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Review of the paleobiogeography of *Eofavartia* Merle, 2002 (Gastropoda: Muricidae) with the description of a new species from the Miocene of Java (Indonesia)

Révision de la paléobiogéographie d'*Eofavartia* Merle, 2002 avec la description d'une espèce nouvelle du Miocene de Java (Indonésie)

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Abstract: The paleobiogeographic range of *Eofavartia* Merle, 2002 (Gastropoda: Muricidae) was until now restricted to the Eocene (Ypresian to Priabonian) of the North Atlantic Ocean and the genus seemed to become extinct after the Priabonian. The description of *E. dharmai* nov. sp. from the Middle Miocene from Java (Indonesia) reveals the persistence of *Eofavartia* during the Neogene in the Indo-Pacific region. In addition, the revision of three South Australian species previously attributed to *Murexiella* and *Subpterynotus* respectively: *M. perculata* Vokes, 1985 (Lower Miocene), *S. antecessens* (Ludbrook 1958) (Pliocene) and *S. tatei* (Verco 1895) (Recent) shows closer morphological affinities to *E. dharmai* nov. sp. and the European and North American Paleogene species. This generic reassignment to *Eofavartia* expands the range of the genus to include South Australia. The extant *E. tatei* represents the last member of the genus, and is herein considered a relict species of *Eofavartia*.

Keywords: Neogene, Indo-Pacific, systematics, biogeography, new species.

Résumé : L'extension paléobiogéographique du genre *Eofavartia* Merle, 2002 (Gastropoda: Muricidae) était jusqu'à lors restreinte à l'Eocène (Yprésien à Priabonien) de l'Océan Atlantique Nord et le genre semblait s'éteindre après le Priabonien en Europe. La description d'*E. dharmai* nov. sp. du Miocène moyen de Java (Indonésie) révèle la persistance d'*Eofavartia* au Néogène dans la région Indo-Pacifique. De plus, la révision de trois espèces

d’Australie du Sud respectivement attribuées à *Murexiella* et *Subpterynotus*: *M. perculata* Vokes, 1985 (Miocène inférieur), *S. antecedens* (Ludbrook, 1958) (Pliocène) et *S. tatei* (Verco, 1895) (actuel) souligne de plus étroites affinités morphologiques avec *E. dharmai* nov. sp. et les espèces paléogènes. Elles sont donc transférées dans *Eofavartia*. Ce résultat étend encore l’extension d’*Eofavartia* à l’Australie du Sud. L’espèce actuelle *E. tatei* est la dernière connue d’*Eofavartia* et peut être considérée comme une espèce relictive du genre.

Mots-clés : Neogène, Indo-Pacifique, systématique, biogéographie, espèce nouvelle.

1. Introduction

In earlier literature, species now attributed to *Eofavartia* Merle, 2002 were attributed to *Murexiella* Clench & Perez Farfante, 1945, a junior synonym of *Favartia* Jousseume, 1880 (e.g., [Cossmann & Pissarro, 1911](#), [Vokes 1968, 1971, 1974, 1985, 1994](#)), as they share several convergent shell characters (subfusiform shape, adapertural face of the varices with imbricated growth laminae, subcircular aperture with closed and rounded shoulder sinus, surface of primary cords with deep spiral grooves). However, new structural homologies identified in muricid shells ([Merle 1999, 2001, 2005](#)) were used in a cladistic analysis ([Merle, 1999, 2002](#)), which enabled the separation of *Eofavartia* from *Favartia*. *Eofavartia* possesses plesiomorphic character states (developed cord P6, P6 on the base of the convex part of the whorl and the presence of D6), which are apomorphic in *Favartia* and other typical Muricopsinae (P6 atrophied, P6 on the top of the siphonal canal, D6 missing). This cladistic analysis also suggested that *Eofavartia* and *Homalocantha* Mörch, 1852 could be potential sister or stem groups of the Muricopsinae (see [Merle, 2002](#); *Subpterynotus* Olsson & Harbison, 1953 was not considered).

Early Neogene species of *Homalocantha* (*H. heptagonata* (Bronn, 1831), *H. perpulcher* (Bellardi, 1872) from Europe and *H. crispangula* (Heilprin, 1887) from North-America) have a rounded and closed shoulder sinus as in *Eofavartia*, but differ by P6 on the top of siphonal canal, by poorly marked growth laminae, by an erect plate of shell matter deposited between the shoulder of each varix and the previous whorl (partition, sensu [Radwin & d’Attilio, 1976](#)) and by lacking D6 and spiral grooves on the cords. Until now, the range of *Eofavartia* was restricted to the Eocene of North Atlantic Ocean ([Merle, 2002](#)). The oldest occurrence of *Eofavartia* is from the Ypresian of Alabama and its last occurrence is from the European Priabonian. The new species described herein demonstrates that the genus had a greater geographical range than previous thought, and was present in the middle Miocene of

Indonesia. This discovery led us to re-examine other Indo-Pacific Neogene and Recent species previously attributed to *Favartia* and *Subpterynotus* and to reconsider the geographical and stratigraphic ranges of *Eofavartia*.

