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The Early Paleogene muricids (Mollusca, Neogastropoda) from the Oiching beds (Haunsberg area, Salzburg, Austria): revision and addition to the knowledge of the evolution of the Paleocene and Lower Eocene *Poirieria*

Didier Merle and Jean-Michel Pacaud*)

with 3 plates and 1 text-figure

Kurzfassung

Die drei Muricidae-Arten, die aus dem oberen Thanet und dem unteren Ypres der Schichten von Oiching bei Salzburg (Österreich) beschrieben worden sind, werden revidiert. *Poirieria braumuelleri* Traub, 1979 wird in die Gattung *Solenosteira* Dall, 1890 (Buccinidae) eingeordnet. *Hexaplex (Paziella) robusta* Traub, 1980, wird als Synonym von *?Poirieria levis* Traub, 1979 angesehen. Die generische Einordnung von *P. levis* wird bestätigt. Ergänzende Erläuterungen werden zu der Skulptur-Entwicklung des *Poirieria*-Arten aus dem unteren Paläogen gegeben.

Abstract

The three muricid species described from the Thanetian and the lower Ypresian of the Oiching beds, near Salzburg (Austria) are revised. *Poirieria braumuelleri* Traub, 1979 is transferred in the buccinid genus *Solenosteira* Dall, 1890. *Hexaplex (Paziella) robusta* Traub, 1980 is regarded as a synonym of *?Poirieria levis* Traub, 1979. The generic assignment of *P. levis* is confirmed. Further comments on the sculptural evolution of the Early Paleogene *Poirieria* are given.

Résumé

Les trois espèces de Muricidae décrites du Thanétien et de l'Yprésien inférieur des couches d'Oiching, près de Salzburg en Autriche, sont révisées. *Poirieria braumuelleri* Traub, 1979 est transférée dans *Solenosteira* Dall, 1890, genre de Buccinidae. *Hexaplex (Paziella) robusta* Traub, 1980 est considérée comme un synonyme de *?Poirieria levis* Traub, 1979. L'assignation générique de *P. levis* est confirmée. Des commentaires supplémentaires sont donnés sur l'évolution sculpturale des *Poirieria* du Paléogène inférieur.

*) Laboratoire de Paléontologie, Muséum national d'histoire naturelle, UMR 8569 CNRS – 8, rue Buffon, 75005 PARIS. (dimerle@aol.com ; pacaud@mnhn.fr)

1. Introduction

Three muricid species have been described from the Thanetian and the lower Ypresian of the Oiching beds, near Salzburg, (TRAUB 1979, 1980, TRAUB & WERNER 1993): *?Poirieria levis* TRAUB, 1979, *Poirieria braumuelleri* TRAUB, 1979 and *Hexaplex (Paziella) robusta* TRAUB, 1980. The opportunity to examine this material and a method to analyse more closely the muricid morphology have encouraged us to propose this small revision.

The descriptive method used here has already been presented in several works concerning the systematics of fossil and recent muricids (MERLE 1999, 2001, 2002, MERLE et al. 2001, HOUART 2000, 2001). Among these works, some primitive species [*Paziella cretacea* (GARVIE, 1991), *P. dyscrita* (COSSMANN, 1889), *P. septemcostata* (ROUAULT, 1850) and *Poirieria subcristata* (D'ORBIGNY, 1850)], slightly similar to the Oiching muricids, have been studied (MERLE & PACAUD 2002). The principle of this method (MERLE 1999, 2001) is based on the research of structural homologies. For the spiral sculpture (cords and internal denticles of the outer lip), they are identified by the ontogenetic and topological correspondences of the characters. These homologies are coded by text-conventions (MERLE 2001, 2002, MERLE et al. 2001) giving a clear presentation of the characters, missing in the traditional descriptive method (HYLLEBERG & NATEEWATHANA 1992).

2. Abbreviations and text-conventions

Repository: ANSP: Academy of natural Sciences, Philadelphia, Pennsylvania, USA; BSP: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; GSA: Geological Survey of Alabama, Tuscaloosa, Alabama, USA; MNHN-LP: Muséum national d'Histoire naturelle, Laboratoire de Paléontologie, Paris, France; NHM: Natural History Museum, London, England; USNM: U.S. National Museum, Washington, USA.

