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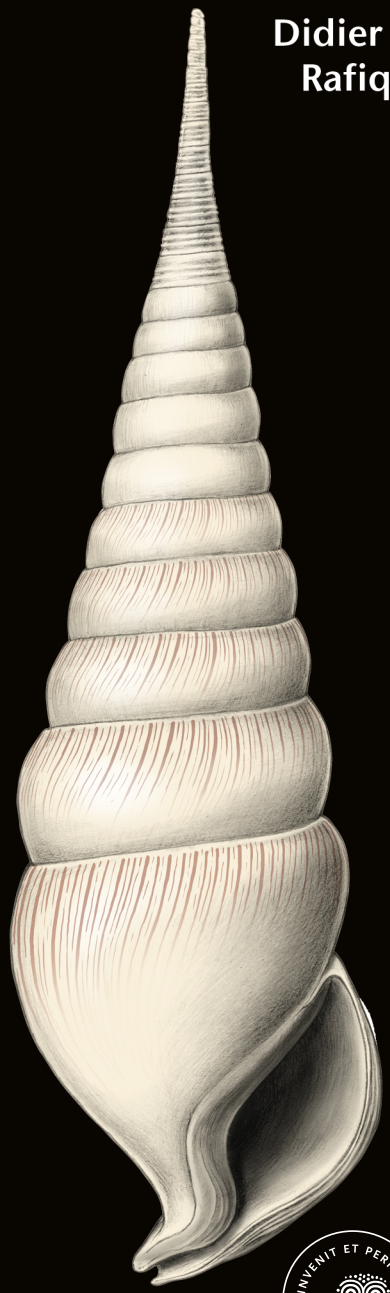

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New campanilids (Mollusca: Gastropoda) from the Ranikot Group (upper Paleocene/early Eocene, Sindh, Pakistan)

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ABSTRACT
In the Lower Indus Basin (Sindh, Pakistan), the Ranikot Group is historically known for its rich malacofauna described in the 19th and early 20th centuries. Recent fieldwork undertaken between 2009 and 2014 has yielded a wealth of material that is intended to supplement the ancient data on the Ranikot Group's palaeobiodiversity. It is in this context that the Campanilidae Douvillé, 1904 assemblage is studied. It includes one ?*Campanile* sp. from the Bara Formation (upper Thanetian) and two new taxa from the Lakra Formation (lower Ypresian): *Campanile metaisi* Merle & Pacaud, n. sp. and *Campanistylus lakhraensis* Merle & Pacaud, n. gen., n. sp. (type species: *Campanistylus lakhraensis* Merle & Pacaud, n. gen., n. sp. by monotypy). With two species known only from the Lower Indus Basin this assemblage of Campanilidae displays a high provincialism at species level. Furthermore, the case of *Campanistylus* Merle & Pacaud, n. gen. also illustrates the emergence of a endemic genus strictly restricted to the Lower Indus Basin.

KEY WORDS
Fossil molluscs,
Campanilidae,
Eocene,
Lower Indus Basin,
new genus,
new species.

RÉSUMÉ
Nouveaux Campanilidae (Mollusca: Gastropoda) du groupe Ranikot (Paléocène supérieur/Eocène inférieur, Sindh, Pakistan).
Dans le Bassin inférieur de l'Indus (Sindh, Pakistan), le groupe Ranikot est historiquement connu pour la richesse de sa malacofaune décrite au XIXe et au début du XXe siècle. De récentes missions de terrain entreprises entre 2009 et 2014 ont permis de collecter un matériel abondant destiné à compléter les données anciennes sur la paléobiodiversité du groupe Ranikot. C'est dans ce contexte que l'assemblage de Campanilidae Douvillé, 1904 est étudié. Il comprend ?*Campanile* sp., provenant de la Formation Bara (Thanétien supérieur) et deux taxons nouveaux provenant de la Formation Lakra, datée de l'Yprésien inférieur : *Campanile metaisi* Merle & Pacaud, n. sp. et *Campanistylus lakhraensis* Merle & Pacaud, n. gen., n. sp. (espèce-type : *Campanistylus lakhraensis* Merle & Pacaud, n. sp. par monotypie). Ce sont les premiers Campanilidae décrits du groupe Ranikot. À l'échelle spécifique, cet assemblage de Campanilidae présente un fort provincialisme, les deux espèces n'étant connues que dans le Bassin inférieur de l'Indus. De plus, le cas de *Campanistylus* Merle & Pacaud, n. gen. illustre aussi l'émergence d'un genre endémique strictement restreint au Bassin inférieur de l'Indus.

MOTS CLÉS
Mollusques fossiles,
Campanilidae,
Eocène,
Bassin inférieur
de l'Indus,
genre nouveau,
espèces nouvelles.

INTRODUCTION

The Indus Basin (Pakistan) has been known since the 19th century for its rich invertebrate faunas from the early Paleogene of the Eastern Tethys. They allow documentation of the biotic impacts of two global events, the Cretaceous/Paleogene crisis and the Paleocene-Eocene Thermal Maximum (PETM) in the context of the India-Asia collision (Jablonski 1998, 2008). The molluscan faunas have been the subject of several monographs: d'Archiac & Haime (1854), Cossmann & Pissarro (1909, 1927), Vredenburg (1923, 1924, 1928) and Douvillé (1929) for the Ranikot Group in Sindh, Eames (1951, 1952) for the Sulaiman Range and Cox (1930) from the Samana Range, but little research has been carried out since the 1950s. The molluscs of the Ranikot Group are typical of this lack of subsequent interest because, although the monographs by Cossmann & Pissarro (1909, 1927) and Vredenburg (1923, 1924, 1928) demonstrated that this fauna is one of the richest found in the early Paleogene of the Eastern Tethys, no recent research has been undertaken. Taking account of the potential for further work, field trips in the Jhirak area and in the Lakhra Dome were organized in 2009, 2010, 2011, 2012 and 2014. During these field trips new material was collected in order to better document different aspects of the paleobiodiversity of the Ranikot Group and particularly, of the Lakhra Formation: reevaluation of the species diversity, evolution of the fauna through time and comparisons with other parts of the Tethyan Ocean.

At the turn of the Palaeocene-Eocene, the Ranikot region was part of the Tethyan seaway connecting the Indo-Pacific to the North-West Atlantic. The Tethys was undoubtedly a marine biodiversity hotspot (Renema *et al.* 2008; Leprieur *et al.* 2015; Yasuhara *et al.* 2022; Tian *et al.* 2024). However, within this ocean, some sub-regions may have been richer than others. For example, the malacological assemblages of the Paris Basin (France) on the edge of the Tethys and northeastern Italy in the western Tethys have an unrivalled species richness (Merle 2008, 2025; Sanders *et al.* 2015). In the eastern Tethys, only the fauna of Ranikot (Pakistan) and the Cambay Basin (India, see Banerjee & Halder 2024) are sufficiently well preserved to give a good idea of the richness of this region. This is why these regions are of such great importance. Fieltrips carried out in Pakistan allowed to collect around 180 fossil species. However, they come from a sandstone in which it is almost impossible to collect small species having an adult size less than 10 mm. This condition introduces a bias in the geological record and the species richness was likely higher.

This study on Pakistan Campanilidae Douvillé, 1904, which are often associated with hotspots throughout the Cenozoic era and are common in the Lakhra Formation, is part of an effort to document the paleobiodiversity of the eastern Tethys. It follows a paper on the volutids (Merle *et al.* 2014) and will be followed by further papers covering other gastropod families. The Campaniloidea are very basal Caenogastropoda (Ponder *et al.* 2008; Strong *et al.* 2011). For a long time, the Campanilidae were confused with the Cerithioidea due to superficial shell similarities, but they are phylogenetically closer to the Vermetoidea than the Cerithioidea (Strong *et al.* 2011). They are represented today by a single living species: *Campanile symbolicum* (Iredale, 1917) from southwestern Australia. This grazer normally occurs subtidally in large populations on sandy patches between rocks on limestone reefs. The substratum may have seagrass, macroalgae or may be predominantly sandy (Houbrick 1989). Campanilids flourished in the Tethys Sea and the Americas during the Paleocene and the Eocene. For the Paleogene of the Indo-Pakistani plate, previous works describing some campanilids are from d'Archiac & Haime (1854), Cossmann & Pissarro (1909), Douvillé (1929), Cox (1930) and Kachhara *et al.* (2011).

