marly facies are restricted to the Southern Aquitaine. The Upper Miocene deposits are poorly documented with only the Messinian deposits in the Loire Basin (corresponding to the local Lower Redonian stage; according to Brébion 1964, it includes the localities of the Maine-et-Loire: Sceaux-d'Anjou, Brigné, Reneauleau, Thorigné). The number of species cited is thus largely underestimated. The Pliocene and Quaternary deposits are not investigated because the data available is very limited. According to Brébion (1964) and Landau et al (2009) at least 10 species occur in the Pliocene of Normandy.

The taxonomic dataset used is the species-level data derived from material collected by the first author or his collaborators. The main data originates from the Oligocene and Miocene deposits. A large set of species are labelled as "sp". From a taxonomic point of view these can be considered as "morphospecies" or "Operational Taxonomic Units" (OTUs). These informal units are here taken to represent specific-level taxa, equivalent to formal "species" (Lozouet 2014). The major literature sources used are:

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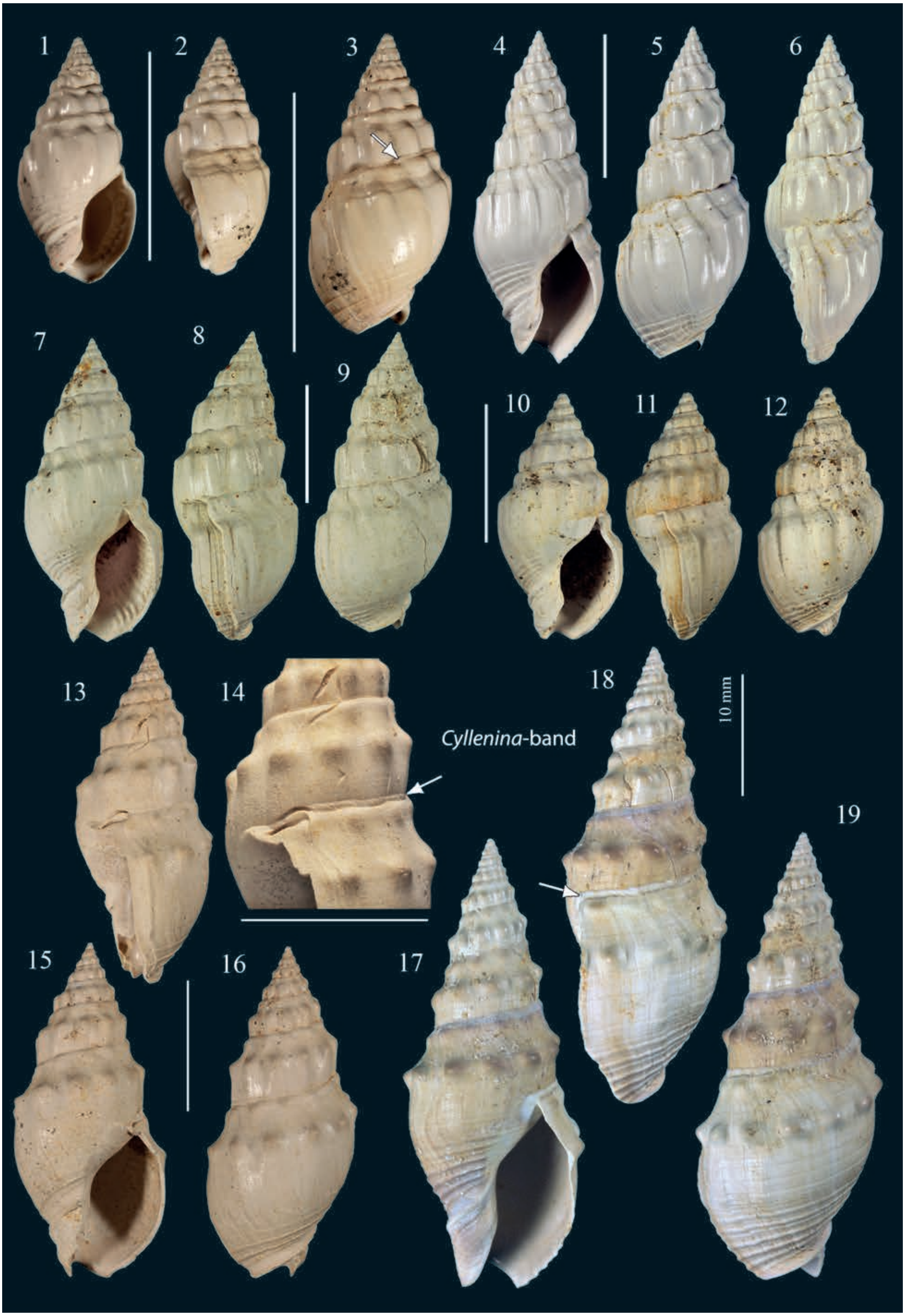
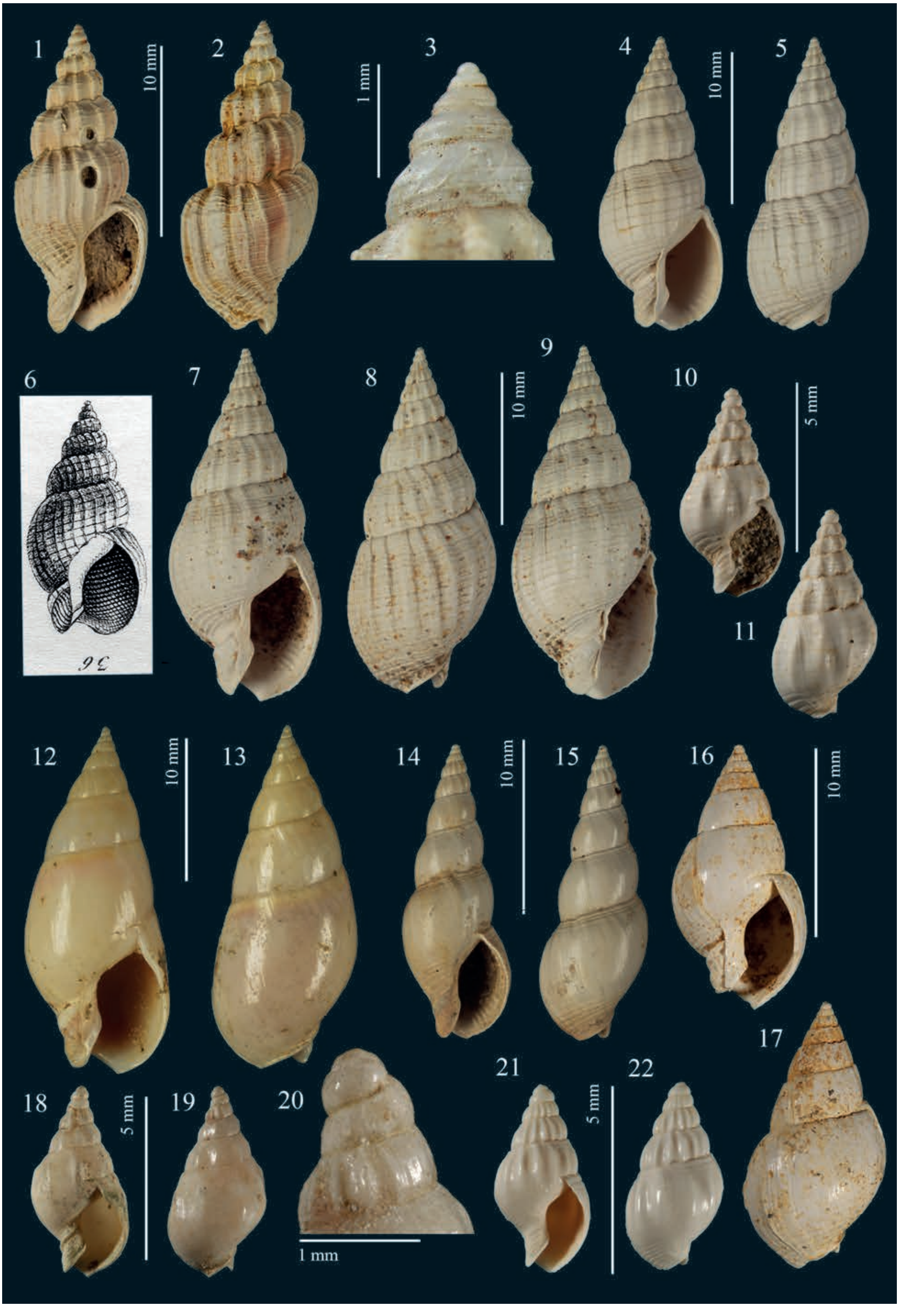
**Plate 3**. Figs 1–12. *Dorsanum aquensis* (Grateloup 1845). Figs 1–3, Lower Miocene, Aquitanian, France, Landes, Meilhan, Carrière Vives, young specimen, (MNHN.F.51556); the arrow in Fig. 3 showing an inconspicuous *Cyllenina*-band; Figs 4–6, Lower Miocene, Aquitanian, France, Gironde, Saucats, Lariey (MNHN.F.51557); Figs 7–12, Lower Miocene, Burdigalian, France, Landes, St-Paul-lès-Dax, Cabanes, 7–9 (MNHN.F.51558), 10–12 (MNHN.F.51559). — Figs 13–19. *Cyllenina baccata* (Basterot 1825). Figs 13–16, Lower Miocene, Aquitanian, France, Gironde, Saucats, Lagus (MNHN.F.51561); Figs 17–19, Lower Miocene, Aquitanian, France, Gironde, Saucats, Pont-Pourquey (MNHN.F.51560). — Scale bars correspond to 10 mm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
Cyllenina-band
18
10 mm
19
15
16
17


