

# New and overlooked occurrences of the rarely reported protochelonibiine “turtle” barnacles from the Oligocene and Miocene of Europe

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## Abstract

15 We report on two clustering chelonibiid shells from Rupelian deposits of southwestern Germany. One of these specimens displays a tripartite rostral complex and disparietal radii that indicate the Oligocene species *Protochelonibia melleni*, which was known so far from isolated compartments only. A literature review reveals two additional, overlooked records of the rarely reported genus *Protochelonibia*, coming respectively from the Burdigalian of  
20 France and the Langhian of Austria. Both these historical finds likely represent the Miocene species *Protochelonibia submersa*. All together, these occurrences support the notion that the protochelonibiines had acquired a broad distribution as early as in Rupelian times, when *P. melleni* occurred along the proto-Gulf of Mexico and in the Western Paratethys. Both *P. melleni* and *P. submersa* grew in form of peltate shells that evoke a superficial adhesion to

25 some kind of quickly moving hosts. The outer wall of the abraded German colony of *P.*  
*melleni* is comprised of pillar-like blocks of shelly material. In other coronuloids, similar yet  
more prominent septa abut outward to form T-shaped flanges and intervening longitudinal  
canals that facilitate the grasping of various kinds of penetrable substrates. Whether the  
diminutive external longitudinal parietal septa of *P. melleni* represent an early stage in the  
30 evolution of the coronuloid shell architecture or vestigial structures cannot be ascertained, but  
the former hypothesis seems to be more likely. New additions to the pre-Pliocene fossil  
record of Coronuloidea will hopefully clarify this and other crucial aspects of the origin and  
early evolution of the turtle and whale barnacles.

### 35 **Key words**

Chelonibiidae, Coronuloidea, Palaeobiogeography, *Protochelonibia*, Rupelian, Western  
Paratethys

### **Declarations**

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have been deposited in a publicly accessible museum collection (see details below).

## 45 **Introduction**

The balanomorph superfamily Coronuloidea includes cirripede epibionts of several marine vertebrates (mostly turtles, cetaceans and sirenians) and invertebrates (mostly crabs, horseshoe crabs and gastropods) (e.g., Darwin 1854; Pilsbry 1916; Newman 1996; Hayashi 2013; Zardus 2021). These epizoic barnacles are classified into four families, namely, the  
50 extant Coronulidae, Chelonibiidae and Platylepadidae, and the extinct (and largely enigmatic) Emersoniidae (e.g., Newman 1996; Collareta and Newman 2020). Among the living coronuloids, those assigned to Chelonibiidae are all classified into the genus *Chelonibia* Leach, 1817, whose members are either turtle-dwellers (e.g., *Chelonibia caretta* (Spengler, 1790) and the *testudinaria* morph of *Chelonibia testudinaria* (Linnaeus, 1758)) or more  
55 generalist epibionts of largely invertebrate hosts (e.g., the *patula* morph of *Chelonibia testudinaria*) (e.g., Darwin 1854; Pilsbry 1916; Newman 1996; Chan et al. 2009; Zardus 2021).

Our understanding of the evolutionary history of the chelonibiid barnacles is still partly wanting, at least as far as the fossil record is concerned. The fossil record of Chelonibiidae is  
60 mostly represented by shells and isolated compartments of *C. testudinaria* from various Pliocene-Quaternary deposits worldwide (e.g., De Alessandri 1906; Ross 1963; Zullo 1982, 1986; Collareta et al. 2016; Collareta 2016, 2020). In deposits older than the Pliocene, fossil chelonibiids are much rarer. Besides a few unquestionable members of *Chelonibia* that originate from early Neogene deposits (e.g., *Chelonibia solida* Withers, 1929 and *Chelonibia*  
65 *zanzibarensis* Collareta & Newman in Collareta et al., 2021), chelonibiids are represented in pre-Pliocene strata by the genus *Protochelonibia* Harzhauser & Newman in Harzhauser et al., 2011. Being diagnosed by large walls with tripartite rostral complexes displaying distinct sutures on the external surface, *Protochelonibia* is currently classified into the monotypic

subfamily Protochelonibiinae (Harzhauser et al. 2011; Collareta and Newman 2020), here  
70 also referred to as the protochelonibiines. In spite of its easily recognizable shell morphology,  
finds of *Protochelonibia* are overly rare, this genus being known on the sole basis of a  
handful of specimens from three fossiliferous deposits worldwide – namely, i) the Oligocene  
(Rupelian) Mint Spring and Byram formations of Mississippi (USA), with *Protochelonibia*  
*melleni* (Zullo, 1982); ii) the lower Miocene (Aquitanian) Ebelsberg Formation of Upper  
75 Austria, with *Protochelonibia submersa* Harzhauser & Newman in Harzhauser et al., 2011;  
and iii) the Pliocene (Piacenzian?) marine deposits exposed at Orciano Pisano, Tuscany  
(central Italy), with *Protochelonibia capellinii* (De Alessandri, 1895).

