The European Tertiary Neritiliidae (Mollusca, Gastropoda, Neritopsina): indicators of tropical submarine cave environments and freshwater faunas

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The oldest freshwater neritiliid, *Neritilia bisinuata*, is described from the Middle Eocene of the Loire Basin. Another European species, *N. neritinoides*, ranging from the Lower Oligocene to Lower Miocene (Upper Burdigalian) is recognized; its habitat appears to have been freshwater, but very close to the sea. Two new marine neritiliid species from the Aquitaine Basin are described: **Bourdieria favia sp. nov.** from the Upper Oligocene and **Pisulinella aucoini sp. nov.** from the Lower Miocene. A third undescribed species from the Lower Miocene is referred to the same family and related to *Pisulinella*. The Oligocene species has a strong spiral sculpture, a character completely absent in previously known neritiliid species. The genus *Agapilia*, founded on juvenile *N. neritinoides* and adult *Vitta picta*, appears to be a junior synonym of the genus *Vitta*. The associated occurrence of shells of the families Neritiliidae, Neritopsidae and Pickworthiidae (well-known inhabitants of Indo-West Pacific submarine caves) at Peyrère suggest the first occurrence of a characteristic assemblage of dark submarine caves during the Oligocene. Both factorial analysis and relative abundance show that at Peyrère these families are associated with other cryptic fossils (various gastropods, bivalves, Brachiopoda, corals, Annelida). However, there are indications of other submarine cave assemblages in various Cenozoic deposits from the Palaeocene to the middle Miocene. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **140**, 447–467.

ADDITIONAL KEYWORDS: biogeography – Oligocene – palaeoecology – protoconch morphology – systematics.

INTRODUCTION

The family Neritiliidae was proposed by Schepman (1908) after analysis of the morphology of the radula had suggested that the tropical freshwater genus *Neritilia* should be separated from the Neritidae and Neritopsidae. Recently, Kano & Kase (2000a, b) provided further proof that there are ample reasons for separating *Neritilia* and its allies from typical Neritidae and that the erection of Neritiliidae is justified. Beyond the anatomical differences, there are marked differences in shell morphology between the two families, especially in the protoconch (Kano & Kase, 2001). Based on shell microsculpture, protoconch morphology and study of the radula of living genera, Kano & Kase (2000a) placed two other genera in the Neritiliidae,

the marine genus *Pisulina* and the closely similar fossil genus *Pisulinella*. Earlier workers (e.g. Knight *et al.*, 1960) had included *Pisulina* in the Neritidae (Smaragdiinae Baker, 1923). For a long time, *Pisulina* was known only from empty shells found at various Indo-West Pacific localities (Herbert & Kilburn, 1991; Hinoide & Habe, 1991). The relatively recent exploration of tropical submarine caves (Hayami & Kase, 1993b; Kano & Kase, 2000b) has shown that extant *Pisulina* are among the most characteristic members of their particular biocenotic association.

It appears that the Neritiliidae (including *Neritilia* and *Pisulina*) tend to be strongly segregated ecologically. *Neritilia* species live in tropical freshwater, although as a rule not very far from the sea, and they extend into brackish waters. An additional species has been described recently from anchialine habitats (Kano, Sasaki & Ishikawa, 2001) in saline water connected by the underground aquifer to sea-water.

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According to Sasaki & Ishikawa (2002), it also occurs in freshwater phreatic communities. *Neritilia* is now the second group of gastropods, together with the hydrobiids, to colonize such environments.

The fossil record of the Neritiliidae is very poor. In 1997, I recorded the presence of a new species of *Pisulina* in the Upper Oligocene of south-western France within an particular assemblage including many cryptic elements. I also noted that *Globularia* (*Deshayesia*) *mollicula* Beets, 1942, from the Neogene of Borneo, is a *Pisulina*. With *P. subpacifica* Ladd, 1966 (a species very close to the extant *P. adamsiana*) and *P. miocenica* Kano & Kase, 2000, both from Pacific islands (Bikini), only four fossil species of Neritiliidae have hitherto been recognized. No species have been described from Europe.

In an attempt to re-evaluate the biodiversity of the Oligocene and Miocene molluscan fauna of the French Atlantic coasts, many new data have been collected (Lozouet, 1997). In particular, the presence of *Neritilia* was recognized in Europe for the first time. I have now identified two freshwater species of *Neritilia* and two (possibly three) marine neritiliids. Of these species three are new. They shed new light on the history of this family and its modern biogeographical distribution, and they are precious bench-marks in research into the origin of the submarine cave biocenoses.

MATERIAL AND METHODS

Most of the fossils examined were collected in the Adour Basin (sub-basin of the Aquitaine Basin, south-western France) (Fig. 1). The Oligocene and Miocene localities are situated in the area of Dax and Mont-de-Marsan. Additional material was collected by Jacques Le Renard (MNHN) from an Eocene outcrop of the Loire Basin and by Didier Aucoin (Paris) from a Lower Miocene outcrop of the Aquitaine Basin. The material is part of a large collection (260 000 specimens) gathered over 15 years; it has already been the subject of an analysis of the mid-Cenozoic gastropod fauna of the European Atlantic (Lozouet, 1997). The extent of the sampling effort may be gauged from the 112 person-days allocated to fieldwork in the Aquitanian outcrop of Meilhan (Lozouet *et al.*, 2001b). Fossiliferous samples were sieved in freshwater. Items larger than 3 mm were sorted in the field and split into bivalves and gastropods; fragile fossils were isolated. Finer fractions were sorted in the laboratory with the aid of a dissecting microscope.

A correspondence analysis (CA; Legendre & Legendre, 1998) was conducted of all gastropods collected in the upper Oligocene of the Adour Basin. It is a classic tool in the study of Recent and fossil continental molluscan associations (Rousseau, 1987; Limondin & Rousseau, 1991) and of marine assemblages such as submarine cave environments (Balduzzi *et al.*, 1989). In contrast to principal component analysis, CA allows simultaneous analysis of variables (columns: outcrops) and observations (rows: species) without affecting the structure of the data (Rousseau, 1990).

SYSTEMATIC PALAEONTOLOGY

CLASS GASTROPODA CUVIER, 1797 SUBCLASS ORTHOGASTROPODA PONDER & LINDBERG, 1995 ORDER NERITOPSINA COX & KNIGHT, 1960 SUPERFAMILY NERITOIDEA RAFINESQUE, 1815 FAMILY NERITILIIDAE SCHEPMAN, 1908

The relationships of the Neritopsina continue to be problematic (Colgan, Ponder & Eggler, 2000), although the Neritiliidae are clearly distinct from the Neritidae. As indicated above, the most important shell character defining the taxonomic position of the Neritiliidae is protoconch morphology. In *Neritilia* and *Pisulina*, the protoconch axis is tilted relative to that of the teleoconch (Herbert & Kilburn, 1991) and bears several spiral ridges.

GENUS *NERITILIA* MARTENS, 1879

Type species (by original designation) *Neritina rubida* Pease, 1867; Recent.

Description: The shell is small, solid, with a relatively flat spire. The protoconch is multispiral tilted relative to the teleoconch coiling axis and ornamented with numerous minute pits. The teleoconch ornament consists principally on growth lines. The inner lip septum is flat and the adaxial margin is straight without teeth; the outer lip is prosocline without teeth.

NERITILIA BISINUATA SP. NOV.
(FIG. 2)

Etymology: From *sinuatus* (Latin), sinuous, referring to the shape of the outer lip.

Type specimens: Holotype, coll. Le Renard (MNHN-LR67776A), 2 paratypes, coll. Le Renard (MNHN-LR67776B).

Type locality and horizon: France, Loire-Atlantique, Saffré 'Le Bois-Gouët', Middle Eocene (Lutetian).

Other material examined: Middle Eocene, France, Loire-Atlantique, Saffré 'Le Bois-Gouët', Middle Eocene (Lutetian), coll. Le Renard, 2 ex. (MNHN-LR6834).

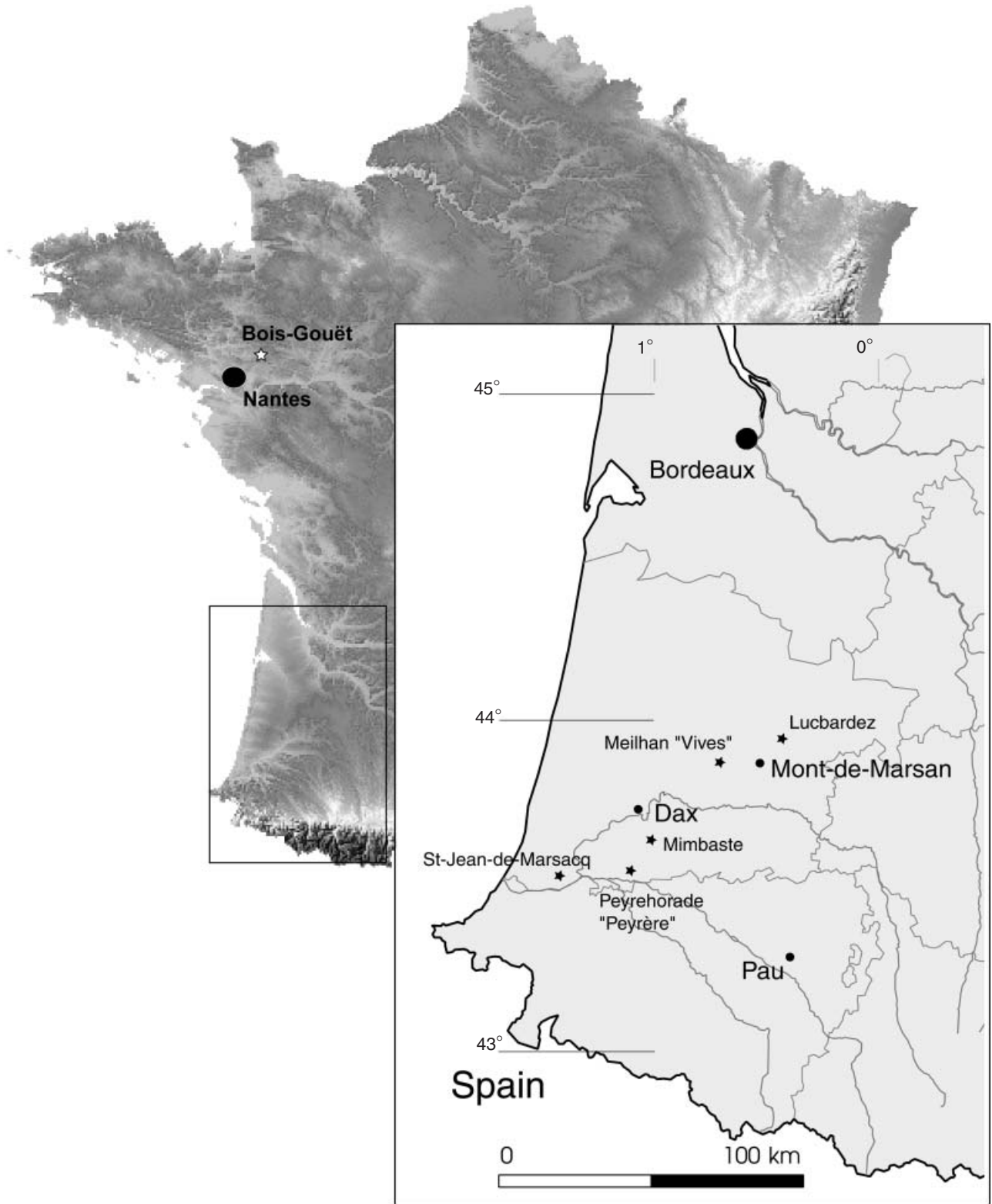*Measurements (holotype):* Height = 1.2 mm; max. width = 1.45 mm.