Text-conventions used in this paper: P: primary cords (= cords appearing in first order); IP: infrasutural primary cord; P1: shoulder cord; P2 to P6: primary cords of the convex part of the whorl; ADP: adapertural siphonal primary cord; MP: median siphonal primary cord; s: secondary cords (= cords appearing in second order); D: denticles of the outer lip (D1 to D6).

3. Systematics

Class Gastropoda CUVIER, 1797

Section Neogastropoda, THIELE, 1929

Superfamily Muricoidea RAFINESQUE, 1815

Family Muricidae RAFINESQUE, 1815

Subfamily Muricinae RAFINESQUE, 1815

Genus *Poirieria* JOUSSEAUME, 1834

Type species: *Murex zelandicus* QUOY & GAYMARD, 1833 (Recent, New-Zealand), by original designation.

Poirieria levis TRAUB, 1979

Pl. 1, figs 1–2; pl. 2, figs 1–2

? Poirieria levis TRAUB, 1979: 107–108, pl. 15, fig. 3a–b.
Hexaplex (Paziella) robusta TRAUB, 1980: 39, pl. 5, fig. 5a–b. (nov. syn.)

Type-locality: Kroisbach, Kch 8 (Oiching beds, Thanetian).

Material: Holotype of *?P. levis,* BSP 1943 II 334 (H: 37.3 mm, W: 36.3 mm including spines); holoype of *Hexaplex (Paziella) robusta,* BSP 1943 II 385, lower Ypresian of Kroisbach, Kch 11a (H: 8.34 mm, W: 5.1 mm).

Description: Two preserved whorls of a conispiral protoconch. Biconical teleoconch up to 37.3 mm in height and up to 11.8 mm in width without P1 spine (36.3 including P1 spine). Five subangular whorls. Last whorl up to 76 % of the total shell height. Apical angle up to 85° (spine included) and up to 50° (spine excluded). Intervarical expression of spiral sculpture with poorly marked spiral cords and varical expression with cord spines. First whorl: spiral sculpture not preserved. Second whorl: formation of a subspinose fold corresponding to the appearance of shoulder cord (P1). Third whorl: appearance of a small spine on shoulder (P1). Fourth whorl: P1 spine developed, open and slightly subtubiform adaperturally. Fifth and last whorl: sutural ramp and siphonal canal smooth: two primary cord spines P1 and P2 poorly developed. Axial sculpture with simple varices of one layer. Aperture up to 62 % of total shell height and up to 40.5 % of width. Outer lip orthocline without internal denticles. Shoulder sinus deep, widely open. Columellar lip smooth, adherent. Siphonal canal open, up to 32.3 % of aperture height. Pseudumbilicus straight.

Comments on the species: While describing *Hexaplex (Paziella) robusta,* TRAUB (1980) thought that the holotype perhaps corresponds to a young specimen. We agree with this point of view, and think that it is a juvenile of *Poirieria levis* TRAUB, 1979. Our opinion is based on the spiral sculpture, which exactly looks like in the first teleoconch whorls of *P. levis* (Pl. 1, figs 1–2). The spiral sculpture forms subangular whorls due to the formation of P1 spine. Despite the holotype of *H. (P.) robusta* is eroded, it is possible to observe the formation of a slightly subtubiform P1 spine (Pl. 2, fig. 2), such as in *P. levis.* The holotype of *H. (P.) robusta* lacks a P2 spine (Pl. 1, figs 2), but in the Lower Tertiary *Poirieria* the development of the P2 spine starts late in the ontogenesis (MERLE & PACAUD 2002). The young and the adult stages of *P. subcristata* (D'ORBIGNY, 1850) from the Anglo-Parisian Ypresian (Pl. 2, figs 3–4), are here illustrated to compare with *P. levis*, and to show that young *Poirieria* are less sculptured than adults. Consequently, *Hexaplex (Paziella) robusta* TRAUB, 1980 is proposed as a junior synonym as *P. levis* TRAUB, 1979.