Here, we report on two clustering protochelonibiine shells from Rupelian deposits of  
southwestern Germany (Fig. 1). Two historical finds of Chelonibiidae that were published by  
80 Withers (1929) are also assigned to *Protochelonibia*. The palaeobiogeographic,  
palaeoecological and evolutionary implications of the Oligo-Miocene species of  
*Protochelonibia* are then discussed, considering our finds, and a general overview of the  
fossil history of the protochelonibiines is provided.

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### **Locality, geology and depositional environment**

The fossil specimens studied herein come from the abandoned Unterfeld claypit near  
Rauenberg (formerly also known as Frauenweiler–Wiesloch), with sediments being deposited  
in the Upper Rhine Valley during the early Oligocene (Rupelian) rifting phase. These  
90 sediments are part of the Hochberg Member of the Bodenheim Formation, dated as  
Calcareous Nannoplankton Zone NP23, or European Mammal Zone MP22-23, respectively,  
which corresponds to the middle part of the Rupelian (Grimm et al. 2002; see also the

summary in Maxwell et al. 2016). This corresponds to an age of ca. 33 to 30 My.

A comprehensive compilation by Maxwell et al. (2016) provides deeper insights into the  
95 depositional environment of Rauenberg. These authors documented 302 identified taxa of  
micro- and macrofossils. Of these, 207 are marine, the rest being terrestrial forms from the  
nearby hinterland. The marine plants and animals thrived in a fully marine, moderately  
shallow, low-energy tropical to subtropical sea area. Organic productivity in this  
palaeoenvironment was generally high, with occasional episodes of seafloor anoxia. Warm  
100 and frost-free (but winter-dry) conditions prevailed on land. The marine vertebrate fauna is  
typically Paratethyan, while the invertebrate fauna shows connectivity to the North Sea.

### **Systematic Palaeontology**

Subclass **Cirripedia** Burmeister, 1834

105 Superorder **Thoracica** Darwin, 1854

Order **Balanomorpha** Pilsbry, 1916 (= Order Sessilia Lamarck, 1818, sensu Buckeridge &  
Newman, 2006)

Infraorder **Neobalaniformes** Gale (sensu Kočí et al. 2017, to accommodate  
Neobalanomorpha Gale in Gale and Sørensen, 2015)

110 Superfamily **Coronuloidea** Leach, 1817

Family **Chelonibiidae** Pilsbry, 1916

Subfamily **Protochelonibiinae** Harzhauser & Newman in Harzhauser et al., 2011

Genus ***Protochelonibia*** Harzhauser & Newman in Harzhauser et al., 2011

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***Protochelonibia melleni*** (Zullo, 1982)

Figures 2, 3

*Chelonibia melleni* new species: Zullo 1982, p. 3, pl. 1, figs. 1-13

120 *Protochelonibia melleni* (Zullo, 1982): Collareta and Newman 2020, p. 179, fig. 1a (right corner)

balanid colony consisting of two individuals: Maxwell et al. 2016, p. 245 (caption), fig. 4E

*Referred material.* SMNK-PAL-7352, two adjacent incomplete shells stored at Staatliches  
125 Museum für Naturkunde Karlsruhe (= SMNK).

*Occurrence.* Abandoned Unterfeld claypit near Rauenberg (formerly Frauenweiler–  
Wiesloch), Early Oligocene (Rupelian), Calcareous Nannoplankton Zone NP23, European  
Mammal Zone MP22-23.

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*Description and comparisons.* The colony consists of two clustering specimens that lack  
conspicuous portions of the outer wall. Both shells are dorsoventrally compressed and locally  
fractured, their outer wall being invariantly abraded.

The largest specimen includes the well-preserved rostral complex (rostrum plus  
135 rostrolatera = RL-R-RL) and right carinolatus<sup>1</sup> (= CL<sup>1</sup>), plus parts of the outer wall of the left  
carinolatus<sup>1</sup> and right carinolatus<sup>2</sup> (= CL<sup>2</sup>). Parts of the sheath (including what appears to be  
the sheath portion of the left CL<sup>2</sup>) are also preserved along with uninformative, heavily  
damaged fragments of the other compartments, possibly including the carina (= C). The  
smaller specimen includes a left carinolatus (CL<sup>1</sup> or CL<sup>2</sup>) plus an adjacent compartment (left  
140 RL or CL<sup>1</sup>) that directly contacts the other shell's left CL<sup>1</sup>; the heavily damaged inner wall of

the other compartments is also preserved.

In apical view (Fig. 2A, 3A), the largest shell is roughly semicircular in outline, and both specimens are low and broadly peltate. The diameter of the orifice is less than half the basal diameter of the shell. The wide rostral complex of the largest specimen is comprised of three  
145 distinct compartments (i.e., the R and the adjacent left and right RLs) that are broadly triangular and subequal in size; these compartments also display distinct sutures on the external surface (Fig. 2B). All the preserved compartments have broad, triangular to trapezoidal parietes and sunken radii. Where preserved (e.g., on the right RL of the largest shell), the upper margin of the radius runs obliquely above the underlying ala of the adjacent  
150 compartment – that is, the radii are disparietal (Fig. 2C). The external surface of most compartment parietes is broadly abraded, thus disclosing an inner fabric of closely appressed, columnar blocks of shelly material (Fig. 2A, B, 3A), whereas the radii are finely striated transversely (Fig. 2C). The displaced sheath fragments are substantially smooth (Fig. 2A, 3A).