1
10 mm
2
3
1 mm
4
10 mm
5
6
36
7
8
10 mm
9
10
5 mm
11
12
10 mm
13
14
10 mm
15
16
10 mm
17
18
5 mm
19
20
1 mm
21
5 mm
22

- Oligocene and the Lower Miocene [Peyrot 1925–1927]
- Middle Miocene [Peyrot 1925–1927, 1938; Glibert 1952]
- Upper Miocene [Brébion 1964] for the Upper Miocene.

The Nassariidae are poorly represented in the Paleocene and Eocene deposits of Europe and the data is based principally on literature (Cossmann 1889; Cossmann & Pissaro 1907–1913). They include also the species revised by Nuttall & Cooper (1973) from the British deposits where the Upper Eocene is well represented.

Five major clades are considered here: *Cyllene* (Cylleninae), *Dorsanum/Cyllenina* (Dorsaninae), Nassariinae, *Phos* (Photinae) and the fossil *Keepingia* group. This last one deserves an explanation.

## The *Keepingia* group

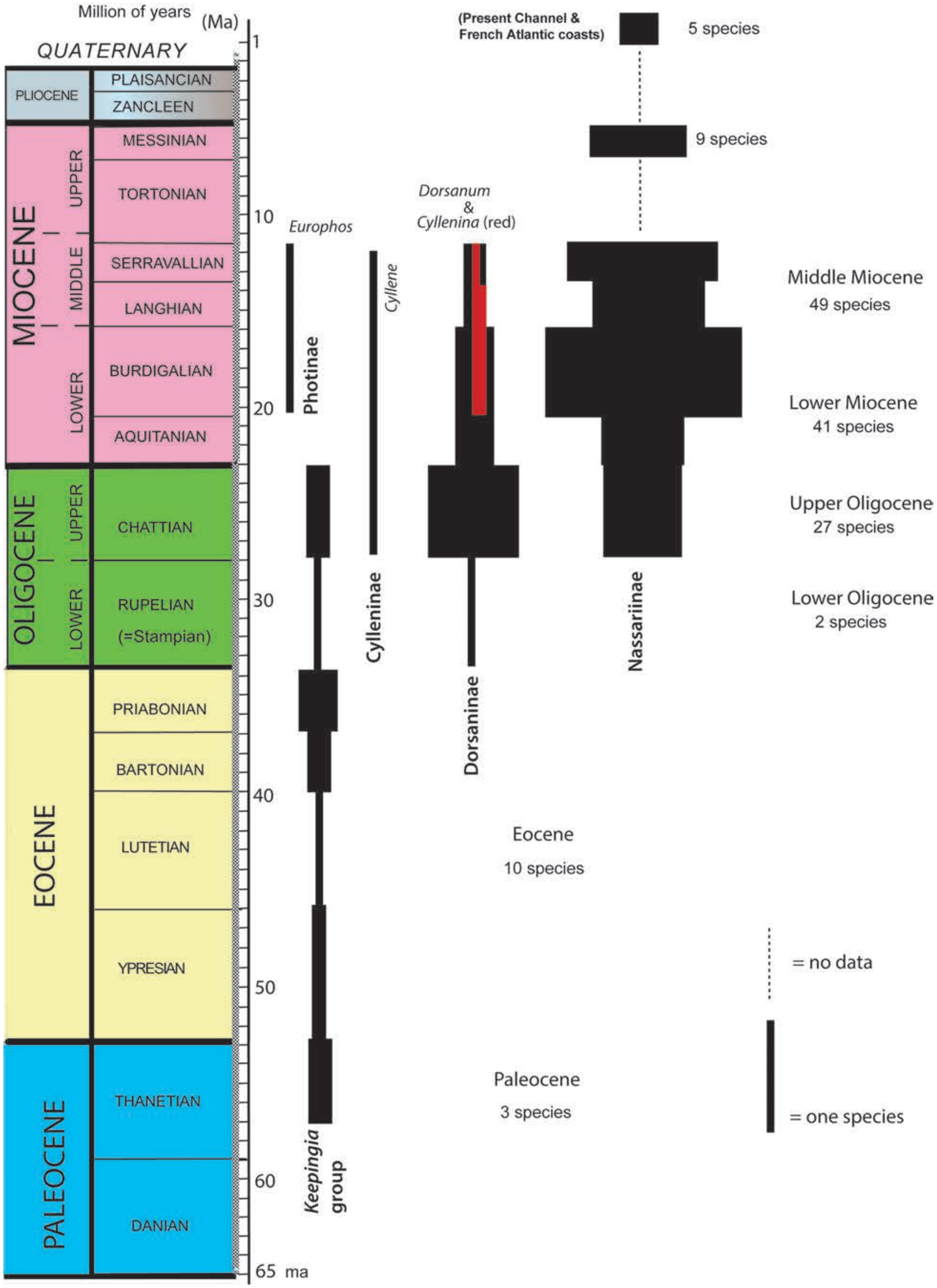
Nuttall & Cooper (1973) established the genera *Keepingia, Pseudocominella, Whitecliffia, Thanetinassa, Desorinassa, Colwellia* for European fossil species (from the Paleocene to the Upper Oligocene) formerly classified in the Buccinidae but recognised as Nassariidae. For Cernohorsky (1984) the conchological features of the type species of *Pseudocominella, Whitecliffia, Keepingia* and *Thanetinassa* genera would indicate a placement in the family Buccinidae rather than in the Nassariidae. But in the same paper *Colwellia* is also considered closely related to the Photinae Buccinidae genus *Cominella* Gray 1850. Cernohorsky (1984) indicated also that the Cylleninae could have evolved from *Colwellia,* and *Desorinassa* is classified in the Dorsaninae. Allmon (1990) stated that four of these genera appear to be closely related to the "*Bullia*-group" (Nassariidae) that includes *Bullia*, *Buccinanops* and *Dorsanum* as defined by Brown 1982. Haasl (2000) included the *Keepingia* group in an informal clade "Buccinoids". However, Nuttall and Cooper's taxa were placed by Haasl (2000) "as part of the photine/dorsanine/nassariine polytomy". Obviously, the systematic position of what we call here the *Keepingia* group is nebulous. Nevertheless, various opinions (Nuttall & Cooper 1973, Haasl 2000, Allmon 1990; Galindo 2014) contribute to demonstrate that the *Keepingia* group is indeed a member of the Nassariidae though its subfamily position is yet unresolved.

The genus *Keepingia* is represented in the European Oligocene deposits by at least seven species. Within the genus *Keepingia* the variability is important. Some species show pronounced spiral and axial external sculpture, whereas others are partially smooth. The outer lip is lirate or smooth. Nuttall & Cooper (1973) indicate that *Keepingia* is very similar to *Colwellia*, differing mainly in the form of the protoconch, which is large, paucispiral, but slightly heterostrophic. This assertion is founded on the examination of some imperfectly preserved specimens and not on a critical analysis of the protoconch of the different species of *Colwellia* and *Keepingia*. Consequently we regard *Colwellia* and *Keepingia* as synonymous. In the same way, Nuttall & Cooper (1973, p. 209) state that *Colwellia* can be distinguished from *Desorinassa* Nuttall and Cooper 1973 by the form of the subsutural ramp: "In *Desorinassa* the ramp is convex and the collabral sculpture is much stronger on the earlier whorls…but some species may form a link between the two genera". We conclude on these grounds that the six new nassariid genera introduced by Nuttall & Cooper (1973) form a homogeneous group. Further studies are needed to clarify the relationships within this group but if we consider the variability of the Nassariidae (e.g. *Nassarius* as defined by Galindo 2014), we suggest to retain, for the time being, the genera *Keepingia, Pseudocominella, Thanetinassa* and *Whitecliffia.*

## Stratigraphical distribution

The total number of taxa found in the Paleocene to the Miocene of the Atlantic coasts amounts to 128 species (Fig. 22; Tab. 1), some of them overlapping over the different stages: the Paleocene contains 3 species, the Eocene 10 species, the Lower Oligocene 2 species, the Upper Oligocene 27 species (29 species for the all Oligocene) and the Miocene 88 species (Lower Miocene: 41 species; Middle Miocene: 49; Upper Miocene: 9 species). During the Paleocene and the Eocene the Nassariidae (*Keepingia* group) range about 3–5 species in each stage and only 2 species are recorded in the Lower Oligocene (1 species of *Keepingia* group, 1 species of Dorsaninae). The main feature of the stratigraphical distribution of Nassariidae is the extinction of the *Keepingia* group (Text-fig. 22) at the end of the Paleogene (Lozouet 2014). With the exception of one species of Dorsaninae described in the Lower Oligocene of Aquitaine, it is the only representative of this family during this