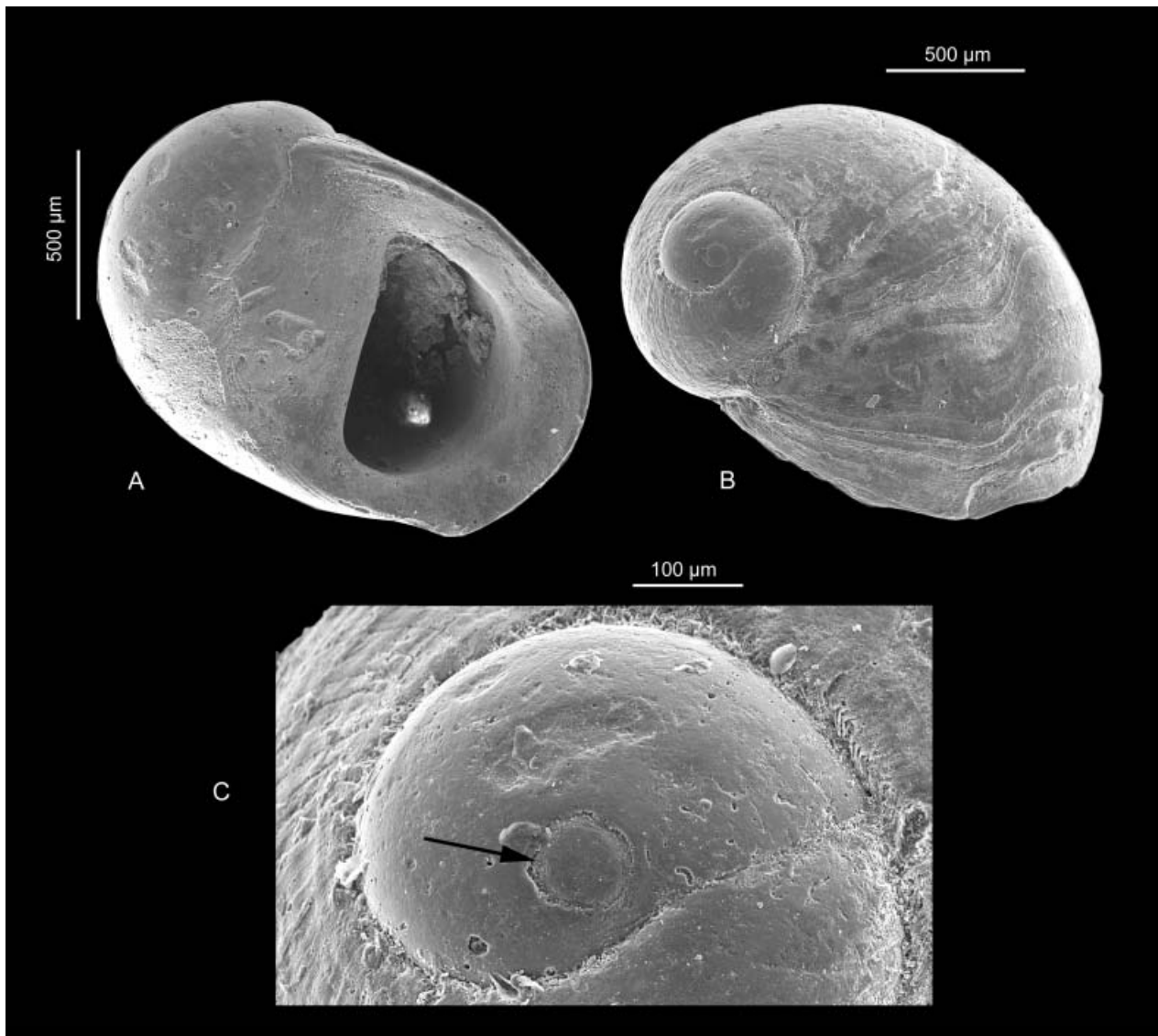**Figure 1.** Location of the fossil localities (★).

Figure 2. *Neritilia bisinuata* **sp. nov.** from Bois-Gouët (Middle Eocene). A, apertural view of the holotype (MNHN-LR67776A); B, apical view of a paratype (MNHN-LR67776B), C, apical view of the protoconch; arrow indicates the embryonic shell.

Description: The shell is minute, solid, very elongate neritiform with a relatively high spire for the group. The protoconch is multispiral, eroded but clearly tilted relative to the teleoconch. Teleoconch whorls up to 1.4 in number, increasing rapidly in size, inflated with a round periphery. The sutural line is gently impressed. The surface of the shell is relatively altered but one can distinguish spiral ridges and sinuous growth lines, which are particularly strong close to the aperture. The semicircular aperture is relatively small and inclined at about 42° relative to the teleoconch coiling axis. The outer lip is prosocline and sinuous with two notches, widely bevelled and slightly dilated outward.

The inner lip is covered with a smooth, extensive callus; the adaxial margin is straight, without teeth.

Remarks: This very small species is unique within *Neritilia* because of the presence of well-developed spiral ridges and strong sinuous growth lines. It is also the smallest *Neritilia* species known.

NERITILIA NERITINOIDES (COSSMANN & PEYROT, 1917) (FIG. 3)

1917 *Teinostoma neritinoides* Cossmann & Peyrot: n°126, pl. 7, figs 11–13.

Material examined: Lower Oligocene (Rupelian stage), France, Landes, Orist (Carrère), 4 ex. (MNHN-PL15357). Upper Oligocene (Chattian stage), Landes, France: Bélus (Marcon), 1 ex. [MNHN-PL14502], Bélus (Tauziède), 2 ex. [MNHN-PL14503]. Lower Miocene (Burdigalian stage), France: Gironde, Pessac (Cap de Bos), 35 ex. [MNHN-PL4185]; Landes, Mimbaste, 1 ex. [MNHN-PL14078]; Landes, Lucbardez (Mondiet) 250 ex. [MNHN-PL15281].

Measurements (specimen from Lucbardez, Fig. 3E): Height 3.2 mm; max. width 3.45 mm.

Description (Lower Miocene specimen from Lucbardez): The shell is small, solid, elongate neritiform, with a moderate spire. The multispiral protoconch is covered by a thin callus, spiral and axial ridges and minute pits entirely covering the surface. The glossy teleoconch is sculptured with very fine axial growth lines only. The large semicircular aperture is inclined at about 28 ° relative to the coiling axis, with a flat thick septum (callus). The adaxial margin of the inner lip is straight; the outer lip is prosocline without teeth. The shell lacks a colour pattern. The operculum is elongate with rounded ends; the outer side shows faint growth lines and an eccentric nucleus, the inner side is smooth with a short apophysis appendage (peg) near the abapical end. Parallel to the abapical margin there is a long muscle scar.

Remarks: In the original description, Cossmann & Peyrot (1917) referred *N. neritinoides* to the genus *Teinostoma* (Vitrinellidae). The punctuated protoconch with its embryonic shell covered by a thin callus (Fig. 3F, G) supports a new assignment to *Neritilia*. Like the Recent *Neritilia* species, the septum is flat and covered by a very slightly pustulated callus. The outer lip has a gently sinuous outline, less strongly so than in *N. bisinuata*, but stronger than in the extant *Neritilia*.

It seems very likely that Harzhauser & Kowalke (2001), in their description of the new genus *Agapilia,* have mistakenly confused a true neritiliid close to *N. neritinoides* for a neritid. The type species is *Neritina picta* Férussac, 1825, a well-known Lower Miocene species of the Aquitaine basin that occurs in many European Neogene deposits. For these authors, *N. picta* combines neritid (teleoconch with numerous columellar teeth and persistent coloration on the shell) and neritiliid (protoconch with minute pits covering the surface) characters. Classically (see Lozouet, Lesport & Renard, 2001a), *N. picta* was assigned to the genus *Vitta* Mörch, 1852 (Neritidae). Our juvenile specimens have been selected from the type basin. Their protoconchs appear to be smooth like those of all the Neritidae (Fig. 3K). The shells of juveniles have a well-known and consistent coloration pattern whereas the juvenile specimen illustrated by Harzhauser &

Kowalke (2001) has no such pattern. I suspect that the authors have mixed up adult specimens of *Vitta picta* with a juvenile specimen of a true smaller species of *Neritilia*. The fact that the so-called young specimen of *Agapilia picta* has a smooth teleoconch without teeth on the inner lip is another clear indication of confusion of specimens belonging to two different taxa. At the same size (half adult whorl), *V. picta* has a colour pattern and well developed tooth on the inner lip (Fig. 3L). Accordingly, I conclude that *Agapilia* with its type species *N. picta* is a junior synonym of *Vitta*. *Agapilia* Harzhauser & Kowalke, 2001 refers pro-parte to *N. picta* (adult specimens) or to a neritiliid, probably *N. neritinoides* (juvenile specimen).

BOURDIERIA GEN. NOV.

Type species: Bourdieria faviai sp. nov.

Etymology: Dedicated to the late Franck Bourdier, one of the most original French Quaternary geologists of the last century.

Description: The shell is small, typically about 3.2–4.4 mm maximum adult width, very solid, with a flat spire. The protoconch is multispiral, tilted relative to the teleoconch coiling axis and ornamented with spiral ridges. The teleoconch is ornamented with strong spiral cords. The inner lip bears five to six teeth and the outer lip bears four strong teeth. The semicircular aperture is highly prosocline.

Remarks: Superficially, *B. faviai* is more similar to members of Neritidae than to any genus of Neritiliidae. In fact, *Bourdieria* is unique among the Neritiliidae because of the presence of strong spiral cords on the teleoconch. Compared to other Neritiliidae, the spire is also especially flat. The protoconch is tilted relative to the teleoconch (Fig. 4I) with spiral ridges (Fig. 4G) clearly indicating its position in Neritiliidae.

BOURDIERIA FAVIAI SP. NOV.
(FIG. 4)

1917 *Nerita* (*Pila*) *basteroti* Recluz, 1850 – Cossmann & Peyrot, n°144, pl. 10, figs 38, 39 [not Recluz, 1850].
1974 *Nerita subcaronis* d'Orbigny, 1852 – Magne & Vergneau-Saubade: 5 (pars) [not d'Orbigny, 1852].

Etymology: Dedicated to Raymond Favia for his assistance in field collection.

Type specimens: Holotype (MNHN-PL1634A), 4 paratypes (MNHN-PL1634B-E).

