

New species of *Eocithara* Fischer, 1883 (Mollusca, Gastropoda, Harpidae) from the Early Paleogene with phylogenetic analysis of the Harpidae

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ABSTRACT

This paper includes an addition to the knowledge of *Eocithara* Fischer, 1883 and a phylogenetic analysis of the related genera. Four *Eocithara* (s.s.) species are newly recorded in the lower Eocene of the Atlantic Ocean (*E.* (s.s.) *mutica* (Lamarck, 1803), *E.* (s.s.) *helenae* n. sp., *E.* (s.s.) sp. 1 and *E.* (s.s.) sp. 2). Three new species are described: *E.* (s.s.) *rosenkrantzi* n. sp. (Thanetian, Greenland), *E.* (s.s.) *helenae* n. sp. (Ypresian, France) and *E.* (s.s.) *eucosmia* n. sp. (Bartonian, France). For the first time, multispiral protoconchs of *Eocithara* (s.s.) are reported (*E.* (s.s.) *helenae* n. sp., *E.* (s.s.) *jacksonensis* (Harris, 1896) (Priabonian, USA) and *E.* (s.s.) *submutica* (d'Orbigny, 1852) (Rupelian, France)). This discovery invalidates the distinction between *Harpa* Röding, 1798 and *Eocithara* based on the protoconch (Rehder 1973). Then, a closer inspection of 31 teleoconch characters is provided and tested in a cladistic analysis including *Morum* Röding, 1798 (one Recent and one fossil species), *Eocithara* (s.s.) (five fossil species), *E.* (*Refluharpa*) Iredale, 1931 (one fossil species), *E.* (*Marwickara*) Laws, 1935 (one fossil species), *Harpa* (four Recent and one fossil species) and *Austroharpa* Finlay, 1931 (four Recent and one fossil species). The matrix has been processed by the software PAUP 4 and generates three equally parsimonious trees. The consensus tree suggests that all *Eocithara* are more closely related to *Harpa* than to *Austroharpa*. A considerable biogeographic congruence is noted (the Austral clades being clearly distinguished from the Thetyan clades) and the stratigraphical congruence is evaluated by the MSM (Manhattan Stratigraphic Measure) at specific and generic levels.

KEY WORDS

Mollusca,
Gastropoda,
Harpidae,
Eocithara,
Paleogene,
homology,
phylogeny,
new species.

RÉSUMÉ

Nouvelles espèces d'Eocithara Fischer, 1883 (Mollusca, Gastropoda, Harpidae) du Paléogène basal. Analyse phylogénétique des Harpidae.

Cette note propose une addition à la connaissance des *Eocithara* Fischer, 1883 et une analyse phylogénétique de genres proches. Quatre *Eocithara* (s.s.) sont nouvellement signalés dans l'Éocène inférieur de l'océan Atlantique (*E. (s.s.) mutica* (Lamarck, 1803), *E. (s.s.) helenae* n. sp., *E. (s.s.)* sp. 1 et *E. (s.s.)* sp. 2). Trois espèces nouvelles sont décrites : *E. (s.s.) rosenkrantzi* n. sp. (Thanétien, Groenland), *E. (s.s.) helenae* n. sp. (Yprésien, France) et *E. (s.s.) eucosmia* n. sp. (Bartoniien, France). Pour la première fois, des protoconques multispirales d'*Eocithara* sont observées (*E. (s.s.) helenae* n. sp., *E. (s.s.) jacksonensis* (Harris, 1896) (Priabonien, USA) et *E. (s.s.) submutica* (d'Orbigny, 1852) (Rupélien, France)). Cette découverte invalide la distinction entre *Eocithara* et *Harpa* Röding, 1798 fondée sur la protoconque (Rehder 1973). De ce fait, une étude détaillée de la téléconque s'est imposée. Ainsi, 31 caractères ont été testés dans une analyse cladistique incluant *Morum* Röding, 1798 (une espèce actuelle et une fossile), *Eocithara* (s.s.) (cinq espèces fossiles), *E. (Refluharpa)* Iredale, 1931 (une espèce fossile), *E. (Marwickara)* Laws, 1935 (une espèce fossile) et *Harpa* (quatre espèces actuelles et une fossile) et *Austroharpa* Finlay, 1931 (quatre espèces actuelles et une fossile). La matrice a été traitée par le programme PAUP 4 qui a généré trois arbres également parcimonieux. L'arbre de consensus strict suggère que les *Eocithara* sont plus proches de *Harpa* que de *Austroharpa*. D'autre part, une grande congruence biogéographique est observée (les clades austraux étant clairement individualisés des clades téthysiens) et la congruence stratigraphique est évaluée par un MSM (Manhattan Stratigraphic Measure) aux niveaux spécifique et générique.

MOTS CLÉS

Mollusca,
Gastropoda,
Harpidae,
Eocithara,
Paléogène,
homologie,
phylogénie,
nouvelles espèces.

INTRODUCTION

The family Harpidae Bronn, 1849 includes two subfamilies, the Moruminae Hughes & Emerson, 1987 and the Harpinae. According to Rehder (1973), the earliest members of the subfamily Harpinae belong to the fossil genus *Eocithara* Fischer, 1883 (type species: *Harpa mutica* Lamarck, 1803 by original designation). In the Thetyan Ocean, it is known through the Thanetian (Ranikot beds) of Pakistan (Cossmann & Pissarro 1909) with *E. (s.s.) morgani* (Cossmann & Pissarro, 1909). A younger species is also reported in the lower Eocene from New Zealand with *Eocithara* (s.s.) sp. (Rehder 1973) indicating the early occurrence of the genus in the South Pacific ocean. In the Atlantic Ocean, *Eocithara* occurs in the Thanetian of Greenland (*Eocithara* (s.s.) *rosen-*

krantzi n. sp.), but between the Thanetian and the Lutetian, no species has been recorded. The present paper fills this gap presenting new material from the lower Eocene (Ypresian) of the Paris and Aquitaine basins. Among the new material, one species possesses a multispiral protoconch and a closer inspection of younger species (*E. (s.s.) jacksonensis* (Harris, 1896) from the Priabonian of Mississippi and *E. (s.s.) submutica* (d'Orbigny, 1852) from Rupelian of Aquitaine) revealed other multispiral protoconchs (Fig. 1A-C). This kind of protoconch probably indicates a planktotrophic larval stage in *Eocithara*; planktotrophic larvae are widespread in Paleogene Neogastropoda (Hansen 1978; Lozouet 1997). However, it poses a problem of the harpid classification, because *Eocithara* is mainly distinguished from *Harpa* Röding, 1798 (type species: *Harpa harpa* Linnaeus, 1758 by ori-

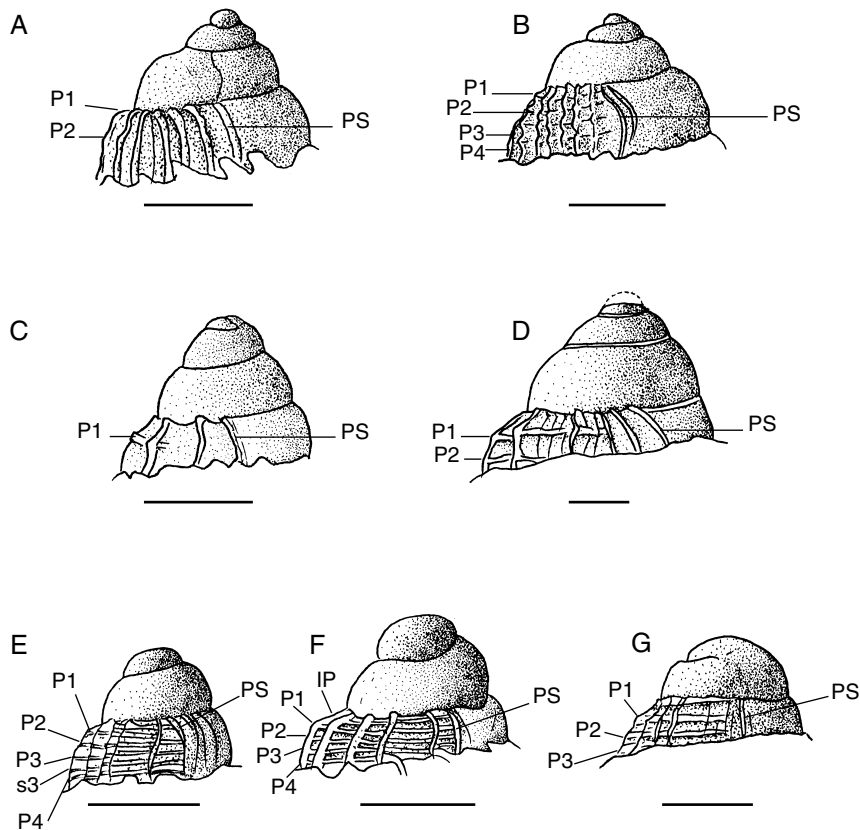


FIG. 1. — Multispiral (A–D), paucispiral protoconchs (E–G) and teleoconch early sculpture of harpids; **A**, *Eocithara* (s.s.) *helena* n. sp., holotype MNHN R63431, Tuilerie de Gan, Pyrénées-Atlantiques, France, Ypresian; **B**, *E. (s.s.) jacksonensis* (Harris, 1896), MNHN J05528 (Cossmann coll.), Jackson, USA, Priabonian; **C**, *E. (s.s.) submutica* (d’Orbigny, 1852), MNHN R63796 (Merle coll.), Gaas, Espibos, Landes, France, Rupelian; **D**, *Harpa doris* Röding, 1798, MNHN R11402 (Lecointre coll.), Praia de Castalho, Cape Verde, Recent; **E**, *Eocithara* (s.s.) *mutica* (Lamarck, 1803), MNHN J05527 (Cossmann coll.), Mouchy-le-Châtel, Oise, France, Lutetian; **F**, *E. (s.s.) elegans* (Deshayes, 1835), MNHN R11401, Vendrest, Seine-et-Marne, France, Bartonian; **G**, *Austroharpa tenuis* (Tate, 1889), MNHN J05731 (Cossmann coll.), Muddy Creek, Australia, Balcombian. Abbreviations: **P1–4**, abapical primary cords; **PS**, protoconch scar; **s**, secondary cords. Scale bars: 1 mm.

ginal designation) by its paucispiral protoconch (Rehder 1973: 223: “the basic character differentiating *Eocithara* from the other genera of Harpidae is the paucispiral protoconch with planate apex”). Moreover, the loss of the planktotrophic larval stage is regarded as highly convergent (Bouchet 1983, 1987, 1989). These observations have encouraged us to check the taxonomic usefulness of the teleoconch characters in a phylogenetic analysis of the Harpinae, comparing more closely *Eocithara* with the related taxa (*Eocithara* (*Refluharpa*) Iredale, 1931 (type species: *Harpa lamellifera* Tate, 1889 by original designation), *E.*

(*Marwickara*) Laws, 1935 (type species: *E. (M.) waihaoensis* Laws, 1935 by original designation), *Harpa* Röding, 1798 and *Austroharpa* Finlay, 1931 (type species: *Harpa pulligera* Tate, 1889 by original designation)).

ABBREVIATIONS

Text-conventions of shell characters

IP	infrasutural primary cord;
P	primary cords (cords appearing in first order);
P1 to P4	abapical primary cords;
PS	protoconch scar;

s	secondary cords (cords appearing in second order);
SP	subsutural cord.
<i>Repository</i>	
MGUH	Geologisk Museum University (Rosentrantz coll.), Copenhagen;
MNHN	Collection domaine Sciences de la Terre, Muséum national d'Histoire naturelle, Paris.

ANALYTICAL METHOD

Considering that the distinction between harpid genera, based on the protoconch (presence or absence of a multispiral protoconch) may represent a taxonomic pitfall, the significance of the teleoconch needs to be considered. For other gastropods families (Architectonicidae, Mathildidae, Calliostomidae, Muricidae), several authors (Bieler 1988, 1995; Marshall 1995; Merle 1999, 2001) have demonstrated that close inspection of the teleoconch sculptural patterns is a fruitful way to carry out the descriptive method, and consequently to evaluate the previous taxonomic distinctions better. This close inspection mainly consists of identifying structural homologies and researching the topological and ontogenetic correspondences through elements of the spiral sculpture (e.g., cords, cord spines, etc.). Another way, applicable to the axial sculpture, consists of examining the different modes of construction of the varices (constructional characters of Miller 1999). In the present paper, we use these two descriptive approaches to compare *Eocithara* and evaluate the teleoconch characters in a phylogenetic analysis of the Harpinae.

The phylogeny of Harpidae remains poorly studied. Firstly, we are still in doubt as to a possible sister-group of Harpidae (Kantor 1996) and we agree with Rehder (1973) that no Mesozoic genera are clearly referable to the family. Secondly, three generic or subgeneric taxa belonging to the Harpinae are exclusively fossil (*Eocithara* (s.s.), *E. (Marwickara)* and *E. (Refluharpa)*) and one generic taxon has a fossil type species (*Austroharpa*) restricting an analysis of the subfamily based on anatomical characters to the two Recent genera

Harpa and *Austroharpa*. Therefore, the addition of fossil taxa is necessary to understand harpid phylogeny better, because as in other zoological groups, it gives character associations that are lacking in the Recent (Donoghue *et al.* 1989; Janvier 1991).