155 The right RL, CL<sup>1</sup> and fragmentary CL<sup>2</sup> of the largest specimen were carefully detached mechanically from the underlying sediment in order to characterise the ventral aspect of the shell (Fig. 3B). The sheath is just slightly dependent and only developed along the upper third or half of the compartments. Its basal edge features no downward projections or prongs. A dense pattern of fine, continuous, internal longitudinal parietal septa emerge below the basal  
160 edge of the sheath; they run radially to reach the shell periphery.

The Rauenberg chelonibiid colony is unambiguously assigned to *Protochelonibia* owing to the observation of a broad tripartite rostral complex rather than a partly fused compound rostrum (Harzhauser et al. 2011). Further supporting this genus-level attribution, SMNK-PAL-7352 resembles *Protochelonibia melleni* and *Protochelonibia submersa* in featuring: 1)

165 a peltate shell morphology; 2) acutely triangular compartment apices; 3) trigonal, rather  
broad radii that are separated from the parietes by sharp angulations; 4) a largely appressed  
sheath that is as long as about one third or half of the paries; and 6) a dense pattern of fine,  
continuous, longitudinal septa running through the inner surface of the outer wall  
(Harzhauser et al. 2011; Collareta and Newman 2020).

170 When Harzhauser & Newman described *P. submersa* (Harzhauser et al. 2011), the  
protochelonibiine affinities of *P. melleni* had not been recognised. Skeletal differences  
between these two species are largely minor (Collareta and Newman 2020), and the new  
German colony of *Protochelonibia* contributes to strengthen this notion. However, we notice  
that the hypodigm of *P. submersa* displays transparietal radii (Harzhauser et al. 2001: figs.  
175 2A, 3A), whereas the type series of *P. melleni* is characterised by disparietal radii (cf.  
diagnosis in Zullo 1982). Considering that the disparietal/transparietal condition of the radii  
is often regarded as species-diagnostic in various lineages of Balanomorpha (e.g., Ross and  
Newman 1996; Prabowo and Yamaguchi 2005; Carriol 2008), SMNK-PAL-7352 is here  
assigned to *P. melleni* on the basis of the observation of disparietal radii.

180 *Protochelonibia melleni* was known so far from the sole type series, which consists of  
isolated compartments only. Therefore, SMNK-PAL-7352 represents the first record of *P.*  
*melleni* since its original description in 1982, as well as the first find of articulated, clustering  
shells of this species.

### 185 **Some overlooked protochelonibiine records from the Oligo-Miocene of Europe**

The discovery of the German colony of *Protochelonibia* fostered a review of palaeontological  
literature that revealed the existence of two additional, overlooked occurrences of this archaic  
chelonibiid genus. Withers (1929) described and figured two chelonibiid fossils from the



Miocene of Europe which he attributed to the extant species *Chelonibia patula* (Ranzani,  
190 1817). These specimens consist respectively of an isolated left carinolateral (Withers 1929:  
pl. 2, figs. 8-10) from Peloua (= Le Péloua), near Soucats (error pro Saucats), France, and an  
isolated carina (Withers 1929: pl. 2, figs. 11, 12) from Kalksburg, near Wien, Austria (Fig. 4).

Withers (1929) regarded the French specimen as Burdigalian and the Austrian one as  
Tortonian. Sediments assigned to the lowermost Burdigalian (ca. 20 Ma) are indeed exposed  
195 at Le Péloua (Cahuzac et al. 1996; Gourinard et al. 1999; Cahuzac and Poignant 2005). The  
Austrian specimen, however, are older than assumed by Withers (1929) and derive from  
middle Badenian deposits, which are correlated with the middle Miocene Langhian stage  
(Harzhauser et al. 2020).

Both these specimens are clearly congeneric of *Protochelonibia submersa* and  
200 *Protochelonibia melleni* in light of the same characters that informed the genus-level  
attribution of the aforementioned German specimens (except for that regarding the tripartite  
rostral complex). With its transparietal radius, the Austrian specimen figured by Withers  
(1929) clearly represents *P. submersa* (Fig. 4). Interpreting the French carina is less  
straightforward, but the sutural surfaces of the radii are not similar to those reported by Zullo  
205 (1982) for the type material of *P. melleni*. Considering also the purported age of the deposits  
that host this specimen, which appears to be close to that of the *P. submersa* stratotype (ca. 22  
Ma according to Gregorova et al. 2009 and Grunert et al. 2010), an attribution of the French  
carina to *P. submersa* seems reasonable.