2. Material and method

2.1 Material and Geological setting

The material described herein is deposited in the Natural History Museum Vienna (NHMW). It was collected by B. Dharma in the Nyalindung area (West Java), the type area of the Nyalindung Formation. This formation is one of the significant accumulations of mainly shallow marine Neogene strata exposed on land in West Java. The lower to middle part of the formation consists of dark sandy siltstone and calcareous sandstone, and contains diverse shallow marine molluscs such as conid, cerithiid and nassariid gastropods, arcid and tridacnid bivalves, and branching corals, suggesting a deposition in a tropical lower intertidal to upper sub-tidal environment (Kase et al. 2015). The precise geologic age of the formation is still debated due to the scarcity of planktonic foraminifers and calcareous nannoplankton (Aswan et al., 2008). It is usually attributed to the Middle Miocene (Aswan 2006; Aswan & Osawa, 2006; Aswan et al. 2008; Wilson & Hall, 2010). However according to Aswan et al. (2017) and Batenburg et al. (2011), the age of the Nyalindung Formation can range between the early Middle Miocene and the early Late Miocene.

2.2 Shell Terminology

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

P: primary cord

s: secondary cord

t: tertiary cord

Ad: adapical (or abapertural)

Ab: abapical (or adapertural)

SP: subsutural cord

IP: infrasutural primary cord (primary cord on shoulder)

adis: adapical infrasutural secondary cord (shoulder)

abis: abapical infrasutural secondary cord (shoulder)

P1: shoulder cord

P2-P6: primary cords of the convex part of the teleoconch whorl

s1-s6: secondary cords of the convex part of the teleoconch whorl (example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc.)

ADP: adapertural primary cord on the siphonal canal

MP: median primary cord on the siphonal canal

ABP: abapertural primary cord on the siphonal canal

ads: adapertural secondary cord on the siphonal canal

ms: median secondary cord on the siphonal canal

abs: abapertural secondary cord on the siphonal canal

ID: infrasutural denticle (internal denticles of the outer lip)

D1-D6: abapical denticles of the outer lip

3. Repository

ANSP: Academy of Natural Sciences of Philadelphia, Pennsylvania, USA

MNHN.F.: Muséum National d'Histoire Naturelle, Paris, France (collection of Paleontology)

MNHN.IM.: Muséum National d'Histoire Naturelle, Paris, France (collection of marine invertebrates)

NHMW: Naturhistorisches Museum, Wien, Austria

NHMUK: Natural History Museum, London, United Kingdom

NMV: National Museum of Victoria, Melbourne, Australia

RGM: Rijksmuseum van Geologie en Mineralogie

UCLB: Université Claude Bernard, Lyon 1, Lyon, France

USNM: National Museum of Natural History, Smithsonian Institution, Washington DC, USA

4. Systematic palaeontology

Class GASTROPODA Cuvier, 1795

Subclass CAENOGASTROPODA Cox, 1960

Order NEOGASTROPODA Wenz, 1938

Superfamily MURICOIDEA Rafinesque, 1815

Family MURICIDAE Rafinesque, 1815

INCERTAE SEDIS

Subfamily MURICOPSINAE Radwin & D'Attilio, 1971

Genus *Eofavartia* Merle, 2002

Type species: *Murex frondosus* Lamarck, 1803 by original designation. Middle Eocene (Lutetian): Paris Basin, France.

Included species: North American Paleogene: *Eofavartia* sp. [= *Murexsul* sp. in [Vokes \(1994\)](#)], Ypresian (Alabama, USA); *E. mantelli* (Conrad, 1834), Bartonian (Alabama). European Paleogene: *E. frondosa* (Lamarck, 1803), Lutetian (Paris Basin, France); *E. marchandi* (Cossmann, 1903), Bartonian (Loire Basin and Normandy, France); *E. subrudis* (d'Orbigny, 1850), Bartonian (Paris Basin, Hampshire and ?Priabonian of North Germany). Indo-Pacific Neogene: *E. perculata* (Vokes, 1985) nov. comb., upper Aquitanian-lower Burdigalian to Langhian, (South Australia); *Eofavartia dharmai* nov sp., Middle Miocene (Western Java, Indonesia); *E. antecedens* (Ludbrook, 1958) nov. comb, Pliocene (South Australia). Recent: *Eofavartia tatei* (Verco, 1895), nov. comb., South West Australia, at 30-37 m deep. For the synonymic list of the species, see [Merle \(1999\)](#) and [Merle et al. \(in press\)](#).

Insert Figure 1

Eofavartia dharmai nov. sp.

Figs 1A-F, 3A-D

References

Homalocantha talahabensis (Martin, 1895) – sensu [Dharma, 2005](#): 338, pl. 134, fig. 5a-c, not *Murex (Homalocantha) talahabensis* Martin, 1895.

Eofavartia sp. 2 – [Merle et al., in press](#): pl. 148, figs 5-6.

Etymology: Named in honour of Bunjamin Dharma (Jakarta), who made these specimens available and in recognition of his contributions to Indonesian malacology.

Type locality: Nyalindung area, Nyalindung Formation, Middle Miocene ([Dharma, 2005](#)), West Java, Indonesia. The exact locality within the Nyalindung area is not known, but the type material is partially covered by a dark sandy siltstone. A dark sandy siltstone corresponds

to the lower to middle part of the formation, contains diverse shallow marine molluscs and is well exposed in the Tjitalahab valley (Kase et al., 2015).

