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On Cretaceous Campanilidae (Caenogastropoda, Mollusca)

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with 2 plates

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Abstract

Six species of the Campanilidae, two of them new, are described from the Late Cretaceous of the Mexcala formation in Mexico, the Puimanyons Olisthostrom in Spain and the Fruška Gora mountains in Serbia. For the first time a planktotrophic larval shell is reported of *Campanile*, recognized on the small *Campanile houbricki* n. sp. from the Maastrichtian of Mexico. It is compared with other Cretaceous species of *Campanile* and with recent *Plesiotrochus*. According to its similar larval shell, *Metacerithium* is transferred to the Campanilidae. Relations to other genera that have previously been placed near *Campanile* are discussed and adapted to the new data. The taxonomic position of *Campanile* within the Caenogastropoda is reconsidered by paleontological data and the placement in its own superfamily confirmed. The new species are: *Campanile houbricki* from Mexico and *Metacerithium ponsi* from Spain.

Zusammenfassung

Sechs Arten der Campanilidae werden aus der oberen Kreide der Mexcala-Formation in Mexico, dem Puimanyons Olisthostrom in Spanien und den Fruška Gora Bergen in Serbien beschrieben, zwei davon neu. Zum ersten Mal kann eine planktotrophe Larvalschale von *Campanile* dokumentiert werden. Aufgrund einer sehr ähnlichen Larvalschale wird die Gattung *Metacerithium* zu den Campanilidae gestellt. Die Beziehungen anderer Gattungen, die bisher den Campanilidae zugehörig galten, wird im Licht unserer neuen Daten diskutiert. Die Stellung von *Campanile* in einer eigenen Überfamilie innerhalb der Caenogastropoda wird bestätigt. Die neuen Arten sind: *Campanile houbricki* aus Mexico und *Metacerithium ponsi* aus Spanien.

1 Introduction

Tracing the history of the largest snail that ever creeped on earth has kept scientists engaged for more than a century. Early workers classified *Campanile* FISCHER, 1884 as cerithiid (LAMARCK, 1804; COSSMANN, 1906; WENZ, 1938) due to similarities of shell ornament and shape. WENZ (1938) united *Campanile* and *Plesiotrochus* FISCHER, 1878 among a few other doubtful genera in the subfamily Campanilinae DOUVILLÉ, 1904 within the Cerithiidae FÉRRUSAC, 1819. DELPEY (1941) presented the first consistent phylogenetic treatment of this group. *Diatinostoma* COSSMANN, 1905, *Ditretus* PIETTE, 1874, and *Pyrazus* MONTFORT, 1810 were discussed as ancestral or related genera. DELPEY, however, considered *Campanile* to be a descendant of *Nerinea* DESHAYES, 1827 because of the occurrence of columellar plates. For a comprehensive outline of earlier works on *Campanile* see HOUBRICK (1981).

Modern biological studies on the spermatozoa (HEALY, 1986), its anatomy (HOUBRICK, 1981 & 1989) and the ultrastructure of the osphradium (HASZPRUNAR, 1992) revealed that recent *Campanile symbolicum* IREDALE, 1917 is quite unique among the Caenogastropoda. It has been placed in its own superfamily, the Campaniloidea (HOUBRICK, 1989). But there has always been some doubt about this treatment. The Eocene type species *Campanile giganteum* LAMARCK, 1804 possesses two columellar plates (JUNG, 1987, plate 3/2) while the recent species shows a smooth columella (HOUBRICK 1981, fig. 2f, g). Although BOUSSAC (1912), WRIGLEY (1940), DELPEY (1941) and HOUBRICK (1981) discussed this matter and concluded that columellar plates alone do not allow generic separation of the Recent and the type species, satisfactory evidence is still lacking.

Plesiotrochus is anatomically so distinct from other Cerithioidea that HOUBRICK (1990) erected an own family, the Plesiotrochidae HOUBRICK, 1990. This family has later been transferred to the Campaniloidea by HEALY (1993) according to similarities he found in their spermatozoans, confirming the earlier placement of WENZ (1938). However, PONDER & LINDBERG (1997) doubted this treatment, and BANDEL (1991) noted that the larval shell of *Plesiotrochus* resembles that of *Bittium* LEACH, 1847 which represents an undoubted Cerithioidean.

2 Materials and methods

The fossils presented herein were collected at three localities. The locality at the Čerević stream in the Serbian Fruška Gora Mountains was visited by NENAD BANJAC, VLADAN RADULOVIĆ and STEFFEN KIEL in spring 1998. The fossils are found in grey, brown and black clayey marls and grey claystones with sporadic intercalation of fine grained yellow sandstone. The presence of rudists, mainly *Sphaerulites solutus* indicates that it belonged to the tropical Tethyan realm. Molluscan fauna and stratigraphy have been described in detail by PETHŐ (1906) and PETKOVIĆ et al. (1976) and the deposits are considered to be of Maastrichtian age.