## 210 **Palaeoecology, functional morphology and evolutionary significance of the Oligo- Miocene *Protochelonibia* species**

The newly identified German colony of *Protochelonibia melleni* demonstrates that, similar to

*Protochelonibia submersa*, this protochelonibiine species attained a low, peltate shell profile (Figs. 2A, 3A). In the widespread extant chelonibiid species *Chelonibia testudinaria*, which  
215 has recently been demonstrated to represent a cluster of morphs (Cheang et al. 2013; Zardus et al. 2014), the low-conical *testudinaria* morph is restricted to the quickly moving sea turtles, whereas the high-conical *patula* morph dwells on slower hosts such as crabs, horseshoe crabs and sea snails, and even on motionless inanimate substrates (Sloan et al. 2014; Collareta and Bianucci 2021). The overall shell morphology of the Oligo-Miocene  
220 species of *Protochelonibia* is thus reminiscent of that displayed by those members of *C. testudinaria* that currently attach onto actively swimming hosts such as sea turtles. Corroborating this morphological inference, Harzhauser et al. (2011) observed surface imprints from the host substratum in one specimen of *P. submersa* that are reminiscent of the sculpture of cheloniid carapacial scutes. Considering also the relatively minor nature of the  
225 skeletal differences observed between *P. melleni* and *P. submersa*, similar lifestyles are expectable for these extinct chelonibiid species. Thus, we feel confident to suggest that both *P. melleni* and *P. submersa* were epizoans on some kind of quickly moving, likely vertebrate hosts.

The German colony of *P. melleni* displays a thoroughly abraded external surface. Acorn  
230 barnacle shells are commonly abraded, especially close to their apex, dehiscence being one of the modalities by which the orifice increases its diameter as the shell grows. Among the living chelonibiids, abrasion is high in *Chelonibia caretta* (Darwin 1854), whose shell is relatively high and not hydrodynamic in outline. In the peltate *P. melleni*, in-vivo abrasion was likely low, hence the often preserved uppermost terminations of the compartments, and  
235 especially, the well-characteristic apex of the rostrum, which is acutely triangular (Harzhauser et al. 2011; Collareta and Newman 2020). Considering also that abrasion seems

to be ubiquitous in SMNK-PAL-7352, it likely occurred post-mortem. Regardless of these considerations, the abraded external surface of the German colony allows for observing that the outer wall of *P. melleni* is comprised of closely appressed, pillar-like blocks of shelly material (Figs. 2A, B, 3A), much like in the *testudinaria* morph of *C. testudinaria*. This is an aspect of the chelonibiid shell that has never been given much attention but by Davis (1972), who commented on the shell architecture of the *testudinaria* morph of *C. testudinaria* as follows:

“A lateral view of the outer lamina shows that it is also ridged and that each ridge terminates at the basal edge as a tooth. [...] In thin section [...], the teeth are represented by dark linear interlaminar figures which represent the centers of calcification of the teeth and of the solid elongate vertical blocks of calcium carbonate to which the teeth give rise. Filets can be seen between adjacent interlaminar figures which represent interfaces between the adjoining blocks. The formation of the structures composing the chelonibiid paries is in marked contrast to the formation of the similarly named structures in the tubiferous Balaninae. [...] In the Chelonibiidae, however, the outer lamina, and longitudinal septa and inner lamina are not discrete entities but are complex structures. The outer lamina is formed compositely of elongate blocks [...]” (Davis 1972: 11-12).

Some pages further on, Davis (1972: 21) presciently linked the outer wall microstructure of the *testudinaria* morph of *C. testudinaria* to that of the whale barnacles (family Coronulidae):

“The structure of the coronulid parietes presents a basic plan. The parietes are composed of an inner lamina connected to the outer lamina by longitudinal septa, forming longitudinal tubes [...]. The longitudinal septa radiate outward from the inner lamina and project below it at the basal edge of the shell where they function as teeth [...]. The outer lamina is formed by the conrescence of the distal edges of the teeth, the secondary result

being the formation of longitudinal tubes. [Note that Davis' inner and outer laminae are to be interpreted as the primary and secondary laminae; see e.g. Collareta et al. 2021.] This contrasts with the teeth of the Chelonibiidae which give rise to solid, elongate, abutting blocks.

265           Although the coronulid laminar complex is different from the outer laminar complex of the chelonibiids, they are essentially similar and may be regarded as homologous. The basic difference between the two is that in the Chelonibiidae the teeth coneresce along their entire length whereas in the Coronulidae only the distal edges coneresce. This results in the formation of a tubed structure with the teeth projecting outward rather than a solid  
270           one with the teeth projecting downward.”

Although Davis (1972) made more detailed observations on the coronuloid outer wall than any cirripedologist before him, his unpublished thesis had little resonance if any. As argued by Collareta et al. (2021), the “elongate vertical blocks” that comprise the outer wall of extant *C. testudinaria* are external parietal septa that grew appressed to each other, thus leaving no  
275           room for any intervening canal. In the early-middle Miocene chelonibiine *Chelonibia zanzibarensis*, these septa are well-spaced from each other and abut outward to form T-shaped flanges, thus defining longitudinal canals in-between them; the latter likely had a role in coring out strings of the host's integument, thus favouring the partial self-burial of the barnacle, as e.g. in *Platylepas hexastylus* (Fabricius, 1798) (Collareta et al. 2021). Relics of  
280           these canals can be found in some extant chelonibiids such as *C. caretta*, a moderately penetrating turtle-dwelling species (Darwin 1854; Pilsbry 1916), and even in the *patula* morph of *C. testudinaria* (Collareta et al. 2021). The Oligo-Miocene species of *Protochelonibia* have low-conical shells, and consequently, they were likely specialised for spreading over the substrate in a way much similar to the living platylepadid species

