

A new Early Miocene barnacle lineage and the roots of sea-turtle fouling Chelonibiidae (Cirripedia, Balanomorpha)

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(Received 6 May 2010; accepted 15 Jul 2010; printed 29 November 2011)

The origin of the mainly sea-turtle fouling balanomorph family Chelonibiidae is still poorly documented. Aside from an Eocene erratic specimen assigned to an extinct subfamily, the extant subfamily Chelonibiinae did not appear in the fossil record before the Late Miocene. Protochelonibiinae Harzhauser & Newman subfam. nov. is here introduced as an extinct sister-group of Chelonibiinae. The subfamily is known so far only from the proto-Mediterranean and the Paratethys seas and ranged from Early Miocene to Late Pliocene. Members of the subfamily are characterized by large walls with tripartite rostra which display distinct sutures on the external surface. The tripartite rostrum, however, has evolved independently several times in the evolution of the balanomorphs and cannot be treated as synapomorphy. The subfamily comprises one new genus and two species. *Protochelonibia* Harzhauser & Newman gen. nov. is the type genus of Protochelonibiinae and *Protochelonibia submersa* Harzhauser & Newman sp. nov. is introduced as type species of this genus. *Chelonobia Capellinii* [sic] De Alessandri, 1895, from the Late Pliocene of Italy, reassigned as *Protochelonibia capellinii* (De Alessandri, 1895), is the youngest record of the subfamily. With the onset of the Pleistocene, Protochelonibiinae were fully replaced by Chelonibiinae, which had co-existed with Protochelonibiinae from the Late Miocene to the Pliocene. Surface imprints from the host substratum in one specimen of *P. submersa* are reminiscent of the sculpture of *Caretta* carapaces. Therefore, the Aquitanian *Protochelonibia* may be the earliest record of sea-turtle fouling in barnacles.

Keywords: Chelonibiidae; Balanoidea; epibionts; sea-turtles; Paratethys Sea; Miocene.

Introduction

The geological evidence for the phylogeny of sessile barnacles comes predominately from intertidal and shallow sublittoral records (Radwanska & Radwanski 2008). Especially in central Europe, in the area of the former Paratethys Sea, Oligocene and Miocene balanids from shallow marine deposits have been reported by Kolosvary (1955), Davadie (1963), Baluk & Radwanski (1967), Zullo (1992) and Wöhrer (1998). Numerous species of balanoid genera such as *Acasta*, *Concavus*, *Perforatus* and *Balanus* have been described. This wealth of data contrasts with the extremely poor knowledge of open marine taxa which obligatorily cling to free-swimming animals such as gars, cetaceans, sirenians, turtles and even sea snakes (Ross & Newman 1967). This group is mainly represented by members of the coronuloid barnacles (chelonibiids, platylepadids and coronulids: Seilacher 2005; Ross & Frick 2007). The oldest record of coronuloids is believed, on the basis of a single specialized rostrum, to be from the Late Eocene with the occurrence of the specialized *Emersonius* Ross (in Ross & Newman 1967) from Florida.

The fossil record of *Chelonibia* Leach, 1817 ranges back only to the Miocene (Buckeridge 1995), although separation of the *Chelonibia*-clade from other balanomorphs by the Early Palaeogene is indicated by palaeontological extrapolation and molecular data (Newman *et al.* 1969; Pérez-Losada *et al.* 2008). Reliable records of the cetacean-affiliated *Coronula* Lamarck, 1802 do not extend below the Late Miocene (Buckeridge 1995; Bianucci *et al.* 2006). All other genera of coronuloid barnacles, such as *Cetolepas* Zullo, 1969 and *Platylepas* Gray, 1825, do not appear before the Plio-Pleistocene in the fossil record (Buckeridge 1995). Taphonomic bias in this group is thus much greater than for intertidal taxa. Occurrences are usually bound to deep-water deposits and serendipitous findings. Balanomorph accumulations formed by winnowing or due to gregarious occurrences so typical of shallow water settings, are completely missing in the deep marine settings. Moreover, specimens and colonies are usually detached from their former hosts and therefore, the origin and development of host-specific fouling by balanomorphs is poorly documented.