ABBREVIATIONS

LOCALITIES (Fig. 1)

stn 1 (25°40'19.6"N, 68°11'23.1"E) Lakhra Dome, Old Indus section, uppermost Lakhra Formation (stn 5 in Merle *et al.* 2014);

stn 2 (25°42'58.0"N, 68°10'34.1"E) Lakhra Dome, East of Lakhra village section, base of the Lakhra Formation (stn 4 in Merle *et al.* 2014);

stn 3 (25°25'15.56"N, 68°11'16.60"E) Jamshoro area, Khnu Brohi coal pit, uppermost Bara Formation (stn 3 in Merle *et al.* 2014).

GEOLOGICAL SETTING

In the lower Indus Basin, the Cenozoic sedimentary deposits are mostly exposed along folded and thrusted belt of the Khirtar and Laki Range (Shah 2009). In the Ranikot area (Laki Range) the lower Paleogene deposits (Paleocene to lower Eocene) are designated as the Ranikot Group. They are well exposed in the Karachi Arc (Sindh Province, southern Pakistan), an invergent fold-thrust belt along the former western margin of the Indo-Pakistan Plate that protrudes eastwards into the Lower Indus Basin (Schelling 1999) and particularly in the Lakhra Dome and in the Jhirak-Jimpir area (Fig. 1). The earliest systematic geological survey in the Hyderabad region was that of Blanford (1879), who produced a geological map showing the Lakhra Dome. The Jhirak-Jimpir area is also historically well-known thanks to the geological description by Vredenburg (1906, 1909) and to the paleontological reports by Cossmann & Pissarro (1909, 1927) and Vredenburg (1923, 1924, 1928). The Ranikot Group consists in ascending order of three distinct lithostratigraphic units: the Khadro (*Cardita beaumonti* beds of early authors), Bara, and Lakhra formations (Cheema *et al.* 1977), but recently some authors included the Sohnari Formation in this group (see Frederiksen 1994). He we focus on new original fossil material collected from the shallow marine Bara and Lakhra formations.

THE BARA FORMATION

This formation includes non-marine, brackish water and inner shelf marine deposits. It ranges in thickness from more than 1 000 m in the Karachi Trough 50 km southwest of the Lakhra Dome (Quadri & Shuaib 1986) to less than 60 m in the northern part of the Sulaiman Range (Williams 1959). At Lakhra, the coal-bearing Bara Formation consists of shales, sandstones, marls and coal bands on the western side. In addition, the presence of marls and lenticular argillaceous limestone bands at Lakhra in the west reflect marine water conditions (Baqri 1997). Following Frederiksen (1994) who studied angiosperm pollen, the age of the Bara Formation is not younger than early Selandian, whereas Wakefield & Monteil (2002) based on foraminiferal and palynological data consider the top of the Bara Formation as late Thanetian. The only specimen of campanilid from the Bara Formation, was collected in the Khnu Brohi coal pit (stn 3) near Hyderabad. The specimen was found on waste heaps resulting from coal extraction in the upper part of this formation. It was associated

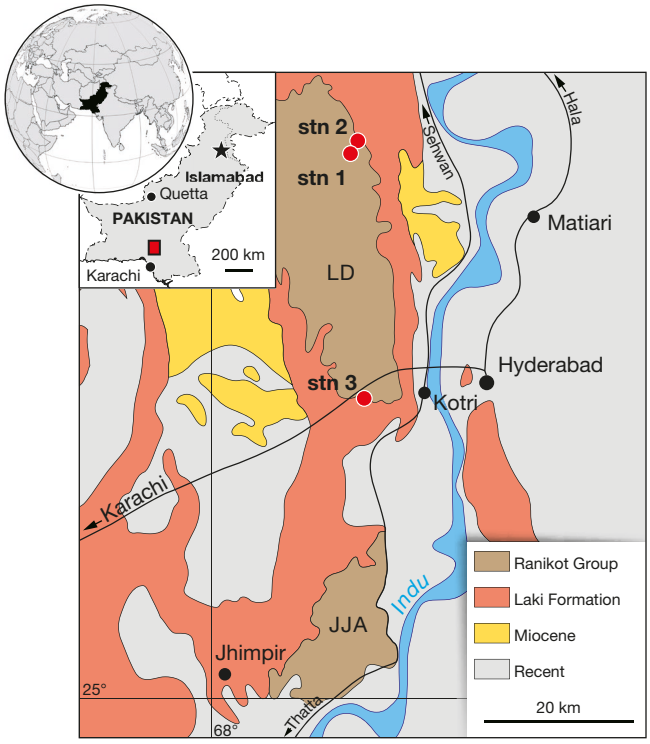

FIG. 1. — Location of the fossil localities (stn 1 to 3) in a simplified geological map showing the Ranikot Group in the Jimpir-Jhirak Area (**JJA**) and the Lakhra Dome (**LD**).

with a diversified marine assemblage in which Merle *et al.* (2014) reported several species of volutids. Unfortunately, the aragonitic shells are often decalcified and many shells are not identifiable at species level.

THE LAKHRA FORMATION

The Lakhra Formation conformably overlies the Bara Formation and consists of evenly bedded impure limestone alternating with bioclastic sandstone and calcareous shale. The most fossiliferous beds correspond to bioclastic sandstones containing a rich molluscan fauna described by Cossmann & Pissarro (1909, 1927) and Vredenburg (1928). The most common gastropods are *Calyptraphorus indicus* Cossmann & Pissarro, 1909 and *Turritella ranikoti* Vredenburg, 1928. The age of the Lakhra Formation is quite controversial in the literature. In the classical book "Stratigraphy of Pakistan", Shah (1977, 2009) indicated that the Lakhra Formation is entirely late Paleocene in age, whereas Wakefield & Monteil (2002) suggested that it straddles the Paleocene/Eocene boundary.

In the Jhirak area, located about 30 km SSE of the Lakhra Dome, the transition between the Bara and Lakhra formations was particularly well exposed on the southern bank outfall drainage channel. Here, in the first calcareous sandstone horizon at the base of the Lakhra Formation, we found a quite well-preserved assemblage of larger foraminifers, characterized by the co-occurrence of *Alveolina vredenburgi* Davies, 1937 *in* Davies & Pinfold (1937) (formerly *A. cucumiformis* Hottinger, 1960), *Miscellanea miscella* (d'Archiac & Haime, 1853) and *Ranikothalia nuttali* (Davies, 1927), which allows