**Plate 4**. Figs 1–3. *Europhos subpolygonum* (d'Orbigny 1852), Middle Miocene, Langhian, Landes, Saubrigues (Tauziets), MNHN.F.51551. — Figs 4–11, *Dorsanum lineolatum* (Grateloup 1834), Lower Miocene, Burdigalian, France, Landes, St-Paul-lès-Dax, Cabanes; Figs 4–5 (MNHN.F.51546), Figs 7–9 (MNHN.F.51547), Figs 10–11 (MNHN.F.5154) young specimen; Fig. 6 original figure from Grateloup 1845 (pl. 36 fig. 36), St-Paul-lès-Dax. — Figs 12–13, 18–20. *Dorsanum miran* (Bruguière 1789), Dakar, Gorée, Figs 12–13 (MNHN-IM-2013-31932), Figs 18–20 (MNHN-IM-2013-31933), young specimen, 20 protoconch and first adult whorl. — Figs 14–15, 21–22. *Dorsanum plicatum* (Grateloup 1845), Lower Miocene, Aquitanian, France, Landes, Meilhan, Carrière Vives, Figs 14–15 (SMF 345996), Figs 21–22, young specimen (MNHN.F.51550). — Figs 16–17. *Dorsanum estotensis* (Lozouet 1999), Upper Oligocene, France, Landes, St-Paul-lès-Dax, Estoti (SMF 345997).


Million of years
(Ma)
QUATERNARY
PLIOCENE
PLAISANCIAN
ZANCLEEN
MIOCENE
UPPER
MIDDLE
LOWER
MESSINIAN
TORTONIAN
SERRAVALLIAN
LANGHIAN
BURDIGALIAN
AQUITANIAN
OLIGOCENE
UPPER
LOWER
CHATTIAN
RUPELIAN
(=Stampian)
EOCENE
PRIABONIAN
BARTONIAN
LUTETIAN
YPRESIAN
PALEOCENE
THANETIAN
DANIAN
1
10
20
30
40
50
60
65 ma
*Europhos*
Photinae
*Keepingia* group
*Cyllene*
Cylleninae
*Dorsanum* & *Cyllenina* (red)
Dorsaninae
(Present Channel & French Atlantic coasts)
5 species
9 species
Nassariinae
Middle Miocene
49 species
Lower Miocene
41 species
Upper Oligocene
27 species
Lower Oligocene
2 species
Eocene
10 species
Paleocene
3 species
= no data
= one species

period. Nuttall & Cooper (1973) attribute to *Keepingia* a stratigraphical distribution ranging from Lower Oligocene to Lower Miocene (Burdigalian). The three species cited by these authors from the Early Miocene originate in fact from the Late Oligocene. Additionally one of them (*Cominella*? *aturensis* Peyrot 1927) is a *Dorsanum* close to *Dorsanum ruidum* Peyrot 1927 or *Dorsanum dubium* Peyrot 1927 (Peyrot 1925–1927, n°955, n°956).

A significant change occurs during the Late Oligocene with the considerable expansion of the Dorsaninae, Nassariinae and the first occurrence of the Cylleninae. The Nassariinae continue to expand in the Early Miocene and in the Middle Miocene. In contrast the Dorsaninae decline in the Middle Miocene and disappear with the Cylleninae from the French Atlantic Coasts in the Late Miocene. Since Cylleninae and Dorsaninae are regarded as thermophilic taxa, this evolution is probably related to the severe cooling during the Middle Miocene time (Serravallian). The modern distribution of these two subfamilies comprises only tropical or subtropical waters. At the Late Miocene, the Nassariinae is the only representative of the family Nassariidae as it is observed in the present day in the Lusitanian province. The stratigraphical distribution of the Nassariidae from the Paratethys shows some significant differences related with the evolution of this basin. In particular the Dorsaninae diversified in the basins of the Eastern Paratethys during the end of the Middle Miocene where ecological factors (brackish water environment) lead to the decline of the Nassariinae. Otherwise, considering that the knowledge on Early Miocene mollusc faunas in the Paratethys is hampered by a taphonomic bias (Harzhauser & Kowalke 2004), we note the same development of the Nassariinae in the Middle Miocene.

## Discussion

*Cyllenina* is a European fossil thermophilic genus (absent in the Boreal region or Nordic province see Lozouet 2014 for terminology) closely related to *Dorsanum* and probably originated from the Lower Miocene *Dorsanum aquensis* group. The major feature of this genus is the presence of a glossy band above the suture, the *Cyllenina*-band and, in some species, the development and occasionally the hypertrophy of the callus on the parietal part (*Cyllenina*-callus). The *Cyllenina*-band was mistaken with the sutural olivid-groove of *Cyllene,* which explains the placement of *Cyllenina* so far in the Cylleninae. The *Buccinum duplicatum* group (=*Duplicatula* =*Duplicata*) is closely related to *Dorsanum aquensis* and *Cyllenina baccata* but especially developed in the Paratethys (Harzhauser & Kowalke 2004). *Buccinum duplicatum* group and *Cyllenina* are encountered in the shallow-water sandy bottom.

Finally with the reappraisal of the systematic position of *Cyllenina,* the Dorsaninae exhibit a great variability and appear flourishing from the Upper Oligocene to Upper Miocene of Southern Europe (including Paratethys). The Paleogene *Keepingia* group is excluded from this subfamily, yet the subfamily position of this group remains unresolved. Compared to the abundance of Dorsaninae in the European Miocene deposits, the present-day distribution of this subfamily with one species on the West-African coasts appears to be clearly relictual. *Dorsanum miran* is the only survivor (Simone & Pastorino 2014; Allmon 1990) and thus the last representative of the subfamily Dorsaninae. Otherwise, the placement of the Lower Miocene species *Buccinum lineolatum* in the *Dorsanum* (Dorsaninae) is confirmed and its recent placement in *Phos* (Photinae) rejected.

In Europe, the rapid diversification of Nassariidae appears at the end of the Paleogene (Late Oligocene) before the extinction of the *Keepingia*-group, the only member of this family present during the Paleocene and the Eocene. The Nassariinae are especially numerous in the Middle Miocene, the same pattern was observed by Harzhauser & Kowalke (2004) in the Paratethys. The diversity of the Dorsaninae is the greatest during the Late Oligocene and Early Miocene on the Atlantic Coasts. In the Central Paratethys the golden age for the Dorsaninae seems to be at the Middle Miocene (*Cyllenina* Badenian; *Dorsanum*, Sarmatian). In Europe the Nassariinae continue their diversification after the Miocene as shown by the 57 species described in the Iberian Pliocene deposits (Landau et al. 2009) but the subfamilies Cylleninae and Dorsaninae did not survive the Pleistocene glaciations. Finally, we note that these patterns on the stratigraphical distribution of the European Nassariidae are globally in accordance with the diversification in time (molecular clock) estimated from molecular data (Galindo 2014).