285 *Platylepas coriacea* Monroe & Limpus, 1979, whose shell is characteristically not embedded  
into the host's tissues (cf. discussion in Collareta et al. 2019). A few compartments of *P.*  
*melleni* display a jagged basal profile (Zullo 1982; Collareta and Newman 2021) that is  
reminiscent of the invaginations and rib-like structures observed at the base of some shells of  
*C. caretta* and the *manati* morph of *C. testudinaria* (a manatee-fouling form; Pilsbry 1916),  
290 thus suggesting a certain degree of penetration into some kind of ductile tissue (Gruvel 1903;  
Monroe 1981); that said, most specimens of *P. melleni* exhibit a regularly rounded periphery  
(Zullo 1982: pl. 1; Fig. 2A, 3A). If *P. melleni* and *P. submersa* mostly adhered superficially  
onto their substrates, managing to develop macroscopic peripheral buttresses and bolsters in  
case of incidental anchoring to relatively soft tissues (as supposed for some specimens of *P.*  
295 *melleni*), this might also correlate with the observation of longitudinally elongated blocks, not  
abutting into T-shaped flanges, running throughout the parietes of the German colony.

Whether the diminutive external longitudinal parietal septa of the Oligo-Miocene species  
of *Protochelonibia* represent an early stage in the evolution of the tubiferous outer wall that is  
typical of the later coronuloids (Collareta et al. 2021) or rather vestigial structures inherited  
300 from a *C. zanzibarensis*-like ancestor (such as hypothesised for the living *testudinaria* morph  
of *C. testudinaria*) cannot be ascertained. On the one hand, the occurrence of a seemingly  
derived coronuloid such as *Emersonius cybosyrinx* in strata as old as the Eocene suggests that  
the key phases of the evolution of shell architecture of the turtle and whale barnacles –  
possibly including the development of longitudinal external parietal septa equipped with T-  
305 shaped flanges and intervening external parietal canals – should be searched for in deposits  
older than the Oligocene. On the other hand, tissue graspers such as of T-shaped flanges only  
appear in the fossil record of Coronuloidea as late as the early or middle Miocene, and the  
peculiar tubiferous outer wall of most coronuloids might have evolved from an ancestral

condition in which some kind of “precursors” of truly abutting longitudinal external parietal  
310 septa were present in form of adjoining columnar blocks of calcium carbonate. Possibly  
supporting an interpretation of the Oligo-Miocene species of *Protochelonibia* as  
representative of the ancestral coronuloid stock, the inner aspect of *P. melleni* and *P.*  
*submersa* features a largely appressed sheath and a dense pattern of fine, continuous, internal  
longitudinal parietal septa that recall the condition observed in some unspecialised, mostly  
315 rock-dwelling balanomorphs (cf. discussion in Zullo 1982). New additions to the fossil record  
of the coronuloids, and especially to the largely fragmentary pre-Pliocene segment of this  
record, are definitively needed for shedding light on this and other crucial aspects of the  
origin and early evolutionary history of the turtle and whale barnacles.

### 320 **General overview of the palaeogeographic and chronostratigraphic distribution of** ***Protochelonibia***

In light of the new and overlooked occurrences of *Protochelonibia* reported herein, the fossil  
history of the protochelonibiines can be summarised as follows.

The oldest records of *Protochelonibia* are Rupelian in age and are assigned to *P. melleni*;  
325 they come from the southern USA and southwestern France (Table 1 and Fig. 4). These finds  
support the notion that the protochelonibiines had acquired a broad distribution as early as in  
Rupelian times, when *P. melleni* occurred in the proto-Gulf of Mexico as well as in the  
Western Paratethys. Such a transatlantic distribution might have been favoured by the fact  
that, during the early Oligocene, the North Atlantic expanse was distinctly narrower  
330 longitudinally than it is today, as well as by *P. melleni* being hosted by some kind of actively  
swimming hosts (see the previous section). Furthermore, given that *Protochelonibia* is the  
sole unquestionable representative of Coronuloidea to be known from Palaeogene strata, and

considering also that the oldest – albeit presumed – coronuloid (namely, *Emersonius cybosyrinx* Ross in Ross and Newman, 1967) also comes from the Gulf region of the USA, 335 the dispersal centre of this superfamily might have been placed in what is currently regarded as the westernmost portion of Tethys (cf. discussion in Collareta and Newman 2020).

The early Miocene finds of *Protochelonibia* conform to *P. submersa*; they come from the Central Paratethys, Central Mediterranean Sea and the Northeastern Atlantic Ocean (Table 1 and Fig. 4). The few data available for the Oligocene and early Miocene protochelonibiines 340 might lead to thinking that *P. melleni* and *P. submersa* comprise a lineage of chronospecies exhibiting little morphological change through time. A single find from the Langhian (Badenian) of the Central Paratethys testifies to the persistence of *P. submersa* as late as in middle Miocene times (Table 1 and Fig. 4).