Type material: Holotype NHMW 2019/0178/0001 (ex. Landau coll.), H: 24.5 mm, W 15.2 mm; paratype NHMW 2019/0178/0002 (ex. Landau coll.), H: 24.5 mm, W: 13.8mm.

Description: Protoconch not preserved. Biconic teleoconch up to 24.5 mm in height, up to 13.8-15.2 mm in width. Moderately high spire, up to six subcarinate whorls. Last whorl (sixth whorl) 81% of total height. Apical angle of 80°. Spiral sculpture with marked primary cords. First whorl: not preserved. Second whorl: presence of P1, P2 and P3. Third whorl: appearance of IP. Fourth whorl: appearance of the secondary cord s3. Fifth whorl: appearance of adis. Sixth whorl (last whorl): adis, IP (sutural ramp); P1 to P6, s1 to s6 (convex part of the whorl) P6 not atrophied, s3, s4 and s6 well developed, s1, s2 and s5 missing; ADP, MP, ABP and EAB1 (siphonal canal), ads, ms and abs present; rare tertiary cords (Fig. 1B, E). Axial sculpture with eight varices on second whorl, nine on third whorl, seven-eight on fourth whorl, seven on fifth whorl and six on sixth whorl. Varices rather thick on last whorl. Adapertural face of the varices with imbricated growth laminae. Axial ornamentation on spire with very short spinelets on P1. On last whorl, short spinelets from P1 to P6 on convex part of whorl and from ADP to EAB1 on siphonal canal. Siphonal canal slightly winged. Squamous microsculpture formed by erected collabral growth lamellae covering surface of shell. Aperture subcircular, up to 22% of diameter and up to 81% of length of last whorl (including siphonal canal). Columellar lip smooth, narrow, erected anteriorly, forming inductura at base. Parietal lip narrow, adherent. No anal sulcus and no parietal callus. Outer lip denticulate. Series of weak denticles including: ID, D1 to D6. ID simple or split, D1-D2 simple, D3-D4 split, D5-D6 simple (Fig. 1C, F). No crenulation at edge of outer lip. Shoulder sinus of P1 not developed. Siphonal canal open, bent to right, slightly dorsally recurved, up to 60% of aperture length. Pseudoumbilicus moderately wide.

Insert Figure 2

Comparisons

[Dharma \(2005, pl. 134, fig. 5a-c\)](#) illustrated a muricid from Nyalindung under the name *Homalocantha talahabensis* from the same locality (Bunjamin Dharma personal

communication BL; 03/07/2020), and conspecific with the type material described herein of *Eofavartia dharmai* nov. sp. However, *Homalocantha talahabensis* (Martin, 1895) is easily separated from *E. dharmai* nov. sp. in having a lower spire, more angulate whorls, developed partitions and a weak P6 on the siphonal canal. These two last characters are typical of the genus *Homalocantha* and are not present in *Eofavartia*. The holotype (RGM 9711-1) of *H. talahabensis* is illustrated here for comparison (Figs 1G-I).

Paleogene *Eofavartia* species: as in all members of *Eofavartia*, *E. dharmai* displays a developed cord P6, P6 on the base of the convex part of the whorl, a series of internal denticles including D1 to D6 and an adapertural face of the varices bearing imbricated growth laminae (Figs 2-3). *Eofavartia* sp. (Ypresian, Alabama) is an immature specimen, but it bears a higher spire compared to *Eofavartia dharmai*. *E. mantelli* (Figs 2C, 3G-H) differs by its inflated last whorl and by having well individualized spines on the siphonal canal (ADP, MP and ABP). *E. frondosa* (Figs 2A-B, 3E-F) differs by its higher spire and its primary cord spines (P1 to P6) dorsally curved and developed on the convex part of the whorl and on the siphonal canal (ADP, MP and ABP). *E. marchandi* (Fig. 2D) strongly resembles *E. frondosa* in shape and sculpture, but its protoconch is paucispiral, whereas the protoconch of *E. frondosa* is multispiral (Merle 1999). *E. subrudis* (Fig. 2E) is as solid-shelled as *E. dharmai*. It shares other similarities such as short spinelets (on P1 to P6) and a slightly winged siphonal canal. The internal denticles are more strongly developed than in *E. dharmai* nov. sp. and the last whorl is more inflated. On the last whorl, the number of varices ranges from 6-7 (*E. mantelli*, *E. frondosa* and *E. dharmai*) to 7-9 in *E. subrudis*.