## Acknowledgements

Thank to Anouchka Sato (MNHN) for reading the manuscript and useful improvements and Victorio Garili for information on Mediterranean species. Thank also to Bernard Landau and Marco Taviani for the gifts of some specimens. Sylvain Pont (MNHN) prepared the SEM pictures. The referees, B. Landau and an anonymous, gave us several precious remarks.

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Text-fig. 22: Stratigraphical distribution of Nassariidae (Nassariinae, Cylleninae, Dorsaninae, Photinae and *Keepingia* group) on the French Atlantic seaboard. The extinction of the *Keepingia* group in parallel to the diversification of the Nassariidae at the Upper Oligocene is the main feature. Lower Miocene and Middle Miocene expansion of the Nassariinae is the second key event. Time scale is from Odin (1994), with Quaternary and Langhian/Serravallian boundaries modified. From Lozouet (2014).

Table 1. Taxonomic dataset used for Figure 20 mainly derived from material collected by the author and collaborators. Genera and species are listed in alphabetical order within subfamily. Paleocene and Eocene species of *Keepingia* group are mainly from Nuttall & Cooper (1973).

| | THANETIAN | YPRESIAN | LUTETIAN | BARTONIAN | PRIABONIAN | RUPELIAN (Paris Basin) | RUPELIAN (Aquitaine Basin) | CHATTIAN | AQUITANIAN | BURDIGALIAN | UPPER BURDIGALIAN | LANGHIAN (Aquitaine Basin) | LANGHIAN (Loire Basin) | SERRAVALLIAN | MESSINIAN (Redonian) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cylleninae** | | | | | | | | | | | | | | | |
| *Cyllene desnoyersi* (Basterot 1825) | | | | | | | | X | X | X | X | X | X | | |
| **Dorsaninae** | | | | | | | | | | | | | | | |
| *Cyllenina ancillariaeformis* (Grateloup 1834) | | | | | | | | | | X | X | | | | |
| *Cyllenina helvetica* (Peyrot 1927) | | | | | | | | | | | | X | | X | |
| *Cyllenina* sp. | | | | | | | | | | | | X | | X | |
| *Cyllenina baccata* (Basterot 1825) | | | | | | | | | | X | X | | | | |
| *Demoulia conglobata* (Brocchi 1814) | | | | | | | | | | | | | | X | |
| *Demoulia nana* (Tournouër 1874) | | | | | | | | | | | | | X | | |
| *Dorsanum aequistriatum* Dollfus 1889 | | | | | | | | | | | | | | X | |
| *Dorsanum aturensis* (Peyrot 1927) | | | | | | | | X | | | | | | | |
| *Dorsanum aquensis* (Grateloup 1845) | | | | | | | | | X | X | | | | | |
| *Dorsanum dubiosum* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Dorsanum dubium* Peyrot 1927 | | | | | | | | X | | | | | | | |
| *Dorsanum estotiensis* Lozouet 1999 | | | | | | | | X | | | | | | | |
| *Dorsanum evanescens* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Dorsanum gaasensis* Lozouet 1999 | | | | | | | X | | | | | | | | |
| *Dorsanum lineolatum* (Grateloup 1834) | | | | | | | | X | X | X | | | | | |
| *Dorsanum plicatum* (Grateloup 1845) | | | | | | | | | X | X | X | X | X | | |
| *Dorsanum raulini* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Dorsanum ruidum* Peyrot 1927 | | | | | | | | X | | | | | | | |
| *Dorsanum singularium* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Dorsanum veneris* (Faujas de Saint fond 1817) | | | | | | | | | | X | X | | | | |
| *Dorsanum* sp. 1 | | | | | | | | X | | | | | | | |
| *Dorsanum* sp. 2 | | | | | | | | | X | | | | | | |
| *Dorsanum* sp. 3 | | | | | | | | X | | | | | | | |
| *Dorsanum* sp. 4 | | | | | | | | X | | | | | | | |
| *Dorsanum* sp. 5 | | | | | | | | X | | | | | | | |
| **Keepingia** group | | | | | | | | | | | | | | | |
| *Colwellia auversiensis* (Deshayes 1865) | | | | X | | | | | | | | | | | |
| *Colwellia flexuosa* (Edwards 1866) | | | | | X | | | | | | | | | | |
| *Desorinassa acies* (Watelet 1853) | X | X | | | | | | | | | | | | | |
| *Desorinassa desori* (Deshayes 1865) | X | | | | | | | | | | | | | | |
| *Desorinassa ovata* (Deshayes 1835) | | X | | | | | | | | | | | | | |
| *Keepingia gossardii* (Nyst 1836) | | | | | | X | X | | | | | | | | |
| *Keepingia laevis* Lozouet 1999 | | | | | | | | X | | | | | | | |
| *Keepingia* sp. | | | | | | | | X | | | | | | | |
| *Keepingia tarbellica* (Grateloup 1834) | | | | | | | | X | | | | | | | |
| *Pseudocominella armata* (J. de C. Sowerby 1850) | | | X | X | | | | | | | | | | | |
| *Pseudocominella deserta* (Solander 1766) | | | | | X | | | | | | | | | | |
| *Pseudocominella semicostata* Nutall & Cooper 1973 | | | | | X | | | | | | | | | | |
| *Pseudocominella solanderi* (Cossmann 1889) | | | | X | | | | | | | | | | | |
| *Thanetinassa bicorona* (Melleville 1843) | X | | | | | | | | | | | | | | |