HARPID SCULPTURAL PATTERN AND STRUCTURAL HOMOLOGIES

SPIRAL SCULPTURE

Harpid spiral sculpture ranges from a lack of ornamentation on the last whorl (e.g., *Austroharpa punctata* (Verco, 1896)) to moderately developed but clearly distinguished spiral cords (e.g., *A. spirata* (Tate, 1889) and *Morum* Röding, 1798). Except in the poorly ornamented species, the early teleoconch whorls of most species often bear three to five well distinguished primary cords on the spire in *Eocithara*, *Harpa* and *Austroharpa* (Fig. 2). The shoulder cord (P1) is the most recognisable and in some species is associated with short spiny processes. Apically, one cord (IP) may be present on the infrasutural ramp (in *Eocithara (Refluharpa) lamellifera*). The subsutural cord (SP), present in the Moruminae genus *Morum* (type species: *Morum oniscus* Linnaeus, 1767), is lacking in the Harpinae. Abapically, two or three primary cords (P2, P3 and P4) are observable (Fig. 2). During the ontogeny, the primary cords become indistinguishable from finer cords in the genera *Eocithara* (s.s.), *E. (Refluharpa)* and *Harpa*, but are well expressed in several austral *Austroharpa* species, such as *A. exquisita* Iredale, 1931 (Recent), *A. spirata* (Fig. 2) and *A. clathrata* (Tate, 1889). Therefore, this loss of cords limits our ability to identify each primary cords in many adults of the Harpinae. Consequently, we will precisely describe and compare harpid spiral sculpture using only the cords IP, P1, P2, P3 and P4, because it is too conjectural to study structural homologies through the other abapical primary cords, which are not visible on the spire and are poorly expressed on the last whorl.

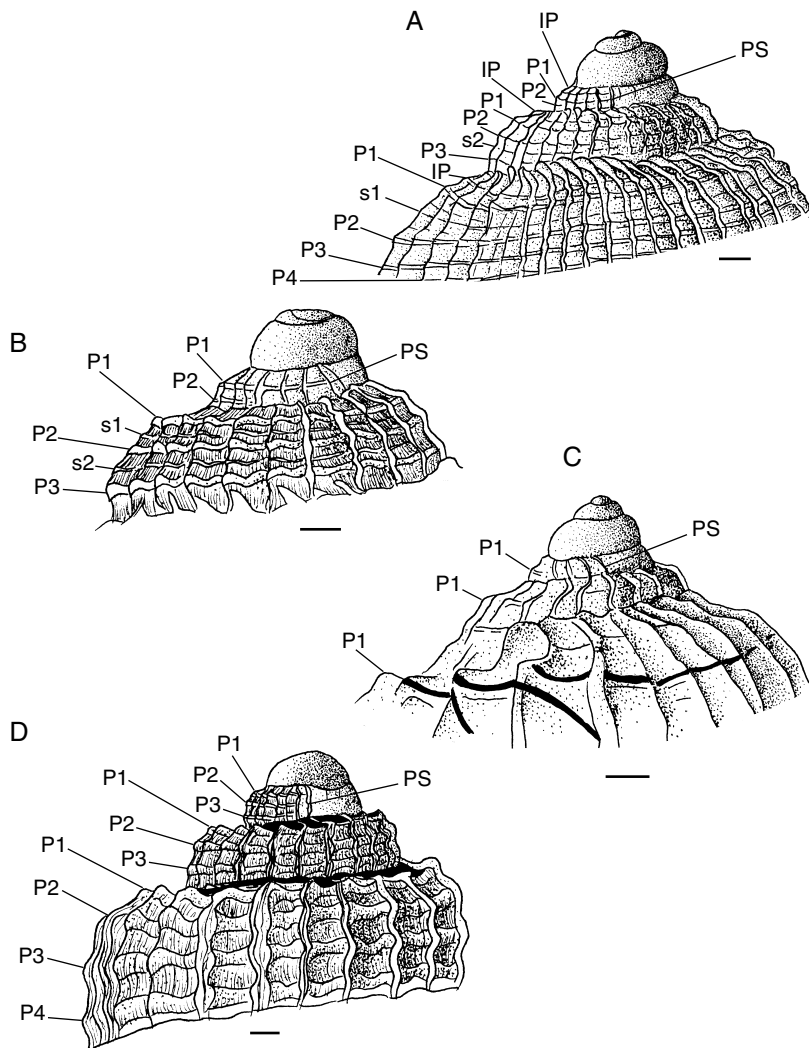


FIG. 2. — Spiral cords appearing on the first teleoconch of the Harpinae; **A**, *Eocithara* (*Refuoharpa*) *lamellifera* (Tate, 1889), MNHN J00612 (Cossmann coll.), Muddy Creek, Australia, Balcombian; **B**, *Harpa articularis* Lamarck, 1822, MNHN R11063 (Lecoindre coll.), Recent, Mauritius Island; **C**, *Harpa major* Röding, 1798, MNHN R63799 (Lecoindre coll.), Recent, Mauritius Island; **D**, *Austroharpa spirata* (Tate, 1889), MNHN J05726 (Cossmann coll.), Schnapper Point, Australia, Balcombian. Abbreviations: **P1-4**, abapical primary cords; **PS**, protoconch scar; **s**, secondary cords. Scale bars: 1 mm.

AXIAL SCULPTURE AND CONSTRUCTIONAL MORPHOLOGIES

The axial sculpture includes poorly ornamented morphologies with rare varices (e.g., *Austroharpa punctata*) as well as moderately ornamented morphologies with more numerous, elongated varices, which are found in the other harpids. In

many species, the varices are associated with a spine (P1 position) delineating the carina and a lamellar expansion near the suture of the preceding whorl. However, a closer analysis demonstrates that varices, spines and lamellar expansions may differ in their construction, suggesting that they are not homologous (Fig. 3).

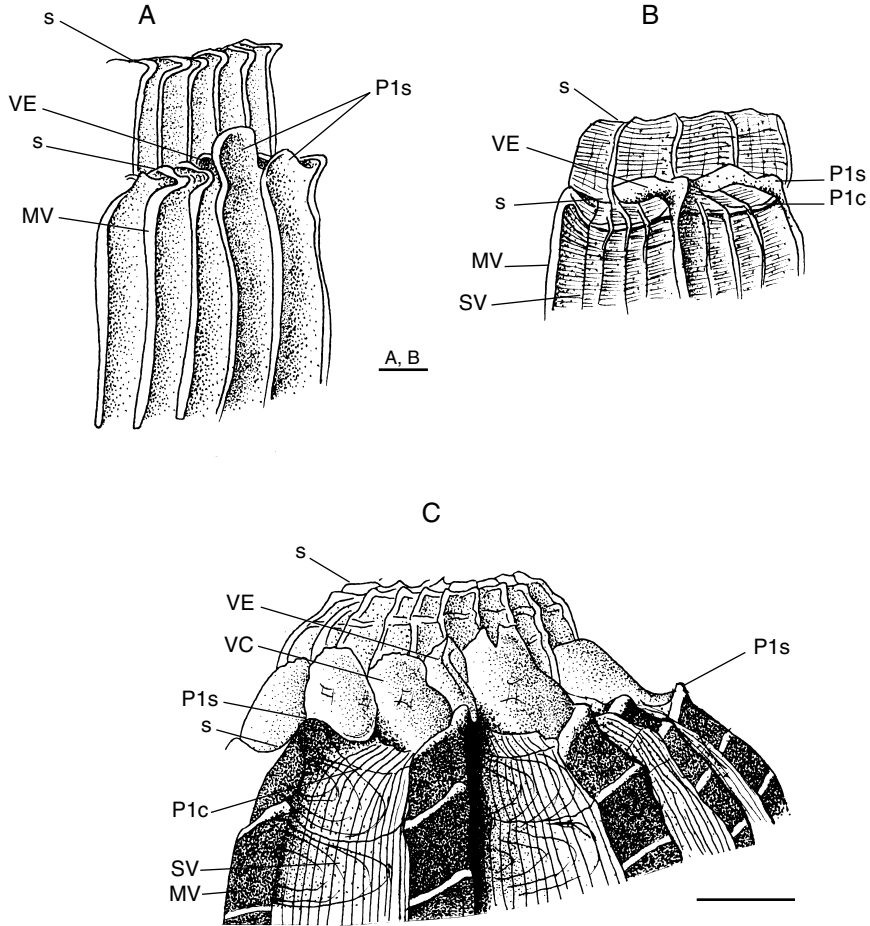


FIG. 3. — Different types of harpin axial sculpture; **A**, portion of *Austroharpa sulcosa* (Tate, 1889), MNHN J05729 (Cossmann coll.), Muddy Creek, Australia, Balcombian, lamellose varices poorly covering the preceding whorl and P1 spine well folded; **B**, portion of *Eocithara* (s.s.) *elegans* (Deshayes, 1835), MNHN R11401 (1965-11 coll.), Vendrest, Seine-et-Marne, France, Bartonian, lamellose varices slightly covering the preceding whorl and P1 spine slightly folded; **C**, portion of *Harpa articularis* Lamarck, 1822, MNHN R11063 (Lecointre coll.), Mauritius Island, Recent, thickened varices largely covering the preceding whorl associating a callus and full P1 spine. Abbreviations: **MV**, major varices; **P1c**, P1 cord; **P1s**, P1 spine; **s**, suture line; **SV**, secondary varices; **VC**, varical callus; **VE**, varical expansion. Scale bars: A, B, 1 mm; C, 5 mm.

SYSTEMATICS

Class GASTROPODA Cuvier, 1797
 Section NEOGASTROPODA Thiele, 1929
 Super-family MURICOIDEA Rafinesque, 1815
 Family HARPIDAE Bronn, 1849

Genus *Eocithara* Fischer, 1883

TYPE SPECIES. — *Harpa mutica* Lamarck, 1803 by original designation.

Eocithara (s.s.) *mutica* (Lamarck, 1803) (Figs 1E; 4A-D; 6D)

Harpa mutica Lamarck, 1803: 167, 168; vélin 3, fig. 24.

Harpa altavillensis Defrance, 1821: 303.

Harpa baylei Mayer, 1877: 93.

Harpa mutica – Lamarck 1805: 227, pl. 44, fig. 14. —
 Deshayes 1835: 642, pl. 86, figs 14, 15; 1865: 524. —
 Kecskeméti-Körmendi & Mészáros 1980: 63, 106,
 pl. 8, fig. 12.