The Neogene and Recent *Eofavartia* species: *E. perculata* (Figs 2F-G, 3I-L) was first attributed to *Favartia* by its author (Vokes, 1985). According to Vokes (1985), an adapertural face of the varices bearing imbricated growth laminae and poorly developed internal denticles of the outer lip are shared with *Favartia*. However, *E. perculata* displays P6 on the convex part of the whorl and the internal denticle D6 is present on the outer lip (Fig. 2F-G). These two character states differ from those of *Favartia* species and other Muricopsinae in which P6 is atrophied and placed on the siphonal canal and D6 is missing. According to Merle (1999, 2002), these character states are plesiomorphic in *Eofavartia*, whereas they are apomorphic in *Favartia*. Therefore, *E. perculata* should be transferred in *Eofavartia*, and might not even represent a muricopsine species. *E. dharmai* nov. sp. and *E. perculata* share short spinelets (on P1 to P6), a slightly winged siphonal canal and poorly developed internal denticles. *E. perculata* differs

from *E. dharmai* in having lower varices and in its more inflated shape (Figs 2F-G, 3I-L, strongly reminiscent of *E. mantelli* (Fig. 3G-H) from the Bartonian of Alabama.

The extant species *Murex tatei* Verco, 1895 (Figs 2H-I, 3M-P) from South West Australia was attributed to *Subpterynotus* Olsson & Harbison, 1953 (type species: *Murex textilis* Gabb, 1873 by original designation, Neogene of Western Atlantic) by numerous authors (Fair, 1976; Radwin & D'Attilio, 1976; Vokes 1974, 1994; Houart, 2018), due to shell characters shared with *S. textilis*: winged varices extending to the siphonal canal, a rounded aperture, an adapertural face of the varices bearing imbricated growth laminae and a scabrous surface. However, as any *Eofavartia* species *Murex tatei* differs from *Subpterynotus* species by lacking trivaricate morphology and intervarical ribs. Three synchronised varices on each whorl characterize muricids having true varices sensu Webster & Vermeij (2017) and according to the definition of varical types given by those authors, *M. tatei* does not display true varices. In addition, *Murex tatei* bears the primary cords: IP on the sutural ramp, P1 to P6 on the convex part of the whorl and ADP, MP, ABP, EAB1 on the siphonal canal (Fig. 2H-I), such as *E. perculata* and *E. dharmai*. The adulthood of *M. tatei* differs only from other *Eofavartia* species by its more winged varices extending the full length of last whorl and siphonal canal (Figs 2H-I, 3M-N). Contrary to the opinion of Vokes (1985: 69), this transformation (the appearance of winged varices extending the full length of last whorl and siphonal canal) does not require considerable changes in morphology. It is a character only developed late in ontogeny of *M. tatei* and it does not should make forget the other important characters of the basic 'bauplan' of *Eofavartia*. In addition, there is great similarity between juveniles of *E. perculata* (Figs 2g, 3K-L) and *M. tatei* (Fig. 3O-P), as they share inflated whorls, cord spines on the siphonal canal, as do the adult of *E. mantelli* (Figs 2C, 3G-H) from the Eocene. Therefore, *Murex tatei* is transferred to *Eofavartia* with the Pliocene South Australian species *E. antecedens* (Ludbrook, 1958) nov. comb., which does not differ strongly from the extant species. *E. dharmai* and *E. tatei* share a moderately elongate shell shape and 6-7 thick varices on last whorls. *E. tatei* differs by having more numerous secondary cords, a rounded aperture with poorly developed internal denticles.

5. Revised paleobiogeography of *Eofavartia* and *Subpterynotus*

Merle (2002) delimited the range of *Eofavartia* to the Eocene [FAD = Ypresian; LAD, Priabonian] of North Atlantic Ocean with records from both North America and Europe. The description of *E. dharmai* and the reevaluation of the characters of *E. perculata* (Vokes, 1985) demonstrate the persistence of *Eofavartia* during the Neogene in the Indo-Pacific region. The

probable presence of the genus in the Tethys Ocean during the Late Paleogene could explain its persistence in the Indo-Pacific Neogene, as open oceanic connections existed between the eastern Tethys and the western Indo-Pacific at the time (Harzhauser et al., 2002). Furthermore, re-examination of extant *Murex tatei* leads us to reject its attribution to *Subpterynotus* and to transfer it into *Eofavartia*. Thus, *E. tatei* can be considered as the single relict species of *Eofavartia*. Therefore, this contribution adds knowledge of the historical link between the Eocene marine fauna of Western Europe and the Miocene-to-Recent fauna of the Indo-West Pacific (IWP), consolidating the idea that the modern southern and southwestern Australian fauna is a relict of past biogeographic distributions. South Australia represents a privileged area for relict living mollusks: among the gastropods, *Campanile symbolicum* Iredale, 1917 for *Campanile* P. Fischer, 1884 (Houbrick 1984a; De Winter et al. 2020), *Diastoma melanioides* (Reeve, 1849) for *Diastoma* Deshayes, 1850 (Houbrick 1984b), *Zoila* Jousseume, 1884 and *Umbilia* Jousseume, 1884 for the Cypraeidae Rafinesque, 1815 (Meyer 2003) and among the bivalves, *Neotrigonia* Cossmann, 1912 for the Trigoniidae Lamarck, 1819 (Stanley 1984; Darragh, 1986).