| | THANETIAN | YPRESIAN | LUTETIAN | BARTONIAN | PRIABONIAN | RUPELIAN (Paris Basin) | RUPELIAN (Aquitaine Basin) | CHATTIAN | AQUITANIAN | BURDIGALIAN | UPPER BURDIGALIAN | LANGHIAN (Aquitaine Basin) | LANGHIAN (Loire Basin) | SERRAVALLIAN | MESSINIAN (Redonian) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Whitecliffia suturosa* (Nyst 1836) | | | | | X | | | | | | | | | | |
| *Whitecliffia tumida* Nuttal & Cooper 1973 | | | | | X | | | | | | | | | | |
| **Nassariinae** | | | | | | | | | | | | | | | |
| *Nassarius andonae* (Bellardi 1882) | | | | | | | | | | | | | X | | |
| *Nassarius aquitanicus* (Mayer 1858) | | | | | | | | X | X | X | | | | | |
| *Nassarius aturensis* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Nassarius basteroti* (Michelotti 1847) | | | | | | | | | | X | X | | X | | |
| *Nassarius beyrichi* (Mayer 1873) | | | | | | | | | | | X | | | | |
| *Nassarius blesensis* (Mayer 1862) | | | | | | | | | | | | | X | | X |
| *Nassarius bouillei* (Degrange-Touzin 1894) | | | | | | | | | | | | | | X | |
| *Nassarius brugnonis* (Bellardi 1882) | | | | | | | | | | | | X | | | |
| *Nassarius caroli* (Dollfus & Dautzenberg 1886) | | | | | | | | | | | | | X | | |
| *Nassarius cf. bouillei* (Degrange-Touzin 1894) | | | | | | | | | | | | X | | | |
| *Nassarius cf. caroli* (Dollfus & Dautzenberg 1886) | | | | | | | | | | | | | | | X |
| *Nassarius cf. cestasensis* (Peyrot 1925) | | | | | | | | | X | | | | | | |
| *Nassarius cf. clathratus* (Born 1778) | | | | | | | | | | | | | | X | |
| *Nassarius cf. crossei* (Mayer 1862) | | | | | | | | | | X | | | | | |
| *Nassarius cf. dujardini* (Deshayes 1844) | | | | | | | | | | | | | | X | |
| *Nassarius cf. lachrymus* (Bellardi 1882) | | | | | | | | | | | | | | X | |
| *Nassarius cf. lambertiei* (Peyrot 1925) | | | | | | | | | | | | | | | X |
| *Nassarius cf. oblitus* (Bellardi 1882) | | | | | | | | | | | | X | | | |
| *Nassarius cf. pseudoangulatus* (Peyrot 1921) | | | | | | | | | | | | X | | | |
| *Nassarius cf. reticulatus* (Linné 1758) | | | | | | | | | | | | | | X | |
| *Nassarius cf. salbriacensis* (Peyrot 1925) | | | | | | | | | | | X | | | | |
| *Nassarius cf. saucatsensis* (Peyrot 1925) | | | | | | | | | X | | | | | | |
| *Nassarius cf. spectabilis* (Nyst 1843) | | | | | | | | | | | | X | | | |
| *Nassarius cf. subecostatus* (Bellardi 1887) | | | | | | | | | | | | X | | X | |
| *Nassarius cf. verrucosus* (Brocchi 1814) | | | | | | | | | | | | | | | X |
| *Nassarius contortus* (Dujardin 1837) | | | | | | | | | | | | X | X | | X |
| *Nassarius crossei* (Mayer 1862) | | | | | | | | | | | | | X | | |
| *Nassarius degrangei* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Nassarius dujardini* (Deshayes 1844) | | | | | | | | | | | | X | X | X | |
| *Nassarius duvergieri* (Peyrot 1925) | | | | | | | | | | X | | | | | |
| *Nassarius emilianus* (Mayer 1872) | | | | | | | | | | | | | | | X |
| *Nassarius girondicus* (Peyrot 1925) | | | | | | | | | X | X | | | | | |
| *Nassarius helveticus* (Peyrot 1925) | | | | | | | | | | | | | | X | |
| *Nassarius incognitus* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Nassarius incommodans* (Peyrot 1925) | | | | | | | | | X | X | | | | | |
| *Nassarius intextus* (Dujardin 1837) | | | | | | | | | | | | | X | | |
| *Nassarius lagusensis* (Peyrot 1925) | | | | | | | | | | X | | | | | |
| *Nassarius lambertiei* (Peyrot 1925) | | | | | | | | | | | | | | X | |
| *Nassarius mancietensis* (Peyrot 1925) | | | | | | | | | | | | X | | | |
| *Nassarius marsooi* (Degrange-Touzin 1894) | | | | | | | | | | | | | | X | |
| *Nassarius* sp. 1 | | | | | | | | | X | | | | | | |
| *Nassarius* sp. 2 | | | | | | | | | X | | | | | | |
| *Nassarius* sp. 3 | | | | | | | | | | | X | | | | |
| *Nassarius* sp. 4 | | | | | | | | | | | X | | | | |