The fossils from the Maastrichtian of the Mexcala Formation in southern Mexico were collected by ROBERTO CÓZATL and STEFFEN KIEL in August 1998. They are exposed 6 km north of the village of Temalac in the Mexican state of Guerrero. Numerous molluscs are described from this locality (ALENCASTER, 1980; PERRILLIAT et al., 2000) but no rudists have been reported. The locality is registered as IGM 2448 in the locality register of the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM) in Mexico City.

Of Campanian age are the fossils from Torallola in the Tremp basin on the southern slopes of the Spanish Pyrenees. They were gathered in the grey to black marls of the Puimanyons Olisthostrom, exposed on the slopes of a valley system between Sensuy, Torallola and Toralla just to the West of Pobla de Segur. Gastropods from this locality have been described by several workers (VIDAL, 1917; BATALLER, 1949; QUINTERO & REVILLA, 1966) and rudists indicate Tethyan affinities. The material presented here was collected by KLAUS BANDEL, STEFFEN KIEL and several colleagues from the University of Hamburg during several field trips since 1989.

All macrofossils have been coated with magnesium oxide for photographing, except the cross-sections. Sediment samples from Spain and Mexico were diluted in an H_2O_2 solution, fractionated with sieves and dried to extract microfossils under a binocular. The microfossils were then coated with gold and photographed with a scanning electron microscope.

The fossils from Temalac in Mexico are deposited in the paleontological collection of the Instituto de Geología, UNAM, labelled IGM 7806-7810. All other fossil are deposited in the type collection of the Geologisch-Paläontologisches Institut, Hamburg University, labelled GPI 3948-3955.

3 The larval shell of *Campanile*

The importance of the shell formed by a planktotrophic larva in gastropod phylogeny has repeatedly been demonstrated by BANDEL (1982, 1997). Unfortunately, the early ontogeny of recent *Campanile symbolicum* is of the lecithotrophic type and this character could hitherto not be used for tracing its phylogenetic history.
The comparably small *Campanile houbricki* n. sp. occurs in the fauna of Temalac, Mexico and here the larval shell is still preserved. The adult shell of this species has a typical sculpture for the genus, but the single columellar plate which is visible in the aperture, is dissolved in the interior of the shell. Its larval shell is quite similar to that of *Plesiotrochus* (plate 2, fig. 5, 6), except that the embryonic portion is larger in the latter, which indicates that the embryo of *Plesiotrochus* was supplied by more yolk than that of *Campanile houbricki*.

4 Systematic paleontology

Superfamily Campaniloidea DOUVILLÉ, 1904

Diagnosis: Members of this superfamily are characterized by a smooth and globular protoconch which consists of 2-2 ½ volutions, is 0.3 to 0.4 mm high and wide, and terminates in a strong varix.

Remarks: HOUBRICK (1989) raised the Campanilidae to superfamily rank in order to exclude them from the Cerithioideans by reason of anatomical differences. However, Houbrick did not present a diagnosis of this superfamily. Since HEALY (1993) included the Plesiotrochidae with small and rather conical shells, we propose the protoconch as seen on *Campanile houbricki* n. sp. to be the unifying shell-character. However, this character can only be used in species with a planktotrophic larva but not in cases of lecithotrophic development.

Family Campanilidae DOUVILLÉ, 1904

Diagnosis: (in part according to HOUBRICK, 1981) The shell is elongate and turreted, has straight-sided or slightly convex whorls and moderately incised sutures. The growth lines are sinuous and sculpture consists of sutural cords and nodes that are frequently absent or weak on later whorls. Its body whorl is truncate, the aperture narrow and fusiform, possesses an anterior canal of moderate length, and the columella is smooth or plaited. The larval shell (if developed) is smooth and provided with a marginally enforced apertural projection.

Genus *Campanile* FISCHER, 1884

Type species: *Campanile giganteum* LAMARCK, 1804 from the Eocene of the Paris Basin.

Diagnosis: The turriform shell has numerous low volutions. The whorls are sculptured with a broad, tuberculate subsutural collar, spiral cords which may be beaded, and a cover of fine incised striae. Columellar and parietal plates may occur and the ornament may change on the last whorls.

Remarks: Members of the Potamididae ADAMS & ADAMS, 1854 are known to produce similar shells. An example is "*Tympanotonus*" *hungaricus* ZITTEL (see SZÖTS, 1953, plate 3, figs 9-18) from the Eocene of Gant, Hungary. However, most Potamididae are restricted to intertidal, often brackish or hypersaline environments (HOUBRICK, 1984, 1991), whereas recent *Campanile symbolicum* lives in the subtidal (HOUBRICK, 1989). According to DONOVAN & BLISSETT (1998) also the Eocene *Campanile* lived in a fully marine subtidal environment. The protoconch of potamidids with a planktotrophic larva have an ornament characterized by two spiral cords (KOWALKE, 1998; BANDEL & KOWALKE, 1999) which contrasts with the smooth protoconch of the Campaniloidea.