Generic assignment: This species cannot be included in *Hexaplex* PERRY, 1811 [type-species: *Hexaplex cichoreum* (GMELIN, 1791) by subsequent designation (IREDALE, 1915)], a genus with numerous and complex sculptural elements from the shoulder to the siphonal canal (MERLE 2001, fig. 10F). *Hexaplex* also possesses an anal sulcus lacking in *Poirieria levis.*

Paziella JOUSSEAUME, 1880 (type-species: *Murex pazi* CROSSE, 1869 by original designation) is most similar to *P. levis* and less sculptured than *Hexaplex.* However, the species of *Paziella* differ by the construction of their shoulder cord spines, which do not become adaperturally subtubiform in the adult stage. Other cord spines are rarely developed in *Paziella* and internal denticles of the outer lip are often present (MERLE 2001, fig. 10A-D, MERLE & PACAUD 2002, text-fig. 3.1–10 and text-fig. 4.1–10).

The fossil genus *Crassimurex* MERLE, 1990 (type-species: *Murex calcitrapa* LAMARCK, 1803 [Lutetien, Paris basin] by O. D.) superficially ressemble to *P. levis* by their general features (developed P1 cord spine, angular teleoconch whorls, open siphonal canal and absence of anal

sulcus). They differ by having more numerous primary cords (P1 to MP which are often without associated cord spines), secondary cords (s3, s5 and s6), internal denticles (D1 to D4) (Pl. 3, fig. 3–4) and by lacking subtubular cord spines. Moreover, the primary cords of the young *Crassimurex* (s.s.) *calcitrapa* are more precocious and more numerous than in *P. levis* (Pl. 3, fig. 3).

Eopaziella Gürs in Welle, 1998, proposed with the type-species *Eopaziella deshayesii* (Nyst, 1836) by O. D. (Welle (1998)), is not available regarding the Article 13 (Name published after 1930) of the I. C. Z. N., because this author gave any description of *Eopaziella* (Art. 13.1.1) and referred to the unpushished thesis of Gürs (1995) (Art. 13.1.2). Gürs (2001) validly described *Eopaziella* with a differential diagnosis and gave the type-species: *Murex capito* Philippi, 1843. Gürs (2001) also introduced *Eopaziella* as subgenus of *Crassimurex*. According to Gürs, *Eopaziella* does not strongly differ from *Crassimurex*, because the same features occur in the two type-species: developed and non tubiform P1 spine, open siphonal canal, absence of anal sulcus, numerous primary cords (P1 to MP), secondary cords (s3, s5 and s6) and internal denticles (D1 to D4). The teleoconch whorls of the Oligocene species *(C. (E.) deshayesii* and *C. (E.) capito* (Philippi, 1843) included in the subgenus *Eopaziella* are only more angular, have less marked cords and are less spiny on the cords P2 to P4 than in typical *C.* (s.s.) *calcitrapa* (= *Murex crispus* Lamarck, 1803). But since the lower Bartonian, some specimens of *C. calcitrapa* from the Paris basin already have angular whorls and primary P2 to P4 without associated spines, showing a morphological transition between the Eocene and the Oligocene species (personal observations, D. M.). Therefore, *Eopaziella* may be regarded as a junior synonym *Crassimurex* Merle, 1990 or at least as a subgenus. In this work, we have preferred to consider *Eopaziella* as subgenus to maintain a disctinction between the Eocene group species (with *C.* (s.s.) *calcitrapa* and *C.* (s.s.) *rouaulti* (Merle, 1990)) and the Oligocene group species (with *C. (E.) deshayesiu* and *C. (E.) capito*).

By their cord spines becoming adaperturally subtubiform, by the few number of primary cords or cord spines (two to four) and by the absence of internal denticles of the outer lip, *P. levis* is most similar to the type-species of *Poirieria* Jousseaume, 1834: *Murex zelandicus* Quoy & Gaymard, 1833, but particularly to Palaeocene and Ypresian members of this genus.