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Geological setting, stratigraphy and palaeoenvironment

The balanomorph colony depicted here is from a temporary outcrop exposed during the construction of a hydropower plant in the vicinity of the small town of Pucking in Upper Austria (N 48° 12' 22"; E 14° 13' 27") (Fig. 1). The grey pelitic deposits are part of the Ebelsberg Formation (Krenmayr & Schnabel 2006) and belong to the North Alpine Foreland Basin fill. According to the regional system, the deposits are part of the upper Egerian stage (Piller *et al.* 2007). The laminated silty clays are dated as Aquitanian (Nannoplankton Zone NN2) and are *c.* 22 Ma (Gregorova *et al.* 2009; Grunert *et al.* 2010).

The section contains a spectacular 'Konservat Lagerstätte' which is described in detail by Grunert *et al.* (2010). According to these authors, the area was part of the outer shelf of the Paratethys Sea. Intense upwelling and episodically increased freshwater influx provided nutrients, stimulating primary productivity. These phases are reflected by pteropod and calcareous nannoplankton blooms. Vertebrates are documented by mass occurrences of fish such as hake and mackerel, along with huge sunfishes and rare dolphins. In addition, littoral algae and shallow water pipe-fishes were transported into the offshore environment by storm events. Bottom waters were dysoxic-anoxic and developed in the upper oxygen minimum zone. Consequently, benthic molluscs are scarce and show low diversity. They mainly consist of lucinid bivalves adapted to anoxic environments. Driftwood falls are also frequent. These are indicated by lignitified wood with algae, mytilid bivalves and stalked barnacles (Harzhauser & Schlögl in press). Within this setting, the balanomorph colony described here can only have occurred on an actively swimming or pelagic organism.

Systematic palaeontology

Abbreviations

NHMW: Natural History Museum Vienna; R: rostrum; RL: rostrulatus; CL: carinolatus; L: latus; C: carina; IP: imbricating plate.

- Class **Thecostraca** Gruvel, 1905
- Subclass **Cirripedia** Burmeister, 1834
- Superorder **Thoracica** Darwin, 1854
- Order **Sessilia** Lamarck, 1818
- Suborder **Balanomorpha** Pilsbry, 1916
- Superfamily **Coronuloidea** Leach, 1817
- Family **Chelonibiidae** Pilsbry, 1916
- (nom. transl. Newman 1996 [ex Chelonibiinae Pilsbry, 1916, p. 262])

Type genus. *Chelonibia* Leach, 1817, p. 68, by original designation of Pilsbry (1916, p. 262).

Definition. Wall eight-plated (R-RL-CL1-CL2-C), rostrum tripartite, or wall six-plated (R-CL1-CL2-C), rostrum totally concrescent (compound); wall bi- or multilamellar, parietes and dependent sheath separated by longitudinal and sometimes transverse septa forming internal canals or spaces (parietes not forming external T-shaped flanges and canals as in coronulids), radii moderately to well developed; opercular plates always present but not filling orifice, apertural (formerly 'opercular' or 'oral') hood absent.

Subfamily **Chelonibiinae** Pilsbry, 1916

Type genus. As for family

Definition. Rostrum tripartite, with sutures visible internally and at least apically externally; R widening little after initial growth and thereby, in remaining narrow compared to RLs, contributing little to diametric growth; bilamellar wall with longitudinal canals and spaces between longitudinal ribs partially to almost completely filled with age.

†Subfamily **Emersoniinae** Ross in Ross & Newman, 1967 (Emersoniinae [sic] Ross in Ross & Newman, 1967, p. 7)

Type genus. †*Emersonius* Ross in Ross & Newman, 1967, p. 7, by original designation.

Definition. Wall presumably six-plated (R-CL1-CL2-C); multi-lamellar (traversed by vertical and horizontal lamella in addition to longitudinal septa, forming box-like cells); known from a single compound R.

†Subfamily **Protochelonibiinae** Harzhauser & Newman subfam. nov.

Type genus. †*Protochelonibia* Harzhauser & Newman sp. nov.

Definition. Wall eight-plated (R-RL-CL1-CL2-C), R tripartite, sutures distinctly visible externally, widening along with RLs during growth and thus continuing to contribute to diametric growth.

†Genus **Protochelonibia** Harzhauser & Newman gen. nov.

Type species. *Protochelonibia submersa* Harzhauser & Newman sp. nov.