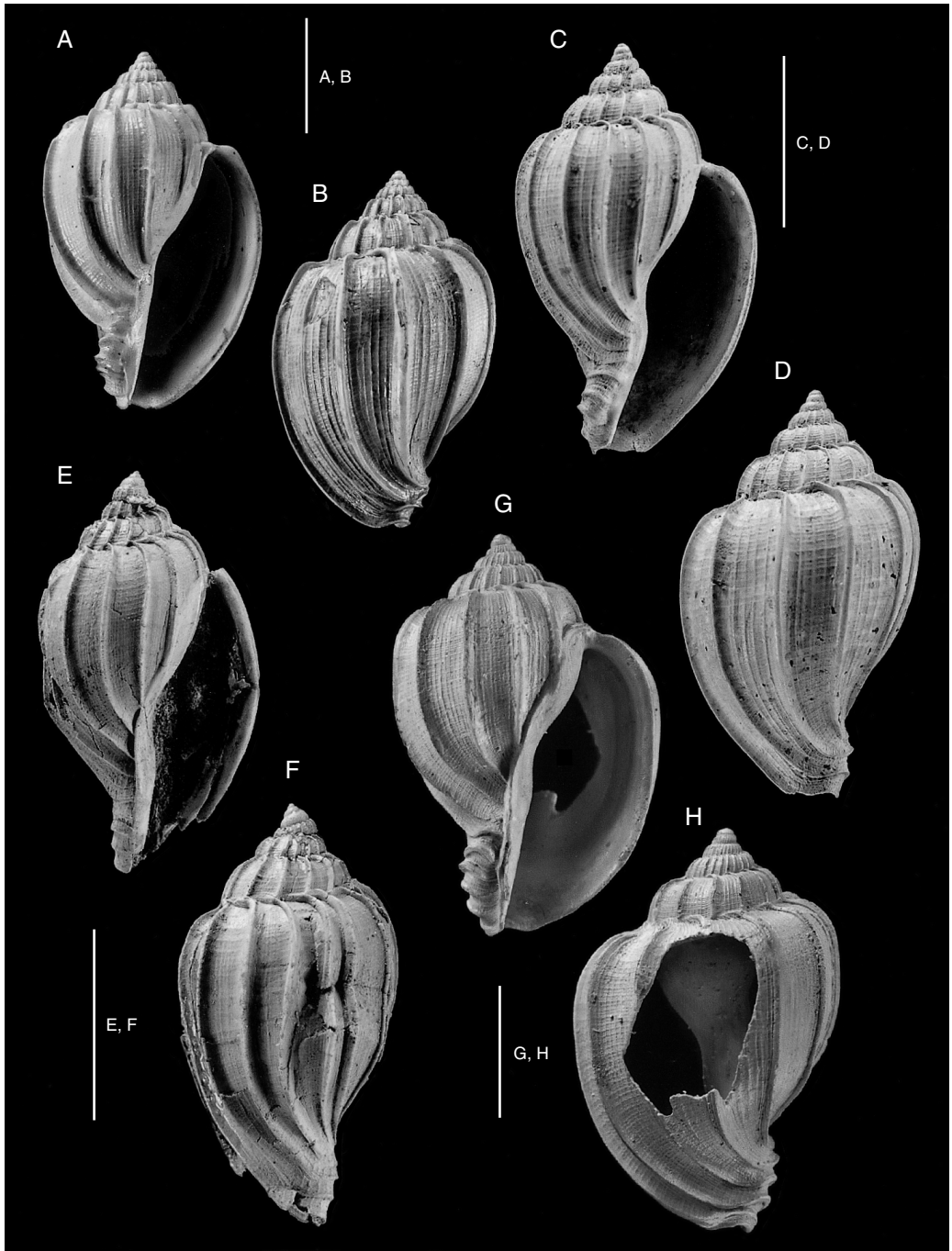


FIG. 4. — **A, B**, *Eocithara* (s.s.) *mutica* (Lamarck, 1803), MNHN R63429 (Schtrock coll.), Chaussy, Val d'Oise, France, Lutetian; **C, D, E**, (s.s.) *mutica*, MNHN R63430 (Leroy coll.), Saint-Gobain, Aisne, France, lower Ypresian; **E, F**, *E. (s.s.) helena* n. sp., holotype, MNHN R63431 (Merle coll.), Tuilerie of Gan, Pyrénées-Atlantiques, France, upper Ypresian; **G, H**, *Eocithara* (s.s.) *eucosmia* n. sp., holotype, MNHN R63798 (Boucher coll.), Bois-Gouët, Saffré, Loire-Atlantique, France, Bartonian. Scale bars: 10 mm.

Harpa cf. mutica – Strausz 1966: 62, 134.

Harpa mutica altavillensis – Deshayes 1865: 524.

Harpa (Eocithara) mutica – Fischer 1883: 601. — Cossmann 1889: 214; 1897: 232, 233 (96, 97), pl. IX, figs 7-9; 1899: 73-75, fig. 10, pl. 3, figs 22, 23. — Cossmann & Pissarro 1901: 33, pl. X, fig. 7; 1913: pl. XLVI, fig. 209-1. — Wenz 1943: 1310, fig. 3732. — Korobkov 1955: pl. 84, figs 8-11. — Glibert 1960: 48. — Le Renard & Pacaud 1995: 120. — Pacaud & Le Renard 1996: 166.

Eocithara (s.s.) mutica – Rehder 1973: 224, 225, pl. 192.

Eocithara (s.s.) mutica altavillensis – Rehder 1973: 225.

TYPE MATERIAL. — Syntypes (Lamarck coll.).

TYPE LOCALITY. — Grignon, Yvelines, France, Lutetian (middle Eocene).

MATERIAL EXAMINED. — **Cuisian.** Saint-Gobain, Aisne, 1 ex. (MNHN R63430, Leroy coll., Fig. 4C, D); 2 ex. (MNHN B65986 and B65997, Lhomme coll.); 1 ex. (MNHN R11390, Schtrock coll.); 1 ex. (Six coll.); Coeuvres-et-Valséry, Aisne, fragments (Leroy coll.).

Lutetian. Brasles, Aisne, 1 ex. (MNHN R11393, Faullummel coll.); Châteauroge, Oise, 1 ex. (MNHN R11397, Faullummel coll.); Chaumont-en-Vexin, Oise, 4 ex. (MNHN R11061, Braillon coll.), 1 ex. (MNHN R11060); Fercourt, Oise, 6 ex. (MNHN R11062, Braillon coll.), 3 ex. (MNHN B65992); 7 ex. (MNHN R11394, Faullummel coll.); Hermes, Oise, 1 ex. (MNHN R11392, Faullummel coll.); Mouchy-le-Châtel, Oise, 1 ex. (MNHN R65996), 3 ex. (MNHN J05527 [Fig. 6D] and J05728, Cossmann coll.); 2 ex. (MNHN R11391, Schtrock coll.); 1 ex. (MNHN R63429, Schtrock coll.) (Fig. 4A, B); Parnes, Oise, 3 ex. (MNHN B65995), 4 ex. (MNHN B65994); Les Boves, Parnes, Oise, 4 ex. (MNHN B65993); Ponchon, Oise, 3 ex. (MNHN R11396, Faullummel coll.); Précý-sur-Oise, Oise, 1 ex. (MNHN J05727, Cossmann coll.); Uilly-Saint-Georges, Oise, 3 ex. (MNHN B65997); Chaussy, Val d'Oise, 1 ex. (MNHN B69171), 2 ex. (MNHN B65988), 2 ex. (MNHN B65999), 1 ex. (MNHN B65990), 1 ex. (MNHN R11059, Boule coll.), 2 ex. (MNHN R11398, Faullummel coll.); Fontenay-en-Vexin, Eure, 2 ex. (MNHN R11399, Faullummel coll.); Saulx-Marchais, Yvelines, 9 ex. (MNHN B65991); Thionville-sur-Opton, Yvelines, 1 ex. (MNHN R11395, Faullummel coll.); Villiers-Saint-Frédéric, Yvelines, 5 ex. (MNHN R11400, Faullummel coll.).

NEW STRATIGRAPHIC RANGE. — Cuisian (lower Ypresian) to upper Lutetian.

MEASUREMENTS (Cuisian material). — R63430: height 24.8 mm, maximal width 14 mm; R65986: height 12 mm, maximal width 7 mm; R65997: height 13 mm, maximal width 7 mm.

DESCRIPTION (based on the Cuisian material). — Shell 25 mm in height and 14 mm in width. Paucispiral protoconch of 2.5 smooth whorls. Teleoconch of five convex whorls. Spire 20% of the total length. Simple, linear suture. Axial sculpture of thin lamellose, abaxially oriented major varices. Posterior part of major varices adapically projecting and moderately covering base of penultimate whorl. 19 major slightly sinuose varices on first whorl and 12 to 13 on last whorl. Four to ten lamellose secondary varices between major varices. Spiral ornamentation of four narrow primary cords (P1 to P4) on first whorl. P1 delineating small carina on end of first whorl. Secondary cords appearing on third whorl. Primary and secondary cords indistinguishable on last whorl. Cord spine P1 forming a simple lamellose spinelet on last whorl. Axial microsculpture with numerous and fine striae. Oblong aperture 72% of the total length, contracted in abapical angle. Centre of columella round, lightly curved on anterior part. Columellar callosity small, well delineated in its labial part. Pseudoumbilicus very narrow, closed by columellar callosity, delineated by umbilical ridge. Umbilical ridge well marked by siphonal fascioles, curved dorsally. Siphonal canal short, curved dorsally. Outer lip thin, slightly thickened by the last varix, orthocone, with parasigmoid outline.

COMPARISONS

These Cuisian *Eocithara* specimens are clearly referable to the Lutetian species *Eocithara (s.s.) mutica*, by having a paucispiral protoconch of 2.5 whorls, by the slightly sinuose varices on the first teleoconch whorl, and by the late appearance of the P1 spine on the last whorl. They only differ from the Lutetian specimens by a smaller size ($L_{max} = 24.8$ mm; $L_{max} = 41$ mm in the Lutetian population). *E. (s.s.) mutica* resembles *E. (s.s.) elegans* (Deshayes, 1835) from the Parisian Bartonian by its protoconch of 2.5 whorls (Figs 1E, F; 6D, E) and by its axial and spiral sculpture on the first teleoconch whorls. It shares the same sculpture on the first teleoconch whorls with *E. (s.s.) submutica* (d'Orbigny, 1852) from the Aquitaine Rupelian. However, *E. (s.s.) elegans* and *E. (s.s.) submutica* have a more strongly developed spiral sculpture (probably the secondary cords) on the last whorl and many specimens possess reinforced varices that are lacking in *E. (s.s.) mutica*. *E. (s.s.) submutica* is also distinguished by having a multispiral protoconch (Figs 1C; 6C). Two other species also seem to be related to *E. (s.s.) mutica*: *E. (s.s.)*

californiensis (Vokes, 1937) from middle Eocene rocks of California (Domengine stage) and *E. (s.s.) hilarionis* (de Gregorio, 1880) from the middle Eocene of northern Italia. *E. (s.s.) californiensis* has been regarded as a subspecies of *E. (s.s.) mutica* (Vokes 1937; Rehder 1973). According to Rehder (1973), the differences between the teleoconch characters of the European and the American specimens are slight, but with the protoconch missing in *E. (s.s.) californiensis*, it is difficult to argue that they represent one species. The same problem occurs with *E. (s.s.) hilarionis*.

Eocithara (s.s.) helena n. sp.

(Figs 1A; 4E, F; 6A)

Eocithara sp. — Merle 1986: 36.

TYPE MATERIAL. — Holotype (MNHN R63431, Merle coll.), 3 paratypes (MNHN R63436, Merle coll.), 1 paratype (MNHN R63800, Merle coll.).

TYPE LOCALITY. — Tuilerie of Gan, Pyrénées-Atlantiques, France, upper Ypresian.

ETYMOLOGY. — For Héléne Merle for her participation to the field research.

MEASUREMENTS. — R63431 (holotype): height 21 mm, maximal width 11 mm; R63436a (paratype): height 19 mm, maximal width 9 mm; R63436b (paratype): height 18 mm, maximal width 7.5 mm; R63436c (paratype): height 31 mm, maximal width 18 mm (broken); R63800 (paratype): height 18 mm, maximal width 11 mm.

DESCRIPTION OF THE HOLOTYPE

Shell 21 mm in height and 11 mm in width. Protoconch multispiral, conical, of 3.5 smooth whorls. Teleoconch of five slightly convex whorls. Conical spire 19% of total length. Simple, linear suture. Axial sculpture of lamellose, abaxially oriented major varices. Posterior part of major varices adapically projected and moderately covering base of penultimate whorl. Twenty-one orthocone major varices on the first whorl and 15 on the last whorl. Five to six lamellose secondary varices between each pair of major varices. Spiral ornamentation of four narrow primary cords (P1 to P4) on first whorl. P1 delineat-

ing a small carina on end of first whorl. Secondary cord (s2) appearing on third whorl. Primary and secondary cords indistinguishable on last whorl. Cord spine P1 not present. Axial microsculpture with numerous and fine striae. Aperture oblong of 81% of total length, contracted in its abapical angle. Centre of the columella straight, lightly curved over anterior part. Columellar callosity small, labial part well delineated. Pseudombilicus very narrow, closed by columellar callosity and delineated by umbilical ridge. Umbilical ridge curved dorsally. Siphonal canal short, curved dorsally. Outer lip thin, but thickened by the last varix, orthocone, with parasigmoid outline.

COMPARISONS

This upper Ypresian species differs from all other European Eocene species by its multispiral protoconch. On the first teleoconch whorl, *E. (s.s.) helena* n. sp. also possesses orthocone varices, while they are sinuose in *E. (s.s.) mutica*, *E. (s.s.) elegans* and in the Rupelian species *E. (s.s.) submutica*. *E. (s.s.) helena* n. sp. is more nearly similar to the American Priabonian species *E. (s.s.) jacksonensis* (Harris, 1896) in its multispiral protoconch (Figs 1B; 6B) and in the sculptural features of its first teleoconch whorl (orthocone varices, poorly marked spiral cords). Nevertheless, the spiral sculpture is more developed in *E. (s.s.) jacksonensis* and no spine in the topological position P1 has been observed in *E. (s.s.) helena* n. sp., whereas it commonly occurs in most specimens of *E. (s.s.) jacksonensis*.

Eocithara (s.s.) euosmia n. sp.

(Figs 4G, H; 5A-C; 6F)

TYPE MATERIAL. — Holotype (MNHN R63798, Boucher coll.), Bois-Gouët; 2 paratypes (MNHN R63434 and MNHN R63435, Pacaud coll.), 1 paratype (MNHN R63797, Faullummel coll.), Bois-Gouët; 1 paratype (MNHN R11404, Ledon coll.), Saint-Aignan-de-Grand-Lieu.

TYPE LOCALITY. — Bois-Gouët, Saffré, Loire-Atlantique, France, Bartonian.

ETYMOLOGY. — From the Greek: well organized.

MEASUREMENTS. — R63798 (holotype): height 32 mm, maximal width 19 mm; R63434 (paratype): height 10 mm, maximal width 4.5 mm (aperture broken); R63435 (paratype): height 7 mm (apex broken), maximal width 3 mm (aperture broken).