Campanile houbricki KIEL & PERRILLIAT n. sp.
Plate 1/1-5

Holotype: IGM 7806, plate 1/4.

Paratypes: IGM 7807, plate 1/3; IGM 7808, plate 1/5.

Derivation of name: In honour of RICHARD S. HOUBRICK who worked on the biology of the recent *Campanile*.
Stratum typicum: The marly Maastrichtian of the Mexcala Formation.
Locus typicus: Locality IGM 2448, about six km north of Temalac, in the Mexican state of Guerrero.

Material: Several fragments from the type locality in Mexico (IGM 7806-7810).

Diagnosis: This small and slender *Campanile* shows one plate low on the columella which is dissolved further inside the shell. The ornament bears two minor spirals below the broad, subsutural belt.

Description: The protoconch is smooth and round, consists of two convex volutions, and terminates with a strong varix that is flaring in its lower half. The embryonic part composing ½ a whorl measures about 0.14 mm across. The entire protoconch is 0.33 mm high and 0.35 mm wide with 1 ½ whorls formed by the larva. The early teleoconch is sculptured with two finely beaded spiral keels. The adult shell is straight-sided, shows a broad, beaded subsutural belt and two minor spirals below. The base is smooth and one plication is present low on the columella. This plate is dissolved in the interior of the shell. The size of a fully grown shell may have been about 60 mm in height, and the largest fragment has a diameter of 11 mm.

Plate 1

Fig. 1-5 *Campanile houbricki* KIEL & PERRILLIAT, n.sp. from the Maastrichtian of the Mexcala Formation near Temalac, Mexico.

- Fig. 1 Early ontogenetic shell with protoconch and two teleoconch whorls, IGM 7810, x 100.
- Fig. 2 Juvenile shell showing ontogenetic changes in sculpture, IGM 7809, x 75.
- Fig. 3 Small specimen showing the transition to the adult sculpture, IGM 7807, x 5.
- Fig. 4 Holotype, IGM 7806, x 3.
- Fig. 5 Cross-section showing the smooth interior, IGM 7808.

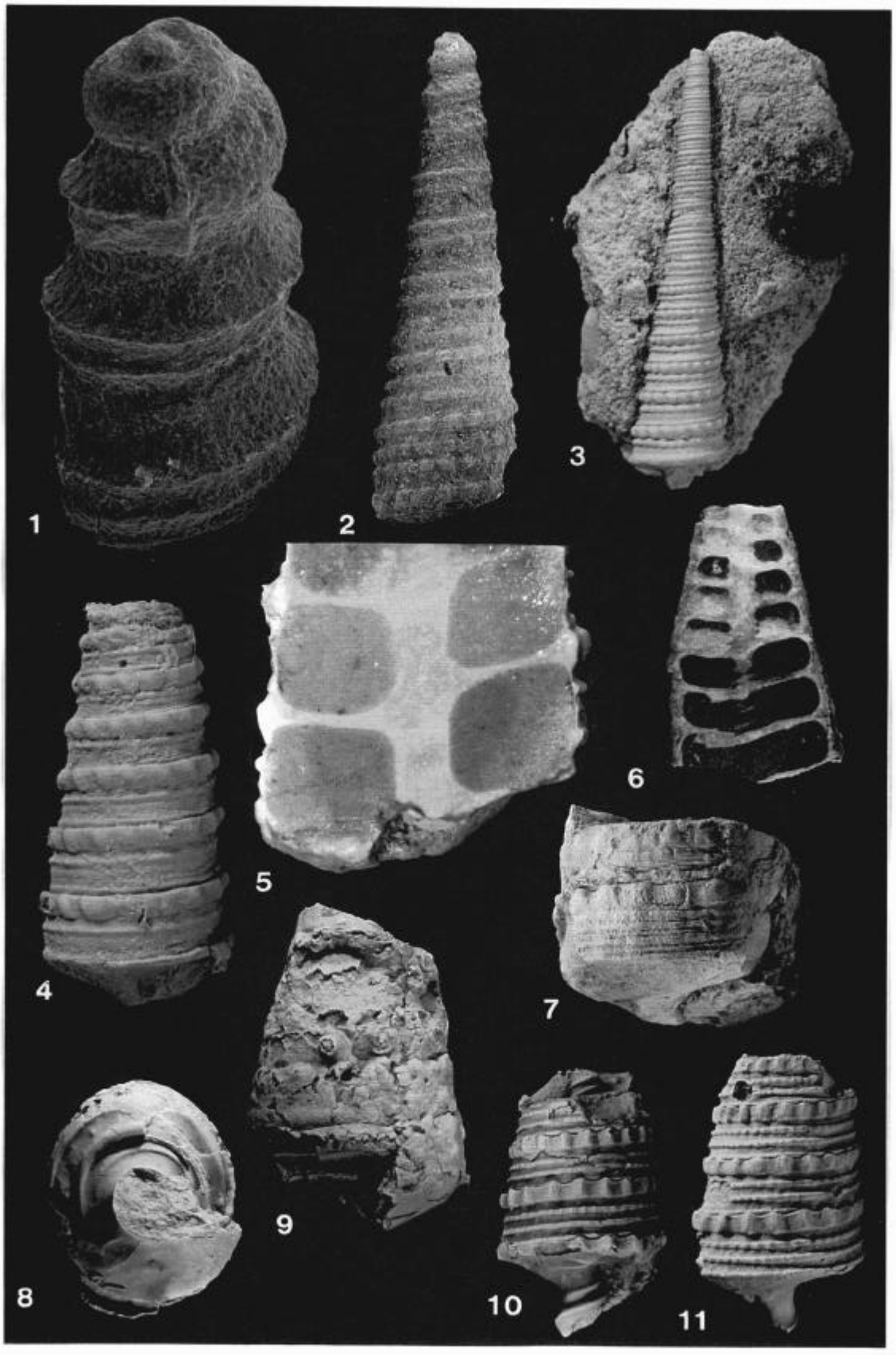
Fig. 6 *Campanile? regens* PETHÖ, 1906 from the Maastrichtian Čerević stream in the Fruška Gora mountains, Serbia, cross-section showing the internal plates, GPI 3950, x 0.9.