Diagnosis. Large shells consisting of eight plates (R-RL-CL1-CL2-C) of which three (RL-R-RL) form a rostral complex with externally visible sutures. The triangular outline of the rostrum is retained throughout life and widens appreciably during ontogeny. Surface nearly smooth except for growth lines and delicate radial threads. Interior surface covered with a dense pattern of longitudinal septa or ribs. Bilamellar section of wall (formed by dependent sheath)

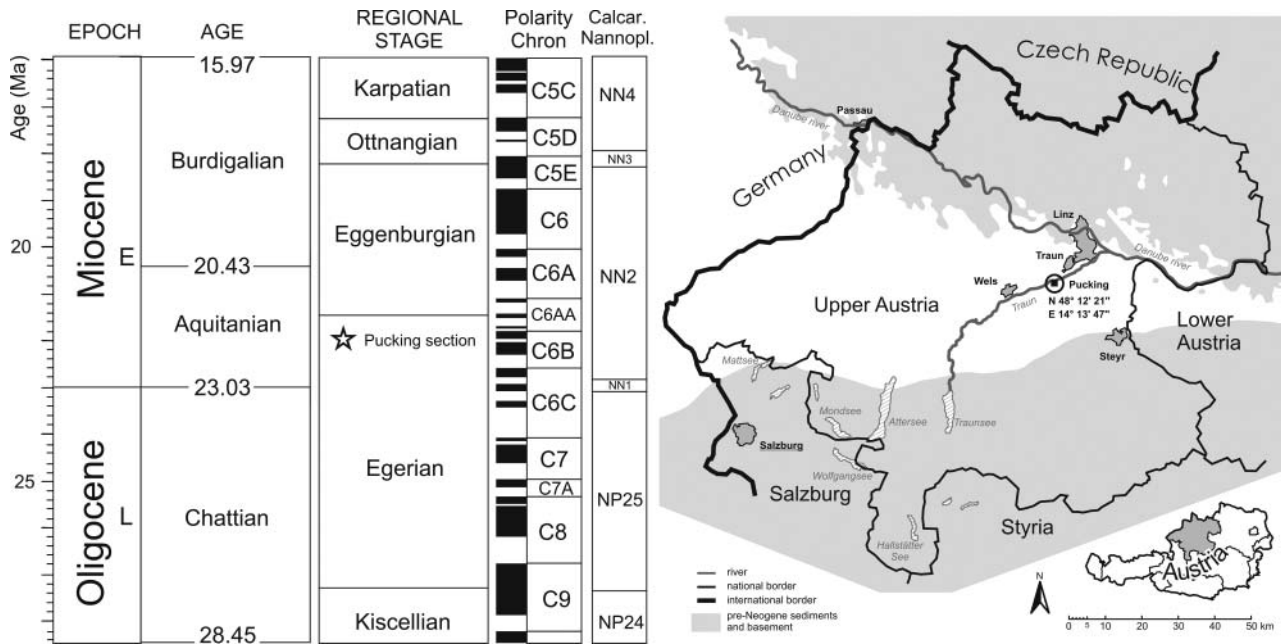


Figure 1. Geographical and stratigraphical position of the Pucking section, after Gregorova *et al.* (2009), Grunert *et al.* (2010) and Piller *et al.* (2007).

approximately half as long as unilaminar section (outer lamina and ribs). Trigonal, moderately broad radii and alae separated from the parietes by sharp angulations. Basis membranous.

Protochelonibia submersa Harzhauser & Newman sp.
nov.
(Figs 2–5B)

Material. Holotype: NHMW 2003z0026/0662a (specimen A in Fig. 2). Paratype: NHMW 2003z0026/0662b (specimen B in Fig. 2).

Etymology. *Submersa*, perfect passive participle of *submergo* (to sink).

Diagnosis. As for genus, with depressed shell and relatively small, elongate and simple scutum without marked articular ridge and without significant muscle pits.

Size. Maximum diameter of colony 88 mm; maximum diameter of holotype (deformed by compaction) 62 mm, and height of rostromerid 30 mm; maximum diameter of paratype 41 mm.

Age. Early Miocene, Aquitanian, (= late Egerian); Nannoplankton Zone NN2 (Gregorova *et al.* 2009; Grunert *et al.* 2010).