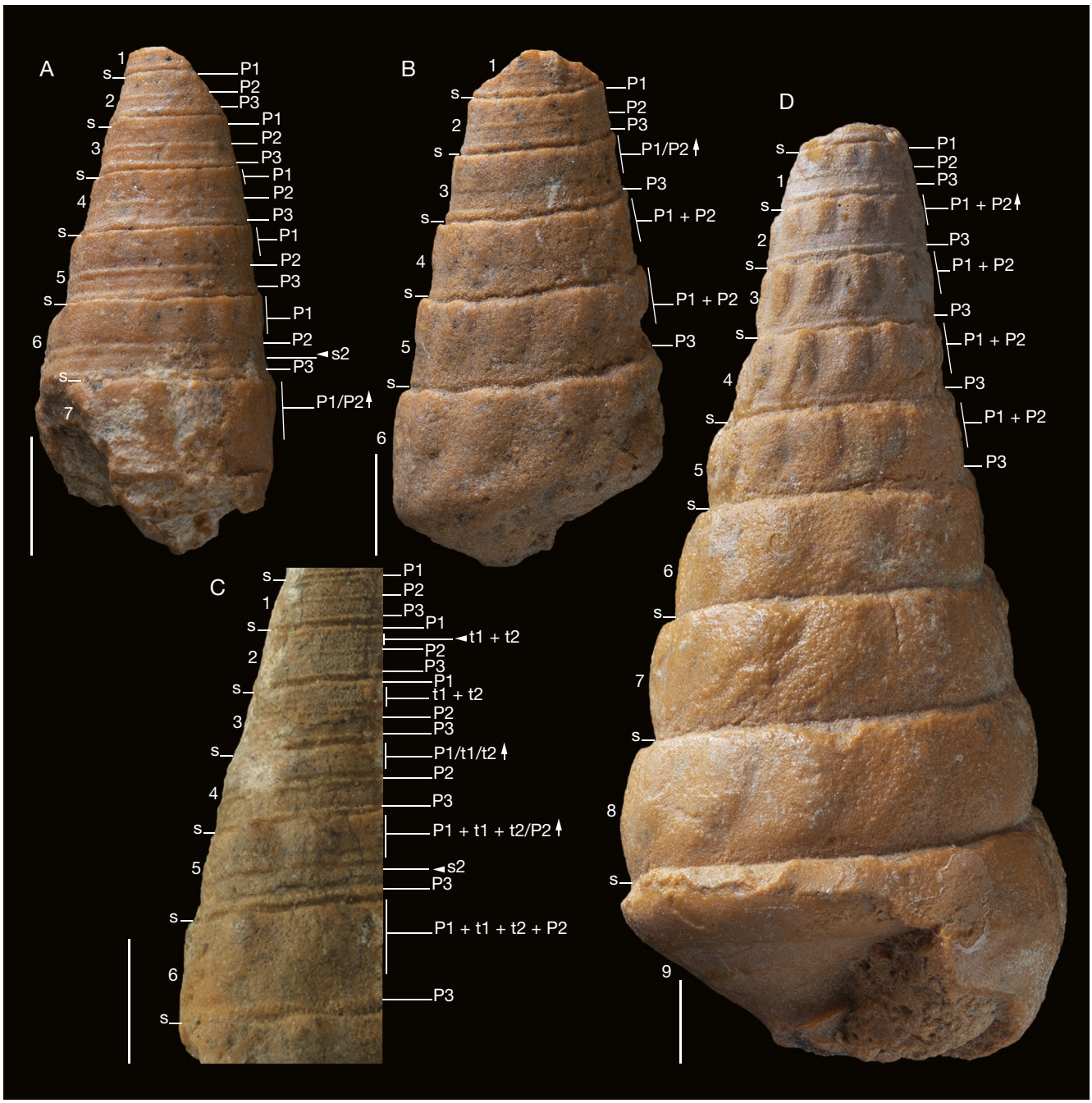

FIG. 2. — Nomenclature of the spiral cords in *Campanile metaisi* Merle & Pacaud, n. sp., Old Indus section (stn 1), Sindh, Pakistan, uppermost Lakhra Formation; early Eocene (Ypresian): **A**, paratype CPAG.RAN.I.90 (cast MNHN.F.A93716); **B**, paratype CPAG.RAN.I.91 (cast MNHN.F.A93718); **C**, paratype CPAG.RAN.I.92 (cast MNHN.F.A93719); **D**, paratype CPAG.RAN.I.88 (cast MNHN.F.A93714). Abbreviation: **s**, suture. On the left of the shells, the numbers from 1 to 9 give the numbers of whorls discussed in the text. Scale bars: 5 mm. Credits: P. Loubry (MNHN/CNRS).

correlation of this horizon with shallow-water benthic biozone SBZ5 (Serra-Kiel *et al.* 1998; Hottinger 2009). According to criteria used to characterize the base of Eocene of the GSSP section (Dababiya, Egypt: Aubry *et al.* 2007), the Paleocene/Eocene (P/E) boundary is defined by the onset of the negative Carbon Isotope Excursion (CIE), which has been correlated directly with the base of the P5b and NP9b planktonic zones. Regarding the standard shallow benthic zonation (Serra-Kiel *et al.* 1998; Hottinger 2009), correlation with the CIE is not obvious, because the shallow-water sediments are generally more affected by diagenesis than deep marine sediments (Zhang *et al.* 2013) and moreover their record is often discontinuous. Following the recalibration of the shallow benthic zonation of Scheibner & Speijer (2009) from Egyptian sections, the P/E boundary should be located between SBZ4 and SBZ5. Consequently, the base of the Lakhra Formation is probably close to the P/E boundary, at least in the Jhirak area, and the occurrence of *Alveolina*

vredenburgi suggests an early Ypresian age. Further studies are required to test the synchroneity or the diachroneity of the base of the Lakhra Formation in other outcrops, including the area of the type section (Lakhra Dome).

We sampled campanilids from two localities situated on two measured logs. The locality stn 2 is close to Lakhra village, documents the base of the Lakhra Formation, whereas the locality stn 1 corresponding to the Old Indus section documents the uppermost Lakhra Formation which is well exposed well exposed here. Stn 2 lies in a bioclastic sandstone located at the base of the Lakhra village section and the fossil assemblage contains a diversified fauna of molluscs (*Calyptraphorus indicus* facies), corals, echinids, crabs, large foraminifers, ray teeth and turtle bones. The *Calyptraphorus indicus* facies also marks the base of the Lakhra Formation in the region of Jhirak (Vredenburg 1909). The main part of the campanilid material described here comes from this bed, in which we identified about 150 species of gastropods. In the uppermost part of the Old Indus section (stn 1), we found another bed of bioclastic sandstone containing a rich assemblage of invertebrates. Both assemblages are comparable to the fauna from Jhirak described by Cossmann & Pissarro (1909, 1927).

MATERIAL AND METHODS

Shell preparation

The shells preserved as calcitic pseudomorphs perfectly replicate the original shell features. However, they are often partially covered by matrix requiring preparation using a pneumatic engraving pen.

Repository

The type and figured material are housed at the Centre for Pure and Applied Geology of the University of Sindh at Jamshoro, Pakistan (CPAG); a copy (plastotype) of this material is housed at the Muséum national d'Histoire naturelle, Paris (collection de Paléontologie, MNHN.F).

Shell terminology

The description of new species and comparisons adopt the terminology suggested by Pacaud *et al.* (2014) and Pacaud (2020).

Primary cords

First sequence of appearance (primary cords): comparisons of different growth stages in several *Campanile* species shows that the onset of the first sequence of spiral cords does not vary from one species to another. The number of primary cords carried by each individual does not vary either. There are only three primary cords on subadult shells. The terminology of primary cords, considering their ontogeny and topological correspondences [see also Merle (2005) for theoretical aspects], is as follows:

P1: primary cord below the adapical suture;
P2: primary cord of the central part of whorl;
P3: primary cord above the abapical suture.

Secondary cords

Second sequence of appearance (secondary cords): after the appearance of primary cords, new spiral cords can be added. These secondary cords are inserted at equal distances between two primary cords. The cords, which are weak when first formed, thicken as they grow. The terminology of secondary cords, considering ontogeny and their topological correspondence, is as follows:

s1: secondary cord placed between P1 and P2;
s2: secondary cord placed between P2 and P3.

Tertiary cords

Third sequence of appearance (tertiary cords): when secondary cords are developed, a third sequence may appear. It differs from the secondary sequence, because the tertiary cords do not always strictly occupy a definite position between a primary and a secondary cord (see Merle [2005: 373] for more details). Tertiary cords are indicated with a t.

Symbols

The use of symbols to indicate changes in the organization of the cords (appearance or fusion) completes the terminology.

◀ Appearance of a cord;
↑ fusing cords;
[+] already fused cord.

Descriptive information

As the early teleoconch whorl of the campanilid specimens described in this paper are missing to varying degrees, the descriptions of the spiral sculpture are composite and based on several specimens. Every specimen described and illustrated is clearly indicated in the descriptions.

SYSTEMATIC PALAEONTOLOGY
(BY D. MERLE & J.-M. PACAUD)

Class GASTROPODA Cuvier, 1795
Subclass CAENOGASTROPODA L. R. Cox, 1960
Order CAENOGASTROPODA *incertae sedis*
Superfamily Campaniloidea Douvillé, 1904
Family Campanilidae Douvillé, 1904

Genus *Campanile* P. Fischer, 1884

Type species. — *Cerithium leve* Quoy & Gaimard, 1834 (*non* Perry, 1811) by subsequent designation (Crosse 1888) (accepted as *Cerithium symbolicum* Iredale, 1917).