| | THANETIAN | YPRESIAN | LUTETIAN | BARTONIAN | PRIABONIAN | RUPELIAN (Paris Basin) | RUPELIAN (Aquitaine Basin) | CHATTIAN | AQUITANIAN | BURDIGALIAN | UPPER BURDIGALIAN | LANGHIAN (Aquitaine Basin) | LANGHIAN (Loire Basin) | SERRAVALLIAN | MESSINIAN (Redonian) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nassarius* sp. 5 | | | | | | | | | X | | X | | | | |
| *Nassarius* sp. 6 | | | | | | | | | | | X | | | | |
| *Nassarius* sp. 7 | | | | | | | | | | | X | | | | |
| *Nassarius* sp. 8 | | | | | | | | | | | X | | | | |
| *Nassarius* sp. 9 | | | | | | | | | | | | | | X | |
| *Nassarius* sp. 10 | | | | | | | | | X | | X | X | | | |
| *Nassarius* sp. 11 | | | | | | | | | | X | X | | | X | |
| *Nassarius* sp. 12 | | | | | | | | | | | X | X | | | |
| *Nassarius* sp. 13 | | | | | | | | | | | X | X | | | |
| *Nassarius* sp. 14 | | | | | | | | | | | | | | X | |
| *Nassarius* sp. 15 | | | | | | | | | | | | | | X | |
| *Nassarius* sp. 16 | | | | | | | | | | | | | | X | |
| *Nassarius* sp. 17 | | | | | | | | | | | | | | X | |
| *Nassarius* sp. 18 | | | | | | | | | | | | | | | X |
| *Nassarius* sp. 19 | | | | | | | | X | | | | | | | |
| *Nassarius* sp. 20 | | | | | | | | X | | | | | | | |
| *Nassarius occidentalis* (Peyrot 1925) | | | | | | | | | | X | | | | | |
| *Nassarius orthezensis* (Tournouër 1876) | | | | | | | | | | | | | | X | |
| *Nassarius prysmaticus* (Brocchi 1814) | | | | | | | | | | | | | X | | X |
| *Nassarius punctiferus* (Degrange-Touzin 1894*)* | | | | | | | | | | | | | | X | |
| *Nassarius pygmaeus* (Schlotheim 1820) | | | | | | | | X | | | | | | | |
| *Nassarius rectus* (Dollfus & Dautzenberg 1886) | | | | | | | | | | | | X | X | | |
| *Nassarius rideli* (Dollfus 1889*)* | | | | | | | | | | | | | | X | |
| *Nassarius ridibundus* Lozouet 1999 | | | | | | | | X | | | | | | | |
| *Nassarius rozieri* (Peyrot 1925) | | | | | | | | | X | X | | | | | |
| *Nassarius salbriacensis* (Peyrot 1925) | | | | | | | | | | | X | X | | | |
| *Nassarius salinensis* (Tournouër 1876) | | | | | | | | | | | | | | X | |
| *Nassarius sallomacense* (Mayer 1860) | | | | | | | | | | | | | | X | |
| *Nassarius saucatsensis* (Peyrot 1925) | | | | | | | | | | X | | | | | |
| *Nassarius sororculus* (Peyrot 1925) | | | | | | | | | | | X | X | | | |
| *Nassarius spectabilis* (Nyst 1845) | | | | | | | | | | | | | X | | X |
| *Nassarius stephanensis* (Peyrot 1925) | | | | | | | | X | | | | | | | |
| *Nassarius subecostatus* (Bellardi 1887) | | | | | | | | | | | | | | X | |
| *Nassarius subincognitus* Lozouet 1999 | | | | | | | | X | | | | | | | |
| *Nassarius subobesus* (Degrange-Touzin 1894) | | | | | | | | | | | | | | X | |
| *Nassarius subtesselatus* (Peyrot 1925) | | | | | | | | | X | X | | | | | |
| *Nassarius subtramineus* (Grateloup 1834) | | | | | | | | | | | X | X | | | |
| *Nassarius tarraconensis* (Tournouër 1879*)* | | | | | | | | | | | X | | | | |
| *Nassarius turonense* (Deshayes 1844) | | | | | | | | | | | | | | X | |
| *Nassarius verrucosus* (Brocchi 1814) | | | | | | | | | | | | X | X | | |
| *Nassarius vulgatissimus* (Mayer 1860) | | | | | | | | | | | X | X | | | |
| **Photinae** | | | | | | | | | | | | | | | |
| *Europhos subpolygonum* (D'Orbigny 1852) | | | | | | | | | | X | X | X | | X | |
| **Number of species** | 3 | 2 | 1 | 3 | 5 | 1 | 2 | 27 | 16 | 20 | 24 | 23 | 15 | 29 | 9 |

## References

Allmon, W.D. (1990): Review of the *Bullia* group (Gastropoda: Nassariidae), with comments on its evolution, biogeography, and phylogeny. — Bulletins of American Paleontology, **99** (335), 1–179, 15 pls.

Bellardi, L. (1882): I Molluschi dei terreni terziari del Piemonte e della Liguria. Parte 3. Gasteropoda (Buccinidae).— Memorie della Reale Accademia delle Scienze di Torino, Cyclopsidae, Purpuridae, Coralliophilidae, Olividae., Series 2, **34**: 219–469, 12 pls.

Brébion, P. (1964): *Les Gastéropodes du Redonien et leur signification*. Thèse de Doctorat, Paris, unpublished, pp. 1–775.

Brown, A.C. (1982): The biology of sandy-beach whelks of the genus *Bullia* (Nassariidae). — Oceanography and Marine Biology, Annual Review, **20**, 309–361.

Bouchet, P. & Rocroi, J.P. (2005): Classification and Nomenclator of Gastropod Families. — Malacologia, **47** (1–2), 1–397.

Cernohorsky, W. O. (1975): The taxonomy of some West American and Atlantic Nassariidae based on their type-specimens. — Record of the Auckland Institute and Museum, **12**:121–173.

Cernohorsky, W. O. (1984): Systematics of the Family Nassariidae (Mollusca: Gastropoda). — Auckland Institute and Museum, Bulletin, **14**: 1–356.

Chirli, C. (2000): Malacofauna Pliocenica Toscana, 2 Superfamiglia Muricoidea. — 142 pp., 42 pls; Firenze (C. Chirli).

Cossmann, M. (1889): Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris. 4ème fascicule. — Annales de la Société royale de malacologie de Belgique, **24**: 3–385 .

Cossmann, M. (1901): Essais de paléoconchologie comparée. vol. 4. —293 pp, 10 pls; Paris, published by the author.

Cossmann, M. & Pissarro, G. (1907–1913): Iconographie complète des coquilles fossiles de l'Eocène des environs de Paris. —T. 2 : Gastéropodes, pl. 1–9 (1907), pl. 10–25 (1910), pl. 26–45 (1911), pl. 46–65 (1913); Hermann, Paris.

Fraussen, K. & Poppe, G.T. (2005): Revision of *Phos* and *Antillophos* from the Central Philippines. — Visaya, **1** (5): 76–115.

Galindo, L. A. (2014): Phylogénie, espèces cryptiques et endémisme chez les Nassariidae: approche intégrative. PhD dissertation (Muséum national d'Histoire naturelle), 232 p.

Glibert, M. (1952): Gastropodes du Miocène moyen du Bassin de la Loire. Deuxième partie. — Mémoire de l'Institut Royal des Sciences Naturelles de Belgiques, Bruxelles, (série 2), **46**: 241–450.

Grateloup, J.-P. (1834): Tableau (suite du) des coquilles fossiles qu'on rencontre dans les terrains tertiaires grossiers (faluns) des environs de Dax, département des Landes. 10ème article. — Actes de la Société Linnéenne de Bordeaux, **6** (4), n°35: 188–212.