Fig. 7 *Campanile inauguratum* (STOLICZKA, 1868) from the Maastrichtian Čerević stream in the Fruška Gora mountains in Serbia, GPI 3949, x 0.9.

Fig. 8-9 *Campanile? carezi* VIDAL, 1917 from the Campanian of the Puimanyons Olisthostrom near Torallola, Spain, GPI 3951.

- Fig. 8 Frontal view of the corroded shell, x 0.7.
- Fig. 9 Basal view showing the parietal folds and their dissappearance near the aperture, x 0.9.

Fig. 10-11 *Campanile cossmanni* VIDAL, 1917 from the Campanian of the Puimanyons Olisthostrom near Torallola, Spain, two views, GPI 3948, x 1.8.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Remarks: Although many workers regard *Campanile* as a predominantely Tertiary genus (HOUBRICK, 1981; HASZPRUNAR, 1992) palaeontologists have described numerous Late Cretaceous species. Distinction between these species is based mainly on the number of minor spiral cords below the subsutural belt, and the number of columellar plates. The oldest species known is probably represented by *Campanile bircki* (GEINITZ, 1875) from the Cenomanian or Turonian of Saxony in Germany. It has two columellar plates in its aperture and three minor and relatively broad spirals in its ornament. *Campanile cossmanni* VIDAL, 1917 as described below appears to be closely related to this species. It is characterized by two equally strong and beaded minor spirals in its ornament, and two columellar plates and two parietal plates in its aperture. Also *Campanile inauguratum* (STOLICZKA, 1868) is closely related. It has minor spirals that are variable in number and strength and two columellar plates. Our newly collected specimen from Serbia shows one parietal plate. Within this relation but somewhat doubtful may be *Campanile hispidium* (ZEKELI, 1852) with only one minor spiral as ornament. While ZEKELI (1852) did not mention columellar plates in his original description, DELPEY (1941) mentioned two to be present in this species. *Campanile houbricki* n. sp. has a sculpture that resembles that of *Campanile inauguratum* but it differs from the latter by its smooth interior. *C. houbricki* is also exceptionally small for the genus.
Campanile? *carezi* VIDAL, 1917 and *Campanile*? *regens* PETHÖ, 1906 show a distinct sculpture of a broad, axially ribbed belt in the upper half of the whorl, as well as columellar and parietal plates. They resemble *Campanile* in general shape and in size but our material is not well enough preserved to decide whether they belong to *Campanile* or even the Campanilidae or represent members of another taxon. However, due to their general similarity they are here tentatively placed within *Campanile*.
WHITE (1887) described some species named *Nerinaea buarquiana* WHITE, 1887, *Nerinaea inaugurata* STOLICZKA, 1868 and *Nerinaea sagrittana* WHITE, 1887 from the late Cretaceous of Brazil of which WRIGLEY (1940) suggested that they rather represent members of *Campanile* and actually lived in the Eocene.

Campanile cossmanni VIDAL, 1917
Plate 1/10-11

1917 *Campanile cossmanni* n.sp. VIDAL, p. 6, pl. 3, figs. 2-4.
1949 *Campanile cossmanni* VIDAL BATALLER, p. 110.

Description: There are two columellar plates in the aperture of which the upper one is much weaker than the second, and two parietal plates of which the outer one is sometimes interrupted. Both the parietal and the weak columellar plates disappear about half a volution before they reach the aperture. The whorls are ornamented with a strongly tuberculate, subsutural collar, two beaded cords below it, and a third smooth ridge that is often obscured by the following whorls. The diameter of the largest specimen is 38 mm.

Material: Eight specimens from the Campanian of Torallola, Spain (GPI 3948).