Campanile metaisi Merle & Pacaud, n. sp.
(Figs 2; 3)

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?*Cerithium (Campanile) subsemicostatum* — Cossmann & Pissarro 1909: 53-54, pl. 5, figs 9, 10 (*non* d'Archiac & Haime, 1854).

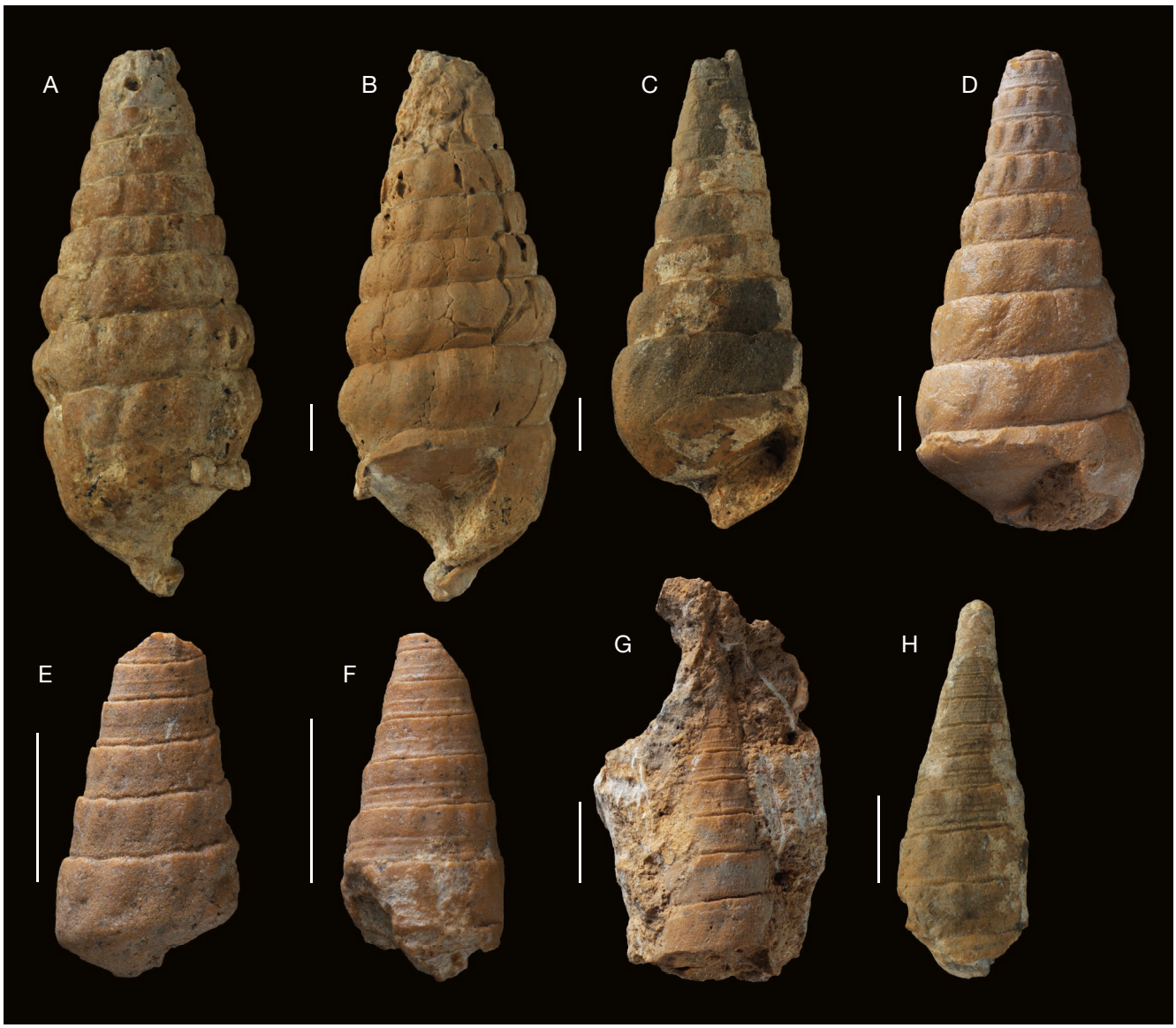

FIG. 3. — Type material of *Campanile metaisi* Merle & Pacaud, n. sp., Old Indus section (stn 1), Sindh, Pakistan, uppermost Lakhra Formation; early Eocene (Ypresian): **A**, **B**, holotype CPAG.RAN.I.93 (cast MNHN.F.A93720); **C**, paratype CPAG.RAN.I.94 (cast MNHN.F.A93722); **D**, paratype CPAG.RAN.I.88 (cast MNHN.F.A93714); **E**, paratype CPAG.RAN.I.91 (cast MNHN.F.A93718); **F**, CPAG.RAN.I.90 (cast MNHN.F.A93716); **G**, paratype CPAG.RAN.I.89 (cast MNHN.F.A93715); **H**, CPAG.RAN.I.92 (cast MNHN.F.A93719). Scale bars: 10 mm. Credits: P. Loubry (MNHN/CNRS).

TYPE MATERIAL. — **Holotype. Pakistan** • Lower Indus Basin, Sindh Province, Jamshoro district; Lakhra Dome, Old Indus section (stn 1), uppermost Lakhra Formation; early Eocene (Ypresian); CPAG.RAN.I.93 (cast MNHN.F.A93720), H: 112 mm (apex and early whorls broken, 10 whorls), D: 46.8 mm; Fig. 3A, B.
Paratype. Pakistan • 1 spm; same data as for the holotype; CPAG.RAN.I.88 (cast MNHN.F.A93714), H: 56.1 mm (shell incomplete, 9 whorls), D: 27.1 mm; Figs 2D, 3D • 1 spm; idem; CPAG.RAN.I.89 (cast MNHN.F.A93715), H: 34.4 mm (shell incomplete, 7 whorls), D: 14.8 mm; Figs 3G • 1 spm; idem; CPAG.RAN.I.90 (cast MNHN.F.A93716), H: 19.3 mm (shell incomplete, 7 whorls), D: 11.4 mm; Figs 2A, 3F • 1 spm; idem; CPAG.RAN.I.91 (cast MNHN.F.A93718), H: 23.3 mm (shell incomplete, 6 whorls), D: 12.1 mm; Figs 2B, 3E • 1 spm; idem; CPAG.RAN.I.92 (cast MNHN.F.A93719), H: 33.7 mm (shell incomplete, 9 whorls), 11.8 mm; Figs 2C, 3H • 1 spm; idem; CPAG.RAN.I.94 (cast MNHN.F.A93722), H: 78.6 mm (shell incomplete, 10 whorls), D: 33 mm; Fig. 3C.

OTHER EXAMINED MATERIAL. — **Pakistan** • 5 spms; same data as for the holotype; MNHN.F.A93713 • 6 spms; idem; MNHN.F.A93717 • 8 spms; idem; MNHN.F.A93721.

ETYMOLOGY. — Dedicated to Grégoire Métais (CNRS), main contributor to the 2011, 2012 and 2014 Franco-Pakistani fieldtrips to Sindh.

TYPE HORIZON. — Diversified mollusc bed of the uppermost Lakhra Formation (top of the Old Indus section, stn 1), early Eocene (Ypresian).

TYPE LOCALITY. — Pakistan, Sindh Province, Jamshoro district; Lakhra Dome, Old Indus section (stn 1).

DISTRIBUTION. — Pakistan, Sindh, Lakhra Formation at Old Indus section (stn 1); Leilan and Jhirak (Cossmann & Pissarro 1909), early Eocene (Ypresian).