Description. The colony consists of six specimens. Of these, only specimen A displays all plates and is chosen

as holotype. The shell consists of eight plates of which the rostrum and the rostromerids (RL-R-RL) are semi-fused to form a tripartite rostrum. The paries of R has an apical angle of *c.* 28° and of the RLs *c.* 30 and 36° respectively. The summits of the RLs and CLs are essentially parallel to the base (transparietal). Their surface is smooth except for a dense pattern of growth lines crossed by very delicate densely spaced radial threads. The upturned growth lines grade into weak ridges on the radii where their terminations form a slightly serrated margin. The apical angles of the parietes of the broad CLs are *c.* 50–110°. Each bears a radius and an ala. What can be seen of the alae includes their separation from the paries by a steep depression on to a moderately wide, flat surface bearing straight growth lines. Carina slightly more convex than other plates, its parietes with angles of *c.* 60–70°; alae similar to those of the other plates.

The interior of the plates is covered by a very dense pattern of primary, secondary and tertiary longitudinal septa. Of these, the tertiary ones appear only in the basal quarter of the plates. No transverse elements are developed. Bilamellar section of wall, formed by the dependent sheath, is approximately half as long as unilaminar section. It forms a row of longitudinal canals between it and the paries, much as in *Chelonibia patula*. Surface of sheath smooth, except for weak concentric growth lines. Basis membranous, no calcareous layer developed.

A small and slender scutum is preserved in specimen D. Only the interior surface is accessible and the apical part is damaged. The maximum length of the restored scutum

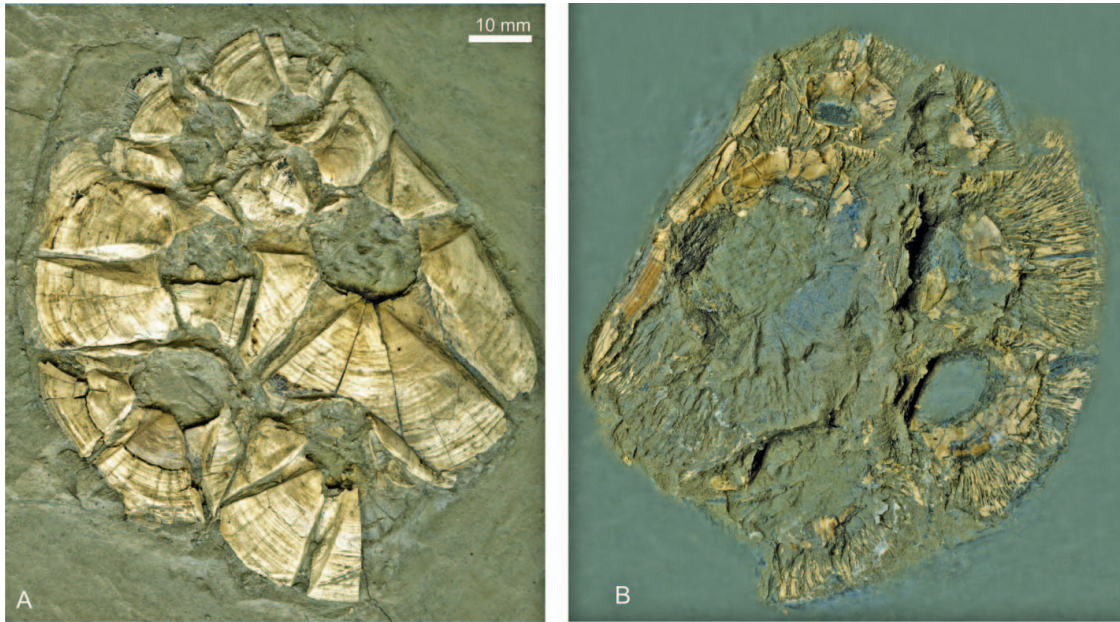


Figure 2. Colony of *Protochelonibia submersa* Harzhauser & Newman sp. nov. consisting of six specimens. **A**, apical view; **B**, basal view.

(Fig. 4) is around 8.5 mm and the maximum width 3 mm. The straight occludent margin forms a weak ridge and a flat-sided edge which bears several oblique ridges and grooves. Basal margin weakly convex and long, grading gently into the shorter and less convex tergal margin. The tergal margin is adjoined by a simple, low articular ridge which

increases in strength towards the apex. No muscle pits are developed.