On the other hand, the transfer of *Murex tatei* into *Eofavartia* modifies our view of the paleobiogeography of *Subpterynotus* (type species: *Murex textilis* Gabb, 1873 by original designation). About the palaeobiogeography and the evolution of *Subpterynotus*, VOKES (1994: 119) concluded that "...the [American *S. textilis*] species disappeared leaving no modern descendant. The only living forms are "Murex" exquisitus G. B. SOWERBY III, 1904, believed to be from South Africa (HOUART, 1980) and the distantly related "Murex" tatei VERCO, 1895, from southern Australia". However, in removing *E. tatei* from *Subpterynotus*, the first conclusion is that this genus was likely never present in Australia, as well as in Indo-Pacific. Moreover, *Murex exquisitus* belongs to another genus than *Subpterynotus* and *Eofavartia* and *S. textilis* (Early Miocene to Plio-Pleistocene) is the last member of its genus (Merle, in press).

Insert Figure 3

6. Conclusion

The description of *E. dharmai* nov. sp. from the Middle Miocene of Java (Indonesia) and the revision of Neogene and living species from South-Australia, previously attributed to

Favartia and *Subpterynotus* by authors, considerably increases the geographic and stratigraphic ranges of *Eofavartia*, which was until now restricted to the North Atlantic Eocene. The extant *E. tatei* represents the last relict species of the genus living in South Australia. Following the generic revision herein, fossil ancestors of *E. tatei* can be found in the same geographical region and are represented by *E. perculata* (Early Miocene) and *E. antecedens* (Pliocene) of South Australia. The middle Miocene molluscan fauna from Java, from which the type material of *E. dharmai* comes, is confirmed as an important means to reconstruct biogeographic connections between the North Atlantic, western Tethys and IWP and this contribution adds evidence to the general ‘Hopping hotspots’ theory (Renema et al., 2008).

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Figure captions

Figure 1: Terminology of the spiral sculpture and the internal denticles of the outer lip in *Eofavartia dharmai* n. sp. and *Homalocantha talahabensis* (Martin, 1895). A-C; holotype (NHMW 2019/0178/0001) of *E.dharmai* in ventral and dorsal view (A-B) and enlarged view of the aperture (C), Middle Miocene, Nyalindung, West Java; paratype (NHMW 2019/0178/0002) of *E. dharmai* in ventral and dorsal view (D-E) and enlarged view of the aperture (F), same locality; G-I; holotype (RGM 9711-1) of *H. talahabensis* in ventral and dorsal view (G-H) and enlarged view of the aperture (I), Tjitalahab, Middle Miocene, West Java Scale bars: 10 mm. Photos A-F: L. Cazes (MNHN); G-I: R. Pouwer (Naturalis biodiversity Center).

Figure 1: Terminologie de la sculpture spiral et des dents internes du labre chez *Eofavartia dharmai* n. sp. et *Homalocantha talahabensis* (Martin, 1895). A-C; holotype (NHMW 2019/0178/0001) d'*E.dharmai* en vue ventrale et dorsale (A-B) et vue agrandie de l'ouverture (C), Miocène moyen, Nyalindung, Ouest de Java; paratype (NHMW 2019/0178/0002) d'*E. dharmai* en vue ventrale et dorsal (D-E) et vue agrandie de l'ouverture (F), même localité; G-I; holotype (RGM 9711-1) d'*H. talahabensis* en vue ventrale et dorsale (G-H) et vue agrandie de l'ouverture (I), Tjitalahab, Miocène moyen, Ouest de Java. Echelle: 10 mm. Photos: A-F: L. Cazes (MNHN); G-I: R. Pouwer (Naturalis Biodiversity Center).

Figure 2: Terminology of the spiral sculpture in ventral view and topological position of D6 in *Eofavartia*. A-B: *E. frondosa* (Lamarck, 1803), type species, A: MNHN.F.A71651, Lutetian, Villiers-Saint-Frédéric (France); B: MNHN.F.J17522, Lutetian, Bracklesham (UK); C: *E. mantelli* (Conrad, 1834), holotype (ANSP 14231), Bartonian, Claiborne, Alabama (USA); D: *E. marchandi* (Cossmann, 1903), UCLB EM31778, Bartonian, Fresville (France); E: *E. subrudis* (d'Orbigny, 1850), MNHN.F.A71843, Bartonian, Auvers-sur-Oise (France); F-G: *F. perculata* (Vokes, 1985), F: holotype (NMV P75075) upper Aquitanian/lower Burdigalian, Fishing Point Marl, Horden Vale Victoria (Australia); G: Paratype A (NMV P74076), same locality; H-I: *E. tatei* (Verco, 1895), H: MNHN.IM, Esperance, Western Australia; I coll. Colomb coll., Western Australia. Scale Bars: 10 mm. Photos: A-B, E: P. Loubry (MNHN), D: D. Serrette (MNHN), C: K. Estes-Smargiassi and E. Wildner (ANSP), F-G: D. J. Holloway (NMV), H-I: photos B. Garrigues.