Comparisons with Paleocene and Ypresian *Poirieria*: from the Paleocene and the Ypresian, three other species of *Poirieria* are recorded in the Atlantic Ocean. Two occur in western Atlantic (Vokes 1992): *Poirieria* sp. (Danian, Alabama) (Pl. 3, fig. 1) and *P. woodsensis* Vokes, 1970 (Thanetian to lower Ypresian, Alabama) (Pl. 3, fig. 2) and one occurs in the eastern Atlantic: *P. subcristata* (d'Orbigny, 1850) (lower Ypresian, England and France) (Pl. 2, figs 3–4). All these species have a low spire, a developed adaperturally subtubiform shoulder spine P1 and, lack spiral sculpture on the siphonal canal and internal denticles on the outer lip. The Danian species is 23.3 mm in height with four or five whorls. It differs from the other Atlantic *Poirieria* species and from *P. levis* in lacking the abapical cord spine on the convex part of the whorl (Pl. 3, fig. 1). *P. woodsensis* is 23 mm in height with five whorls. It bears the major cord spines (P3 and P4), which do not appear in *P. levis* possessing only P1 and P2 (Pl. 3, fig. 2). The largest specimens of *P. subcristata* reach 50 mm for 6 or 7 whorls. They look very much like to *P. woodsensis* because of the presence of the cord spines P1, P2 and P3 (Pl. 2, figs 3–4), but P4 is absent in *P. subcristata* (Merle & Pacaud 2002).

Family Buccinidae RAFINESQUE, 1815

Genus *Solenosteira* DALL, 1890

Type species: *Fusus pallidus* BRODERIP & SOWERBY, 1829 (Recent, West-America) by original designation.

Solenosteira braumuelleri (TRAUB, 1979) nov. comb.

Pl. 1, fig. 4

? Poirieria braumuelleri TRAUB, 1979: 107, pl. 15, fig. 2a–b.

Type-locality: Kroisbach, Kch11a (Oiching beds, lower Ypresian).

Material: Holoype of *S. braumuelleri* BSP 1943 II 335 (H: 42.9 mm, W: 20.5 mm).

Comments: This species has been previously compared with the Lutetian muricid *Crassimurex* (s.s.) *calcitrapa* (LAMARCK, 1803) (Pl. 1, fig. 6 and Pl. 3, fig. 3–4), due to some similarities (size, biconic shell, presence of spiral sculpture on the siphonal canal). *C.* (s.s.) *calcitrapa* differs from *Solenosteira braumuelleri* by having true abaxially oriented varices, a muricid familial character, and in lacking nodules. The shoulder spine P1, is also deeper in *C.* (s.s.) *calcitrapa* than in *S.* (s.s.) *braumuelleri*, and *C.* (s.s.) *calcitrapa* has more numerous cord spines (P1 to P4) with irregular appearance of secondary cords (s1, s3, s5 and s6). The anal notch and numerous growth striae on the siphonal canal are characters missing in the muricid *C.* (s.s.) *calcitrapa*.

Compared to other neogastropods, *S. braumuelleri* seems to be more closely related to the Lutetian buccinid *S. subcarinata* (LAMARCK, 1803) (= *Fusus muricoides* DESHAYES, 1835) (Pl. 1, fig. 5). The two species have nodulose varices, nodules becoming slightly spinose on the shoulder of the last teleoconch whorls, an anal notch and growth striae on the siphonal canal. *S. braumuelleri* differs from *S. subcarinata* in having a deeper anal notch, a less angular columella, and more developed shoulder spinelets. *S. braumuelleri* may be considered as the oldest known species of the genus *Solenosteira*.

4. Additional comments on the sculptural changes of the Lower Paleogene *Poirieria* members

In a previous paper (MERLE & PACAUD 2002), we discussed about the sculptural modifications in lower Paleogene *Paziella* and *Poirieria*, comparing the oldest authenticated muricid *Paziella cretacea* (GARVIE, 1991) (Late Campanian-Early Maastrichtian) with lower Eocene *Paziella* and with *Poirieria subcristata*. We showed that the spiral sculpture of these old muricids is poorly developed, particularly in the first stages of their growth. We also suggested that the sculptural changes probably result from ontogenetic heterochronies (ALBERCH et al. 1979, DAVID et al. 1986). A peramorphic evolution of sculptural characters (eg.: cords) may generate an increase in the sculptural development, while a paedomorphic evolution may generate a decrease in the sculptural development (MERLE & PACAUD 2002).