Type locality and horizon: France, Landes, Peyrehorade (Peyrère), Upper Oligocene, marls with *Eulepidina*.
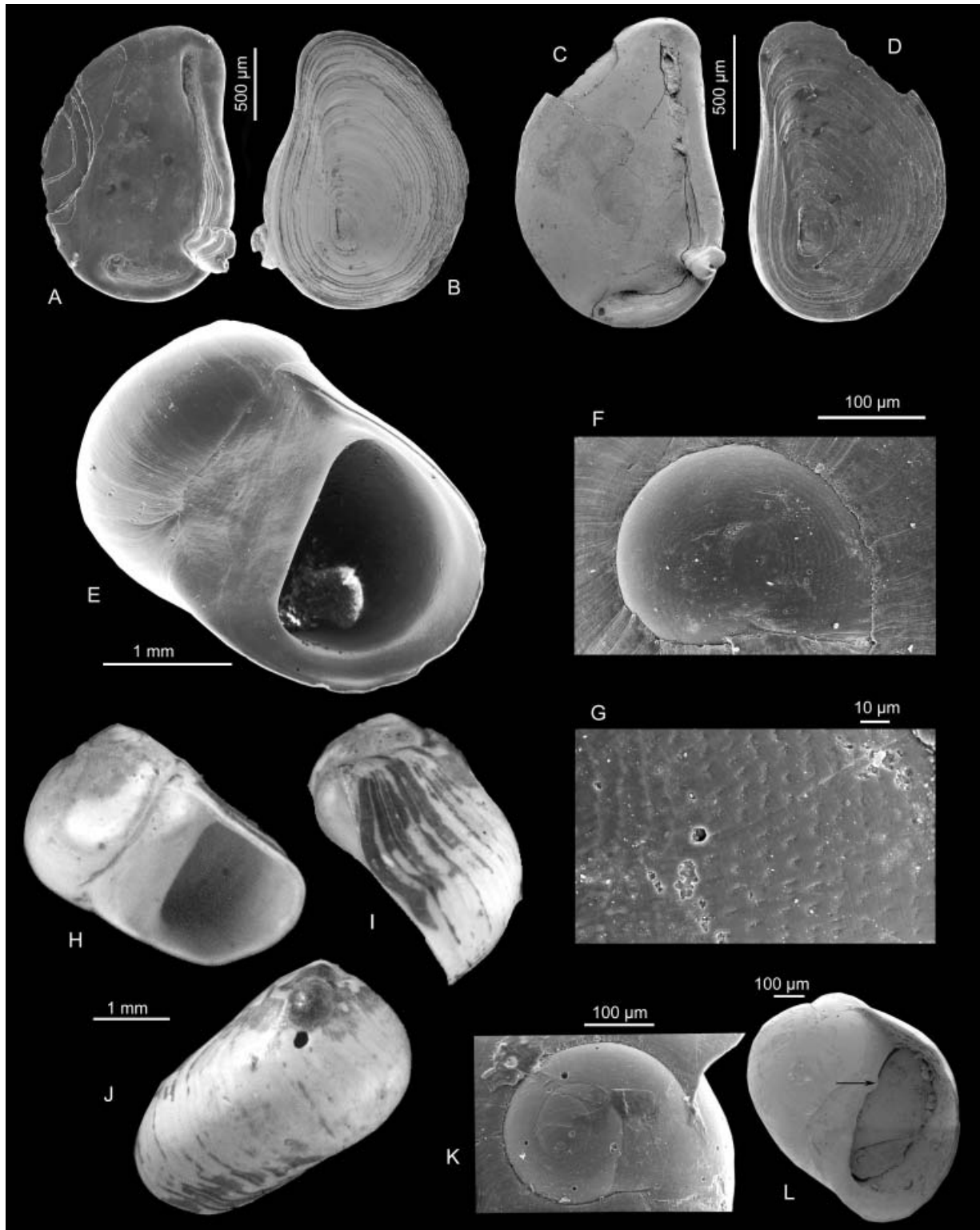
Figure 3. A–J, *Neritilia neritinoides* (Cossmann & Peyrot, 1917). K & L, *Vitta picta* (Férussac, 1825). A–D, operculum. E, apertural view (MNHN-PL15281). F, apical view of the protoconch. G, enlarged portion of the protoconch showing minute pits (MNHN-PL4185). H, apertural view. I, right lateral view. J, dorsal view (MNHN-PL14078). K, apical view of the protoconch. L, juvenile specimen of 0.8 whorl with operculum showing a tooth (arrowed) on the inner lip (MNHN-PL15385). *Sources of specimens:* A–E, Lucbardez; F & G, Pessac; H–L, Mimbaste (all Lower Miocene).
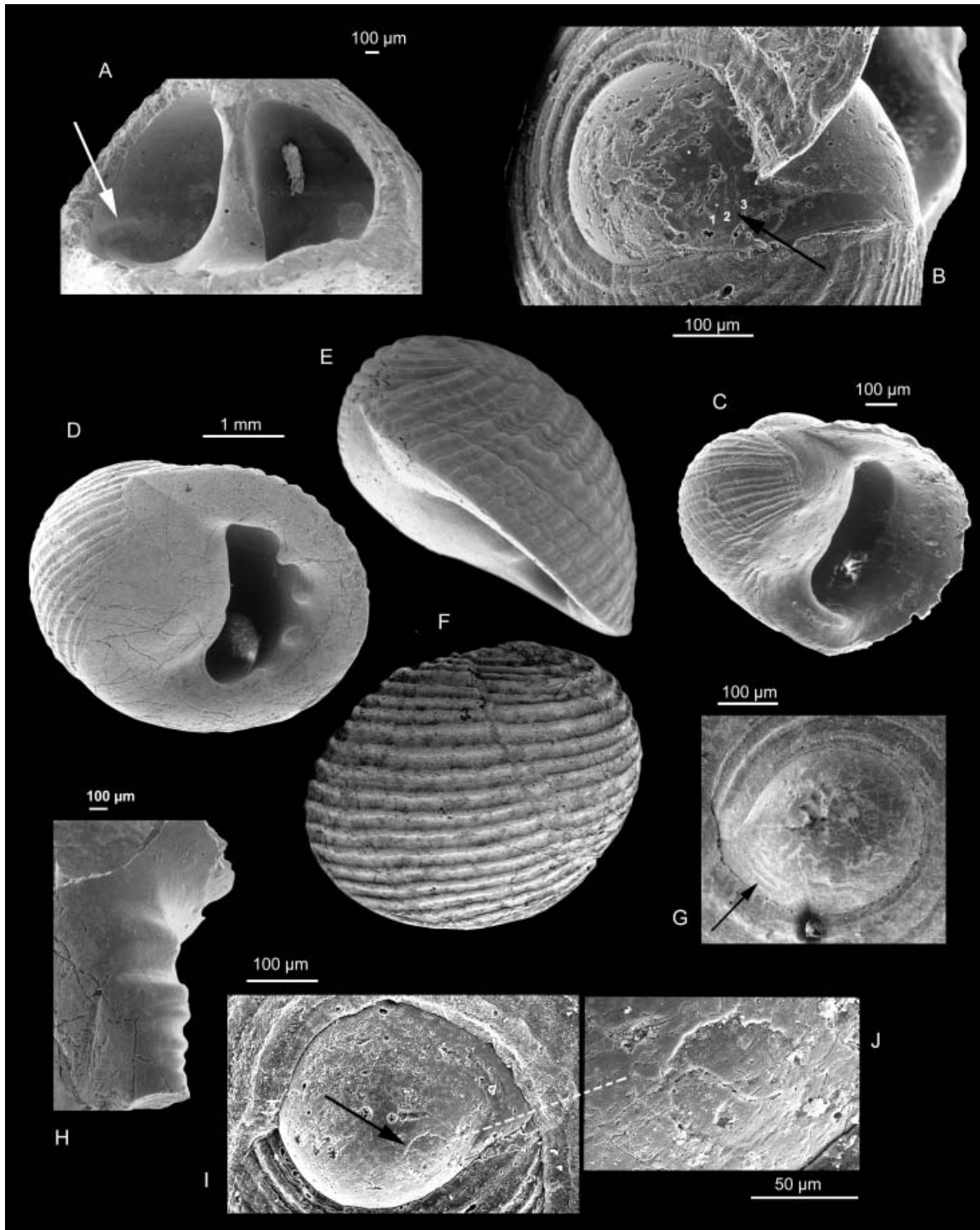
Figure 4. *Bourdieria faviai* **sp. nov.** from Peyrère (Upper Oligocene). A, broken specimen (apical whorls removed) showing (arrowed) the ridge inside the aperture (MNHN-PL1634E). B & C, juvenile specimen of 0.8 adult whorl (MNHN-PL1634C). B, apical view of the protoconch showing the position of three weak ridges (arrowed). D–F, views of the holotype (MNHN-PL1634A); D, apertural view, E, right lateral view, F, dorsal view. G, view of the apical part showing the ridges of the protoconch (arrow). H, broken specimen showing internal view of the columellar area. I & J, apical view of the protoconch; arrow indicates the embryonic shell. I, detail of the embryonic shell.

Other material examined: Upper Oligocene, France, Landes, Peyrehorade (Peyrère), 50 ex. (MNHN-PL1634F).

Measurements (holotype): Height 3.0 mm; max. width 4.0 mm.

Description: The shell is small, very solid, obliquely ovate in shape, with a very flat spire. The teleoconch consists of more than 2.5 rounded whorls, increasing very rapidly, with a depressed suture line that is difficult to observe due to the development of spiral cords. The globular protoconch (poor state of preservation in available material) is partially covered by the first teleoconch whorl; the boundary between protoconch and teleoconch is very clearly differentiated. Three or four spiral ridges are present close to the apertural line; the suture separating embryonic and larval shells is not clearly visible on the available specimens. The teleoconch is sculptured with 14–15 spiral cords and axial growth lines. The semicircular aperture is highly prosocline (about 49° relative to the shell axis) with a thick septum (inner lip callus) and a very blunt outer line; the arcuate septum is slightly convex and smooth. The columellar area bears 5–6 blunt teeth deeply situated inside the aperture, the adapical three being smaller. The blunt outer lip is thickened by a well-developed inductura, bearing four regularly spaced strong teeth. Inside the aperture there is a relatively long ridge near the base probably representing the innermost limit of the opercular retraction.

Remarks: Bourdieria faviai has been variously interpreted. Cossmann & Peyrot (1917) incorrectly identified it as a young specimen of one of the most common neritids (*Nerita basteroti*) of the Lower Miocene. Magne & Vergneau-Saubade (1974) identified young specimens of *N. basteroti sensu* Cossmann & Peyrot with *N. subcaronis* d'Orbigny, 1852, a problematic Lower Miocene species initially described by Grateloup (1847) under the name *N. caronis*. Despite several visits to the collections of the University of Bordeaux-Talence, where the Grateloup collection is housed, I have been unable to locate the figured and only known specimen of *N. subcaronis*. According to the figures of Grateloup (1847: pl. 5, fig. 45) and Magne & Vergneau-Saubade (1974), the septal lip of *Nerita subcaronis* bears many small denticles which *B. faviai* lacks. *B. faviai* is therefore easily differentiated from the Neritidae by its small size, the heavy, smooth, convex callus, the large regular teeth on the outer lip and the tilted protoconch typical of the Neritiliidae. *B. faviai* occurs only in the Saubrigues palaeocanyon and is only common in one site.