Figure 2: Terminologie de la sculpture spirale et position topologique de D6 chez *Eofavartia*. A-B: *E. frondosa* (Lamarck, 1803), espèce-type, A: MNHN.F.A71651, Lutétien, Villiers-Saint-Frédéric (France); B: MNHN.F.J17522, Lutétien, Bracklesham (UK); C: *E. mantelli* (Conrad, 1834), holotype (ANSP 14231), Bartonien, Claiborne, Alabama (USA); D: *E. marchandi* (Cossmann, 1903), UCLB EM31778, Bartonien, Fresville (France); E: *E. subrudis* (d'Orbigny, 1850), MNHN.F.A71843, Bartonien, Auvers-sur-Oise (France); F-G: *F. perculata* (Vokes, 1985), F: holotype (NMV P75075) Aquitanien supérieur/Burdigalien inférieur, Fishing Point Marl, Horden Vale Victoria (Australia); G: Paratype A (NMV P74076), même localité; H-I: *E. tatei* (Verco, 1895), H: MNHN.IM, Esperance, Australie occidentale; I: coll. Colomb, Australie occidentale. Echelle: 10 mm. Photos A-B, E: P. Loubry (MNHN), D: D. Serrette (MNHN), C: K. Estes-Smargiassi et E. Wildner (ANSP), F-G: D. J. Holloway (NMV), H-I: B. Garrigues.

Figure 3: Paleogene, Neogene and Recent *Eofavartia* in ventral and dorsal view. A-D: *E. dharmai* nov. sp., A-B: holotype (NHMW 2019/0178/0001), Middle Miocene, Nyalindung West Java; C-D: paratype (NHMW 2019/0178/0002), same locality; E-F: *E. frondosa* (Lamarck, 1803), MNHN.F.A71652, Lutetian, Villiers-Saint-Frédéric (France), G-H; *E. mantelli* (Conrad, 1834) MNHN.F.J05467, Bartonian, Claiborne, Alabama (USA); I-L: *E. perculata* (Vokes, 1985), I-J: holotype (NMV P75075), upper Aquitanian/lower Burdigalian, Fishing Point Marl, Horden Vale, Victoria (Australia); K-L: paratype D (USNM 375462), juvenile, Langhian, Muddy Creek, West of Hamilton, Victoria (Australia); M-P: *E. tatei*

(Verco, 1895), M-P: I: Colomb coll, Western Australia; O-P: NHMUK 1899.12.7.5, juvenile, South Australia, H: 10.5 mm. Scale bars: A-J, M-N: 10 mm, K-L, O-P: 5 mm. Photos: A-D: L. Cazes (MNHN), E-F: P. Loubry, G-H: J. Mouchart, I-J: D. J. Holloway (NMV), K-L: M. Florence (USNM), M-P: B. Garrigues.

Figure 3: *Eofavartia* paléogènes, néogènes et actuelles en vue ventrale et dorsale. A-D: *E. dharmai* nov. sp., A-B: holotype (NHMW 2019/0178/0001), Miocène moyen, Nyalindung Ouest de Java; C-D: paratype (NHMW 2019/0178/0002), même localité; E-F: *E. frondosa* (Lamarck, 1803), MNHN.F.A71652, Lutétien, Villiers-Saint-Frédéric (France), G-H: *E. mantelli* (Conrad, 1834) MNHN.F.J05467, Bartonien, Claiborne, Alabama (USA); I-L: *E. perculata* (Vokes, 1985), I-J: holotype (NMV P75075), Aquitanien supérieur/Burdigalien inférieur, Fishing Point Marl, Horden Vale, Victoria (Australie); K-L: paratype D (USNM 375462), juvénile, Langhien, Muddy Creek, Ouest de Hamilton, Victoria (Australie); M-P: *E. tatei* (Verco, 1895), M-P: I: Colomb coll, Australie occidentale; O-P: NHMUK 1899.12.7.5, juvénile, Australie du Sud, H: 10.5 mm. Echelle: A-J, M-N: 10 mm, K-L, O-P: 5 mm. Photos: A-D: L. Cazes (MNHN), E-F: P. Loubry, G-H: J. Mouchart, I-J: D. J. Holloway (NMV), K-L: M. Florence (USNM), M-P: B. Garrigues.