Description

Medium sized, elongate, conical shell of more than ten convex teleoconch whorls (based on the holotype); apical angle 30°. Antepenultimate and penultimate whorls slightly more inflated that earlier spire whorls. Last whorl nearest 39.4% total height (holotype). Whorls separated by narrowly impressed suture. Protoconch and first teleoconch whorls unknown. Spiral sculpture (composite description). Specimen MNHN.F.A93716 (H: 19.3 mm, D: 11.4 mm, seven whorls, Fig. 2A) on whorls 1 to 5, P1 to P3 present; P1 close-set to adapical suture and more prominent than P2 and P3; P1-P2 fine but well-marked; P3 close-set to abapical suture. On whorl no. 6 (see Fig. 2A), appearance of s2 and appearance of weakly nodular varical ribs on P1. On whorl no. 7, P1-P2 merging – Specimen MNHN.F.A93718 (H: 23.3 mm, D: 12.1 mm, six whorls, Fig. 2B) on whorl nos. 1-2, P1 to P3. On whorl no. 3, P1 and P2 merging. On whorls nos. 4-6 (see Fig. 2B), P1-P2 fused and nodular varical ribs devoid of traces of spiral cord becoming more prominent on whorl no. 6 – Specimen MNHN.F.A93719 (H: 33.7 mm, D: 11.8 mm, six whorls, Fig. 2C), on whorl no. 2, appearance of two tertiary cords (t1+ t2) between P1 and P2. On whorl no. 4, P1, t1, t2 fusing. On whorl no. 5, P2 fusing with P1, t1 + t2 already fused. Appearance of s2. On whorl no. 6, disappearance of cord except P3 – Specimen MNHN.F.A93714 (H: 56.1 mm, D: 27.1 mm, nine whorls, Fig. 2D), on whorl no. 1, P1-P3. On whorl no. 2, P1 and P2 fusing. On whorl no. 3 to no. 5, P1 and P2 fused and P3 close set to the abapical suture. On whorls no. 6 to no. 9, no spiral sculpture – Holotype MNHN.F.A93714 (H: 112 mm, D: 46.8 mm, ten whorls, Fig. 3A, B) no cord even on early whorls. Axial sculpture appearing approximately after disappearance of spiral cords and consisting of 15 moderately thick varicose ribs on penultimate and last whorls, and between 12-16 ribs on preceding whorls. First ribs more varicose on adapical part of whorls. Aperture narrow 54.8% of diameter and 48.8% of length of last whorl. Anal canal indistinct. Columella weakly concave, with two folds. Siphonal canal short.

Comparisons

Cossmann & Pissarro (1909) identified similar specimens from the Lakhra Formation as ?*Cerithium (Campanile) subsemicostatum* d'Archiac & Haime, 1854. Indeed, they are reminiscent of that species, which is also a *Campanile* and displays nodular varical ribs (see d'Archiac & Haime 1854: pl. 29, fig. 5). However, *Campanile subsemicostatum* differs in its more numerous ribs (8-9 on the ventral side, instead 6-7 in *C. metaisi* Merle & Pacaud, n. sp.), in its opistocyrt ribs and in its wider apical angle. Moreover, d'Archiac & Haime (1854: 300) noticed that the matrix containing *Campanile subsemicostatum* is associated with *Nummulites garansensis* (accepted as *Nummulites garansiana* Joly & Leymerie, 1848), a Rupelian Large Benthic Foraminifera (LBF) and for this reason, Cossmann & Pissarro (1909: B53) placed a query after their identification. Considering their morphological differences and also their distant stratigraphic age, there is no doubt that *C. subsemicostatum* (d'Archiac & Haime, 1854) and *C. metaisi* Merle & Pacaud, n. sp. belong to two distinct species. *Campanile metaisi* Merle & Pacaud, n. sp. is reminiscent to *Campanile cornucopiae* (J. Sowerby, 1818) from the middle Eocene of the Paris Basin, Normandy and Hampshire in its medium size and in its nodular varices. However, *Campanile cornucopiae* differs by its early whorls that are more ornamented (see Wrigley 1940, figs 1, 4 and Pacaud *et al.* 2014: pl. 8).

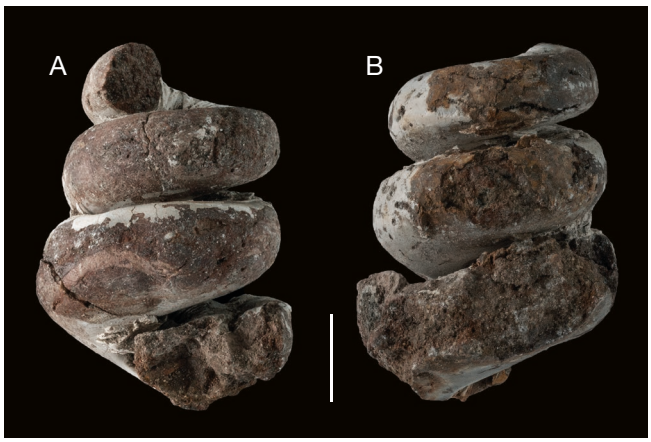

Fig. 4. — ?*Campanile* sp. from Khnu Brohi coal pit (stn 3), Sindh, Pakistan, uppermost Bara Formation, late Paleocene (Thanetian). Specimen MNHN.F.A93703 (internal mold): **A**, ventral face; **B**, dorsal face. Scale bar: 10 mm. Credits: P. Loubry (MNHN/CNRS).

?***Campanile*** sp.
(Fig. 4)

Material. — **Pakistan** • 1 spm; Lower Indus Basin, Sindh Province, Jamshoro district, Jamshoro area, Khnu Brohi coal pit (stn 3); uppermost Bara Formation, late Paleocene (Thanetian); MNHN.F.A93703.

Distribution. — Uppermost Bara Formation, late Paleocene (Thanetian).

Description

Internal mold, displaying three rounded whorls of 36.5 mm in length and 29.2 mm in width. Base showing a large foramen corresponding to place of columella. Remains of shell on surface of mold.

Comments

This large internal mold corresponds most likely to a campanilid, but there is no character that allows an identification at species or genus level.

Genus *Campanistylus* Merle & Pacaud, n. gen.

urn:lsid:zoobank.org:act:0DA1619A-ACDE-4170-BD12-B7F2AAF647FA

Type species. — *Campanistylus lakhraensis* Merle & Pacaud, n. gen., n. sp.

Species included. — Type species.

ETYMOLOGY. — From *Campanile* and *stylus* (from Greek name *στύλος* meaning column reflecting the straight-sided shape of the early teleconch whorls). Gender, male.

DIAGNOSIS. — Medium sized shell; early spire very slender turriculate, resembling a column, followed by whorls gradually increasing in growth rate resulting in broader, more convex whorls. Overall aspect of shell, turriculate, coleoconid. Whorls separated by narrowly impressed suture. Delicate spiral sculpture present on around 25 early teleoconch whorls, disappearing on later whorls. Series of cords including P1, P2, s2, P3. Surface of cords usually smooth, sometimes slightly granulose. Aperture narrow, ovoid, compressed adapically. Anal canal short, narrow. Columella weakly concave, one fold. Siphonal canal moderately short, bent and dorsally recurved. Outer lip prosocyrt, not thickened. Remains of periostracum imprints. Residual colour pattern consisting of red stripes, approximately parallel, with inclination varying from slightly sinuous to sigmoidal.