GENUS *PISULINELLA* KANO & KASE, 2000

Type species (by original designation): *Pisulinella pacifica* Kano & Kase, 2000; Miocene of Eniwetok Atoll.

Description: The shell is small, about 4 mm maximum adult width, globulous, very solid. The protoconch is multispiral, tilted relative to the teleoconch coiling axis and ornamented with spiral ridges. The shell surface is smooth and ornamented with fine growth lines. The inner lip septum is slightly convex and the adaxial margin bears three or four inconspicuous teeth. A shallow groove on the inner lip callus extends along the inner line. The outer lip is prosocline and bears many weak tubercles.

PISULINELLA? AUCOINI SP. NOV.
(FIG. 5)

Etymology: Dedicated to Didier Aucoin, a very active fossil collector in the Paris and Aquitaine Basins.

Type specimens: Holotype (MNHN-PL15355A), 1 paratype (MNHN-PL15356B).

Type locality and horizon: France, Landes, Meilhan (Vives), Lower Miocene (Aquitanian stage).

Other material examined: Lower Miocene, Landes, Meilhan (Vives), 1 ex. (coll. Aucoin, private collection)

Measurements (holotype): Height 2.6 mm; max. width 2.9 mm.

Description: The shell is small, very solid, obliquely ovate in shape, with a low spire. The teleoconch, which consists of little more than two rounded whorls, increases rapidly, with an impressed suture. The globular protoconch is poorly preserved in the available material and while partially covered by the first teleoconch whorl, the limit between protoconch and teleoconch is clear; the suture between the embryonic and larval shells is not distinguishable in our specimens. The glossy teleoconch is sculptured with fine axial growth lines only, which are better developed close to the aperture. The semicircular aperture is highly prosocline (38–40° relative to the shell axis), with a thick septum (callus) and a blunt outer line. The septum is slightly convex, smooth, the columellar area bearing two main teeth; a third results from the subdivision of the abapical tooth. The outer lip is blunt, thickened by a well-developed inductura, and bears five strong teeth. Inside the aperture there is a relatively long ridge near the base, probably representing the innermost limit of the opercular retraction.

Remarks: P. aucoini differs from *B. faviai* by a more elongate shell form and the absence of spiral cords. The presence of spiral cords being unique among the
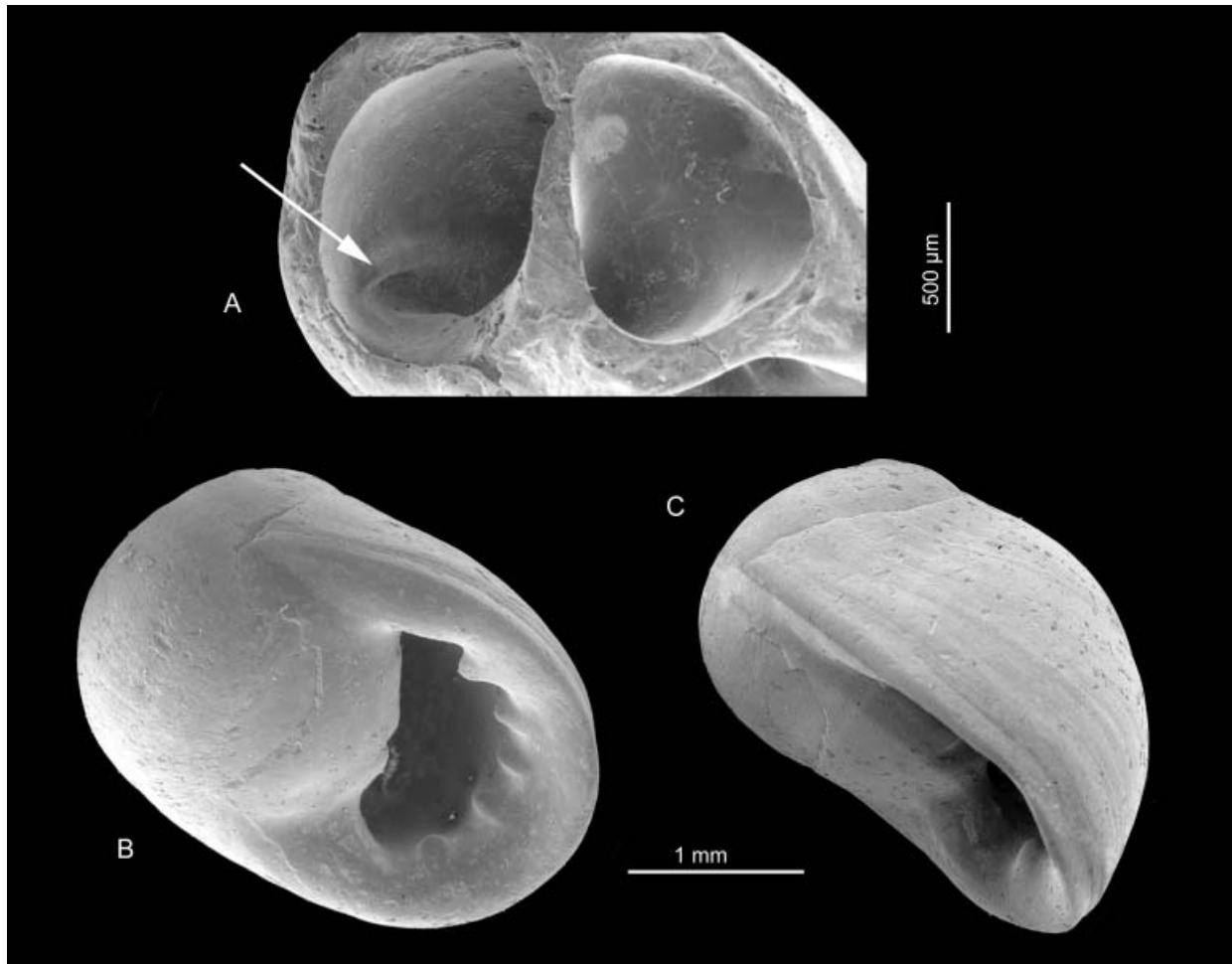
Figure 5. *Pisulinella? aucoini* **sp. nov.** from Meilhan (Lower Miocene). A, broken specimen (apical whorls removed) showing (arrowed) the ridge inside the aperture (MNHN-PL15356B). B & C, holotype (MNHN-PL15355A). B, in apertural view; C in right lateral view.

Neritiliidae, their absence in *P. aucoini* excludes a placement in *Bourdieria*. *P. aucoini* is very similar in shape to *Pisulinella miocenica* Kano & Kase, 2000a, but is easily distinguished by the large teeth on the outer lip; it is possible that the absence of a shallow groove on the inner lips callus of *P. aucoini* could be an apomorphic character of *Pisulinella* (Kano & Kase, 2000a) resulting from the poor preservation of the available specimens. In any event, the generic assignment of *P. miocenica* cannot be clearly indicated.

The three specimens of *P. aucoini* were collected together with abundant reef coral debris (*Pocillopora*) and many other rare molluscs such as the muricid *Galeropsis lavenayanus* Hupé, 1860 (see Lozouet & Renard, 1998). Judging from the morphology of coral fragments and the limited thickness of this layer, it is not possible to be sure that a true coral reef was their habitat. Nevertheless, the layer yielded coral patches

of *Porites* exceeding 3 m in length and 1.5 m in height (Lozouet *et al.*, 2001b). It may be suggested with some confidence that *P. aucoini* was a cryptic species living in crevices of a coral patch-reef.

PISULINELLA? SP. (FIG. 6)

Material studied: Lower Miocene (Burdigalian), France, Landes, Mimbaste; 1 ex. (MNHN-PL15356). Only one juvenile specimen of this form has been collected from the Lower Miocene (Burdigalian) of Mimbaste (Landes). This outcrop has yielded some elements of hard bottom and cryptic fauna (Neritopsidae, Pickworthiidae) associated with a rich marine littoral sand fauna. The protoconch of *Pisulinella?* sp. bears several ribs similar to those observed in the genera *Pisulinella* and *Bourdieria*. The teleoconch is sculptured with fine spiral ribs that exclude assignment to *B. faviai*. *P. aucoini* differs by the absence of
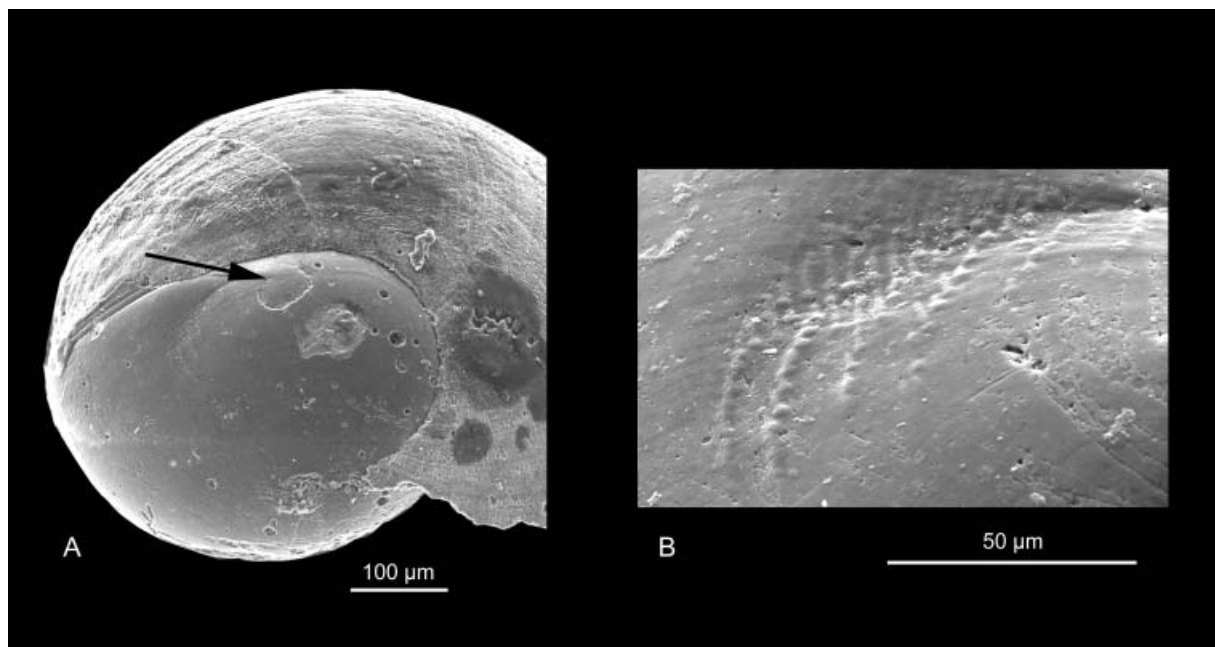
Figure 6. *Pisulinella* sp. from Mimbaste (Lower Miocene). A, apical view of the protoconch; arrow indicates the embryonic shell (MNHN-PL15356). B, enlarged portion of the protoconch showing the spiral ridges.

spiral ribs on the teleoconch. I consider that this specimen represents a third undescribed marine neritiliid species, although a full description and clear indication of generic position is postponed until further material becomes available. Placement within the genus *Pisulinella* is based on the fact that the sculpture comprises only very fine spiral ribs – specimens of *B. faviai* which are the same size already bear strong spiral cords.