Campanile inauguratum (STOLICZKA, 1868)
Plate 1/7

1868 *Cerithium inauguratum* n.sp. STOLICZKA, p. 193, pl. 15, figs.19, 20.
1902 *Cerithium* sp. cf. *inauguratum* STOLICZKA QUAAS, p. 262, pl. 26, figs. 27a, b.
1922 *Campanile inauguratum* (STOLICZKA) COTTREAU, 61, pl. 8, figs. 3-5.

Description: The large, high spired shell has low whorls and is ornamented with a tuberculate, subsutural belt with fine incised striae and four spiral cords of different strength below. In a cross section, two columellar and one parietal plate are visible. Its largest diameter is 45 mm.

Material: One specimen from Čerević stream in the Serbian Fruška Gora mountains (GPI 3949).

Campanile? *regens* PETHÖ, 1906
Plate 1/6

1906 *Campanile regens* n.sp. PETHÖ, p. 161, pl. 10, fig. 12.

Description: The large, high spired shell consists of more than 12 low volutions and is sculptured with axial ribs that are strongest near the upper suture. The columella bears two plates and the aperture ends in a basal canal. The figured specimen is 140 mm high and 60 mm in diameter.

Remarks: *Campanile*? *carezi* is distinct by its three parietal plates while *Campanile*? *regens* shows only one.

Material: One specimen from Čerević stream in the Serbian Fruška Gora mountains (GPI 3950).

Campanile? *carezi* VIDAL, 1917
Plate 1/8-9

1917 *Campanile carezi* n.sp. VIDAL, p. 7, pl. 3, fig. 6.
1949 *Campanile carezi* VIDAL BATALLER, p. 109-110.

Description: The large, high spired shell consists of numerous low volutions which are sculptured with axial ribs that thin out on the lower half of the whorl. The columella shows three parietal plates, the first at the outer margin of the whorl, the second and strongest in the centre and a last weak one near the columella. All three plates disappear at least half a volution before they reach the aperture. The damaged specimen is 74 mm high and 54 mm wide.

Material: One specimen from the Campanian of Torallola, Spain (GPI 3951).

Genus *Metacerithium* COSSMANN, 1906

Type species: *Cerithium trimonile* MICHELIN, 1838 from the Aptian/Albian of France.

Diagnosis: The small to medium sized, high spired shell has volutions with three beaded spiral cords, of which the central one may be weak. Its base is a little rounded and the anterior canal is straight (WENZ, 1938).

Remarks: ABBASS (1973, p. 133, pl. 4, figs. 2, 3, 7, 8, 10) described and illustrated well preserved specimens of the type species. Accordingly, opisthocline axial ribs are present on the earliest whorl and a subsutural band appears from the fourth whorl onwards. The ornament then gradually becomes tuberculate. This coincides with the development of ornamentation observed by us on the new species described below. The new species has the protoconch preserved, while its shape and ornament is not known from the type. Due to these similarities of the teleoconchs and the *Campanile*-like protoconch of the new species, *Metacerithium* is herein regarded to belong to the Campanilidae. *Metacerithium* is distinct from *Campanile* by its strong, beaded spiral ridge near the base of the volutions.

Metacerithium ponsi KIEL & BANDEL n. sp.
Plate 2/1-4

Holotype: GPI 3953, plate 2/1, 3.

Paratype: GPI 3952, plate 2/4.

Derivation of name: Named after JOSE MARIA PONS (Barcelona) for his introduction to the geology of the Tremp Basin and the locality of Torallola.
Stratum typicum: The Campanian Puimanyons Olisthostrom of the Vallcarga Formation.

Locus typicus: The valley of the Barranc de Sensui between the villages of Torallola and Sensuy near Pobla de Segur, Catalania, Spain.

Material: Three specimens from the type locality in Spain (GPI 3952-3954).

Diagnosis: This *Metacerithium* has two tuberculate spiral cords and a smooth base.

Description: The protoconch is smooth and roundish, is made of 2 ½ volutions and terminates at a varix. It is 0.25 mm high and 0.33 mm wide. The teleoconch is slender turriform. The first 8 whorls have a subsutural row of tubercles and a strong, beaded spiral ridge near the base. The aperture has a straight columella without plates and its anterior siphonal canal is constricted and short. The holotype is 6.4 mm high and the paratype is 9 mm high.

Remarks: Metacerithium ponsi has more denticles per whorl on the basal keel than are present in the type species Metacerithium trimonile.