Campanistylus lakhraensis Merle & Pacaud, n. gen., n. sp. (Figs 5; 6)

urn:lsid:zoobank.org:act:501A660A-F529-48F8-8D9D-D49A3571A5F5

TYPE MATERIAL. — **Holotype. Pakistan** • Lower Indus Basin, Sindh Province, Jamshoro district; Lakhra Dome, East of Lakhra village section (stn 2), lower Lakhra Formation; early Eocene (Ypresian); CPAG. RAN.I.95 (cast MNHN.F.A93729); H: 136.8 mm (*c.* 32 whorls), D: 40.1 mm; Fig. 6A, B.
Paratypes. Pakistan • 1 spm; same data as the holotype; CPAG. RAN.I.102 (cast MNHN.F.A93726), H: 31.9 mm (shell incomplete, 6 whorls), D: 17.9 mm; Fig. 5D • 1 spm; idem; CPAG. RAN.I.103 (cast MNHN.F.A93725), H: 57.1 mm (shell incomplete, 8 whorls), D: 27.1 mm; Fig. 5C • 1 spm; idem; CPAG. RAN.I.104 (cast MNHN.F.A93727), H: 29.2 mm (shell incomplete, 7 whorls), D: 14 mm; Fig. 5B • 1 spm; idem; CPAG.RAN.I.105 (cast MNHN.F.A93728), H: 58.6 mm (shell incomplete, 8 whorls), D: 29.7 mm; Fig. 5A • 1 spm; same data as for the holotype; CPAG. RAN.I.96 (cast MNHN.F.A98131), H: 159.4 mm (*c.* 27 whorls), D: 43.3 mm; Fig. 6C • 1 spm; idem; CPAG.RAN.I.97 (cast MNHN.F.A98129), H: 114.9 mm (shell incomplete, 6 whorls), D: 43.8 mm • 1 spm; idem; CPAG.RAN.I.98 (cast MNHN.F.A93712), H: 91.4 mm (shell incomplete, 3 whorls), D: 46.1 mm; Fig. 6H, I • 1 spm; idem; CPAG.RAN.I.99 (cast MNHN.F.A98132), H: 115.4 mm (shell incomplete, 7 whorls), D: 44.1 mm; Fig. 6F, G • 1 spm; idem; CPAG.RAN.I.100 (cast MNHN.F.A93711), H: 98.2 mm (*c.* 23 whorls), D: 28.8 mm; Fig. 6D, E • 1 spm; idem; CPAG.RAN.I.101 (cast MNHN.F.A93724), H: 17.8 mm (shell incomplete, 3 whorls), D: 12.3 mm.

OTHER EXAMINED MATERIAL. — Pakistan • 1 spm; same data as the holotype; MNHN.F.A93696 • 1 spm; idem; MNHN.F.A93697 • 1 spm; idem; MNHN.F.A93698 • 2 spms; idem; MNHN.F.A93699 • 1 spm; idem; MNHN.F.A93700 • 2 spms; idem; MNHN.F.A93701 • 3 spms; idem; MNHN.F.A93702 • 1 spm; idem; MNHN.F.A93704 • 5 spms; idem; MNHN.F.A93705 • 1 spm; idem; MNHN.F.A93706 • 3 spms; idem; MNHN.F.A93707 • 2 spms; idem; MNHN.F.A93708 • 1 spm; idem; MNHN.F.A93709 • 2 spms; idem; MNHN.F.A93710.

ETYMOLOGY. — From the type formation: Lakhra Formation.

TYPE HORIZON. — Diversified molluscs bed, base of the East-Lakhra village section (stn 2), lower Lakhra Formation, early Eocene (Ypresian).

TYPE LOCALITY. — Pakistan, Sindh Province, Jamshoro district; Lakhra Dome, East-Lakhra village section (stn 2).

DISTRIBUTION. — Lakhra Formation, early Eocene (Ypresian).

DESCRIPTION

Medium sized shell (H = 136 mm) of more than 33 teleoconch whorls starting with 24 turriculate whorls resembling a column, followed by eight whorls becoming increasingly convex; overall aspect of shell, turriculate, coleoconid. Antepenultimate and penultimate whorls slightly more inflated that earlier spire whorls. Apical angle 18-19°. Last whorl 29.3% total height (holotype). Whorls separated by narrowly impressed suture. Protoconch and first teleoconch whorls unknown. Delicate spiral sculpture present on early teleoconch whorls, disappearing on last whorls – Detailed composite description of the spiral sculpture: holotype MNHN.F.A93729 (Fig. 6A, B, H: 136.8 mm), primary cords P1-P3 present until 20th whorl, P1 close-set to the adapical suture more prominent than P2 and P3, P2 less prominent. On whorl no. 21, appearance of s2 between P2 and P3, P2 less prominent than the other primary cords. From whorl no. 22 to no. 24 (Fig. 6B), s2 becoming larger and subequal to P2, s2 and P2 less prominent that the other cords; small granules visible on cords. On whorls nos. 25-26 (Fig. 6B), P1, P2 and s2 starting to fade gradually, P3 still prominent. On whorl no. 27 (Fig. 6B), loss of spiral sculpture – Paratype MNHN.F.A93728 (Fig. 5A, H: 58.6 mm) on whorls no. 1 to no. 4, P1-P3 and s2 present; P1 prominent, close-set to adapical suture; P3 close-set to abapical suture; s2 close-set to P2 and less prominent. On whorls nos. 5-6, P1, P2 and s2 starting to fade gradually, P3 still prominent. On whorl no. 7, P1 tending to fuse with P2. On whorl 8, loss of the spiral sculpture – Paratype MNHN.F.A93727 (Fig. 5B, H: 29.2 mm), on whorls no. 1 to no. 3, P1-P3 and s2 present; P1 prominent, close-set to adapical suture; P3 close-set to abapical suture; s2 close-set to P2 and less prominent. On whorl nos. 4-5, P1, P2 and s2 starting to fade, P3 still prominent. On whorl no. 6, loss of the spiral sculpture – Paratype MNHN.F.A93725 (Fig. 5C, H: 57.1 mm), on whorls no. 1 to no. 3, P1-P3 and s2 present; P1 prominent, close-set to adapical suture; P3 prominent close-set to abapical suture; P2 and s2 weaker; small granules on P2, s2 and P3. On whorl no. 4, P1, P2 to tending to fuse and s2 starting to fade gradually, P3 still prominent. On whorl no. 5, only P3. On whorl no. 6, loss of the spiral sculpture – Paratype MNHN.F.A93726 (Fig. 5D, H: 31.9 mm), on whorls nos. 1-2, P1-P3 and s2 present; P1 close-set to adapical suture; P3 close-set to abapical suture; s2 close to P2 and less prominent. On whorl no. 3, P1 and P2 tending to fuse. On whorl no. 4, only P3. On whorl no. 5, total loss of the spiral sculpture – No axial sculpture, except some growing striae. Aperture narrow, ovoid, compressed adapically, of 88.7% of diameter and 84.33% of length of last whorl. Anal canal short and narrow. Columella weakly concave with one fold; columellar lip slightly erect; parietal lip adherent. Siphonal canal moderately short, bent, turning left and dorsally curved. Outer lip prosocyrt, not thickened. Remains of periostracum imprints (paratype MNHN.F.A93711). Residual colour pattern consisting of red stripes, approximately parallel, with inclination varying from slightly sinuous to sigmoidal (paratype MNHN.F.A98132, Fig. 6F, G).