DESCRIPTION OF THE HOLOTYPE

Shell 32 mm in height and 19 mm in width, weakly inflated. Protoconch eroded, of one large whorl. Teleoconch of 5.25 weakly convex whorls. Conical spire 17% of total length. Suture simple, linear. Axial sculpture of sigmoid, lamellose, and abaxially oriented major varices. Posterior part of each major varix adapically projected and moderately covering base of penultimate whorl. Forty-five major varices on first whorl, 31-32 equally spaced major varices on third and 11 on last whorl. Eleven to 14 very lamellose secondary varices between each pair of major varices on last whorl. Spiral cords lacking on the first whorl, but appearing on second whorl as four narrow cords (P1 to P4). P1 delineating a small carina on third whorl, but not on last whorl. Secondary cord appearing on third whorl. Primary and secondary cords indistinguishable on last whorl. Cord spine P1 absent, but only a small angle on the whorl. Axial microsculpture faint. Oblong aperture of 75% of total length, contracted in its abapical angle. Centre of columella straight, lightly curved in anterior part. Columellar callosity slightly expanded in parietal area and well delineated in its labial part. Pseudoumbilicus narrow, closed by columellar callosity and delineated by umbilical ridge. Umbilical ridge curved dorsally. Siphonal canal short, curved dorsally. Outer lip thin, but thickened by the last varix, orthocline, with parasigmoid outline.

COMPARISONS

This new Bartonian species is known by five specimens from Bois-Gouët and Saint-Aignan-de-Grand-Lieu. They have the same sculpture at the two localities. On the first whorl, it is characterized by very sinuous varices and by lacking spiral cords. This sculpture represents a previously unknown character in *Eocithara*, as all other species have spiral cords. Moreover, the number of

varices on the first (45) and the second (31-32) whorls is much higher than in the other European species. It also has more numerous and more lamellose secondary varices (12-14) than in *E. (s.s.) helenae* n. sp. (5-6) and in *E. (s.s.) mutica* (4-10).

Eocithara (s.s.) *rosenkrantzi* n. sp. (Fig. 5D, E)

Eocithara sp. – Rosenkrantz 1970: 441.

Harpa sp. – Kollmann & Peel 1983: 87, fig. 196A (*non* B).

TYPE MATERIAL. — Holotype (MGUH 15818, copy MNHN R63692).

TYPE LOCALITY. — Sonja Lens, East of Turritelakløft, Nuussuaq Peninsula, West Greenland, Agatdal Formation, Thanetian.

ETYMOLOGY. — For Professor Alfred Rosenkrantz who collected the studied specimens.

MEASUREMENTS. — MGUH 15818 (copy MNHN R63692) (holotype): height 9.5 mm (the two first teleoconch whorls are broken), maximal width 6.2 mm.

DESCRIPTION OF THE HOLOTYPE

Shell 9.5 mm in height and 6.2 mm in width. Protoconch missing. The last three teleoconch whorls are preserved. Whorls conical, weakly convex. Spire 21% of total length. Suture simple, linear. Axial sculpture of lamellose, abaxially oriented major varices. Posterior part of major varices adapically projecting, moderately covering base of penultimate whorl. Ten major varices on first preserved whorl and 14 equally spaced varices on last whorl. No secondary varices present between major varices. Spiral sculpture not preserved or absent. Oblong aperture of 63% of total length, contracted in its abapical angle. Centre of columella straight, weakly curved in its anterior part. Columellar callosity small, well delineated in its labial part. Pseudoumbilicus very narrow, closed and delineated by columellar callosity. Umbilical ridge poorly expressed. Siphonal canal short, slightly curved dorsally. Outer lip thin, but thickened by last varice, orthocline, with parasigmoid outline.

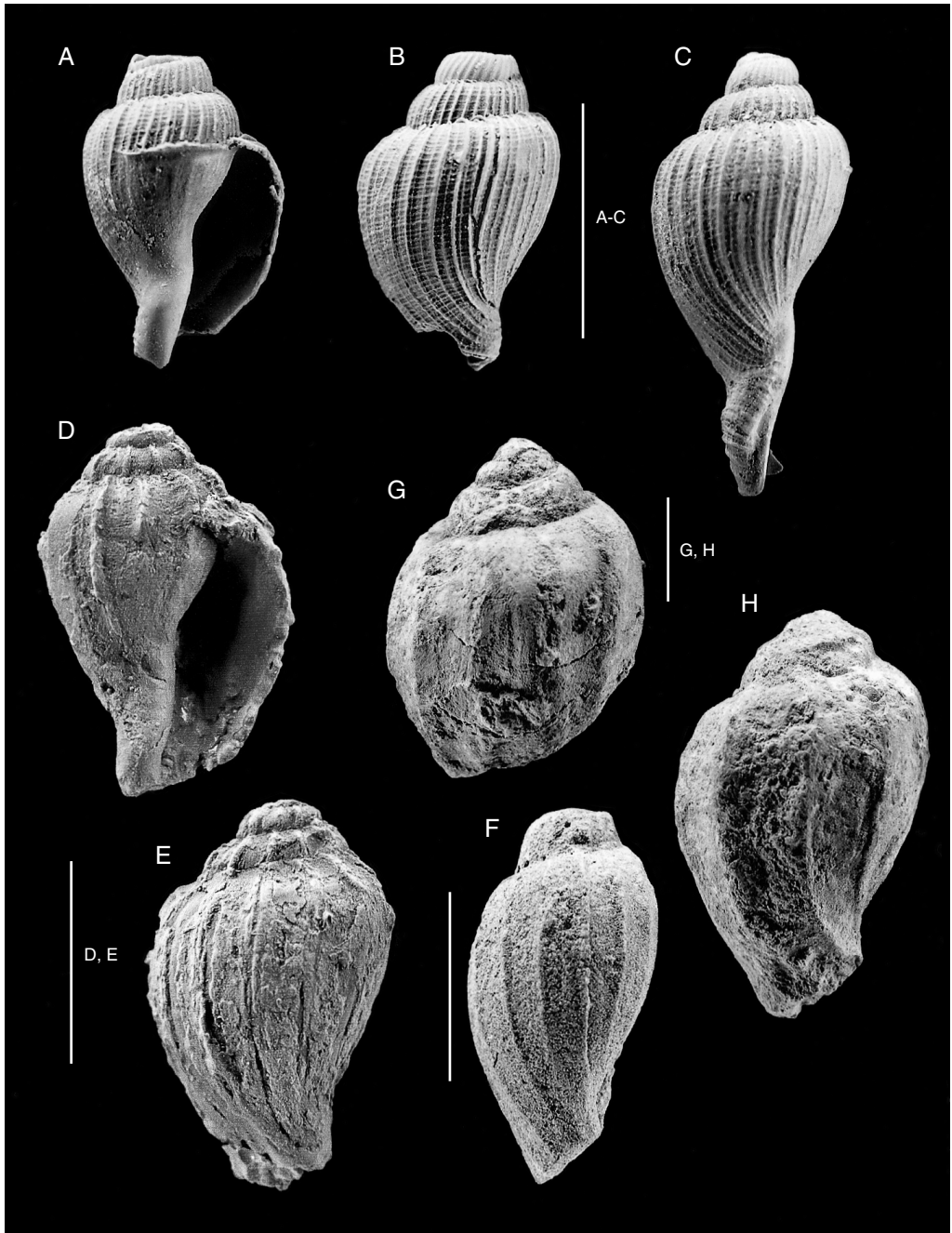


FIG. 5. — **A-C**, *Eocithara* (s.s.) *eucosmia* n. sp., paratypes, MNHN R63434 et R63435 (Pacaud coll.), Bois-Gouët, Saffré, Loire-Atlantique, France, Bartonian; **D-E**, *E.* (s.s.) *rosenkrantzi* n. sp., holotype, MGUH 15818 (copy MNHN R63692), Sonja Lens, East of Turritellakløft, Nuussuaq Peninsula, West Greenland, Thanetian (Agatdal Formation); **F**, *E.* (s.s.) sp. 1, MNHN J05430 (Cossmann coll.), Coustouge, Aude, France, lower Ypresian; **G-H**, *Eocithara* (s.s.) sp. 2, MNHN R63432 and R63433 (Courtessole-Griffe coll.), Les Capitelles, North of Aragon, Aude, France, lower Ypresian. Scale bars: A-E, 5 mm; F-H, 10 mm.

COMPARISONS

This Paleocene species is the oldest known from the Atlantic Ocean. It has been already presented under the name *Harpa* sp. by Kollman & Peel (1983), who figured two specimens (fig. 196A, B). A closer inspection of the material reveals that the specimen in figure 196B cannot be referred to the Harpidae, but is a young *Volutocorbis* Dall, 1890. Conversely, the specimen in figure 196A, chosen here as the holotype of *E. (s.s.) rosenkrantzi* n. sp., may be attributed to *Eocithara* (Fig. 5F, G). The holotype has rounded whorls, as in some *E. (s.s.) mutica*, but differs in its less developed spiral sculpture and, in particular, lacks a P1 spine.

Eocithara (s.s.) sp. 1 (Fig. 5F)

LOCALITY. — Coustouge, Aude, France, lower Ypresian.

MATERIAL EXAMINED. — 1 ex. (MNHN J05430, Cossmann coll.).

MEASUREMENTS. — Height 22.8 mm (penultimate and last whorl only preserved), maximal width 12 mm.

DESCRIPTION

Oval and poorly inflated shell 22.8 mm in height and 12 mm in width. Protoconch missing. Last two teleoconch whorls preserved. Whorls weakly convex. Conical spire 18% of total length. Suture simple, linear. Axial sculpture of lamellose, abaxially oriented major varices. Posterior part of major varices adapically projecting, moderately covering base of penultimate whorl. Fourteen to 15 equally spaced major varices on last whorl. Several poorly preserved secondary varices between each pair of major varices. Spiral sculpture not preserved. Oblong aperture of 68% of total length. Columellar callosity small, well delineated in its labial part. Siphonal canal short, curved dorsally. Outer lip orthocone, with parasigmoid outline.

COMPARISONS

This external mold is characterized by an elongated final teleoconch whorl. In the number of its major varices and in its elongated morphology, it

looks most like *E. (s.s.) helenae* n. sp., which also comes from the Aquitaine basin.

Eocithara (s.s.) sp. 2 (Fig. 5G, H)

LOCALITY. — Les Capitelles, North of Aragon, Aude, France, lower Ypresian.

MATERIAL EXAMINED. — 2 ex. (MNHN R63432 and MNHN R63433, Courtesolle-Griffe coll.).

MEASUREMENTS. — R63432: height 31 mm (broken base and broken first whorls), maximal width 25 mm; R63433: height 42 mm (broken first whorls), maximal width 26 mm.

DESCRIPTION

Oval, inflated shell 42 mm in height and 26 mm in width. Protoconch missing. Three preserved teleoconch whorls. Whorls convex. Conical spire 12% of total length. Suture simple, linear. Axial sculpture of lamellose, abaxially oriented major varices. Posterior part of major varices adapically projecting, moderately covering base of penultimate whorl. Ten equally spaced major varices on last whorl. No secondary varices preserved between major varices. Spiral sculpture not preserved. Oblong aperture of 71% of total length. Columellar callosity small, well delineated in its labial part. Siphonal canal short, curved dorsally. Outer lip orthocone, with parasigmoid outline.

COMPARISONS

These two other lower Ypresian specimens of *Eocithara (s.s.)*, preserved as external molds, mainly differ from *Eocithara (s.s.)* sp. 1 and from *E. (s.s.) helenae* n. sp. by having more inflated whorls and by their greater size. They look more like *Eocithara (s.s.) mutica* than *E. (s.s.) helenae* n. sp.

PHYLOGENETIC ANALYSIS

OUTGROUPS

Two taxa are used as outgroups. For the first one, we have referred to the phylogenetic study by Kantor (1996) based on anatomical characters. Kantor (1996) was the first to discuss the phylogeny of the Muricoidea including the Harpidae.