The comparisons with *Paziella cretacea* already indicated, that the strong development and the appearance of the cord spines P2 and P3 of *Poirieria subcristata* can be regarded as the result of an ontogenetic acceleration and a pre-displacement, which correspond to peramorphic heterochronies (MERLE & PACAUD 2002). The present study, concerning all Paleocene and lower Eocene *Poirieria*, brings more details on the sculptural evolution in this genus (fig 1). In

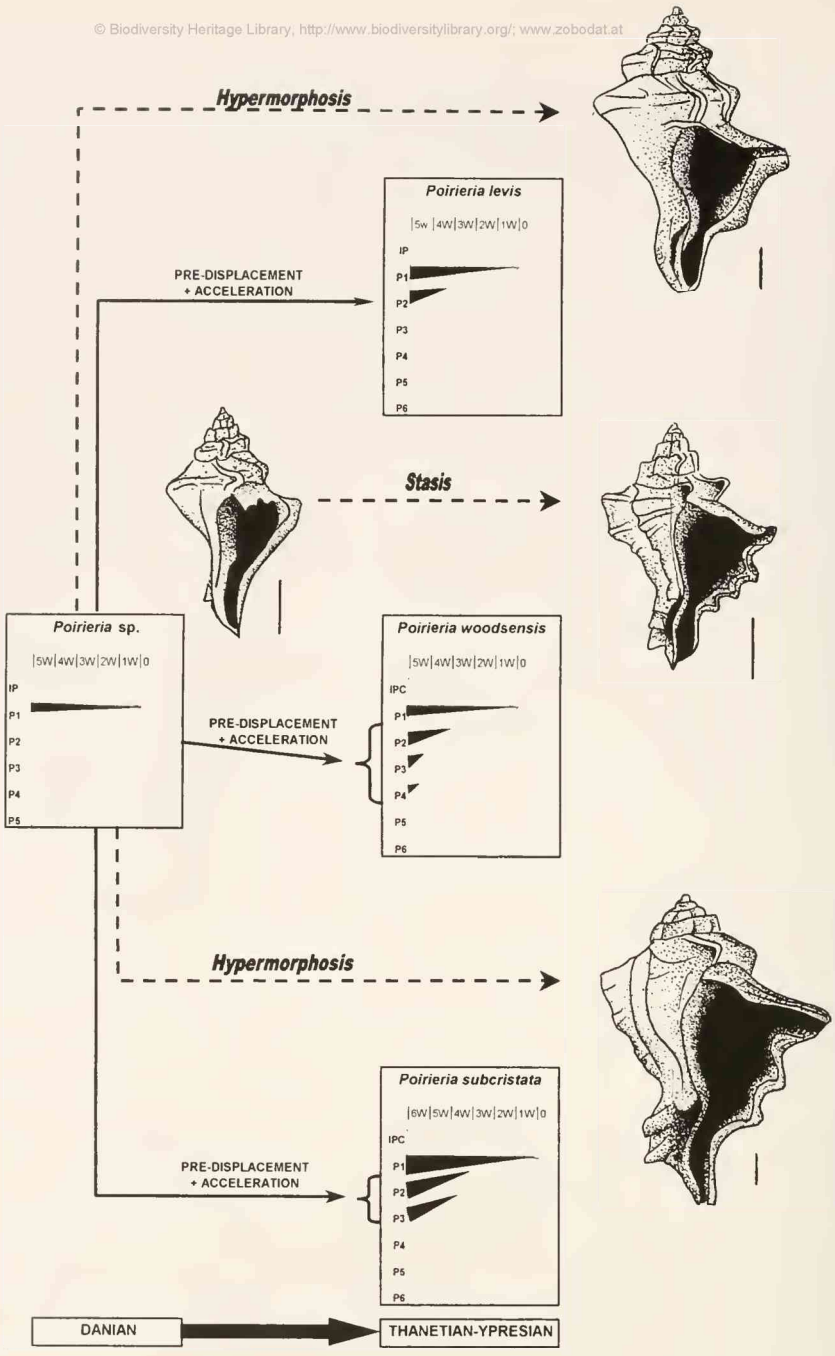

Fig. 1: Ontogenetic trajectories of the primary cords in *Poirieria*. *Poirieria* sp. (Danian, USA) is chosen as the primitive morphological reference. In *P. levis* (Thanetian-Ypresian, Austria), the pre-displacement and the acceleration of P2 cord spine are associated to a hypermorphic shell. In *P. woodsensis* (Thanetian, USA), P2, P3 and P4 cord spines are pre-displaced and the accelerated. In *P. subcristata* (Ypresian, England and France), P2 and P3 cord spines are associated to a hypermorphic shell. w = whorl. Scale bars = 5 mm.