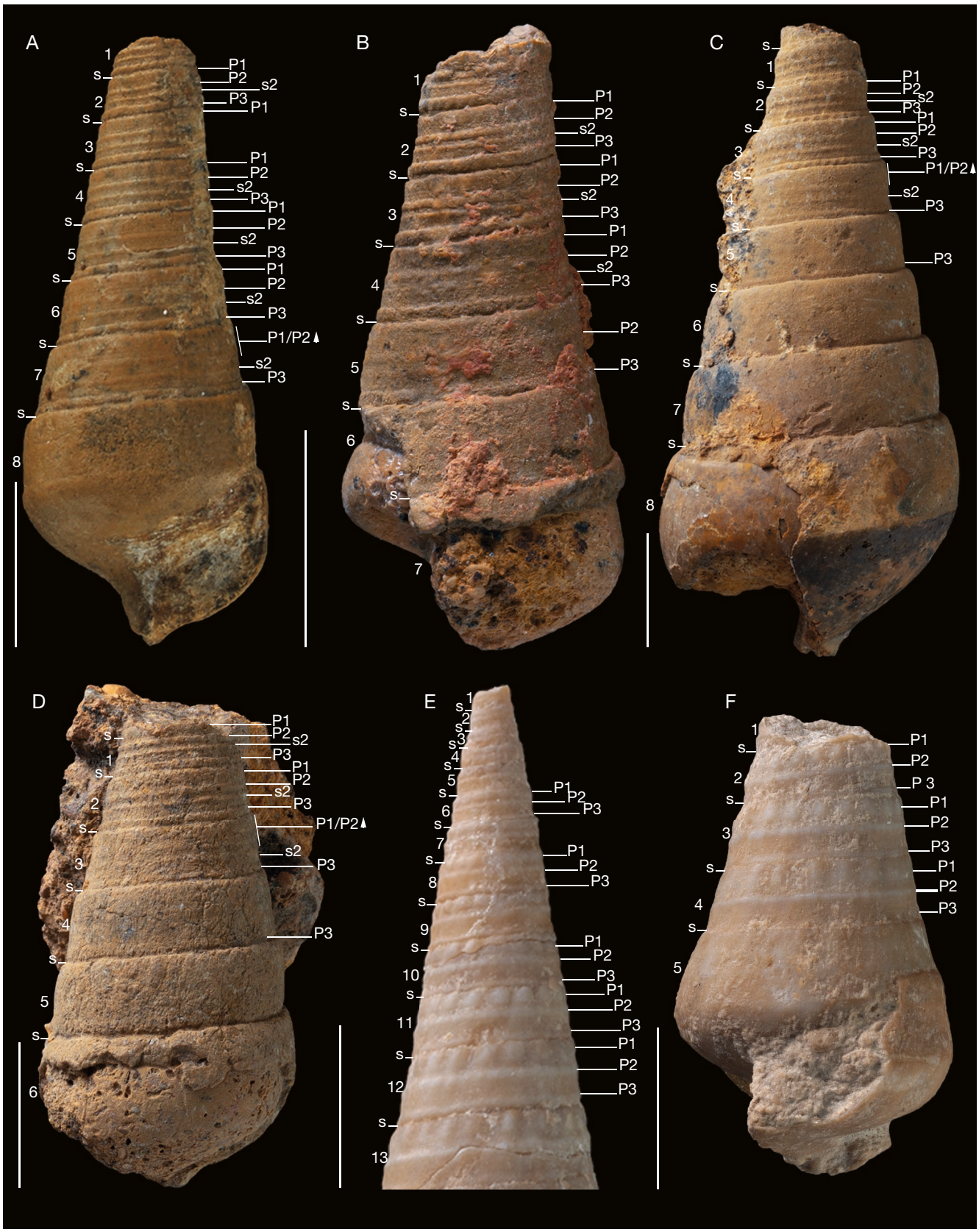

Fig. 5. — Nomenclature of the spiral cords in *Campanistylus lakhraensis* Merle & Pacaud, n. gen., n. sp. (**A**-**D**), base of the East-Lakhra village section (stn 2), lower Lakhra Formation, early Eocene (Ypresian), and *Campanile gomphoceras* (Bayan, 1870) (**E**, **F**), middle Eocene (Lutetian), Monte Postale (Italy), for comparison (**E**, **F**): **A**, paratype CPAG.RAN.I.105 (cast MNHN.F.A93728); **B**, paratype CPAG.RAN.I.104 (cast MNHN.F.A93727); **C**, paratype CPAG.RAN.I.103 (cast MNHN.F.A93725); **D**, paratype CPAG.RAN.I.102 (cast MNHN.F.A93726); **E**, specimen MNHN.F.A94698; **F**, specimen MNHN.F.A94699. On the left of the shells, the numbers from 1 to 13 give the numbers of whorls discussed in the text. Scale bars: 10 mm. Credits: P. Loubry (MNHN/CNRS).

Fig. 6. — Type material of *Campanistylus lakhraensis* Merle & Pacaud, n. sp. and its reconstruction, East-Lakhra village section (stn 2), lower Lakhra Formation, early Eocene (Ypresian): **A**, **B**, holotype CPAG.RAN.I.93 (cast MNHN.F.A93729): **A**, general view; **B**, enlarged view showing the progressive loss of sculpture, 23 to 27, number of whorls; **C**, paratype CPAG.RAN.I.96 (cast MNHN.F.A98131); **D**, **E**, paratype CPAG.RAN.I.100 (cast MNHN.F.A93711): **D**, ventral face; **E**, dorsal face; **F**, **G**, paratype CPAG.RAN.I.99 (cast MNHN.F.A98132): **F**, general view of the specimen showing a residual colour pattern; **G**, enlarged view of two whorls showing the residual colour pattern; **H**, **I**, paratype CPAG.RAN.I.98 (cast MNHN.F.A93712); **H**, profil view showing the outer lip; **I**, ventral view; **J**, reconstruction of a complete specimen with its colour pattern drawn by Charlène Letenneur (MNHN): reconstruction based on the holotype and the paratypes CPAG.RAN.I.96, CPAG.RAN.I.99 and CPAG.RAN.I.98. On the left of the shell in **B**, the numbers from 21 to 27 give the numbers of whorls discussed in the text. Scale bars: 10 mm. Credits: P. Loubry (MNHN/CNRS).

Discussion and comparisons

The oldest record of *Campanile* has been traced back to the Late Cretaceous (Douvillé 1904; Cossmann 1906, 1908; Delpey 1941; Kiel *et al.* 2000; Pacaud 2020). Their members flourished in the Tethys Sea and the Americas, but their diversity declines abruptly during the Oligocene (Cossmann 1908; Wrigley 1940; Delpey 1941). Today, *Campanile symbolicum* Iredale, 1917, is the sole living species and survives in the warm-temperate waters of southwestern Australia (Ludbrook 1971; Houbrick 1981; Healey & Wells 1998). Matsubara (2009) proposed a checklist of 98 species names of Cenozoic *Campanile*. Although around 100 species are known, they display there is little intrageneric variability, which historically prompted authors to place them all in the same genus. The shape is globally elongate turriculate with a more or less developed shoulder carina. The aperture bears one or two columellar folds. The spiral sculpture displays P1 to P3 on early teleoconch whorls with occasional adjunction of minor cords (secondary or tertiary cords) on later whorls. Spiral cords are usually granulose to nodulose. A strong development of the area of P1 often leads to the formation of a peripheral carina associated with more or less developed nodules, as in *Campanile giganteum* (Lamarck, 1804). As far as the spiral sculpture on the early whorls is concerned, *Campanistylus* is no different from any other *Campanile*. This shared character allows us to place it without hesitation in the family Campanilidae and to distinguish it from many Cerithioidea. However, *Campanistylus* Merle & Pacaud, n. gen. differs from species of *Campanile* by its cyrtoconoid shape beginning with a turriculate spire, by its almost smooth cords particularly P1, by its convex whorls and, above all, by having a loss of sculpture bearing smooth last whorls. Some specimens of the present day species *Campanile symbolicum* Iredale, 1917 often reduce their spiral sculpture, but they are many specimens displaying slightly nodulose P1 and P3 (see the syntypes of *Cerithium leve* Quoy & Gaimard, 1834, *non* Perry, 1811: https://science.mnhn.fr/institution/mnhn/collection/im/item/2000-27072). *Campanile brookmani* Cox, 1930, from the Danian (early Paleocene) of Hangu Shales (Samana Range, Pakistan) is known from a few poorly preserved specimens (Cox 1930: pl. 17, figs 2-5). Its spiral cord P3 is strongly developed, whereas it is small or absent in *Campanistylus lakhraensis* Merle & Pacaud, n. gen., n. sp. The last whorls of the largest specimen of *Campanile brookmani* (Cox, 1930) (Cox 1930: pl. 17, fig. 4), the holotype, are flat, simply widened abapically with a P3 close-set to the abapical suture, and therefore are very different from those of *Campanistylus lakhraensis*, which are convex and slightly constricted near the abapical suture. Among all other known fossil, *Campanile gomphoceras* (Bayan, 1870), from the middle Eocene (Lutetian) of Monte Postale (Italy), is the only other species to feature last whorls that are devoid of ornamentation (Fig. 7). However, the spiral sculpture on early whorls is more reminiscent of others *Campanile* and displays a strongly nodulose P1 (Fig. 5E, F). In addition, its last whorls are not convex but quite straight and its aperture is narrower with a longer anal canal. Although it is easily distinguished from *Campanistylus lakhrensis*, *Campanile gomphoceras* is not a typical *Campanile* and probably requires a separate genus. It was placed in the pachychilid genera *Bellatara* Strand, 1928 by Malaroda (1954) and *Pseudobellardia* Cox, 1931 by Dominici (2014), but in agreement with Delpey (1941), we confirm its place in the Campanilidae. Finally, another feature distinguishing *Campanistylus* from *Campanile* is the presence of colour pattern (Fig. 6F, G), as no colour pattern has been described in any *Campanile,* even in the type species *C. symbolicum*, still living in Australia. All these differences justify the proposed generic separation between *Campanistylus* and *Campanile*.