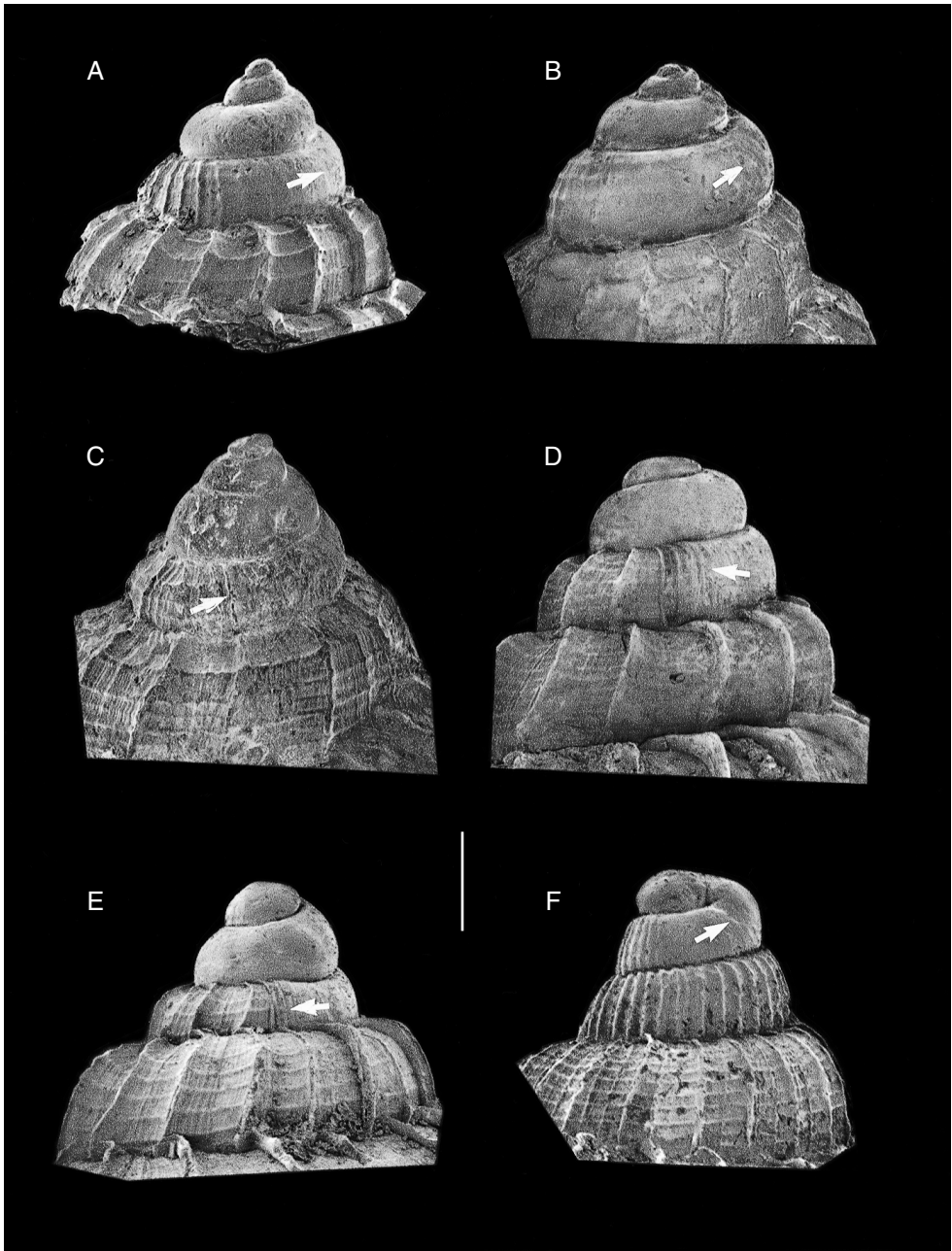


FIG. 6. — SEM views of multispiral and paucispiral *Eocithara* (s.s.); **A**, *Eocithara* (s.s.) *helenae* n. sp., paratype, MNHN R63800 (Merle coll.), Tuilerie of Gan, Pyrénées-Atlantiques, France, upper Ypresian; **B**, *E.* (s.s.) *jacksonensis* (Harris, 1896), MNHN J05528 (Cossmann coll.), Jackson, USA, Priabonian; **C**, *E.* (s.s.) *submutica* (d'Orbigny, 1852), MNHN R63801 (Aucoin coll.), Gaas, Espibos, Landes, France, Rupelian; **D**, *Eocithara* (s.s.) *mutica* (Lamarck, 1803), MNHN J05527 (Cossmann coll.), Mouchy-le-Châtel, Oise, France, Lutetian; **E**, *E.* (s.s.) *elegans* (Deshayes, 1835), MNHN R11401, Vendrest, Seine-et-Marne, France, Bartonian; **F**, *Eocithara* (s.s.) *eucosmia* n. sp., paratype, MNHN R11404 (Ledon coll.), Saint-Aignan-de-Grand-Lieu, Loire-Atlantique, France, Bartonian. The white arrow indicates the protoconch scar. Scale bar: 1 mm.

His analysis placed the Harpidae as a sister-group of the Colubrariidae (Kantor 1996: fig. 19.6), inside an unresolved clade containing the Volutomitridae and Mitridae. The shell morphology of the members of these three families has evolved greatly since the Early Tertiary, and we have preferred to choose, as first outgroup a member of the Volutidae (Athletinae), the most basal Muricoidea according the Kantor's phylogeny. In particular, we have used the Lutetian species *Athleta (Volutospina) spinosa* (Lamarck, 1803), because of the great number of available specimens.

For the second outgroup, we have referred to the fossil record. Two genera need to be discussed: *Eoharpa* Stephenson, 1955 (type species: *E. sinuosa* Stephenson, 1955 by original designation (Campanian, USA)) and *Cryptochorda* Mörch, 1858 (type species: *Cryptochorda stromboides* (Hermann, 1781) by original designation (Eocene, Europe)). *Eoharpa* was proposed as a genus in the family Harpidae. However, according to Rehder (1973), the attenuation of the anterior end into a fairly long siphonal canal is absent from all fossil and Recent members of the Harpidae. Moreover, the preservation of this rare fossil is too poor to be very useful in our study. More interesting is the genus *Cryptochorda* placed by Cossmann (1899: 76, 77) in the Harpidae, because the shell is shaped as in Harpidae, although it lacks sculpture. Since Wenz (1943), Pchelintsev & Korobkov (1960) and Rehder (1973), this genus is excluded from the Harpidae, belonging to the family Cryptochordidae Pchelintsev & Korobkov, 1960 or to the Volutidae (Wenz 1943), but it is important to stress that *Cryptochorda* strongly resembles the unornamented species *Austroharpa punctata* and it appears logical to discuss this genus more closely in our phylogenetic analysis. The type species of *Cryptochorda* has been selected as an outgroup.

ANALYSED TAXA

The matrix is composed of the two outgroups and the 18 species of the ingroup. The ingroup includes eight *Eocithara*, four *Harpa*, four *Austroharpa* and two *Morum* species. The *Eocithara*

group contains the type species of *Eocithara* (s.s.), *E. (Refluharpa)* and *E. (Marwickara)* and also five species of *Eocithara* (s.s.) from the lower Eocene to the lower Oligocene of Europe and Mississippi. The *Harpa* group contains two Recent Indo-Pacific species, one Neogene species from Europe and one Recent West African species. The *Austroharpa* group contains: 1) *Austroharpa punctata* (Recent, Australia) a poorly ornamented species that is interesting to compare with *Cryptochorda*; 2) *A. spirata*, a Neogene species closely related to *A. exquisita* Iredale, 1931, the type species of the subgenus *Palamharpa*; and 3) *A. tenuis*, another Neogene species that is very similar to *A. pulligera* (the type species of *Austroharpa*) in its teleoconch. The *Morum* group (Moruminae) includes *Morum oniscus* (Linnaeus, 1767), the type species of the genus, and a fossil from lower Miocene of Aquitaine (France): *M. harpaeformis* Grateloup, 1827. The species of Moruminae are not used as outgroups, but they allow us to test the monophyly of the Harpinae. Except for two species, *A. (P.) punctata* and *E. (M.) waihaensis* (middle Eocene, New Zealand), all material has been examined (Table 1) and possesses well preserved first teleoconch whorls. For these species, the descriptions and the figures of Rehder (1973) and Laws (1935) have been used to complete the matrix.

Character list

1. Spiral sculpture on the spire: present (0); absent (1). Comment: the total absence of spiral sculpture is regarded as the apomorphic state. It is restricted to the outgroup *Cryptochorda stromboides*. On the first teleoconch whorl of *Austroharpa punctata*, a residual cord P1 delineates the sutural ramp and a small carina.
2. Distribution of the primary cords on the last whorl: present on the whole whorl, with a decrease in the centre of the whorl (0); only on the base of the whorl (1); equally distributed on the whole whorl until the siphonal canal (2); absence of cords (3). Comment: states 2 and 3 occur in the ingroup.
3. Internal denticles of the outer lip: absent (0); present (1). Comment: denticles occur inside the outer lip in *Morum*.

TABLE 1. — Material, stratigraphic and geographic ranges of the examined taxa used in the phylogenetic analysis.

Taxa	Collections	Stratigraphic range	Geographic range
<i>Athleta (Volutospina) spinosa</i> (Lamarck, 1803)	MNHN (several coll.)	Lutetian (middle Eocene)	Paris basin
<i>Cryptochorda stromboides</i> (Hermann, 1781)	MNHN (several coll.)	Ypresian-Lutetian (lower to middle Eocene)	Paris basin and Belgium
<i>Morum harpaeformis</i> Grateloup, 1827	MNHN (Cossmann coll.)	Aquitanian-Burdigalian (lower Miocene)	Aquitaine basin (France)
<i>Morum oniscus</i> (Linnaeus, 1767)	MNHN (Lecointre coll.)	Recent	French West-Indies
<i>Eocithara</i> (s.s.) <i>mutica</i> (Lamarck, 1803)	MNHN (several coll.)	Ypresian-Lutetian (lower to middle Eocene)	Paris basin
<i>E.</i> (s.s.) <i>elegans</i> (Deshayes, 1835)	MNHN (several coll.)	Bartonian (middle Eocene)	Paris basin
<i>E.</i> (s.s.) <i>jacksonensis</i> (Harris, 1896)	MNHN (Cossmann coll.)	Priabonian (upper Eocene)	Mississippi (USA)
<i>E.</i> (s.s.) <i>submutica</i> (d'Orbigny, 1852)	Merle coll.	Rupelian (lower Oligocene)	Aquitaine basin, Gaas
<i>E.</i> (s.s.) <i>helenae</i> n. sp.	MNHN (Merle coll.)	Ypresian (lower Eocene)	Aquitaine basin, Gan
<i>E. (Refluharpa) lamellifera</i> (Tate, 1889)	MNHN (Cossmann coll.)	Balcombian (middle Miocene)	Victoria basin (South Australia), Muddy Creek
<i>Austroharpa sulcosa</i> (Tate, 1889)	MNHN (Cossmann coll.)	Balcombian (middle Miocene)	Victoria basin, Muddy Creek
<i>A. tenuis</i> (Tate, 1889)	MNHN (Cossmann coll.)	Balcombian (middle Miocene)	Victoria basin, Muddy Creek
<i>A. spirata</i> (Tate, 1889)	MNHN (Cossmann coll.)	Balcombian (middle Miocene)	Victoria basin, Schnapper Point
<i>Harpa brochoni</i> Benoist in Cossmann, 1899	MNHN (Cossmann coll.)	Aquitanian-Burdigalian (lower Miocene)	Aquitaine basin
<i>H. major</i> Röding, 1798	MNHN (Lecointre coll.)	Upper Miocene to Recent	East Africa to Hawaiian and Marquesas Islands
<i>H. articularis</i> Lamarck, 1822	MNHN (Lecointre coll.)	Upper Miocene to Recent	Philippines, Indonesia to Western Australia, Queensland, and Fiji
<i>H. davidis</i> Röding, 1798	MNHN (Lecointre coll.)	Recent	Maldives, Ceylon and eastern India to Burma, Thailand and northwestern Sumatra
<i>H. doris</i> Röding, 1798	MNHN (Lecointre coll.)	Recent	West Africa, Cape Verde Islands to Luanda, Angola, Ascension Island

4. Morphology of the primary cord P1 on the first teleoconch whorl: fine, clearly distinct, without delineating the sutural ramp (0); fine, clearly distinct, delineating the sutural ramp (1); indistinct, delineating the sutural ramp (2); obvious, delineating the sutural ramp (3); absence of cords (- = not applicable).

5. Development of the cord spine P1: well developed and abaxially placed (0); poorly developed (Fig. 3B) and adaxially placed (1); developed (Fig. 3A, C) and adaxially placed (2); absence of spine (3); absence of the cord P1 (- = not applicable).

6. Morphology of the cord spine P1: full and non-lamellar spine throughout ontogeny (0);

lamellar spine without lamellar fold in the adult stages (1) (Fig. 3B); lamellar spine with lamellar fold throughout ontogeny (2) (Fig. 3A); lamellar in the young stage and very thick following an adapertural relief in the adult stage (3) (Fig. 3C); absence of the spine P1 (- = not applicable).

7. Development of the subsutural cord: developed (0); absent in the spiral sculpture (1); absence of cord on the spire (- = not applicable). Comment: a developed subsutural cord on the spire occurs in *Athleta* (*V.*) *spinosa* (outgroup) and in *Morum* (ingroup).

8. Morphology of the adapical primary cords P2 and P3 on the first whorl: spiral alignment of small nodules (0); clearly distinct cords (1); indistinct cords (2); absence of cord on the spire (-). Comment: the ingroup is characterized by continuous cords (states 1 and 2). In *Austroharpa sulcosa*, these cords are poorly marked (state 2).