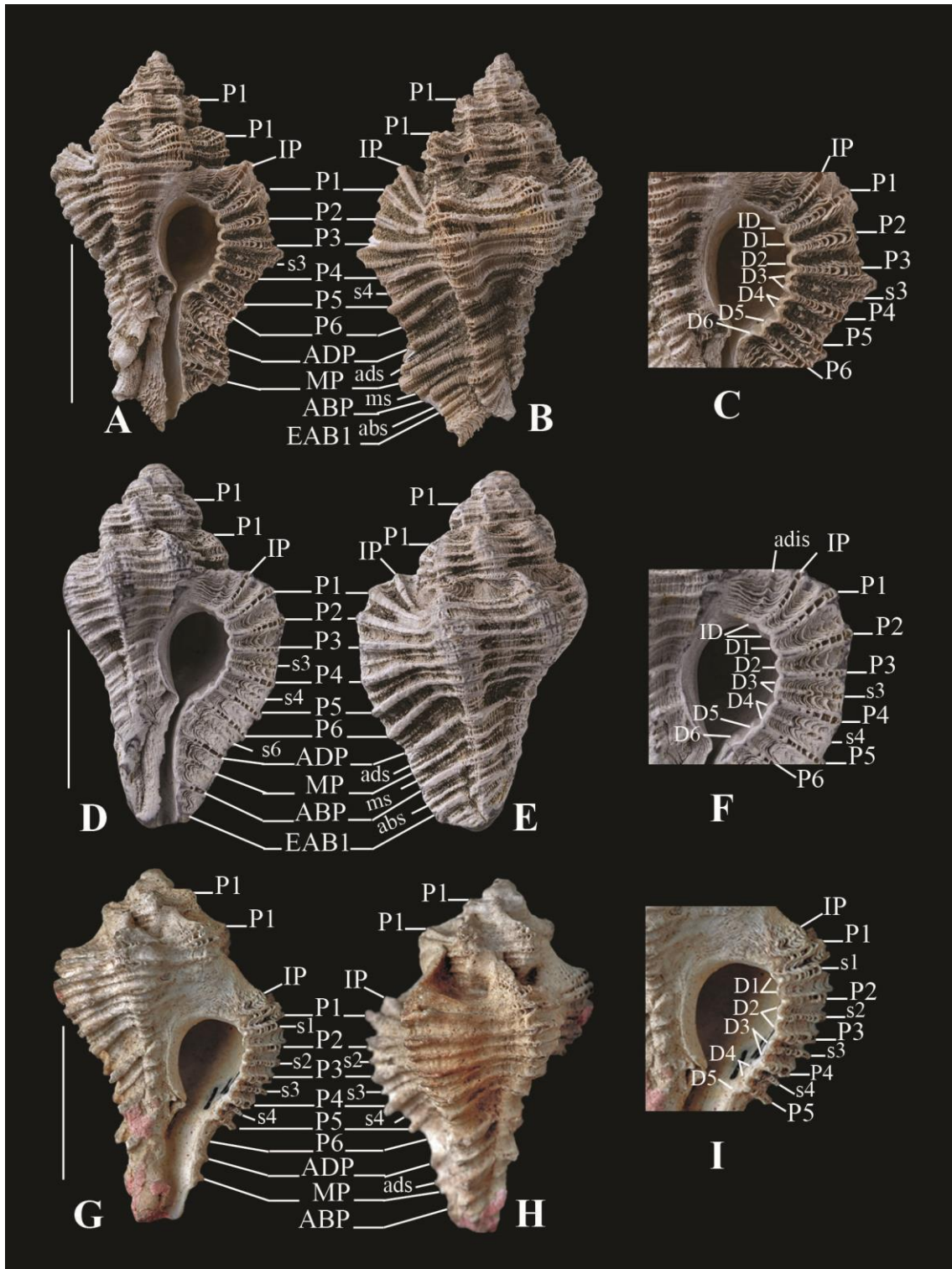


Fig. 1

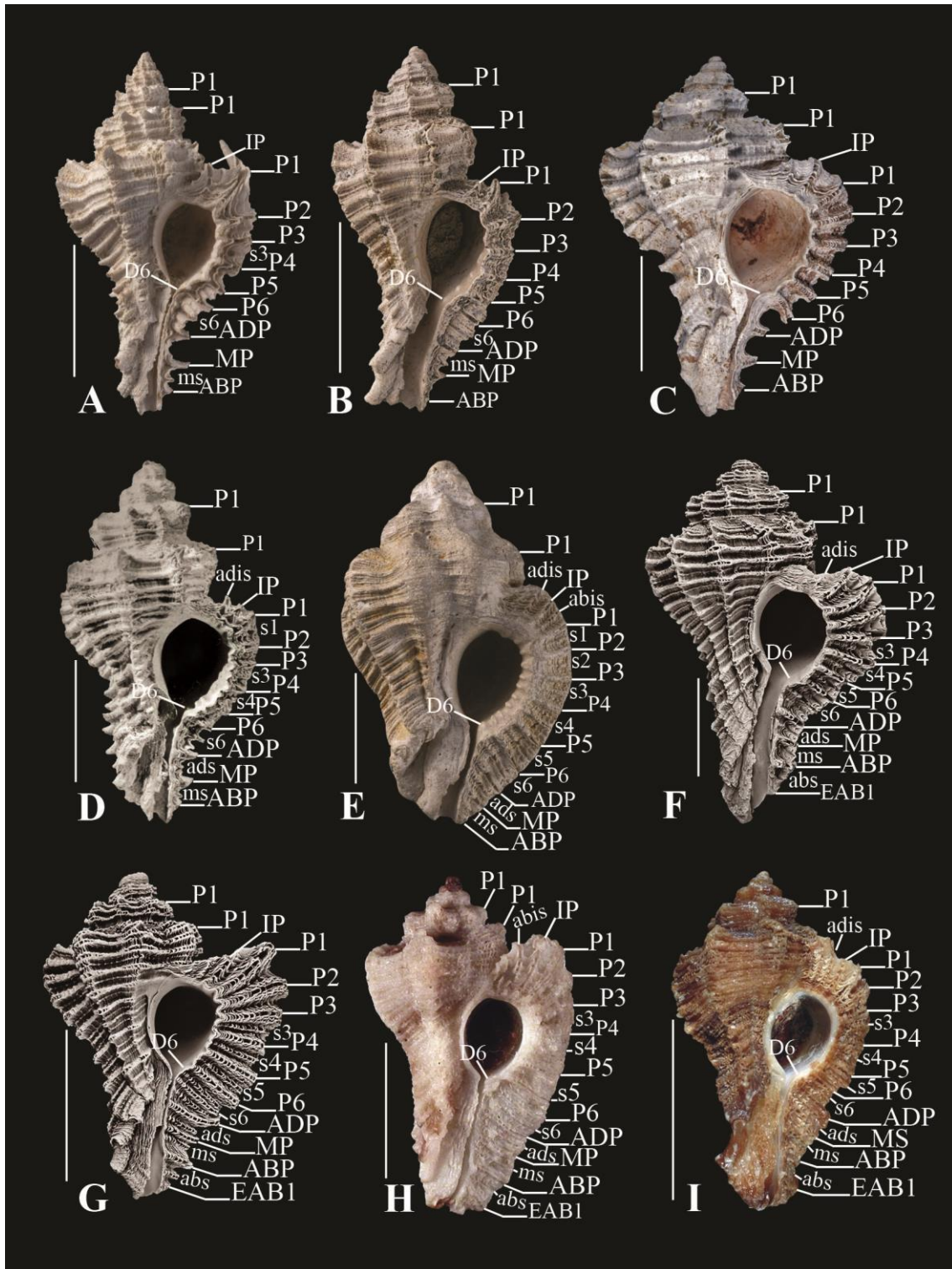