Fig. 7. — *Campanile gomphoceras* (Bayan, 1870), middle Eocene (Lutetian), Monte Postale (Italy): **A**, subadult specimen MNHN.F.A94698; **B**, adult specimen MNHN.F.A98193. Scale bars: 10 mm. Credits: P. Loubry (MNHN/CNRS).

DISCUSSION

The campanilid assemblage and endemism

Although campanilids have been described in Pakistan and India in earlier works (d'Archiac & Haime 1854; Cossmann & Pissarro 1909; Douvillé 1929; Cox 1930; Kachhara *et al.* 2011) the campanilid assemblage from Ranikot documents an obvious provincialism, the two newly described species not recorded outside the Lower Indus Basin. A Tethyan provincialism of littoral assemblages was already reported within the western Tethys with the pachychilids and the potamidids by Harzhauser *et al.* (2012) and in the eastern Tethys (Pakistan) with the volutids by Merle *et al.* (2014). Moreover, the

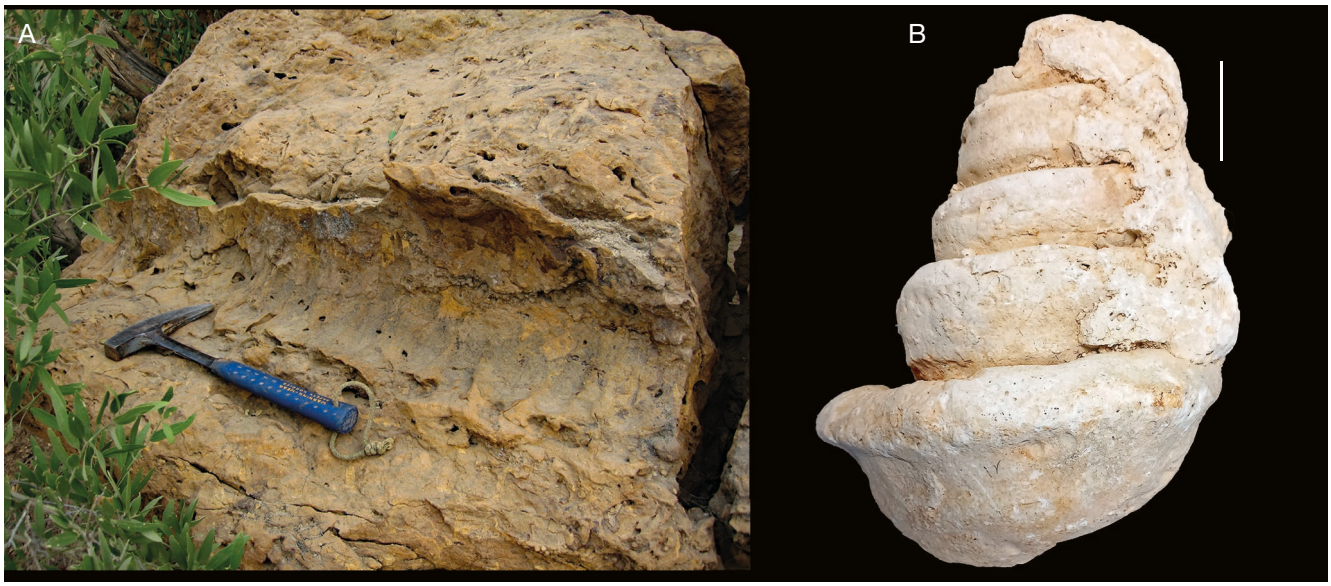

FIG. 8. — Large and unidentified *Campanile* P. Fischer, 1884 from the Ypresian of the Lakhra Formation (**A**) and the Lutetian of the Tyon Formation (**B**), Sindh, Pakistan: **A**, external imprint, Khanun Brohi, Jamshoro district; **B**, internal mold, MNHN.F.A94252, Thano Bula Khan, Jamshoro district. Scale bar: B, 50 mm. Credits: A, Grégoire Métais (CNRS/MNHN); B, Didier Merle.

case of *Campanistylus* Merle & Pacaud, n. gen. also illustrates an endemic genus strictly restricted to the Lower Indus Basin. A similar case is known with the strange volutid genus *Pakiluta* Merle & Pacaud *in* Merle *et al.* (2014) for which no other species of the genus is known outside this basin. The restricted geographical ranges of *Campanistylus* and *Pakiluta* are reminiscent of those of relict benthic Cenozoic molluscs from South Australia such as *Campanile* (Houbrick, 1984a), *Diastoma* Deshayes, 1850 (Houbrick,1984b), *Eofavartia* Merle 2002 (Merle & Landau 2020) and among the bivalves, *Neotrigonia* Cossmann, 1912 (Stanley 1984; Darragh 1985). The ranges of these genera illustrate the geographical isolation of the Australian continent, which favoured the appearance of such relict areas. For *Campanistylus* and *Pakiluta*, the isolation of the Indian subcontinent, described as an "Indian raft" (Krause & Maas 1990; Parmar & Prasad 2020, see also Patriat & Achache 1984: fig. 1), likely played a role in fostering relict areas, as it remained separated from other continents throughout the Mesozoic and early Cenozoic. A study of the entire malacological fauna from the Lakhra Formation will make it possible to identify and assess the number of taxa with identical biogeographical characteristics and would allow to confirm or refute this hypothesis of endemism resulting from the "Indian raft" applied to benthic molluscs.

ON THE SMALL SIZE OF THE DESCRIBED *CAMPANILE*

The two species of Campanilidae described herein are just a few centimeters long, 13 cm at most (the reconstructed specimen in Figure 6J), just like the modern Australian species (*Campanile symbolicum*) and only extant representative of the family (12 cm: Houbrick 1981). They lived during an interval of time close to the Paleocene-Eocene Thermal Maximum (PETM) when the warmest temperatures are registered in the Cenozoic. This small size is an interesting point, as it could suggest a tendency for the Campanilidae to be smaller in warmer habitats and vice versa. This rule (Bergman rule) on size variation according to temperature has been demonstrated for a large number of monophyletic clades of ectotherms. For the molluscs, it has been demonstrated in Cypraeaidae Rafinesque, 1815 and Ovulidae J. Fleming, 1822 (Irie & Fischer 2009; Dominici *et al.* 2020). However, it seems difficult to verify it in the case of the Campanilidae. Indeed, in the early Eocene of Jamaica, during the warmest period of the Cenozoic, the size of *Campanile trevorjacksoni* Portell & Donovan, 2008 could be around one metre long. In the middle Eocene of the Paris Basin, where the waters were quite warm (Huyghe *et al.* 2012, 2015), giant *Campanile* appeared (*Campanile giganteum* (Lamarck, 1804) and *Campanile auvertianum* d'Orbigny, 1850) with other species of smaller size. In the Rupelian, a colder period following Eocene-Oligocene transition (EOT), *Campanile charpentieri* (de Basterot, 1825), the single Rupelian *Campanile* species known from the Paris and Aquitaine basins does not exceed 100 mm. In the early Eocene from Lakhra Formation, we describe these two small species of Campanilidae, but during the preliminary fieldtrip in 2009, the Franco-Pakistan team found the imprint of a very large *Campanile* of more 40 centimeters long (Fig. 8A), which unfortunately could not be recovered. In addition, in the Lutetian of the Tyon Formation (Kirthar Range, Pakistan), internal moulds of large *Campanile* exceeding 25 centimeters have been found (Fig. 8B).

CONCLUSION

This study, which focuses on the *Campanile* from the Lakhra Formation (base of the lower Eocene), provides important new information on the family, including the description of

a new genus. Furthermore, it demonstrates the importance of this Indo-Pakistani fauna for understanding the structure of the eastern Tethys biodiversity hotspot, which has been little studied compared to the western Tethys. The high number of new species and genera recently discovered in the Lakhra Formation suggests that its mollusc fauna is still "under study" and that further new species can be expected.

Acknowledgements
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