PALAEOENVIRONMENT OF EUROPEAN FOSSIL NERITILIIDS

DID *NERITILIA NERITINOIDES* INHABIT FRESH OR BRACKISH WATER?

In the Lower Oligocene (Orist), four juvenile specimens of *Neritilia* have been collected on a beach sand deposit and are very abraded. In the Upper Oligocene, *N. neritinoides* has been found in a very fine sand layer (5–10 mm thick) included in a marly sequence. The predominantly marine molluscs are mixed with species which inhabit fresh and brackish water, suggesting that they originate from a variety of environments (Lozouet, 2003). The temporarily accessible outcrops of Pessac (Lower Miocene) have also yielded a rich mixed fauna (Lozouet & Gourgues, 1995) in a sequence 4 m thick of very fossiliferous calcareous sand, including cross-bedded and shell lenses, indicating the influence of tidal currents. The studied sample of Cap de Bos contains 1345 gastropod specimens rep-

resenting 125 species. Of these 114 (1123 specimens) are marine, six (129 specimens) are freshwater and five (93 specimens) are possibly brackish-water species. Brackish and freshwater specimens account for 16.5% of the total fauna. This layer also contains many pieces of lignitized wood and a few fossils of mammals and crocodilians have been reported (Duranthon & Cahuzac, 1997), which confirms the influence of a river.

In the Lower Miocene (Lucbardez 'Mondiet'), *N. neritinoides* occurs at the top of a 5-m thick section with alternating sandy marls, limestone banks and sandy limestones. It is one of the commonest species, and the specimens are perfectly preserved. Analysis of the variation of the faunistic components of this outcrop should help provide a more precise description of the environment of *N. neritinoides*. The sequence from base to top is as follows:

(1) 0–35 cm, calcareous sandy marl with numerous potamid gastropods (*Granulolabium plicatum* (Bruguière, 1792)).
(2) 35–135 cm, sandy marls including two limestone banks (10 and 20 cm thick); molluscs are dominated by one carditid (Bivalvia) species accumulated in the shelly limestones.
(3) 135–285 cm, yellow calcareous sand containing only very fine mollusc debris.
(4) 285–305 cm, heterogeneous limestone with sandy patches.
(5) 305–315/320 cm, yellow sand with *Melanopsis*.

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(6) 320–370 cm, brown-red humic sand, with very fine lignitic beds including *Melanopsis*.

(7) 370–395 cm, weathered clay with preserved fauna (*Melanopsis*, *Congeria*) only at the bottom.

(8) 395–495 cm, Quaternary sand, 'Sable des Landes'.

Layers 1 and 2 were probably deposited under shallow marine/lagoon conditions as indicated by the genus *Granulolabium* (see Lozouet *et al.*, 2001a). This Lower Miocene biocenosis, of low diversity and dominated by *Venericardia* and *Granulolabium*, strikingly resembles the lagoonal community described by Gitton, Lozouet & Maestrati (1986) at the top of the marine sequence of the Lower Oligocene of the Paris Basin (Ormoy fauna).

In layer 3, the shells are very scattered. A more careful study of a sample rich in mollusc fragments revealed that the dominant species are the small *Ervilia* and *Lentidium* bivalves. A species of Lucinidae was also recorded. The most commonly found gastropods are young specimens of *Hydrobia* cf. *aturensis* and *Granulolabium plicatum*. In the finest fraction, the species *Pelecydion* sp. (Pelecydionidae) is unusually abundant. Species of this tropical family are generally considered as very rare. However, during the 'Expédition Montrouzier' to New Caledonia (Bouchet *et al.*, 2002), an association of small Mollusca including *Pelecydion*, Iravadiidae, Cornirostridae was collected in coarse beach sediments (C. Erseus, pers. comm.). The bivalve *Lentidium* is a characteristic genus of the 'Upper clean sand' assemblages of the Mediterranean Sea (Pérès, 1982) having been reported in the same environment since the Oligocene of the Paris Basin (Gitton *et al.*, 1986). As this corresponds to the surf zone of the lower beach, it concurs with the presence of *Pelecydion* sp.

Layer 3 may be interpreted as a spillover deposited on the subtidal sediment of the estuarine side of a littoral spit. Intrusion of material from a dynamic marine environment into relatively static and brackish areas is characteristic of storm deposits. An additional corroboration of this interpretation is the ecology of the more abundant species of layers 5–7, in decreasing order of frequency: *Melanopsis dufourii* Férussac, 1822, *Gyraulus balizacencis* (Peyrot, 1931), *Neritilia neritinoides*, *Hydrobia* spp. (three species). The predominance of *Congeria basteroti* (Deshayes, 1836) is significant. All these species are very well preserved. The numerous *N. neritinoides* have a glossy surface and details of the protoconch are clearly preserved. In contrast, the rare brackish elements of the malacofauna (estuarine or lagoonal) have been collected only in layer 5 (Gastropoda: *Granulolabium plicatum*, Bivalvia: *Anadara cardiiformis* (Basterot, 1825), *Venericardia pinnula* (Basterot, 1825)), and are highly abraded.

Melanopsis dufourii Férussac, 1822 is very close to the extant *M. praemorsa* (Linné, 1758), a circum-Mediterranean species living in running water (brooks, irrigation canals, rapids and springs) rather than stagnant water, and tolerating desiccation and moderate salinity (Brown, 1994). Dreissenidae also live in freshwater and tolerate moderate salinity (Archambault-Guezou, 1976). The Planorbidae, such as *Gyraulus*, are a typically freshwater element but the extant species *G. laevis* (Alder, 1838) (very similar to *G. balizacencis*) may occur in inland waters close to the sea, tolerating slightly brackish conditions (Kerney, 1999). *Gyraulus* species generally live in quiet water, among weeds. The two most common hydrobiid species do not belong to the brackish-water fossil group of *Hydrobia andreaei* Boettger, 1892 (Lozouet *et al.*, 2001a) but resemble hydrobiids that inhabit waters of low to moderate salinity. Another species is suggestive of the extant *Mercuria confusa* (Frauenfeld, 1863), a hydrobiid mostly restricted to freshwater in estuaries and pools. I also add one species of Unionidae and the gastropods *Acroloxus cestasensis* (Peyrot, 1932) (Acroloxidae) and *Ferrissia* sp. (Planorbidae); these species belong to freshwater groups. The extant *Ferrissia wautieri* (Mirolli, 1960) lives in stagnant or slowly moving water with ample vegetation (Kerney, 1999). A displaced terrestrial found in this assemblage species belongs to the genus *Carychium* (Ellobiidae).

Analysis of the fauna of this sequence shows the evolution of the shallow water and lagoonal community towards a freshwater environment. As indicated by the good state of preservation of the molluscs and the habitats of their modern counterparts, layers 5–7 are freshwater deposits. This provides evidence that *N. neritinoides* belongs to a freshwater community probably able to tolerate slight salinity. Like the other species of *Neritilia*, it has a planktotrophic stage (as indicated by the protoconch); it has been postulated that this type of larval veliger, after hatching in freshwater, needs to reach the sea and then return to an inland environment (Kano *et al.*, 2001). Due to the lack of palaeotopographic information one cannot be precise about previous environmental conditions where *N. neritinoides* has been collected, but it is presumed that it was an estuary or freshwater lake close to the sea.

IS THE PRESENCE OF ***BOURDIERIA FAVIAI*** SP. NOV. INDICATIVE OF SUBMARINE CAVES?

The new marine neritiliid *Bourdieria faviai* is very common in only one outcrop (Peyrère), which is situated near the head of a submarine palaeocanyon (Fig. 7). The Saubrigues palaeocanyon, which is several hundred metres deep, results from a major erosion phase located at the Lower–Upper Oligocene
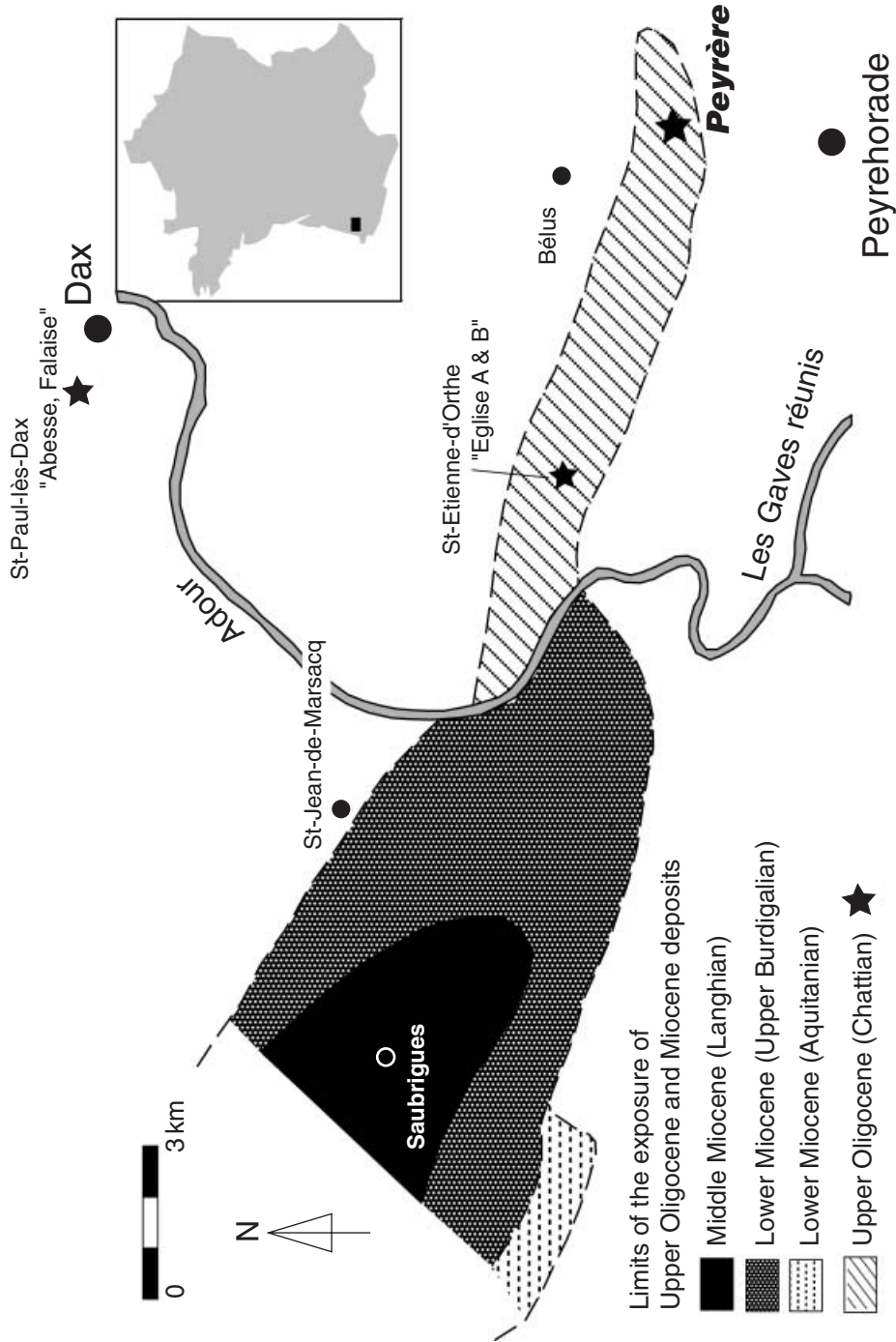
Figure 7. Location of the Peyrère outcrop in the late Oligocene to mid Miocene fill of the Saubrigues palaeocanyon (from Kieken, 1973; Cahuzac *et al.*, 1995).

boundary (Kieken, 1973) that coincides (Dolin, Dolin & Lozouet, 1985) with an important low-stand of the eustatic sea-curve of Vail *et al.* (1977). The palaeocanyon became immersed during the Late Oligocene due to the eustatic rise in sea-level. As a result it preserved the only accessible Upper Oligocene outcrops in France, rich in circalittoral and bathyal faunas. The palaeocanyon is filled extensively with Late Oligocene and Early to Middle Miocene sediments (Dolin *et al.*, 1985; Cahuzac, Janin & Steurbaut, 1995).