the Danian *Poirieria* sp. (pl. 3, fig. 1a, b), only P1 spine is more developed than in *Paziella cretacea*, indicating a low sculptural divergence between the two genera in the Early Paleocene. Therefore, the addition and the development of abapical cord spines observed in *Poirieria* seems to occur later than the Danian. It is only observed in the three most recent species (Text. fig 1). Compared to *Poirieria* sp., P2 is added in *P. levis* (pl. 2, figs. 1, 2), P2 and P3 are added in *P. subcristata* (pl. 2, figs. 3, 4) and P2, P3 and P4 are added in *P. woodsensis* (pl. 3, fig. 2). *P. levis* shares the development of P2 spine with the two other species, but P3 and P4 spines do not appear at the end of its ontogenesis, showing that one part of the juvenile morphology of *Poirieria* seems to continue into adulthood of *P. levis*.

5. Conclusion

Only one muricid species, *Poirieria levis* TRAUB, 1979, is recognized, because *Hexaplex (Paziella) robusta* TRAUB, 1980 is regarded as a synonym of *P. levis* and *P. braumuelleri* TRAUB, 1979 is transferred in the genus *Solenosteira* DALL, 1890 (family: Buccinidae). *P. levis*, closely related to the Paleocene and lower Ypresian *Poirieria* from the North-Atlantic Ocean, is the oldest member of the genus in the Tethysian Ocean, while no *Poirieria* species are reported in the South-Atlantic Ocean and in the Pacific Ocean before the Middle Eocene (MAXWELL 1971). A disjunction of the Paleocene *Poirieria* biogeographic area due to the closure of the Carpathian sea way (PLAZIAT 1981, SMITH, SMITH & FUNNELL 1994) may explain two observations: the closest relationships of *P. levis* with the North-Atlantic *Poirieria* and its old occurrence in the Tethysian Ocean.

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Plates

Plate 1

Fig. 1a–b: *Poirieria levis* TRAUB, 1979, holotype (BSP 1943 II 334), Thanetian, Kroisbach, Kch 8, Austria (X 1.5)

Fig. 2a–b: *P. levis*, holoype of *Hexaplex (Paziella) robusta* TRAUB, 1980 (BSP 1943 II 385), Ypresian, Kroisbach, Kch 11a, Austria (X 6)

Fig. 3a–b: *Poirieria subcristata* (D'ORBIGNY, 1850), specimen MNHN-LP R62957 (coll. Pacaud), Ypresian, Celles-sur-Aisne, France (X 4)

Fig. 4: *Solenosteira braumuelleri* (TRAUB, 1980), holotype (BSP 1943 II 335), Ypresian, Kroisbach, Kch 11a, Austria (X 1.5)

Fig. 5: *Solenosteira subcarinata* (LAMARCK, 1803), specimen MNHN-LP R62967 (coll. Schtrock), Lutetian, Beynes, France (X 2)

Fig. 6: *Crassimurex (s.s.) calcitrapa* (LAMARCK, 1803), figured specimen of COSSMANN & PISSARRO (1911) MNHN-LP J02583 (coll. Cossmann), Lutetian, Villiers-St-Frédéric, France (X 2).

Plate 2

Poirieria levis TRAUB, 1979: dorsal and apertural views of the spiral sculpture

Fig. 1a–b: young specimen (BSP 1943 II 385) from Kroisbach, Kch 11a, Ypresian, Austria

Fig. 2a–b: adult specimen (BSP 1943 II 334) from Kroisbach, Kch 8, Thanetian, Austria

P. subcristata (D'ORBIGNY, 1850): dorsal and apertural views of the spiral sculpture

Fig. 3a–b: young specimen (MNHN-LP R62957, coll. Pacaud) from Celles-sur-Aisne, Ypresian, France

Fig. 4a–b: adult specimen (NHM 43731) from Highgate, Ypresian, England.
Scale bars = 5 mm.