5 Discussion

DELPEY (1941) suggested *Diatinostoma* and *Ditretus* (see COSSMANN, 1906, pl. 5, figs 1-10) to represent possible ancestors of *Campanile*. The former possesses axial ribs which are strongest near the upper suture and fine spiral lines below; this may be regarded as similarities to *Campanile*. The latter shows a strong, nodose spiral cord near the base of the whorls resembling those of young *Metacerithium*. However, the protoconch morphology of *Diatinostoma* and *Ditretus* are still unknown, and thus their relations to the Campanilidae remain in doubt. DELPEY (1941) also discussed a possible relation of *Pyrazus* to *Campanile*. However, *Pyrazus* is based on a recent Australian species which belongs to the Batillariidae HOUBRICK, 1991 (BEESLY et al., 1998).
Nerineans possess columellar and parietal plates but often also show labral plates, unknown from *Campanile*. Since several nerinean species have been documented with a heterostrophic, sinistrally coiled protoconch (BIGOT, 1896; BANDEL, 1993; KOWALKE & BANDEL, 1996), this family is regarded to belong to the Allogastropoda (Heterostropha). However, their adult shells can be quite similar to those of the Campanilidae.

Plate 2

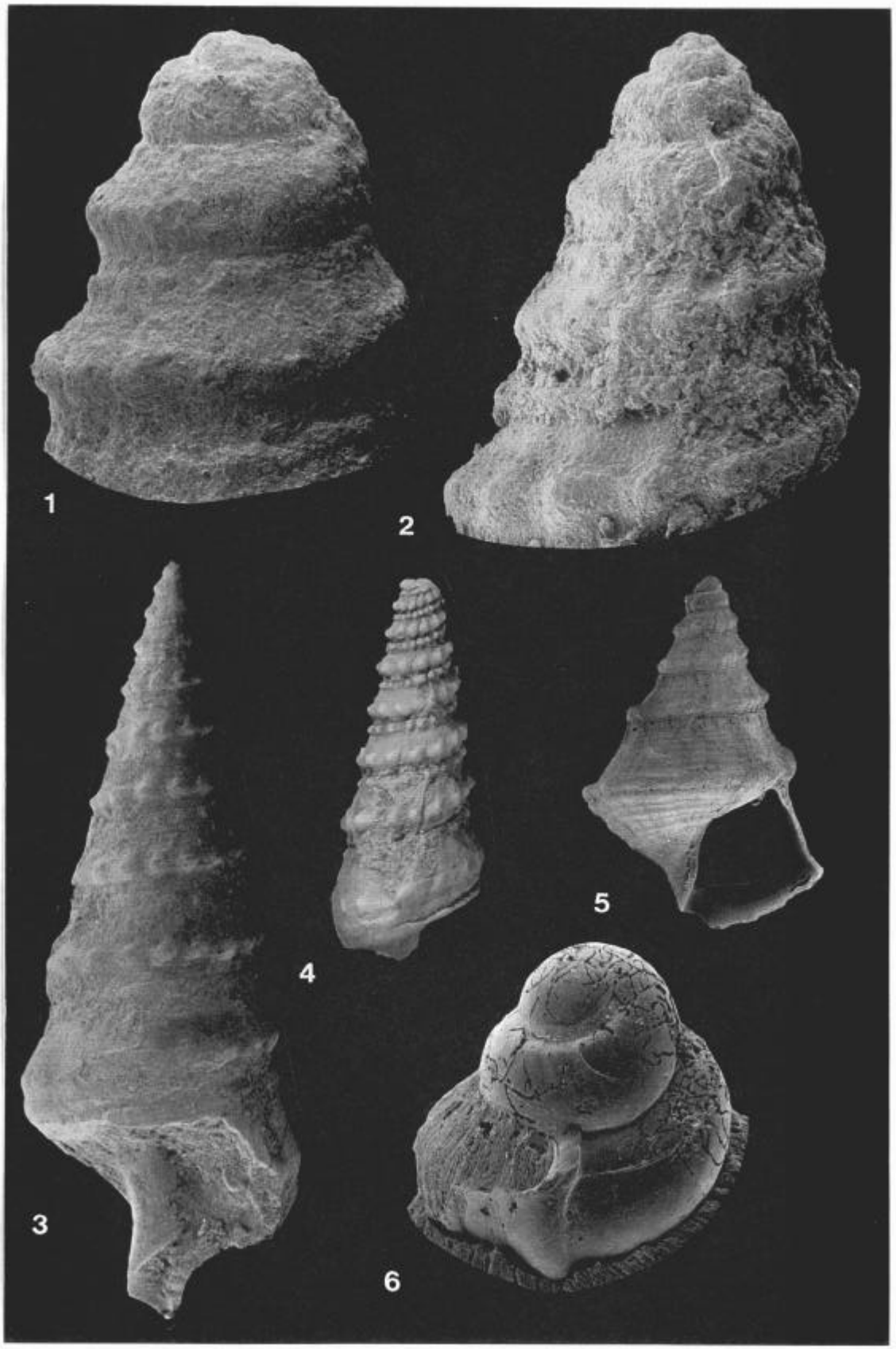
Fig. 1-4 *Metacerithium ponsi* KIEL & BANDEL, n.sp. from the Campanian of the Puimanyons Olisthostrom near Torallola, Spain.