9. Varical expression of the abapical primary cords on the last whorls (centre of the last whorl): no varical expression (0); varical undulations (1); no spiral cords (- = not applicable). Comment: a varical expression of the cords is restricted to the *Austroharpa* species, except in *Austroharpa punctata*.

10. Morphology of the adapical primary cords (centre of the last whorl): cords pinched (0); cords narrow (1); cords well developed and convex (2); cords poorly expressed and convex (3); cords only expressed near the abapertural face of the varices (4); no spiral cords (- = not applicable). Comment: in Recent *Harpa* species, the spiral sculpture on the centre and base of the whorl does not totally disappear. A closer analysis shows residual spiral cords near the abapertural face of the varices (state 4).

11. Abapical secondary cords on the spire: absent (0); present (1); no primary cords (- = not applicable).

12. Spines on P2: absent (0); present (1); no cords (- = not applicable).

13. Type of axial sculpture (first whorl): axial folds (0); orthocline lamellae (1); sigmoid lamellae (2); axial growing ridges (3). Comment: orthocline lamellae on the first whorl (state 1) are widespread in the harpids, except in several *Eocithara* species (*E.* (s.s.) *mutica*, *E.* (s.s.) *elegans* and *E.* (s.s.) *submutica*) having sigmoid lamellae (state 2).

14. Type of axial sculpture (adult stage): axial folds (0); axial growing ridges (1); thin, abaxially projected lamellae (2); thick projected lamellae (3). Comment: thick projected lamellae (state 3) are present in all *Harpa* species. They are missing in *Austroharpa* and in *Eocithara*, except in several *E.* (s.s.) *elegans* and *E.* (s.s.) *submutica*.

15. Overlapping of the preceding whorl by the axial sculpture: no overlapping (0); preceding whorl poorly covered (1 to 5%) (1) (Fig. 3A); preceding whorl moderately covered (6 to 10%) (2) (Fig. 3B); preceding whorl strongly covered (11 to 20%) (3) (Fig. 3C). Comment: a preceding whorl strongly covered by the lamellae is an apomorphy of *Harpa*.

16. Number of major varices on the first whorl: 20 to 30 varices (0); 15 to 19 varices (1); more than 30 varices (2); fewer than 15 varices (3); no varices (- = not applicable).

17. Number of major varices on the last whorl: 10 to 20 varices (0); more than 20 varices (1); fewer than 10 (2); no varices (- = not applicable).

18. Secondary varices: absent (0); present (1); no major varices (- = not applicable).

19. Morphology of the secondary varices: rare and irregular ridges (0); fine lamellae (1); numerous (more than 25) ridges (2); equally (less than 25) spaced ridges (3); no secondary varices (- = not applicable).

20. Parietal expansion: overlapping the beginning of the last whorl (0); restricted to the edge of the inner lip (1). Comment: a parietal expansion overlapping the beginning of the last whorl occurs in *A.* (*V.*) *spinosa* and *Cryptochorda* (outgroup) and in *Harpa* and *Morum* (ingroup). Conversely, it is lacking in *Eocithara* and *Austroharpa*.

21. Columellar folds: present (0); absent (1). Comment: an absence of columellar folds is character state occurring in *Cryptochorda* and in the ingroup.

22. Expression of the siphonal fascioles on the columella: fascioles not making an umbilical ridge (0); fascioles making an umbilical ridge without forming columellar relief (1); fascioles making an umbilical ridge and forming columellar relief (2).

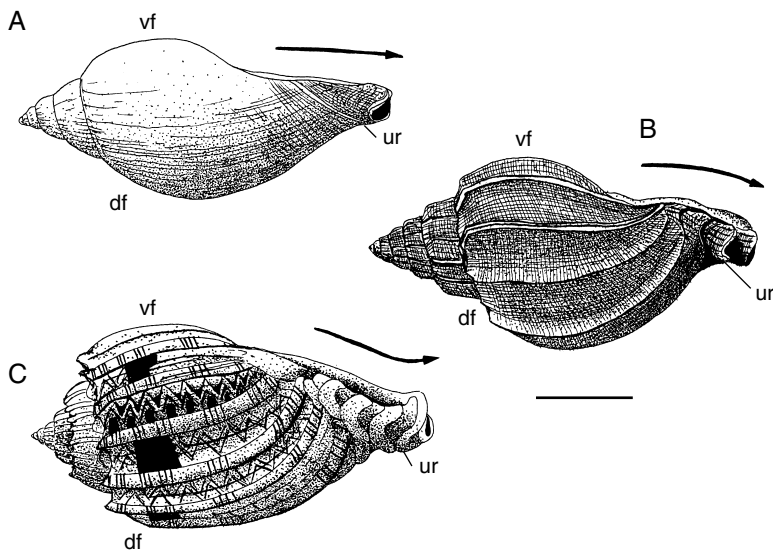


FIG. 7. — Direction of the umbilical ridge on the ventral face (character 23); **A**, state 0: straight umbilical ridge, e.g.: *Cryptochorda strombooides* (Hermann, 1781), MNHN R11405, Grignon, Yvelines, France, Lutetian; **B**, state 1: dorsally oriented umbilical ridge, e.g.: *Eocithara* (s.s.) *jacksonensis* (Harris, 1896), MNHN R11406 (L. Dolin coll.), Jackson, USA, Priabonian; **C**, state 2: ventrally oriented, e.g.: *Harpa doris* Röding, 1798, MNHN R11402 (Lecointre coll.), Praia de Castalho, Cape Verde, Recent. Abbreviations: **vf**, ventral face; **df**, dorsal face; **ur**, umbilical ridge. The black arrow indicates the direction of the umbilical ridge. Scale bar: 10 mm.

23. Direction of umbilical ridge on the ventral face: straight (0); dorsally oriented (1); ventrally recurved (2). Comment: an umbilical ridge ventrally recurved (state 2) is an apomorphy of *Harpa* (Fig. 7).

24. Direction of the siphonal canal: straight (0); dorsally oriented (1).

25. Number of teleoconch whorls: more than four whorls (0); fewer than four whorls (1).

26. Morphology and carina on the first teleoconch whorl: slightly convex whorl with a small angularity (0); whorl with an obvious angularity (1); distinctly convex whorl with a small angularity (2).

27. Umbilical ridge: umbilical fascioles not delineating a ridge (0); umbilical fascioles delineating the ridge (1); umbilical fascioles delineating the ridge, but covered by a callus expansion (2). Comment: states 1 and 2 occur in the ingroup.

28. Axial microsculpture: absent (0); fine axial striae (1). Comment: fine axial microstriae have been observed only in *Eocithara*.

29. Spiral microsculpture: absent (0); fine spiral striae between the secondary varices (1).

30. Columellar tubercles: absent (0); present (1). Comment: columellar tubercles only occur in *Morum*.

31. Labral thickening: absent (0); present (1). Comment: a labral thickening is developed in *Morum*.

MATRIX TREATMENT AND CONSENSUS TREE

The matrix (Fig. 8) has been treated by the software PAUP 4 (option Branch and Bound, optimisations Acctran and Deltran), Hennig86 (option ie) and Winclada 0.9.9 (option max. trees: 10,000, 100 reps, mult*max*) and all characters were unordered. The results obtained by each software are largely similar and the same topology has been found. PAUP 4 generated three equally parsimonious trees having a consistency index of 81.7, a retention index of 89 and a length of 71 steps, Hennig86 generated three trees with a consistency index of 80 and a retention index of 89, and Winclada generated the same number of trees with a consistency index of 81 and a retention index of 88.

	1	1	2	3
	0	0	0	0
<i>Athleta spinosa</i>	0 0			
<i>Cryptochorda stromboides</i>	1 1 0 - - - - - - - - 3 1 0 - - - - 0 1 2 0 1 0 2 0 0 0 0 0			
<i>Morum harpaeformis</i>	0 2 1 3 0 0 0 1 0 2 ? 0 1 0 0 3 0 0 0 0 1 2 1 1 0 1 1 0 0 1 1			
<i>Morum oniscus</i>	0 2 1 3 0 0 0 1 1 2 ? 0 1 0 0 3 0 0 0 0 1 2 1 1 0 1 1 0 0 1 1			
<i>Eocithara</i> (s.s.) <i>elegans</i>	0 2 0 1 1 1 1 1 0 1 1 0 2 3 2 1 0 1 1 1 1 2 1 1 0 2 1 1 0 0 0			
<i>E.</i> (s.s.) <i>submutica</i>	0 2 0 1 1 1 1 1 0 1 1 0 2 3 2 1 0 1 1 1 1 2 1 1 0 2 1 1 0 0 0			
<i>E.</i> (s.s.) <i>jacksonensis</i>	0 2 0 1 1 1 1 1 0 1 1 0 1 2 2 0 0 1 1 1 1 2 1 1 0 2 1 1 0 0 0			
<i>E.</i> (s.s.) <i>mutica</i>	0 2 0 1 1 1 1 1 0 1 1 0 2 2 2 1 0 1 1 1 1 2 1 1 0 2 1 1 0 0 0			
<i>E.</i> (s.s.) <i>helena</i>	0 2 0 1 3 - 1 1 0 1 1 0 1 2 2 0 0 1 1 1 1 2 1 1 0 2 1 1 0 0 0			
<i>E. (Refluharpa) lamellifera</i>	0 2 0 1 3 - 1 1 0 1 1 0 1 2 1 2 1 1 1 1 1 2 1 1 1 2 1 1 0 0 0			
<i>E. (Marwickara) waihaoensis</i>	0 2 0 1 3 - 1 1 0 1 1 0 2 2 1 ? 0 1 ? 1 1 2 1 1 1 2 1 ? 0 0 0			
<i>Austroharpa sulcosa</i>	0 2 0 1 2 2 1 2 1 3 0 0 1 2 1 2 1 0 0 1 1 1 1 1 1 1 1 0 0 0 0			
<i>Austroharpa spirata</i>	0 2 0 3 2 2 1 1 1 2 0 0 1 2 1 0 1 0 0 1 1 1 1 1 1 1 1 0 0 0 0			
<i>Austroharpa tenuis</i>	0 2 0 1 1 2 1 1 1 3 0 0 1 2 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 0 0			
<i>Austroharpa punctata</i>	0 3 0 2 - - - - - - - - 1 2 1 ? 2 0 0 1 1 1 1 1 1 1 2 2 0 0 0 0			
<i>Harpa articulata</i>	0 2 0 1 2 3 1 1 0 4 1 1 1 3 3 0 0 1 2 0 1 2 2 1 1 2 2 0 1 0 0			
<i>Harpa davidis</i>	0 2 0 1 2 3 1 1 0 4 1 0 1 3 3 0 0 1 2 0 1 2 2 1 1 2 2 0 0 0 0			
<i>Harpa major</i>	0 2 0 1 2 3 1 1 0 4 1 0 1 3 3 1 0 1 2 0 1 2 2 1 1 2 2 0 0 0 0			
<i>Harpa broconi</i>	0 2 0 1 2 3 1 1 0 4 1 0 1 3 3 ? 0 1 3 0 1 2 2 1 1 2 2 0 0 0 0			
<i>Harpa doris</i>	0 2 0 1 2 3 1 1 0 4 1 0 1 3 3 1 0 1 3 0 1 2 2 1 1 2 2 0 0 0 0			

FIG. 8. — Matrix of the characters.

The strict consensus tree (Fig. 9) gives the following topology: 1) no node branching *Cryptochorda* with the Harpidae, and particularly with *Austroharpa punctata*, has been found. Consequently, this result suggests the monophyly of the Harpidae (node 35) excluding *Cryptochorda*; 2) the tree presents two main nodes: the Moruminae (node 21) and the Harpinae (node 34), distinguishing the two

subfamilies; 3) the Harpinae also are divided in two nodes, the *Austroharpa* node 33 and the *Harpa-Eocithara* node 30; and 4) *Eocithara* (node 26) has *Harpa* as sister-group (node 29). This last result also demonstrates the importance of the teleoconch characters for the distinction between *Eocithara* and *Harpa*, no protoconch character being introduced in the matrix.