Earlier investigations carried out on the Peyrère assemblage led to quite contradictory results. For Dolin *et al.* (1985) it resembled a present-day detritic community living in the sublittoral zone, at depths between 50 and 100 m (Pérès, 1982). This interpretation does not differ from that of Steurbaut (1982) derived from fish otoliths, or that of Chevalier (1963) based on corals. On the contrary, Cahuzac & Chaix (1996) claimed that the presence of corals indicates a quiet, soft muddy bottom between 30 and 50 m or less. Contradictions are also apparent within the gastropod fauna. Some well preserved molluscs such as the saco-glossan *Julia douvillei* (Cossmann & Peyrot, 1914) or the *Amphithalamus immigrus* (Lozouet, 1998) live and feed on very shallow-biotope green algae (*Caulerpa* for the Sacoglossa; see Le Renard, 1983). This demonstrates that at least part of the fauna lived in the higher photic zone. On the other hand, some very common gastropods (such as *Alvania peyreirensis* Cossmann & Peyrot, 1919, and *Benthonellania antepelagica* Lozouet, 1990 developed in the darker circalittoral zone of the canyon and possibly penetrated the top of the bathyal zone.

As establishing the ecological significance of *B. faviai* requires a detailed study of the Peyrère assemblage, I first compare the latter's gastropod fauna with that of the Upper Oligocene of the Adour Basin in order to identify the significant species. In view of the diversity and abundance of the material (1138 species) an analysis based on data processing with multivariate methods has proved to be particularly efficient (Fig. 8). I then compare these results with analyses of the dominant gastropod fauna and other associated groups.
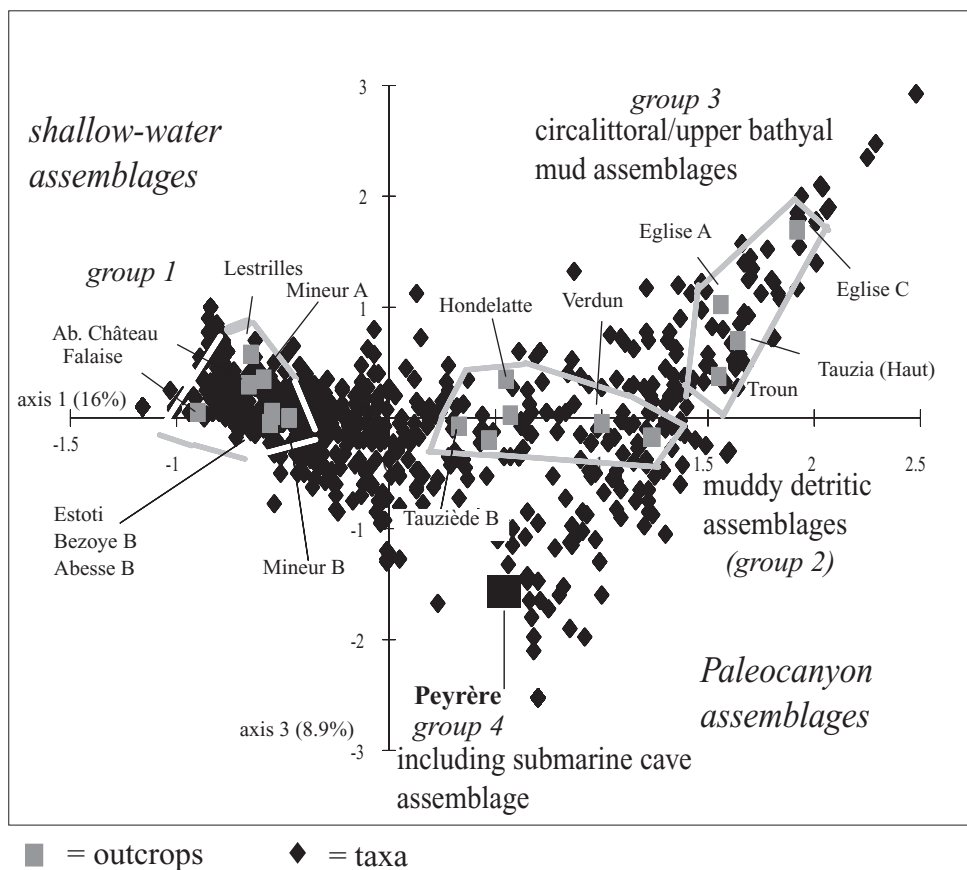

Figure 8. Relationships between taxa (1138 species) and sites (20 outcrops) using the second factorial plane (F1 and 3) of the CA. The distribution of the assemblages suggests segregation into four groups.

Gastropod factor analysis

The analysis involved 20 outcrops from which 80 000 specimens were taken, resulting in the identification of 1138 species. The material came from different sampling projects in a number of localities. The biodiversity data are not exactly comparable because the duration of excavation and sorting was not equal for all the sites; thus frequency is coded using a 4.3 ratio geometric progression (coded strengths vary between 0 and 6. Thus 0 = no specimens; 2 = 4–8; 3 = 19–80; 4 = 81–350; 5 = 350–1500; 6 = > 1500). For Frontier & Pichod-Viale (1991) this coding was adapted specifically for CA because it reduces the numerical difference between well and poorly represented species and more easily retains the patterns of variation in representation.

The three axes (F1–3) represent 35.3% of the total variability (information) of the global sample (F1 16%, F2 10.4%, F3 8.9%). F1 distinguishes, on the negative side, outcrops from the littoral zone and on the positive side, outcrops from the palaeocanyon zone (see Fig. 8). F2 discriminates a single outcrop, St-Paul-lès-Dax 'Falaise', which contributes 86% of the data. Species featuring strongly include *Olivia pygmaea* (Cossmann & Peyrot, 1917) (1.6%), *Strombus bonellii* Brongniart, 1823 (2.1%), *Bistolida* cf. *proflavicula* (Sacco, 1894) (2.1%), *Trivia* cf. *excoccinella* Sacco (1894) (1.6%), *Dorsanum lineolatum* (Grateloup, 1834) (2.1%), *Oliva dufresnei* Basterot, 1825 (2.1%), *Tudicla rusticula* (Basterot, 1825) (1.1%). It is interesting to note that these Miocene species appear for the first time in the Falaise outcrop. In fact, it contains a notably larger number of Miocene species than any other upper Oligocene deposit in the Adour Basin and has therefore been interpreted as the uppermost Oligocene layer of the basin (Lozouet, 1997).

F3 is characterized by the high contribution of Peyrère (60.4%) and of the two other outcrops of the palaeocanyon (St-Etienne-d'Orthe 'Eglise A', 11.6%; 'Eglise C', 16%). The second factorial plane (F1 and 3, Fig. 8) reveals the peculiar position of the Peyrère assemblage within the Adour Basin faunas, particularly those of the palaeocanyon. The distribution of the diverse assemblages suggests segregation into four groups:

(1) contains the shallow-water calcareous facies outcropping in the vicinity of Dax;
(2) contains muddy sand assemblages localized in the palaeocanyon;
(3) contains palaeocanyon mud assemblages (circalittoral to upper bathyal);
(4) is limited to the Peyrère fauna, another palaeocanyon locality.

Characteristic gastropod species of the Peyrère assemblage

Species which feature prominently in F3 can be considered as the most characteristic of the Peyrère assemblage. They are: *Nassarius aturensis* (Peyrot, 1925) (1.5%) *Alvania argillensis* Lozouet, 1988 (1.3%), *Gemmula rotata peyreirensis* (Peyrot, 1931) (1.3%), *Microglyphis* sp. (1.3%), *Calliotropis rivulusensis* Lozouet, 1999 (1.1%), *Bourdieria faviai* sp. nov. (1.1%), *Cantharus* sp. (1.1%), *Drilliolia sedentaria* Lozouet, 1998 (1%), *Bela pyrenaica* (Peyrot, 1931) (1%), *Praescissurella peyreirensis* Lozouet, 1998 (0.8%), *Emarginula teneraeformis* Lozouet, 1999 (0.8%), *Neritopsis moniliformis* Grateloup, 1832 (0.8%), *Hipponyx benoisti* (0.8%), *Ataxocerithium degrangei* (Cossmann & Peyrot, 1919) (0.8%) and *Triforis tertia* Lozouet, 1998 (0.8%).

Among these, *C. rivulusensis*, *Microglyphis* sp., *N. aturensis* and *G. rotata peyreirensis* are exclusive to the mud assemblages of the palaeocanyon; they were not collected in the outcrop (despite the name 'peyreirensis' for the *Gemmula*).

Those restricted to the outcrop include *B. faviai*, *P. peyreirensis* and *N. moniliformis*, while those which are simply found more frequently within it include *A. argillensis*, *E. teneraeformis*, *H. benoisti*, *A. degrangei*, *T. tertia*, *Cantharus* sp. and *B. pyrenaica*.

The presence of *Alvania*, *Cantharus* and *Bela* does not indicate a specific biotope. Conversely, *Bourdieria* and *Neritopsis* are significant indicators. In the Indo-West Pacific, *Neritopsis* is restricted to submarine caves (Kase & Hayami, 1992). The genus is also recorded from the Caribbean but only as dead shells; thus the habitat is not yet known. As mentioned above, *Bourdieria* is close to *Pisulina*, one of the best modern indicators of a submarine cave biocenosis. The other species have specialized feeding habitats and fit well into a sciaphilous sessile epifauna. The Cerithiopsidae (*Ataxocerithium*), Triforidae (*Triforis*) and Fissurellidae (*Emarginula*) feed on sponges. *Hipponyx* is semisessile. *Praescissurella* sp. has been collected from the outer reef slope in New Caledonia (Koumac, Expédition Montrouzier; see Bouchet *et al.*, 2002). The Scissurellidae move freely on rocky or gravelly substrates but also live in submarine caves where they are particularly common (Kase & Hayami, 1992; Di Geronimo *et al.*, 1997). Apart from these highly characteristic species, I have also identified in the Peyrère assemblage the earliest fossil species of *Larocheopsis* (*Larocheopsis marshalli* Lozouet, 1998; Scissurellidae, Larocheinae). This Oligocene species is very close to *L. tesselata* (Kase & Kano, 2002), which lives in a Pacific submarine cave. Kase & Kano (2002) proposed including *L. marshalli* and *L. tesselata* within a new genus, *Trogloconcha*. Another Recent species referred to *Trogloconcha* (*T. ohashii* Kase & Kano, 2002) is

widely distributed throughout the Indo-West Pacific. It lives at depths of between 4 and 51 m, in gloomy to totally dark caves that are incompletely filled with calcareous muddy sands (Kase & Kano, 2002).