Plate 3

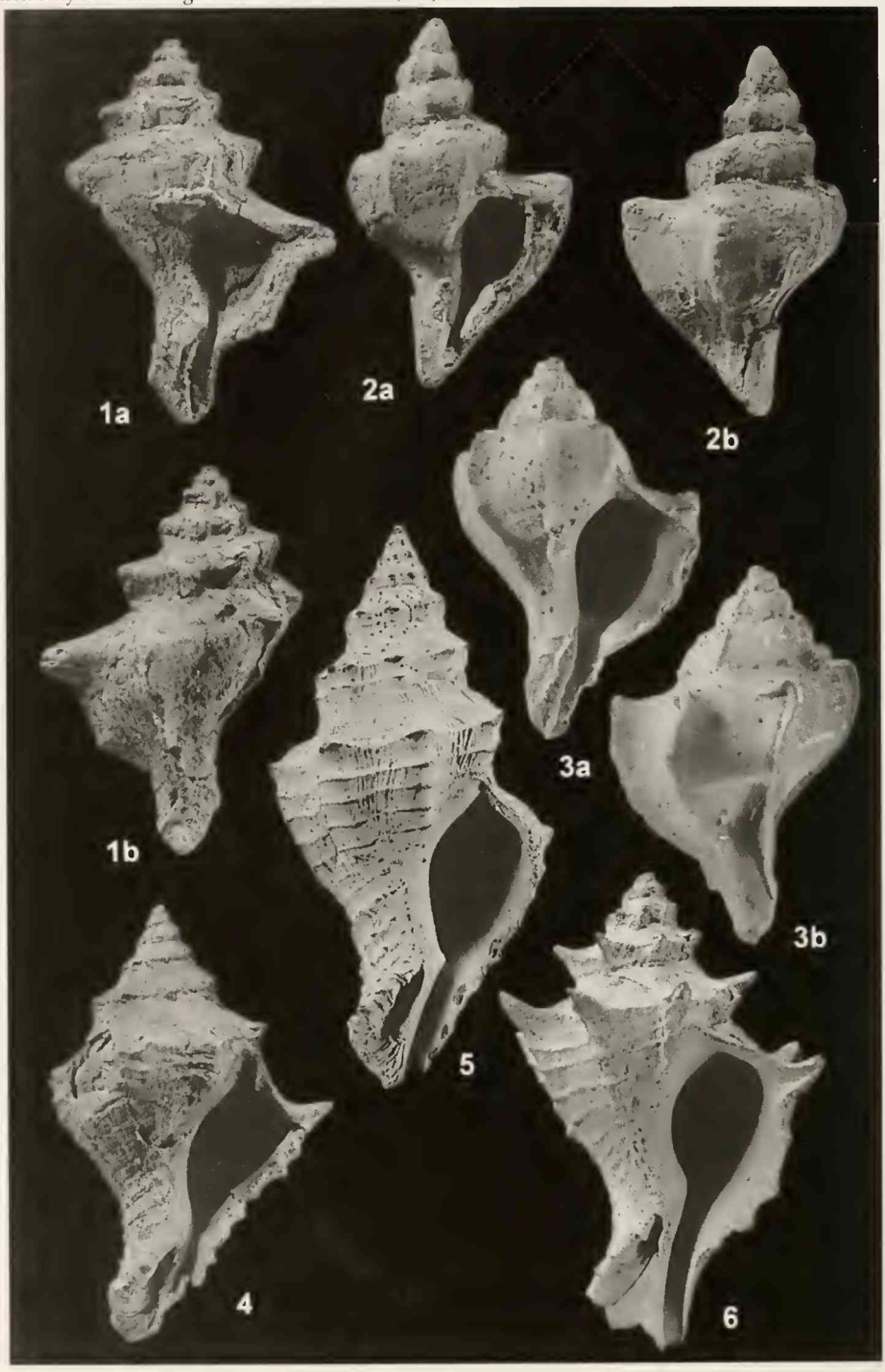
Fig. 1a–b: *Poirieria sp.*: dorsal and apertural views of the spiral sculpture, specimen GSA 160.2 from Matthews Landing, Danian, Alabama, USA (after VOKES, 1992)

Fig. 2: *P. woodsensis* VOKES, 1970: dorsal and apertural views of the spiral sculpture, holotype ANSP 7059 from Woods Bluff, Thanetian, Alabama, USA (after VOKES, 1992)

Crassimurex (s.s.) calcitrapa (LAMARCK, 1803): dorsal and apertural views of the spiral sculpture

Fig. 3a–b: young specimen (MNHN-LP R63472, coll. Merle) from Villiers-St-Frédéric, Lutetian, France

Fig. 4a–b: adult specimen (MNHN-LP R63473, coll. Merle) from Grignon, Lutetian, France.
Scale bars = 5 mm.