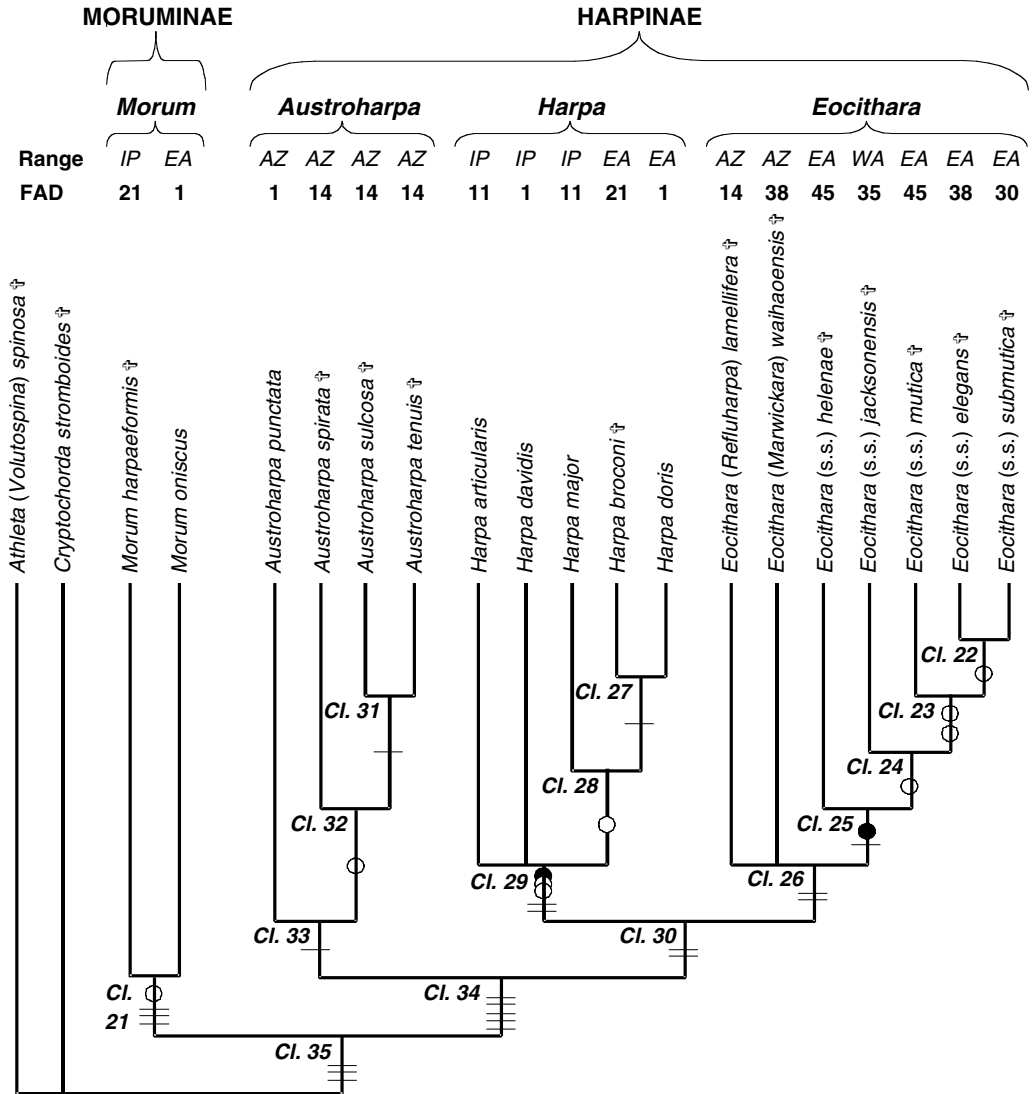


FIG. 9. — Redrawn consensus tree obtained using PAUP 4 (option: Branch and Bound; trees: 3; length: 71, CI: 81.7; RI: 89). Explanations: **clade 35**: ua = 20(1), 23(1), 27(1); **clade 34**: ua = 5(2), 7(1), 14(2), 15(1), 25(1); **clade 21**: ua = 3(1), 16(3), 30(1), 31(1), ha = 26(1); **clade 33**: ua = 22(1); **clade 32**: ha = 26(1); **clade 31**: ua = 10(3); **clade 30**: ua = 11(1), 18(1); **clade 29**: ua = 15(3), 23(2), ha = 14(3), 27(2), r = 20(0); **clade 28**: ha = 16(1); **clade 27**: ua = 19(3); **clade 26**: ua = 5(3), 28(1); **clade 25**: ua = 15(2), r = 25(0); **clade 24**: ha = 5(1); **clade 23**: ha = 13(2), 16(1); **clade 22**: ha = 14(3). Abbreviations and symbols: **FAD**, First Appearance Data in Mya; **ua**, unambiguous synapomorphy; **ha**, homoplastic synapomorphy; **r**, reversion; **AZ**, Australia and New Zealand; **EA**, eastern Atlantic; **IP**, Indo-Pacific; **WA**, western Atlantic; †, fossil taxa; —, non homoplastic apomorphy; O, homoplastic apomorphy; ●, reversion.

CHARACTER ANALYSIS

More detailed information concerning the possible relationships between *Eocithara* and the

other harpid genera is provided in this part. For the character analysis, we will only discuss the unambiguous synapomorphies regarding the topology of the tree.

HARPIDAE CLADE

Node 35

This basal node is supported by three synapomorphies. A reduced parietal expansion to the edge of the inner lip (character 20) is regarded as an apomorphic state (transformation 0 → 1). This interpretation basically depends on the polarisation using the selected outgroups, which both have a parietal expansion overlapping the beginning of the last whorl (state 0). However, this character state is rare in primitive Neogastropoda and probably represents an apomorphy. Actually, early harpids (e.g., *Eocithara*) possess the character state 1 (reduced parietal expansion on the edge of the inner lip) such as in many neogastropods, and we cannot exclude the possibility that this state would be better interpreted as a plesiomorphic state. The two other apertural characters [23 (1) and 27 (1)] indicate changes of the umbilical ridge (morphology of umbilical fascioles and dorsal orientation). They are diagnostic indicators for the distinction between the Harpidae and the Cryptochordidae.

HARPIDAE (MORUMINAE) CLADE

Node 21

Five apomorphic characters support the node 21, containing the Moruminae. Among them, four are distinctive for the Harpinae and concern the aperture: internal denticles of the outer lip [3 (1)], less than 15 major varices on the first whorl [16 (3)], columellar tubercles [30 (1)] and developed labral thickening [31 (1)]. The fifth synapomorphy, first teleoconch whorl with an obvious angularity [26 (1)] is homoplastic with *Austroharpa*.

HARPIDAE (HARPINAE) CLADE

Node 34

The internal node 34 is supported by five basal synapomorphies for the Harpinae. Two characters concern the spiral sculpture (5 and 7), two the axial sculpture (14 and 15) and one the coiling (25). Regarding the spiral sculpture, two

transformations are proposed: developed and adaxially oriented P1 spine (5 (0) → 5 (2)) and loss of the sutural cord (7 (0) → 7 (1)). For character 5, a transformation (0 → 2) is more parsimonious than a transformation 0 → 1 (poorly developed and adaxially placed) or 0 → 3 (absence of spine), but the earliest (*Eocithara*) taxa possess the states 1 or 3, probably suggesting a polarisation problem of this character. For character 7, the state 1 may be regarded as a good basal synapomorphy, distinguishing the Harpinae from the Moruminae. It is the same case for axial characters 14 and 15, respectively indicating the appearance of abaxially projected lamellae (transformation 0 → 2) and a penultimate whorl poorly covered by the adaxial expansion of the varices (transformation 0 → 1). The topology of the tree also indicates having fewer than four whorls [25 (1)] as an apomorphy. This interpretation is slightly ambiguous because, while *Harpa*, *Austroharpa* and the Australian and New Zealand subgenera *E. (Refluharpa)* and *E. (Marwickara)* effectively share this character state, it is lacking in the Paleogene *Eocithara* (s.s.), which are older.

AUSTROHARPA CLADE

Node 33 (Austroharpa punctata + node 32)

The node 33 is supported by a single synapomorphy: siphonal fascioles making a ridge and forming a columellar relief [22 (2)]. This character state is restricted to the genus *Austroharpa* and, in the case of *A. punctata*, it is distinctive from *Cryptochorda*. We can also point to the absence of apomorphies found through the sculpture. A detailed analysis of the matrix allows us to understand that this absence does not come from homoplasies, but from the diversity of types of spiral sculpture in the studied taxa.

Node 32 (A. spirata and node 31)

This node is supported by a single apomorphy: a carina on the first teleoconch whorl forming an obvious angularity [26 (1)]. This character state is regarded as homoplastic with the Moruminae.

Node 31 (*A. sulcosa* and *A. tenuis*)

Poorly expressed and convex primary cords in the centre of the last whorl [10 (3)] is the single synapomorphy of this terminal node, indicating a transformation (2 → 3). This apomorphy is interesting, because despite the sculptural diversity of *Austroharpa* species, two main groups may be distinguished, one being *A. spirata* and *A. exquisita* (type species of *A. (Palamharpa)*) with well expressed convex spiral cords (state 2), and the other including *A. sulcosa*, *A. tenuis* and *A. pulligera* (type species of *Austroharpa*).

Rehder (1973) considered *Austroharpa* (s.s.) as monospecific, because of mamillate protoconch in *A. pulligera*, while he classified *A. tenuis* and *A. sulcosa* in *A. (Palamharpa)*. Our observations suggest that *A. pulligera*, *A. sulcosa* and *A. tenuis* are probably more closely related than the other species are. In this case, it would be preferable to transfer *A. sulcosa* and *A. tenuis* to *Austroharpa* (s.s.), or more simply to regard *Palamharpa* as a junior synonym of *Austroharpa*, considering the few characters distinguishing both subgenera, and especially as protoconch, this developmental character being no longer considered to separate genera.

HARPA + EOCITHARA CLADES*Node 30*

The internal node 30 is supported by two synapomorphies: presence of adapical secondary cords on the spire [11 (1)] and presence of secondary varices [18 (1)]. These sculptural characters are restricted to *Harpa* and all *Eocithara* species.

HARPA CLADE*Node 29* (*Harpa articulata*, *H. davidis* and *node 28*)

The *Harpa* clade is well supported by two synapomorphies of the axial sculpture, two of the aperture and one reversion. The sculptural character states 14 (3) (abaperturally projected lamellae, transformation 2 → 3) and 15 (3) (axial sculpture largely covering (11-20%) the preceding whorl, transformation 1 → 3) indicate an increase in the

development of axial sculpture. The character state 14 (3) is homoplastic with two species of *Eocithara* (*E. (s.s.) elegans* and *E. (s.s.) submutica*), while the character state 15 (3) is autapomorphic. The apertural autapomorphy [23 (2)] suggests a change in the orientation of the umbilical ridge (transformation 1 → 2), which is ventrally turned and not dorsally turned as in other harpids. The character state 27 (2) (umbilical fascioles covered by a callus expansion, transformation 1 → 2) is a widespread character in *Harpa*, but homoplastic with *Austroharpa punctata*. An overlapping of the parietal expansion [20 (0)] is regarded as a reversion (transformation 1 → 0), because it is present in the outgroup and absent in all the other members of the ingroup. Regarding the Paleogene Neogastropoda, this kind of aperture is rare, but its occurrence in *Athleta*, *Cryptochorda* and *Harpa* probably corresponds to a homoplasy.

Node 28 (*H. major* and *node 27*)

The node is supported by a single apomorphy concerning the number of varices in the first whorl [16 (1)]. This character state, homoplastic and occurring in *Austroharpa* and *Eocithara*, has a low consistency index (0.50).

Node 27 (*H. broconi* and *H. doris*)

This node containing two Atlantic *Harpa* is characterized by spaced ridges corresponding to the secondary varices [19 (3)], while the studied Indo-Pacific *Harpa* have numerous (more than 25) ridges [19 (2)].

EOCITHARA CLADE*Node 26* (*E. (Refluharpa)*, *E. (Marwickara)* and *Eocithara (s.s.) clade*)

A polytomy is observed at the base of this node containing *E. (Refluharpa)*, *E. (Marwickara)* and the *Eocithara* (s.s.). Homoplasies in the characters 13 (axial sculpture on first whorl), 15 (overlapping of the axial sculpture on the precedent whorl) and 16 (number of major varices on the first whorl) are responsible for conflicts in the topology. The node 23 is supported by two synapomorphies found in the sculpture: absence

of the spine P1 in the adult [5 (3)] and fine axial microsculpture [28 (1)]. The character state 5 (3) is restricted to *E. (Refluharpa)*, *E. (Marwickara)* and to *E. (s.s.) helenae* n. sp. and a fine axial microsculpture [28] has been observed only in *Eocithara*.

EOCITHARA (s.s.) CLADE

Node 25 (*Eocithara (s.s.) helenae* n. sp. and *node 24*)

A penultimate whorl moderately covered (6 to 10%) by the axial sculpture [15 (2)] is regarded as an apomorphy of this node (transformation 1 → 2). It corresponds to an increase in the adapical development of the varices. The topology also suggests a reversion for character 25 (more than five teleoconch whorls, transformation 1 → 0). We have already discussed the ambiguity of this result for node 35.

Node 24 (*Eocithara (s.s.) jacksonensis* and *node 23*)

Node 24 is supported by a single synapomorphy of the sculpture: poorly developed and adaxially placed cord spine P1 [5 (1)]. The topology suggests an increase of the development of the spine P1 in the adult, compared with basal *Eocithara* (transformation 3 (= absence of spine) → 1). This character is also homoplastic with *Austroharpa tenuis*, but in this species, the suggested transformation is 2 → 1 indicating a decrease of the development of this character in the adult.