Thus, the characteristic species of Peyrère identified by the CA are those which inhabit cryptic environments or hard substrates with sessile fauna.

Common gastropods

The most common species of the Peyrère assemblage are listed in Table 1. The outcrop contains more than 400 species of Gastropoda. In the studied samples, 387 species were identified among 12 117 specimens; of these, only 25 comprise 66% (7980 specimens) of the total. Members of the muddy detrical assemblage (*Alvania peyreirensis*, *Ringicula semidecorata*, *Benthonellania antepelagica*, *Alvania discazorum*, *Turritella raulini*, *Diastoma ultimum*, *Ceritoturris fecunda*,

Streptodictyon (*s.l.*) sp. and *Circulus pseudogymnobasis*) are common in several localities of the palaeocanyon, accounting for 49.6% of the total.

Homalopoma, a common group of hard bottom dwellers, includes several species adapted to cryptic environments: *H. sanguineum* (Linné, 1758) is frequent in Mediterranean submarine caves (Di Geronimo *et al.*, 1997), while other *Homalopoma* species are common in the Ryukyu submarine caves (T. Kase, pers. comm.).

Species of the family Pickworthiidae, such as *Mareleptopoma* cf. *kenneyi*, are very characteristic of modern submarine cave environments (Kase, 1998) but are not strictly restricted to them. They have been also collected hidden under stones in the littoral zone (Touho, New Caledonia; S. Gofas & A. Warén, pers. comm.). Considering the size of the Pickworthiidae (ranging between 0.5 mm and a few millimetres), cryptic conditions are easily found in coarse detrital

Table 1. The 25 most common species of Peyrère (66% of the total specimens) ranked in decreasing order of abundance. *Species characteristic of muddy bottom environments. †Species restricted to, or commonest in, the outcrop. Substrate conditions and food sources are deduced from those of their modern counterparts

Taxa	Substrate conditions	Food source	Number of specimens
Alvania peyreirensis Cossmann & Peyrot, 1919*	vagile on muddy bottom	detritus	1100
Ringicula semidecorata Morlet, 1882*	vagile on muddy bottom	foraminifera, detritus	980
Crisilla vera (Cossmann & Peyrot, 1919)	vagile on algae	algae, detritus	790
Homalopoma granulosa (Grateloup, 1828)	vagile on hard bottom	algae detritus	627
Benthonellania antepelagica Lozouet, 1990*	vagile on muddy bottom	detritus	560
Alvania argillensis Lozouet, 1998†	vagile on muddy bottom?	algae, detritus	398
Alvania discazalorum Lozouet, 1998*	vagile on muddy bottom	algae, detritus	356
Mareleptopoma cf. *kenneyi* (Ladd, 1966)†	vagile on hard bottom	detritus?	333
Turritella raulini Cossmann & Peyrot, 1922*	vagile on muddy bottom	suspended material	280
Pusillina cf. *grateloupi* (Vergneau-Saubade, 1968)	vagile on algae	algae, detritus	251
Monodontella peyreirensis (Cossm. & Peyrot, 1917)†	vagile on hard bottom	algae, detritus	247
Jujubinus quantulus Lozouet, 1999†	vagile on algae	algae, detritus	234
Diastoma ultimum Cossmann & Peyrot, 1922*	vagile on muddy bottom	detritus	213
Ceritoturris fecunda Lozouet, 1999*	vagile on muddy bottom	polychaetes	195
Streptodictyon (*s.l.*) sp.*	vagile on muddy bottom.	carrion, polychaetes, etc.	171
Scissurella lamellosa Benoist, 1875	vagile on hard bottom	algae, detritus	162
Bourdieria faviai sp. nov.†	vagile on hard bottom	detritus	138
Agathodonta moulinsii (Grateloup, 1827)†	vagile on hard bottom	algae, detritus	134
Volvarina aturensis (Peyrot, 1928)	vagile on hard/muddy bottom	carrion?, fish	130
Stosicia buccinalis (Grateloup, 1828)†	vagile on algae or hard/muddy bottom	algae, detritus	129
Hespererato cf. *rhenana* Schilder, 1933†	vagile on hard/muddy bottom	ascidians	117
Olivia oligocaenica Lozouet, 1999†	vagile on hard bottom	algae, detritus	114
Cantharus sp.†	vagile on hard/muddy bottom	carrion, polychaetes, etc.	110
Circulus pseudogymnobasis Lozouet, 1998	vagile on muddy bottom	detritus?	107
Amphithalamus immigrus Lozouet, 1998	vagile on algae	algae, detritus	104
Total			7980

habitats. *Crisilla vera* and *Pusillina* cf. *grateloupi* are very common in calcareous shallow-water facies and probably fed on algae. In any case, these species cannot be associated with a muddy bottom. The Trochidae (*Monodontella*, *Agathodonta*, and *Olivia* (= *Danilia*)) live on hard substrates. *Olivia* spp. were probably restricted to deep-water coral communities (Hickman & McLean, 1990). *Jujubinus* as well as the rissoid *Stosicia* occur more frequently on algae and sea grasses, although some species of the latter are possible inhabitants of cryptic environments. *Volvarina* occurs not only in the palaeocanyon sediments but also in the littoral calcareous sand near Dax. The Triviidae (*Hesperato*) prey on ascidians. The ecology of the genus *Amphithalamus* is not known with certainty although Keen & Smith (1961) indicated that some species are very common at the bases of *Caulerpa*. *Amphithalamus* and the pickworthiid *Mareleptopoma* are very common in the Chattien deposits of the Adour Basin. These species are well preserved in the shallow-water facies and in the Peyrère assemblage. In the other palaeocanyon outcrops, they are poorly preserved.

Comparison between the global Adour Basin malacofauna and the more specific locality of Peyrère demonstrates that the palaeocanyon assemblages are products of the mixture of contrasting biocenoses. One assemblage suggests life in muddy sediments at depths corresponding to the outer shelf or upper slope (circalittoral to upper bathyal), while the others were probably transported from shallower biotopes including biogenic substrates and cryptic habitats.

Other molluscs and sessile or encrusting animals

The other principal molluscs are bivalves, with the Arcidae making up the bulk of the biomass. The commonest species, *Barbatia lithomoides*, seems to be restricted to Peyrère. The deformation of the valves indicates a habitat in crevices and microcavities. Morphology of *B. lithomoides* is very similar to that of *Litharca lithodomus* (Sowerby, 1833) of the Panamic province (R. von Cosel, pers. comm.) which is cryptophilic (Keen, 1971: fig. 76). Among other common bivalves we note *Venericardia ruginosa*, *Spondylus* sp. and *Dimya* sp., all of which are sessile. Some oysters doubtfully referred to *Pycnodonte* might have been encrusting hard substrates at the entrance of submarine caves (Kase & Hayami, 1992; Hayami & Kase, 1996). Hayami & Kase (1993b) have also indicated as occurring in the submarine caves of the Ryukyu islands, the arcids *Bentharca*, *Bathyarca* (common at Peyrère), the mytiloid genera *Brachidontes*, *Septifer*, *Crenella*, *Urumella* and various Philobryidae. Apart from *Urumella*, all are present in Peyrère. In the Japanese submarine caves there are also members of the Propeamussiidae (not present in Peyrère), Limidae

and Carditidae (common at Peyrère). The biodiversity of Bivalvia is not as high as in Ryukyu, with many small, fragile elements absent. This suggests that Peyrère does not represent the primary environment of most of the molluscs. Because the assemblage brings together various biocenoses from diverse environments, it is to be expected that the most fragile transported elements are absent.

Many large and minute brachiopods including megathyridids (*Megathiris*, *Argyrotheca*) and thecideids (*Lacazella mediterranea* (Risso, 1826)) have been collected at Peyrère. The definitely sciaphilous affinity of *Lacazella* and *Argyrotheca* suggest either a circalittoral or shaded substrate (Pajaud & Plaziat, 1972). For Laubier (1966), *Megathiris* and *Argyrotheca* are strictly cryptobiotic, being found in closed cavities. Among the abundant Serpulidae (Polychaeta) of Peyrère, *Placostegus* is restricted to cryptic environments. Coral debris is very frequent; the most common type collected in the sample of marl of about 800 kg is a caryophylliid identified by H. Zibrowius (pers. comm.) as *Polycyathus*, a genus generally living on rocky circalittoral cliffs. An overturned large block of *Porites*, 1 m long and 80 cm high clearly demonstrates transportation in a mud flow. The shallow water interpretation of Scleractinaria (Cahuzac & Chaix, 1996) is obviously based on these reworked littoral elements, whereas a major part of the coral assemblage is of circalittoral affinity, as demonstrated by Chevalier (1963).

Palaeoenvironmental interpretation of the fossil assemblage of Peyrère

The modern ecology of most of the representative genera suggests that this assemblage results from the amalgamation of circalittoral muddy bottom molluscs and hard substrate dwellers including those from cryptic habitats. However, some species could also be related to photophilic (infralittoral) algae (*Julia*, *Amphithalamus*). A precipitous slope must have limited a shallow platform favourable to hermatypic corals and marine phanerogams, with its cliff and caves or crevices. Overhangs, crevices or caves favour sciaphilic organisms, even at the limited depth compatible with photophilic assemblages.

As a result, the very rich fauna of this locality illustrates the ecological diversity of adjacent biotopes brought together by the steep canyon topography. Rock and cave dwellers of various depths accumulated in the circalittoral mud at the base of a cliff. Slumping and mud-flow processes might account for the mixture of well-preserved shells of diverse origins but the most important feature is the topographic contrast of this setting. It is also apparent that the littoral contribution is mainly gastropods living on algae and hard

substrates. The most common fossils of the sandy shallow-water facies collected in the Adour Basin are missing: Naticidae (*Natica, Neverita, Polinices*), Nassariidae (*Keepingia*), Ampullospiridae, Olividae (*Oliva, Anazola*), Terebridae (only two specimens of *Hastula*), Cylichnidae (*Acteocina*), Ringiculidae (*Ringicula minor, R. ventricosa*). This indicates clearly that the shallow-water malacofauna of Peyrère is contributed by fauna from hard bottom biotopes.