Grateloup, J.-P. (1845–1847): Conchyliologie fossile des terrains tertiaires du Bassin de l'Adour (environs de Dax). 1, Univalves. Atlas. — 1845, 45 planches et leurs textes explicatifs (1, 3, 5–10, 12–48). 1847, 3 planches et leurs textes explicatifs (2, 4, 11), I–XX. Lafargue, Bordeaux (see Lesport et al. 2012).

Haasl, D.M. (2000): Phylogenetic relationships among nassariid gastropods. — Journal of Paleontology, **74**: 839–852.

Harzhauser, M. & Cernohorsky, W. (2011): Nomenclatorial rectifications and comments on some European Neogene nassariid and buccinid Gastropoda (Prosobranchia: Nassariidae; Buccinidae). — Archiv für Molluskenkunde, **140** (1): 29–35.

Harzhauser, M. & Kowalke, T. (2004): Survey of the nassariid gastropods in the Neogene Paratethys (Mollusca: Caenogastropoda: Buccinoidea). — Archiv für Molluskenkunde, **133** (1/2): 1–61.

Kolesnikov, V. (1939): Contribution to the Taxonomy of Sarmatian Gastropods. — Doklady Akademii Nauk Trudy Zoologicheskogo Instituta [Leningrad], **42**, R, 25(8): 700–703.

Landau, B. Da Silva, C.M. & Heitz, A.: Systematics of the gastropods of the upper Lower-lower Middle Miocene of Cantaure, Paraguaná Peninsula, Venezuela. — Bulletins American Paleontology (in review process).

Landau, B. Da Silva, C.M. & Gili, C. (2009): The Early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 8: Nassariidae. — Palaeontos, **17**: 1–101, 22 pls.

Landau, B. Da Silva, C.M. & Mayoral, E. (2011): The Lower Pliocene gastropods of the Huelva Sands Formation, Guadalquivir Basin, Southwestern Spain. — Paleofocus, **4**: 1–90.

Landau, B.M. Harzhauser, M. & Islamoglu, Y. & Marques Da Silva, C. (2013): Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. — Cainozoic Research, **11–13**: 584 p.

Landau, B.M. & Marquet, R. (1999): A new species of *Cyllene* (*Cyllenina*) (Mollusca, Mesogastropoda) from the Arenas de Huelva Formation (Pliocene, southern Spain). — Contribution to Tertiary and Quaternary Geology, **36** (1–4): 41–44.

Lesport, J.F. Cluzaud, A & Verhecken, A. (2012): Les publications du Docteur Jean-Pierre Sylvestre de Grateloup sur les mollusques fossiles du Bassin d'Aquitaine (S.-O. France) : dates de parutions et commentaires). — Bulletin de la Société Linnéenne de Bordeaux, **147**, nouv. série **40** (4): 417–485.

Lozouet, P. (2014): Temporal and latitudinal trends in the biodiversity of European Atlantic Cenozoic gastropod (Mollusca) faunas. A base for the history of biogeographic provinces. — Carnets de Géologie [Notebooks on Geology], **14**: 273–314.

Lozouet, P. Lesport, J.F. & Renard, P. (2001): Révision des Gastropoda (Mollusca) du stratotype de l'Aquitanien (Miocène inf.): site de Saucats "Lariey", Gironde, France. — Cossmanniana, Hors série **n°3**: 189 pp., 37 pls.

MacNeil, F. S. & Dockery, D. T. (1984): Lower Oligocene Gastropoda, Scaphopoda, and Cephalopoda of the Vicksburg group in Mississippi. — Mississippi Bureau of Geology, Bulletin, **124**: 1–415.

Michelotti, G. (1847): Description des fossiles des terrains miocènes de l'Italie septentrionale. — 408 pp., (A. Arnz & Comp.) Leide.

Odin, G.S. (1994): Geological time scale (1994) . — Comptes Rendus de l'Académie des Sciences, série II, **238**: 59–71.

Peyrot, A. (1903): Note sur quelques fossiles des faluns de la Touraine (Helvétien infér.) et des environs d'Orthez (Helvétien supérieur). — La Feuille des Jeunes Naturalistes, **388**: 53–56.

Peyrot, A. (1925–1927): Conchologie néogénique de l'Aquitaine. — Actes de la Société Linnéenne de Bordeaux, **77** (2): 51–194 (1925); **78**: 199–256 (1927).

Peyrot, A. (1938): Les mollusques testacés univalves des dépôts helvétiens du Bassin Ligérien. Catalogue critique, descriptif et illustré. — Actes de la Société Linnéenne de Bordeaux, **89**: 1–300.

Nuttall, C. P. & Cooper, J. (1973): A review of some English Palaeogene Nassariidae, formerly referred to *Cominella*. — Bulletin of the British Museum (Natural History), **23** (3): 177–219, 9 pls.

Sacco, F. (1890): Catalogo paleontologico del Bazino terziaro del Piemonte. — Bolletino della Società Geologica Italiana, **9**: 185–340.

Sacco, F. (1904): I molluschi dei terreni terziairii del Piemonte e della Liguria. Vol. 30. — 203 p., 31 pls; C. Clausen (Torino).

Simone, L.R.L. & Pastorino, G. (2014): Comparative morphology of *Dorsanum miran* and *Bullia granulosa* from Morocco (Mollusca: Caenogastropoda: Nassariidae). — African Invertebrates, **55** (1): 125–142.

Tournouër, R. (1875): Note sur le groupe des *Cyllene* fossiles des terraines miocènes de l'Europe. — Journal de Conchyliologie, **23**: 329–335, pl. l5.

Vokes, E.H. (1969): The genus *Trajana* (Mollusca: Gastropoda) in the New World. — Tulane Studies in Geology and Paleontology, **7**: 75–83.

Wenz, W. (1938–1944): Teil 1: Allgemeiner Teil und Prosobranchia. — In: O.H. Schindewolf [Ed.]: Handbuch der Paläozoologie, Band 6, Gastropoda: xii + 1639 pp; Borntraeger, Berlin.

Zhang, Shuqian & Zhang, Suping (2014): The genus *Antillophos* Woodring, 1928 (Gastropoda: Buccinidae) from the China seas, with description of a new species. — Molluscan Research, DOI:10.1080/13235818.2014.948256.

Manuscript submitted: 15.12.2014
Revised manuscript accepted: 16.04.2015