In Pliocene strata, the protochelonibiines are represented by *Protochelonibia capellinii*, 345 which is known from the sole Central Mediterranean (i.e., Italian) holotype (Table 1 and Fig. 4). While sharing with the Oligo-Miocene species of *Protochelonibia* a distinctly tripartite rostral complex featuring a transversely broad rostrum, *P. capellinii* resembles *Chelonibia testudinaria* in having a dome-shaped shell morphology and a clearly dependent sheath, as well as in the general arrangement of the internal longitudinal parietal septa. These characters 350 evoke some degree of morphological convergence with the coeval chelonibiines, among which members of the living species *C. testudinaria* were already present (De Alessandri 1906; Collareta 2016, 2020). The protochelonibiines did not persist into the Pleistocene, thus eventually leaving *Chelonibia* as the sole representative of Chelonibiidae in the present-day global ocean.

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## Figure captions

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**Fig. 1** Geographic setting of the abandoned Unterfeld claypit near Rauenberg, southwestern Germany. Geographic coordinates: 49°16'14"N; 8°40'22"E

**Fig. 2** SMNK-PAL-7352, colony of *Protochelonibia melleni* (Zullo, 1982) from the Rupelian of southwestern Germany, in apical view. **a** – General view of the colony. **b** – Close-up of the apex of the tripartite rostral complex (note the elongate vertical blocks that comprise the outer wall and the well individualised, acutely triangular rostrum and rostromerals). **c** – Detail of the right rostromeral-carinolateral<sup>1</sup> suture (note the disparietal radius). Figure legend: *al* = ala, *CL*<sup>1</sup> = carinolatus<sup>1</sup>, *rd* = radius, *R* = rostrum, *RL* = rostromerus. Squares in the scale bar have sides of 1 mm each

550 **Fig. 3** SMNK-PAL-7352, colony of *Protochelonibia melleni* (Zullo, 1982) from the Rupelian of southwestern Germany. To improve contrast and highlight detail, the specimen was coated with ammonium chloride, a whitening technique described by Cooper (1935) and Feldman (1989). **a** – General view of the colony in apical view. **b** – Close-up of the ventral view of the right rostromerus, carinolatus<sup>1</sup> and fragmentary carinolatus<sup>2</sup>, in basal view (note the largely appressed sheath and the dense pattern of fine, continuous, longitudinal internal parietal septa). Figure legend: *CL*<sup>1</sup> = carinolatus<sup>1</sup>, *CL*<sup>2</sup> = carinolatus<sup>2</sup>, *R* = rostrum, *RL* = rostromerus

**Fig. 4** Reproduction of the original plate depicting the specimens of *Protochelonibia* Harzhauser & Newman, 2011 described by Withers (1929) under the name *Chelonibia patula* (Ranzani, 1817). Panels 8, 9 and 10 illustrate a lower Miocene French carina (here assigned to *Protochelonibia* cf. *submersa* Harzhauser & Newman, 2011). Panels 11 and 12 illustrate an upper Miocene Austrian carinolatus (here assigned to *Protochelonibia*



*submersa*). Note that the holotype of *Chelonibia solida* Withers, 1929 is also illustrated in panels 5, 6 and 7. A scale bar has been added at the bottom of the plate; this equals 10 mm for panels 11–12, 5 mm for panels 8–10, and 2.5 mm for all other panels. After Withers (1929: pl. 2)

**Fig 5** (Palaeo)geographic and chronostratigraphic distribution of the finds of *Protochelonibia* spp. Figure legend: red stars = occurrences of *Protochelonibia melleni* (Zullo, 1982), yellow stars = occurrences of *Protochelonibia submersa* Harzhauser & Newman, 2011, green stars = occurrences of *Protochelonibia capellinii* (De Alessandri, 1895). The palaeogeographic maps reproduced in the four panels are after Scotese (2014a, b). See Table 1 for distributional data sources