The malacofauna is therefore consistent with deposition at depths corresponding to the circalittoral zone at around 60–95 m, according to the Mediterranean data collected by Pérès (1982). This is in good agreement with evidence from fish otoliths (Steurbaut, 1982) and corals. The mass transport resulted from nonbiological processes (debris flow rather than the action of currents) because only a few specimens are worn. The outcrop is located near the head of the palaeocanyon (Fig. 7), so it may be inferred that the submarine morphology includes cliffs submerged during the previous immersion of the Adour Basin. During the fieldwork, some huge blocks of Eocene limestone (containing *Nummulites*) were discovered in the marine marl sequences, thus corroborating submarine cliff collapse.

However, the originality of the Peyrère assemblage is clearly due to the abundance of elements of hard substrates and cryptic habitats. The CA highlights the distinctiveness of its malacofauna among the various sites of the palaeocanyon, the presence of *Neritopsis* and *Bourdieria* being particularly characteristic. The collection of marine neritiliids is thus part of the remains of an Upper Oligocene submarine cave fauna and could be the best indicator of such an environment.

Other European faunas suspected of concealing submarine-cave fossils

We have no record of a specific submarine cave malacofauna in the European Cenozoic; however, in light of the Peyrère assemblage it is possible to identify some likely localities. Five such environments are now examined, ranging from the Palaeocene (Danian), Lower Eocene (Ypresian) and Lower Miocene (Aquitanian and Burdigalian) to the Middle Miocene.

The rich malacofauna of the coral limestones of the Danian of Fakse (Denmark) has been recently compared to that of Peyrère (Schnetler, Lozouet & Pacaud, 2001). Some species are very similar (e.g. *Praescissurella peyreirensis* Lozouet, 1998 and *P. ravni* Schnetler, Lozouet & Pacaud, 2001). The Pickworthiidae are present, although the Neritopsidae and Neritiliidae were not recorded (K. I. Schnetler, pers. comm.). In the Paris Basin, the Vigny assemblage (Danian) is very similar to that of Fakse according to

Meyer (1987) and Pacaud, Merle & Mayer (2001), with neritopsids found. The Lower Eocene (middle Ypresian) of the 'Tuilerie de Gan' (Pyrénées-Atlantiques, south-western France) has a very rich malacofauna (Cossmann, 1923). According to Merle (1985) it is similar to the Hungarian Upper Oligocene 'Hinia and *Cadulus* community' of Baldi (1973), and interpreted as a circalittoral to upper bathyal muddy bottom association. Dolin *et al.* (1985) also suggested that it is a silty or muddy detrital assemblage. As the Hungarian assemblage closely resembles those of the Adour palaeocanyon (confirmed by Nolf & Brzobohaty, 1994, in a study of the fish otoliths), the supposed global autochthony of the Gan malacofauna becomes doubtful (Dolin *et al.*, 1985). It is clear that the latter cannot be interpreted as a homogeneous community. Analysis reveals a mixture of inhabitants typically found in cryptic environments: *Neritopsis* and the Pickworthiidae (*Gania carinata* Bandel & Kowalke, 1997) are particularly common (J. Le Renard, pers. comm.). Various sessile organisms have been also collected: Brachiopoda, Serpulidae, Bivalvia (*Spondylus*, *Dimya*) and Gastropoda (Vermetidae, Siliquariidae). Sponge-eating Gastropoda (Cerithiopsidae, Triforidae) are common. The cryptic species of Gan are therefore not as abundant as at Peyrère, though clearly present.

In the Lower Miocene Saubrigues palaeocanyon (Upper Burdigalian) (Fig. 7) several outcrops yielded submarine cave molluscs indicating assemblages typical of muddy bottom environments. At St-Martin-de-Hinx a new neritopsid and three species of Pickworthiidae have been identified. In the Paratethys, Badenian stage (lower part of the Middle Miocene), Kostej (Romania) is one of the most famous outcrops yielding a rich malacofauna from which many new species of gastropods have been described (von Zilch, 1934). It is clear that the similarity between the Kostej and the Peyrère faunas reflects the same diversity of environments (Lozouet, 1997). Cryptic elements are the Neritopsidae and Pickworthiidae associated with Brachiopoda (Megathyridae, Thecideidae) and numerous sponge-eaters (Cerithiopsidae, Triphoridae).

These assemblages have been deposited in a circalittoral muddy environment at the foot of a submarine relief. However *Neritopsis moniliformis* and *Mareleptopoma* cf. *kenneyi*, both indicators of cryptic environments, are also very common in the very shallow-water facies of St-Paul-lès-Dax 'Maïnot' (Lower Miocene, Aquitanian). This is not a contradictory situation; in the Ryukyu archipelago (Hayami & Kase, 1993b) the entrances of submarine caves containing typical cave malacofauna range between mean sea level and depths of *c.* 40 m. The fauna is therefore easily reworked in beach deposits.

These brief analyses show that remains of submarine cave faunas are present in some outcrops. Future

investigations should uncover further assemblages with submarine cave elements.

DISCUSSION

The fossil record of the Neritiliidae is now known to begin with the European Middle Eocene *Neritilia bisinuata* sp. nov. In Europe *N. neritinoides* ranges from the Lower Oligocene to the Lower Miocene (upper Burdigalian). The present-day biogeographical range of *Neritilia* (Fig. 9) includes West Africa, the Caribbean Islands and the Indo-West Pacific tropical province; all species live in freshwater close to the sea in tropical environments except for two species extending to south-western Japan (Kano *et al.*, 2001; Sasaki & Ishikawa, 2002) and subtropical eastern South Africa (Bandel & Kowalke, 1999).

Neritilia neritinoides is recognized as an element of freshwater fauna. Like other freshwater elements of the Tertiary fauna, such as the Stenothyriidae, Pomatiopsidae and Thiaridae (*Brotia*), the Neritiliidae probably disappeared from the European Atlantic domain during first major cooling period of the Tertiary, probably in the Middle Miocene (Serravallian) (Valdès & Lozouet, 2000). This climatic event constitutes one of the most important steps in the definition of the present-day freshwater Palaearctic fauna. The disappearance of the Pomatiopsidae and Stenothyridae can be correlated with the expansion of other prosobranchs like the Hydrobiidae (Lozouet, 1997) now dominant in the European brackish and freshwater malacofaunas.

Modern neritiliids lack conspicuous sculpture – the fossil *Bourdiera faviai* is the only known species with strong ribs. Therefore, fossil neritiliid species might easily be allocated to the Neritidae, which are in general strongly sculptured. In the Lower Miocene species *Pisulinella aucoini*, large teeth on the outer lip (as in *B. faviai*) are associated with a smooth shell. In the same way, *P. aucoini* closely resembles the Indo-West Pacific Miocene species *P. miocenica*; both have a smooth shell but differ in the thickness and size of teeth on the outer lip. The earlier *P. aucoini* has five strong teeth on the outer lip, whereas *P. miocenica* has many obscure tubercles. In modern *Pisulina*, teeth are totally absent. The fossil record is still too poor to make a strong claim for a direct phyletic line between *Pisulina* and *Bourdieria*, but it is possible to posit a hypothesis of a two-way evolutionary pathway of marine Neritiliidae during the Neogene, leading to the loss of sculpture and outer lip teeth.

Modern neritiliids are also restricted to the environment of submarine caves in the Indo-West Pacific (Kano & Kase, 2000b). The abundance of well preserved *B. faviai* in the Upper Oligocene outcrop of Peyrère, in association with the Neritopsidae and Pickworthiidae and other elements of cryptic faunas, can be seen as providing the first evidence of a submarine cave ecosystem during the Tertiary. While our knowledge of this environment is restricted to synchronously displaced fossil remains, its *in situ* preservation must be considered exceptional (Taylor & Palmer, 1994). Few studies have been carried out on the molluscan faunas of submarine caves because these are among the most difficult habitats to study. The first detailed works address the littoral marine caves of the Mediterranean (Starmühlner, 1955; Cattaneo-Vietti & Fluvio-Russo, 1987; Balduzzi *et al.*, 1989). Because the Mediterranean suffered various extinctions of climatic and eustatic origin, in addition to recolonization events during the Pleistocene, neoendemisms do not appear to have occurred. While it may be argued that
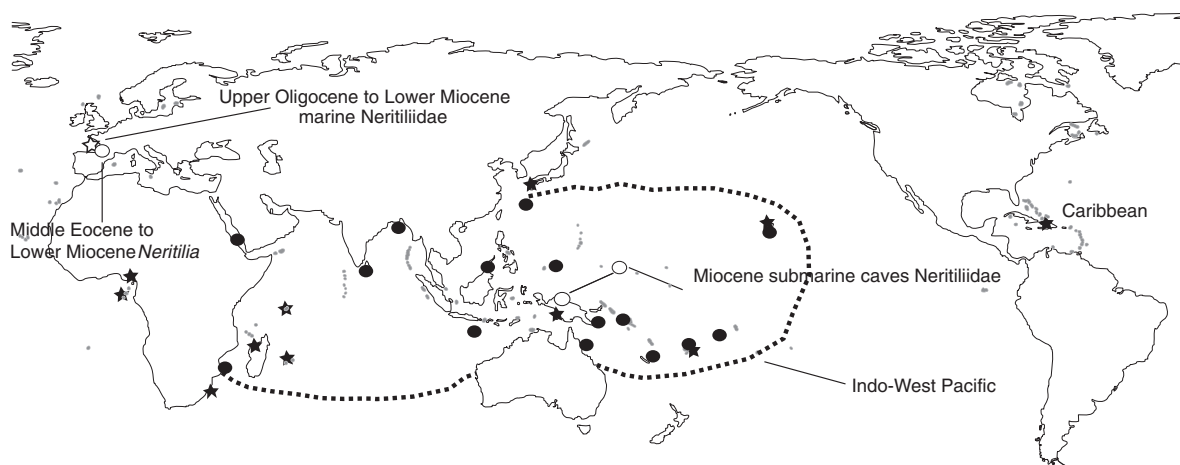

Figure 9. Geographic distribution of the Recent marine Neritiliidae (dotted line) and principal occurrences of the genus *Pisulina* (●); fossil occurrences of the marine Neritiliidae (○); occurrences of the Recent (★) and fossil (☆) freshwater Neritiliidae.

the submarine cave environments of the Mediterranean are not particularly noteworthy (Balduzzi *et al.,* 1989), the Indo-West Pacific shoreline did not undergo similarly dramatic events. It appears that the submarine coral-reef caves preserved a very original fauna (Kase & Hayami, 1992; Hayami & Kase, 1993a). The Indo-West Pacific province inherited its fauna from the vast pan-tropical Mesogean (Palaeogene Tethyan) province. Because of its relative stability and its great latitudinal extension, this area harbours the greatest species diversity for any group, particularly molluscs (Bouchet *et al.*, 2002). The presence of the Neritopsidae, Pickworthiidae and marine Neritiliidae in the Peyrère assemblage reveals a pan-tropical biogeography rather than an anachronistic Indo-West Pacific affinity. It provides evidence of ancient and modern submarine cave faunas, traced definitively to the Upper Oligocene, but probably appearing earlier, in the Tertiary, with associations becoming differentiated at the genus level prior to the Eocene. Its presence suggests that Tertiary fossils from similar environments will continue to be found in Europe.

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