Node 23 (*Eocithara (s.s.) mutica* and *node 22*)

Node 23 is supported by two synapomorphies of the axial sculpture. Character 13 (type of axial sculpture on the first whorl) suggests the acquisition of sigmoid lamellae (state 2) on the first whorl from orthocone lamellae (transformation 1 → 2). This state is restricted to *Eocithara*, but it is homoplastic, occurring in *E. (Marwickara)*. Character 16 (number of major varices on the first whorl) indicates a reduction in the number of varices (transformation 0 → 1 = 15 to 19 varices), but this state is highly homoplastic and also occurs in *Harpa* and *Austroharpa*.

Node 22 (*Eocithara (s.s.) elegans* and *E. (s.s.) submutica*)

This terminal node is supported by a single synapomorphy of the adult axial sculpture: character 14 (3). The topology indicates the derivation of thick projected lamellae (found in several *E. (s.s.) elegans* and *E. (s.s.) submutica*) from thin and abaxially projected lamellae (transformation 2 → 3). This character state is homoplastic with *Harpa*.

BIOGEOGRAPHIC AND STRATIGRAPHIC CONGRUENCES

BIOGEOGRAPHIC CONGRUENCE

In this part, we will deal with the biogeographic congruence of the resultant tree, simultaneously regarding the protoconchs, because the two larval types (multispiral and paucispiral protoconchs) are important for the biogeography of many marine gastropods including the Harpidae. Two main observations may be made. Firstly, multispiral protoconchs indicate a planktotrophic larval stage, often correlated with a wide dispersion (e.g., *Harpa major*, Recent), while paucispiral protoconchs indicate a lecithotrophic larval stage corresponding to a short life (if any) in the plankton and correlated with a restricted dispersion (e.g., *Austroharpa punctata*, Recent). Secondly, the acquisition of a paucispiral protoconch from species having a multispiral protoconch is a hypothesis corroborated by paleontological studies (Bouchet 1987), but the reverse evolution has been never confirmed (Bouchet 1983, 1987).

Austroharpa clade

The *Austroharpa* clade (Fig. 9) exclusively contains South Australian species. This result is highly congruent with the geographic range of the whole genus, restricted to the warm temperate waters of South Australia. However, it is interesting to point out that all *Austroharpa* species, known from the Upper Oligocene to the Recent, possess a paucispiral protoconch. This observation may explain the restricted geographic range of *Austroharpa*, but it is enigmatic that no

Austroharpa with a multispiral protoconch has been found, such as in *Harpa* or *Eocithara*. Two hypotheses may be proposed: 1) *Austroharpa* corresponds to an endemic radiation, exclusively composed of species having paucispiral protoconchs; 2) the *Austroharpa* clade may be paraphyletic, because it does not include species with a multispiral protoconch (gap in the paleontological record, incongruence in the cladogram, etc.). For example, species placed in *Austroharpa* all possibly evolved from other genera (such as *Eocithara*) by loss of planktotrophy. A longer discussion would be too conjectural.

Harpa clade

The *Harpa* clade (Fig. 9) contains Recent Indo-Pacific, West African and European Burdigalian (Aquitaine basin) species. The protoconch of the European species is still unknown, but they are multispiral in the other species. In the tree file, the Burdigalian and the West African species form a terminal node and are not mixed with Indo-Pacific species. The result appears congruent, because the Burdigalian fauna from Aquitaine is closely related to the Western African fauna and belongs to the primitive Euro-West-African Paleo-Province (Lozouet 1997).

Eocithara clade

The *Eocithara* clade (Fig. 9) forms a basal polytomy including *E. (Refluharpa)*, *E. (Marwickara)* and the *Eocithara* (s.s.) clade, but no node mixing the austral species (*Refluharpa* and *Marwickara*) with the Atlantic species (*Eocithara* (s.s.)) has been found. In the tree file, one tree suggesting a subdivision of the *Eocithara* clade into two nodes, the *Eocithara* (s.s.) node and *Marwickara* + *Refluharpa* node is more congruent with the biogeography of the considered taxa. *Marwickara* and *Refluharpa* also possess paucispiral protoconchs. In *Marwickara* and *Refluharpa*, this larval character is correlated with a restricted biogeographic range (South Australia and New Zealand), contrasting with the wider range of *Eocithara* (s.s.). We still cannot consider *Marwickara* and *Refluharpa* as a true species radiation because they are both monospecific, but they show once again that the South Australian sec-

tor is an endemic sector for the Harpids. The *Eocithara* (s.s.) clade includes four European species and one American species. The two basal taxa (in the nodes 21 and 22) of this pectinate clade are represented by the Ypresian European species *E. (s.s.) helena* n. sp. and the Priabonian American species *E. (s.s.) jacksonensis*. This result does not appear to be geographically congruent, but it is interesting to point out that these Eocene basal species both possess a multispiral protoconch, which is often correlated with wide geographic and stratigraphic ranges (Hansen 1978, 1982). More congruent is node 21 proposing a distinction between *E. (s.s.) jacksonensis* and a European branch (node 20) including the two Eocene European species with paucispiral protoconchs.

STRATIGRAPHIC CONGRUENCE

The question of stratigraphic congruence can be counted by the statement that cladograms predict the order in which fossil taxa appear and may be tested with the stratigraphic record (Benton & Storrs 1994, 1996; Benton *et al.* 1999; Wagner 1995; Siddal 1998; Pol & Norell 2001). Nevertheless, the question of the fit of the cladogram with the stratigraphic record generates a methodological debate with two opposite points of view (Zaragueta & Lelièvre 2001). The first uses coefficients (e.g., Spearman coefficient) that modifies the cladogram to adapt it to the stratigraphy (e.g., Norell & Novacek 1992), while the second one, considering the independence between temporal data and hierarchic hypotheses, preconises the measure of the fit of the cladogram with the stratigraphic record by an index (e.g., Siddal 1998; Pol & Norell 2001; Zaragueta & Lelièvre 2001). According to the second opinion, which does not require an alteration of the cladogram, a measure of the fit of the harpid tree with the stratigraphic record is presented here using the MSM (Manhattan Stratigraphic Measure) of Siddal (1998) modified by Pol & Norell (2001). The principle of this measure is based on the optimisation of a Sankoff character on the tree. "This character is set assigning a different character state to each taxon and the cost of the transformation between character states are defined in

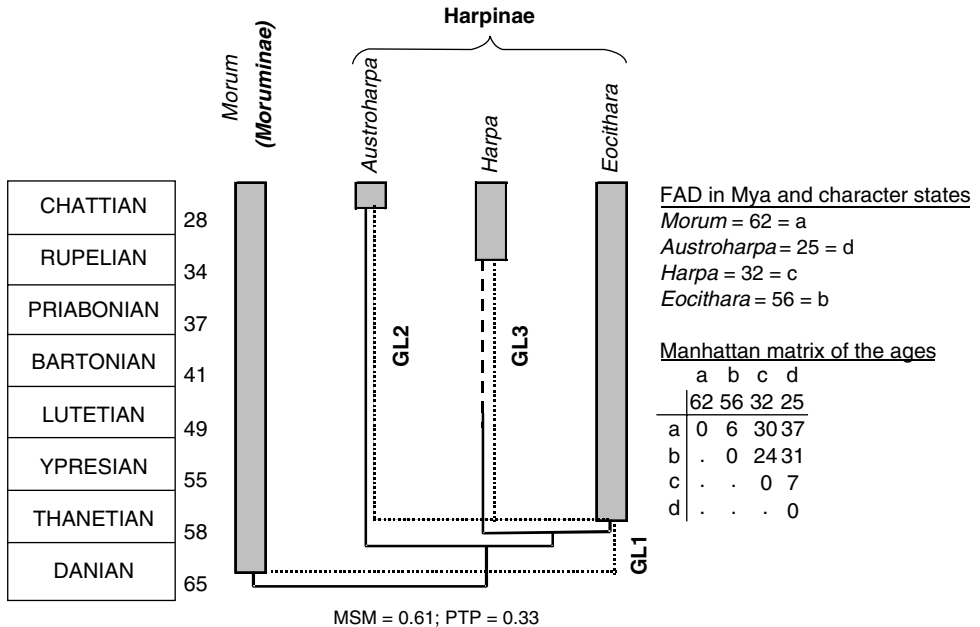


FIG. 10. — Generic comparison between the order of appearance of the taxa in the consensus tree and the stratigraphical record, codification of the character age and Manhattan matrix of the ages. Abbreviations and symbols: **FAD**, First Appearance Data; **GL1**, ghost line between the *Moruminae* and the *Harpinae* clades; **GL2**, ghost line between the *Austroharpa* and the *Harpa-Eocithara* clades; **GL3**, ghost line between the *Harpa* and the *Eocithara* clades; **dark cells**, stratigraphic range of the taxa in the Paleogene.

a symmetrical step matrix [Manhattan matrix, Fig. 10], based on the absolute difference in first appearance ages [FAD = First Appearance Data] between each pairwise comparison of taxa. Then, the character is optimized using Sankoff parsimony in the phylogenetic hypothesis and its length (L_o) is compared to the minimum length (L_m) that the age character can have in any phylogenetic hypothesis (MSM = L_m / L_o) (Pol & Norell 2001). The procedure to calculate the MSM is given by Pol & Norell (2001) and it may be processed by the software PAUP 4.

Two MSM have been calculated, one for the consensus tree using the FAD of the studied species (Fig. 9) and one at generic level (Fig. 10) using the FAD of oldest species belonging to the genera considered (*Morum*, *Austroharpa*, *Harpa* and *Eocithara*) which are not included in the matrix for diverse reasons (missing material or too badly preserved). These last FAD have been found in Furon & Kouriatchy (1953) and Chabaglian (1959) for

the *Moruminae*, in Rehder (1973) for *Austroharpa*, in MacNeil & Dockery (1984) and Vokes (1984) for *Harpa* and come from this work for *Eocithara*. The FAD of the *Moruminae*, often reported from the Oligocene (Wenz 1943) with *Morum*, is here reported from the Danian of Togo with "*Oniscia* (= *Morum*) (*Oniscidia*)" *chavani* Furon & Kouriatchy, 1959. The attribution to the subgenus *Oniscidia* Mörch, 1852 seems doubtful, but the African species possesses apertural apomorphies (internal denticles, labral thickening and columellar ornamentation) found in *Morum*. The FAD of *Eocithara* is reported with *Eocithara rosenkrantzii* n. sp. from the Thanetian of Greenland, that of *Austroharpa* is reported from the austral Chattian with *A. pachycheila* (Tate, 1894) and that of *Harpa* is reported from the American Rupelian with *H. vicksburgiana* Dockery, 1984 and from Peruvian Rupelian with *H. myrmia* Olsson, 1931. Palmer (1937) and Rehder (1973) also presented a fragmentary spec-

imen with axial sculpture (abaxially projected lamellae) from the middle Eocene of Texas, which is similar to those of *Harpa* and to some *Eocithara*. So, new data from the Texan Eocene will be necessary to verify the FAD of *Harpa*.

At specific level, the value of the MSM is 0.20 ($L_o = 218 / L_m = 44$). It is significantly low and clearly indicates conflicts between the stratigraphic record and the topology of the tree, despite the value (= 0.053) of the PTP test, the probability of finding a length shorter than L_o after 1000 replications, is also significantly low. Conflicts between the stratigraphic record and the topology are evident regarding the Moruminae, *Austroharpa* and *Harpa* and can only be resolved by the introduction of long ghost taxa. If the entire stratigraphic range of each genus is considered, the value of MSM increases to 0.61 ($L_o = 61 / L_m = 37$) and the PTP value (0.33) also increases. The increase of the MSM probably results from a reduction in the length of the ghost taxa in the case of the Moruminae and *Harpa*. However, other parameters may influence the value of the MSM, which decreases when the number of taxa increases (Siddal 1998; Pol & Norell 2001; Zaragueta & Lelièvre 2001). Regarding this point, the fact that two different topologies (one poorly pectinate topology with 18 taxa and one pectinate topology with four taxa) are being tested needs to be stressed.

CONCLUSION

This paper adds to the knowledge of *Eocithara*, providing new biostratigraphic data for the genus and describing three new species. Among this material, the discovery of three species with multispiral protoconchs (Figs 3; 6) in the Paleogene invalidates the protoconch as a distinctive character in the harpid classification used by Rehder (1973). This is particularly true in the case of the distinction between *Eocithara* and *Harpa*. Therefore, the usefulness of the teleoconch characters has been re-evaluated. A closer inspection of these characters using a performed descriptive method, suggests their usefulness for a phyloge-

netic analysis. The cladistic analysis firstly shows that they may be exclusively used to distinguish the different harpid genera (*Morum*, *Austroharpa*, *Harpa* and *Eocithara*), without using the protoconch as a criterion. Secondly, the consensus tree (Fig. 9) is particularly congruent with the biogeographic data and at the generic level, the value of the MSM do not indicate major conflicts between the order in which taxa appear in the cladogram and the stratigraphic record. These congruencies encouraged the addition of fossil taxa to aid the understanding of the harpid phylogeny and demonstrate the importance of a performed descriptive method for the shell, as a fruitful means of investigation.

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