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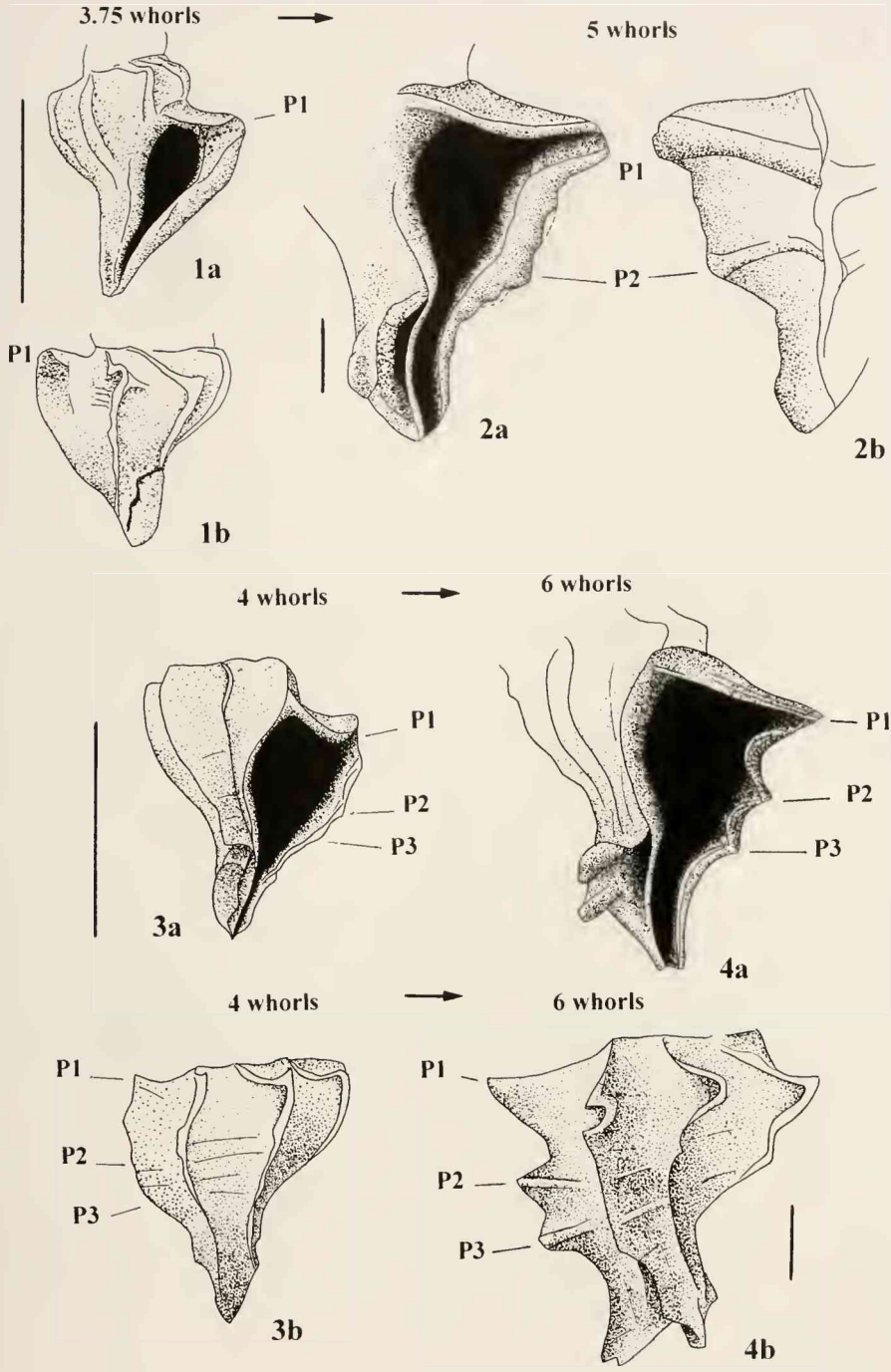
Tafel 1



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Tafel 2