575

Fig. 1



Fig. 2



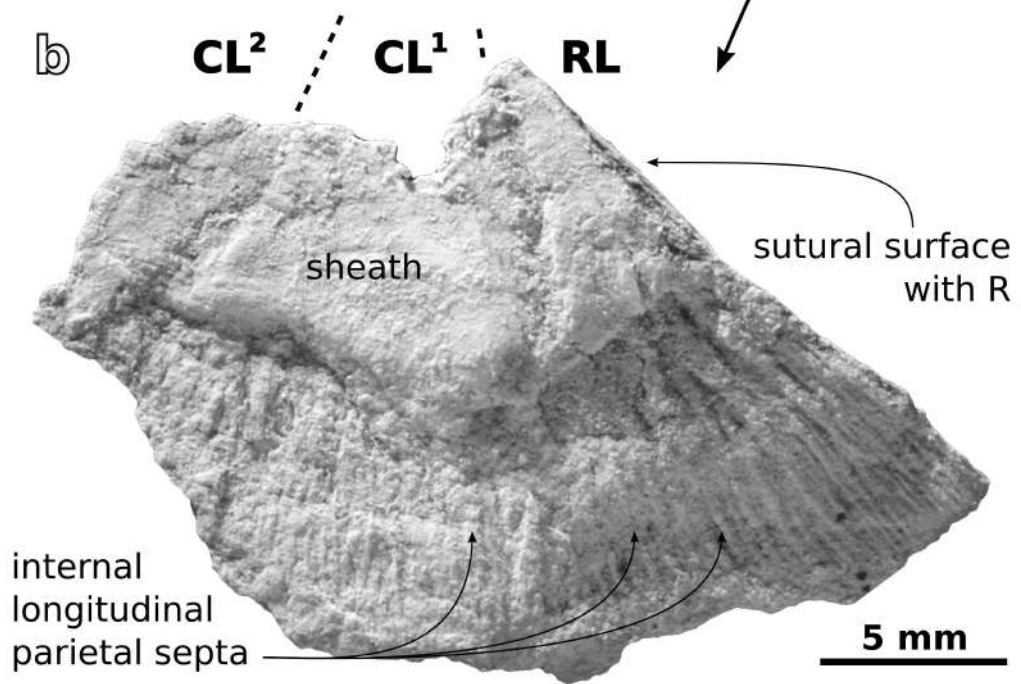
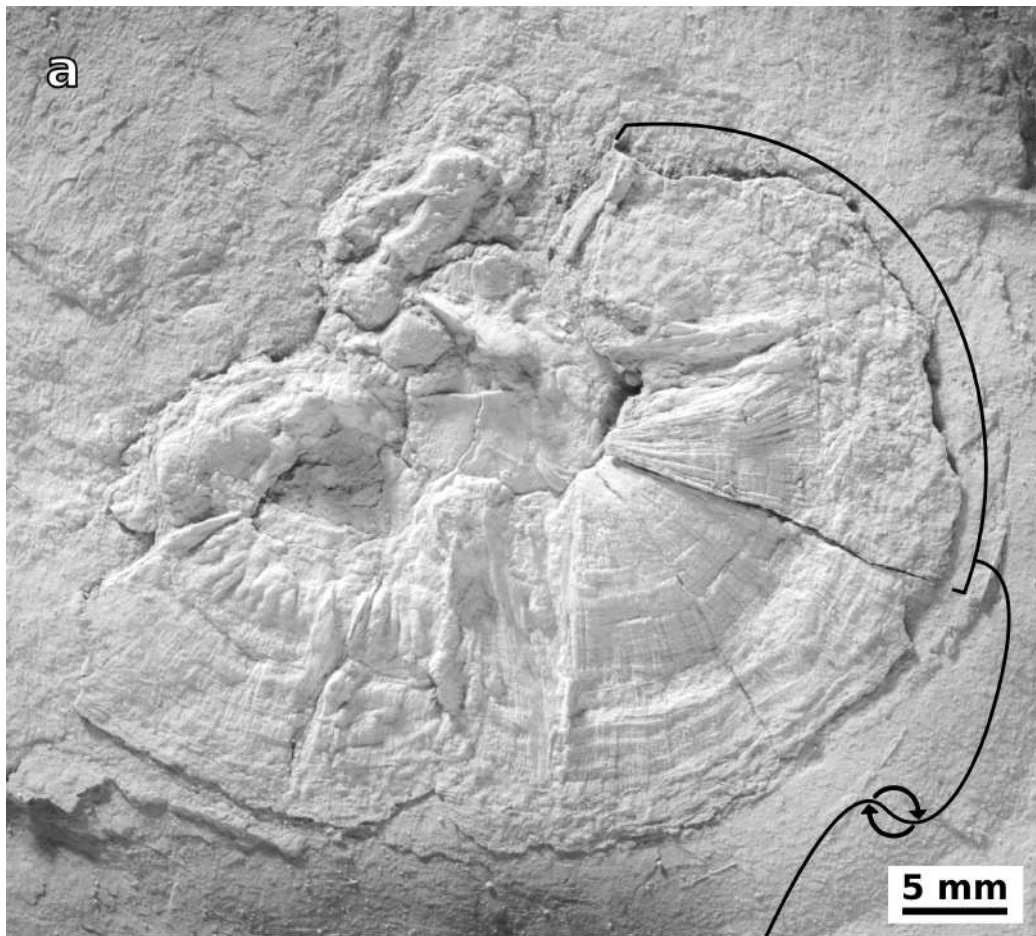