Fig. 2

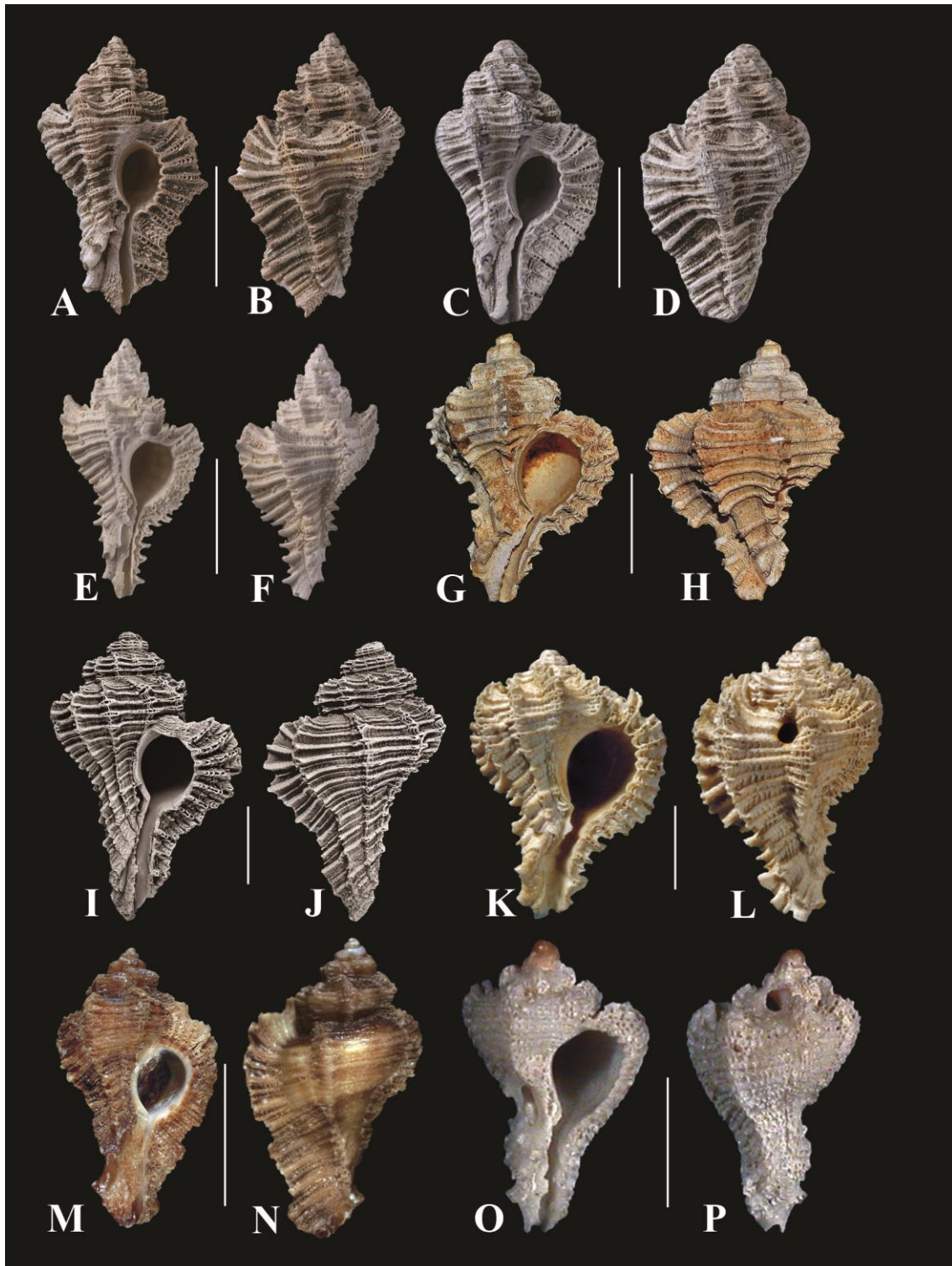


Fig. 3