Fig. 1 Protoconch of the holotype, GPI 3953, x 144.
Fig. 2 Protoconch of another specimen, showing the characteristic varix, GPI 3954, x 125.
Fig. 3 Holotype, GPI 3953, x 20.
Fig. 4 Paratype, GPI 3952, x 7.

Fig. 5-6 *Plesiotrochus* spp. from Lizard Island, Australia, GPI 3955.

Fig. 5 Apertural view on the adult shell, x 34.

Fig. 6 Protoconch of the same specimen, x 185.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Another problematic genus often assigned to the Campanilidae is *Diozoptyxis* COSSMANN, 1896. As VAUGHAN (1988) pointed out, COSSMANN (1896) and D'ORBIGNY (1843) independently named two different species as *Nerinea monilifera*. COSSMANN's species, which he defined as the type species of *Diozoptyxis,* bears three internal plates and an open umbilicus, whereas D'ORBIGNY's only shows one plate and no umbilicus. VAUGHAN (1988) suggested to assign Cossmanns *Nerinea monilifera* to a new species *Diotoptyxis monilifera*. According to this treatment, *Diozoptyxis* contains umbilicate shells with three internal plates. It is therefore well distinguished from *Campanile* and could very well represent a member of the Nerineidae ZITTEL, 1873.

HOUBRICK (1989) included *Dirocerithium* WOODRING & STENZEL, 1959 from the Panamese Eocene in the Campanilidae based on WOODRING's (1959) comments on similarities of *Dirocerithium* and *Campanile gomphoceras* BAYAN, 1870. In fact, Woodring never mentioned *Campanile* in this context but included *"Campanile" gomphoceras* in *Bellatara* STRAND, 1928 and both genera *Dirocerithium* and *Bellatara* are placed within the Cerithiidae. The early ornament of *Dirocerithium wechesense* STENZEL (in WOODRING, 1959, pl. 24, fig. 14) consists of axial ribs crossed by three to four spiral cords and resembles that of *Cerithium* rather than *Campanile*.

Our new species of *Metacerithium* possesses a protoconch similar to that of *Campanile houbricki*. Its teleoconch sculpture resembles that of the early shell of *Metacerithium trimonile* which was well described and figured by ABBASS (1973) from the English Aptian, and represents the type species of this genus. Because of its protoconchmorphology, we transfer *Metacerithium* to the Campanilidae.

This raises the question whether the other genera constituting the Metacerithiinae also belong to the Campanilidae. *Microschiza belgica* D'ARCHIAC, 1841 was defined by COSSMANN (1906) as the type species of *Cimolithium* COSSMANN, 1906 which is thought to be a member of the Metacerithiinae (WENZ, 1938). The same species was considered by DELPEY (1941) as a possible early *Campanile*. Upper Cretaceous species of *Teretrina* COSSMANN, 1912, members of the Mathildidae DALL, 1889 (Heterostropha) resemble *Bathraspira* COSSMANN, 1906, another member of the Metacerithiinae. A specimen of *Bathraspira* sp. with heterostrophic protoconch and two teleoconch whorls was illustrated by KOLLMANN (1982, pl. 8, figs. 3-5). But KOLLMANN was not sure whether his assignment was correct due to some apertural features of *Bathraspira*. His data also indicate that this genus may not belong to the *Metacerithium*-relation. However, neither the protoconchs of the type species of *Cimolithium* or *Bathraspira* are known, nor those of any further metacerithiinid, so their placement remains uncertain.

Only a few Neogene fossils of *Plesiotrochus* are known (LADD, 1972). However, comparing the early teleoconch sculpture of *Metacerithium* and *Plesiotrochus* (plate 2/5-6), *Metacerithium* may be considered as possible stem group representative of the Plesiotrochidae.

Protoconchs similar to those of *Campanile houbricki* can be found in the Triassic *Settsassia* BANDEL, 1992 (BANDEL, 1992, pl. 11, fig. 4) and *Angularia* KOKEN, 1892 (BANDEL, 1993, pl. 14, fig. 4), on the upper Carboniferous *Palaeostylus* MANSAY, 1914 and *Orthonema* MEEK & WORTHEN, 1861 (NÜTZEL, 1998, pls. XXXII, XXXIII), and *Stegocoelia* (YOO, 1988, fig. 71, 79; 1994, pl. 15). But possible relations of these genera to *Campanile* and *Metacerithium* are still open.

6 Conclusions

The larval shell of *Campanile houbricki* n. sp. is globular, consists of 2-2 ½ smooth and convex volutions, is about 0.4 mm wide, 0.3 mm high and the embryonic portion measures 0.15 mm across. The protoconch terminates in a strong varix which is flaring in the lower half. A very similar protoconch type can be observed on the recent *Plesiotrochus* which is closely related to the recent *Campanile symbolicum* regarding sperm ultrastructure (HEALY, 1986). We therefore conclude that the here presented larval shell is representative for *Campanile* and the Campaniloidea.