Fig. 4

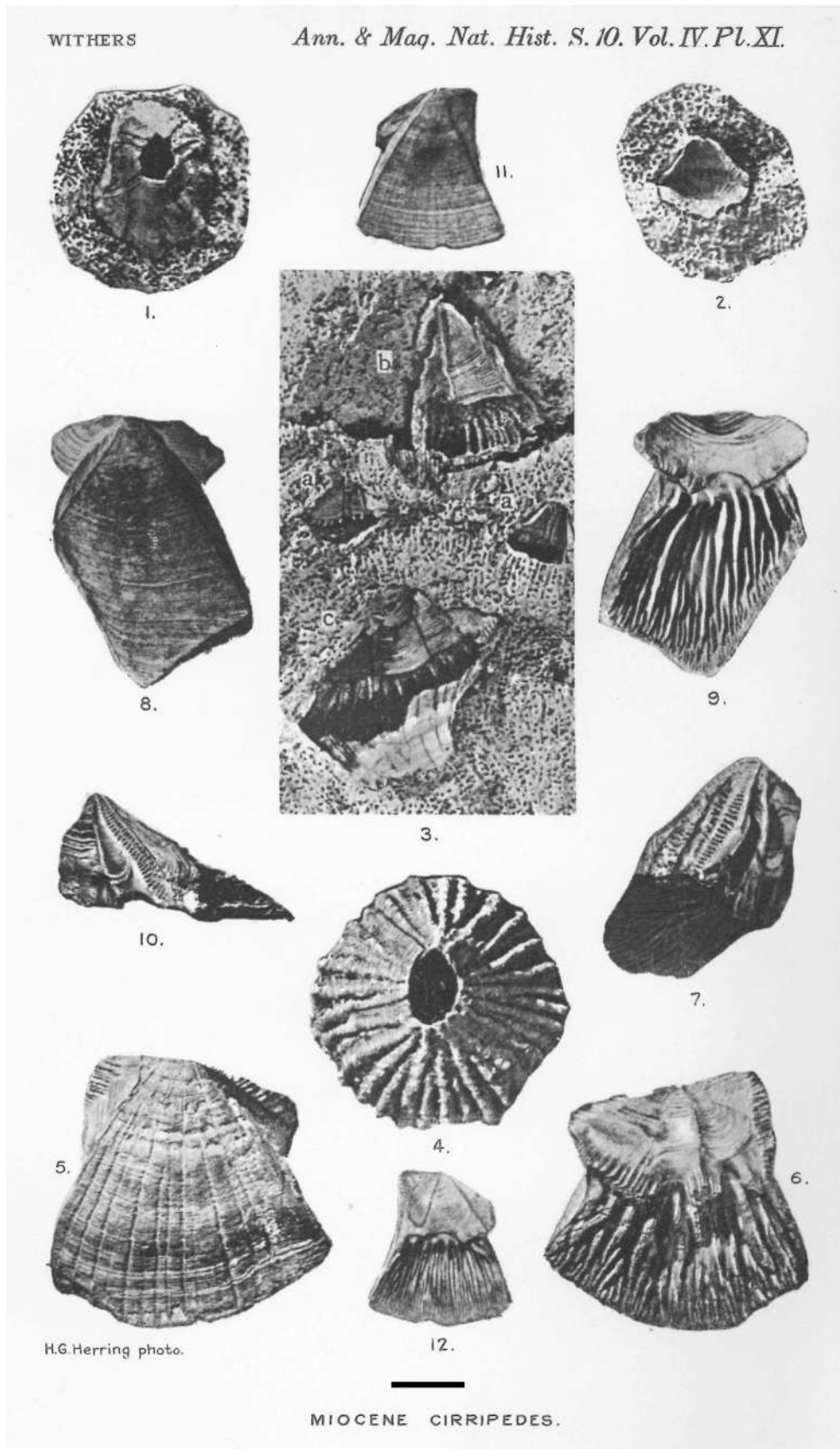
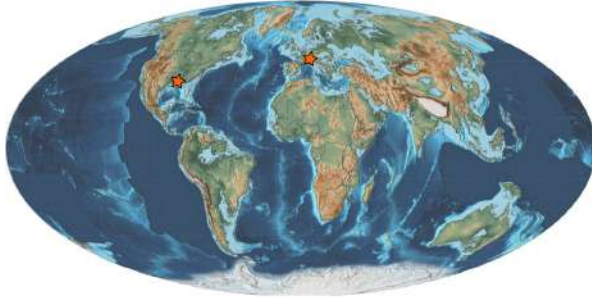
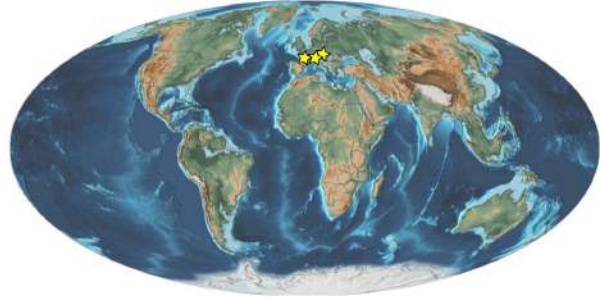


Fig. 5

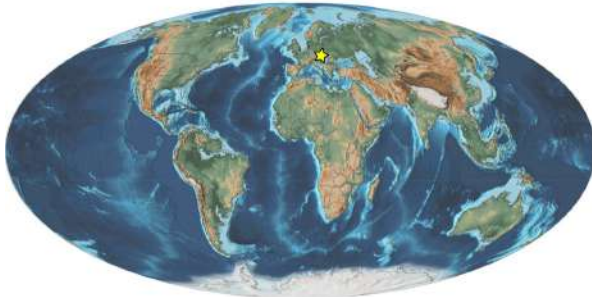
**Late Oligocene**  
(23.03–15.97 Ma)



**Early Miocene**  
(23.03–15.97 Ma)



**Middle Miocene**  
(15.97–11.63 Ma)



**Pliocene**  
(5.33–2.59 Ma)