The above described larval shell certainly places *Campanile* in the subclass Caenogastropoda. A relation to *Nerinea* and related Heterostropha can be rejected since they have sinistrally coiled protoconchs.

Two species of *Metacerithium* similar to its type species possess protoconchs resembling those described for *Campanile houbricki*. *Metacerithium* is therefore transferred to the Campanilidae.

Including *Metacerithium*, the Campanilidae can be traced back into the mid-Cretaceous. Similar larval shells described from the Triassic and Carboniferous may indicate that the Campaniloidea represent an even older caenogastropod lineage.

Another problematic genus often assigned to the Campanilidae is *Diozoptyxis* COSSMANN, 1896. As VAUGHAN (1988) pointed out, COSSMANN (1896) and D'ORBIGNY (1843) independently named two different species as *Nerinea monilifera*. COSSMANN's species, which he defined as the type species of *Diozoptyxis,* bears three internal plates and an open umbilicus, whereas D'ORBIGNY's only shows one plate and no umbilicus. VAUGHAN (1988) suggested to assign Cossmanns *Nerinea monilifera* to a new species *Diotoptyxis monilifera*. According to this treatment, *Diozoptyxis* contains umbilicate shells with three internal plates. It is therefore well distinguished from *Campanile* and could very well represent a member of the Nerineidae ZITTEL, 1873.

HOUBRICK (1989) included *Dirocerithium* WOODRING & STENZEL, 1959 from the Panamese Eocene in the Campanilidae based on WOODRING's (1959) comments on similarities of *Dirocerithium* and *Campanile gomphoceras* BAYAN, 1870. In fact, Woodring never mentioned *Campanile* in this context but included *"Campanile" gomphoceras* in *Bellatara* STRAND, 1928 and both genera *Dirocerithium* and *Bellatara* are placed within the Cerithiidae. The early ornament of *Dirocerithium wechesense* STENZEL (in WOODRING, 1959, pl. 24, fig. 14) consists of axial ribs crossed by three to four spiral cords and resembles that of *Cerithium* rather than *Campanile*.

Our new species of *Metacerithium* possesses a protoconch similar to that of *Campanile houbricki*. Its teleoconch sculpture resembles that of the early shell of *Metacerithium trimonile* which was well described and figured by ABBASS (1973) from the English Aptian, and represents the type species of this genus. Because of its protoconchmorphology, we transfer *Metacerithium* to the Campanilidae.

This raises the question whether the other genera constituting the Metacerithiinae also belong to the Campanilidae. *Microschiza belgica* D'ARCHIAC, 1841 was defined by COSSMANN (1906) as the type species of *Cimolithium* COSSMANN, 1906 which is thought to be a member of the Metacerithiinae (WENZ, 1938). The same species was considered by DELPEY (1941) as a possible early *Campanile*. Upper Cretaceous species of *Teretrina* COSSMANN, 1912, members of the Mathildidae DALL, 1889 (Heterostropha) resemble *Bathraspira* COSSMANN, 1906, another member of the Metacerithiinae. A specimen of *Bathraspira* sp. with heterostrophic protoconch and two teleoconch whorls was illustrated by KOLLMANN (1982, pl. 8, figs. 3-5). But KOLLMANN was not sure whether his assignment was correct due to some apertural features of *Bathraspira*. His data also indicate that this genus may not belong to the *Metacerithium*-relation. However, neither the protoconchs of the type species of *Cimolithium* or *Bathraspira* are known, nor those of any further metacerithiinid, so their placement remains uncertain.

Only a few Neogene fossils of *Plesiotrochus* are known (LADD, 1972). However, comparing the early teleoconch sculpture of *Metacerithium* and *Plesiotrochus* (plate 2/5-6), *Metacerithium* may be considered as possible stem group representative of the Plesiotrochidae.

Protoconchs similar to those of *Campanile houbricki* can be found in the Triassic *Settsassia* BANDEL, 1992 (BANDEL, 1992, pl. 11, fig. 4) and *Angularia* KOKEN, 1892 (BANDEL, 1993, pl. 14, fig. 4), on the upper Carboniferous *Palaeostylus* MANSAY, 1914 and *Orthonema* MEEK & WORTHEN, 1861 (NÜTZEL, 1998, pls. XXXII, XXXIII), and *Stegocoelia* (YOO, 1988, fig. 71, 79; 1994, pl. 15). But possible relations of these genera to *Campanile* and *Metacerithium* are still open.

6 Conclusions

The larval shell of *Campanile houbricki* n. sp. is globular, consists of 2-2 ½ smooth and convex volutions, is about 0.4 mm wide, 0.3 mm high and the embryonic portion measures 0.15 mm across. The protoconch terminates in a strong varix which is flaring in the lower half. A very similar protoconch type can be observed on the recent *Plesiotrochus* which is closely related to the recent *Campanile symbolicum* regarding sperm ultrastructure (HEALY, 1986). We therefore conclude that the here presented larval shell is representative for *Campanile* and the Campaniloidea.

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