Remarks. The closest relative is a species from the Late Pliocene of Orciano in Italy which was described by De Alessandri (1895, 1906) as *Chelonobia* [sic] *Capellinii*

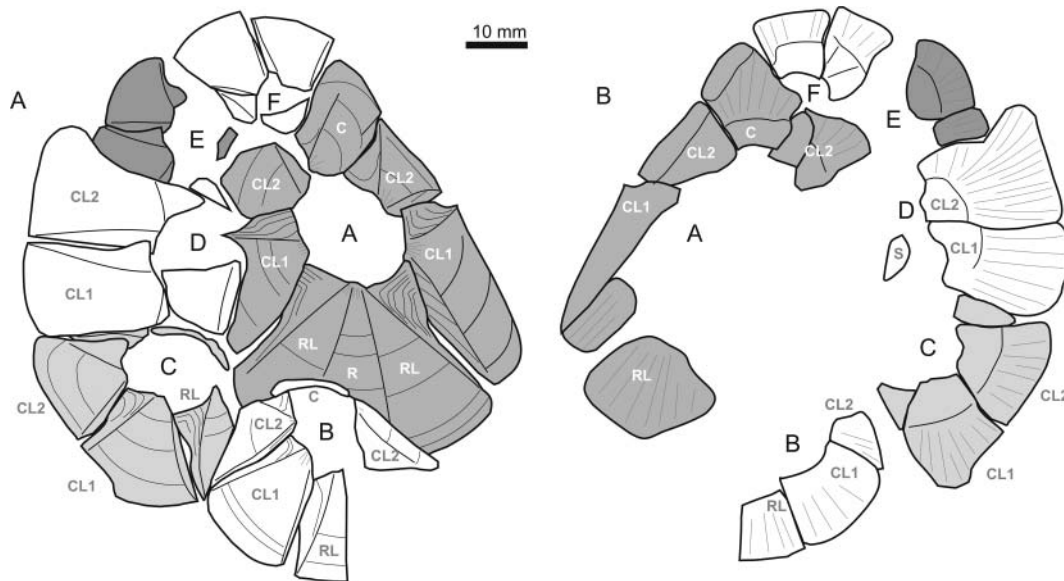


Figure 3. Line drawings of *Protochelonibia submersa* Harzhauser & Newman sp. nov., as shown in Fig. 2. Specimens A–F are indicated in different shades of grey in apical (**A**) and basal (**B**) views. Specimen A is the holotype (NHMW 2003z0026/0662a) and specimen B the paratype (NHMW 2003z0026/0662b). Abbreviations: R: rostrum; RL: rostro-lateral; C: carina; CL: carino-lateral, CL2 by replication of CL1; S: scutum.

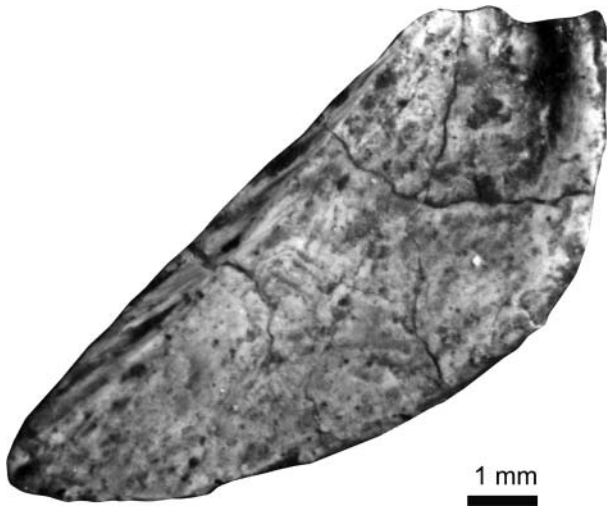


Figure 4. Interior view of the scutum of *Protochelonibia submersa* Harzhauser & Newman sp. nov., specimen D; indicated also in Fig. 2B.

[sic]. It is reassigned here as *Protochelonibia capellini* (De Alessandri, 1895). Despite the similar tripartite rostra of the Early Miocene species and Pliocene Italian forms, there are several features which justify a separation on the species level. These include a high rather than depressed profile, an orderly rather than disorderly arrangement of secondary and tertiary internal ribs, and weak radial furrows and threads on the parietes of the Pliocene species. De

Alessandri (1906) also mentioned an Early Miocene plate from the Burdigalian Termofourâ Formation of the Turin Mountains, which he assigned to *Chelonibia capellini*. This isolated plate has a smooth surface and a sheath that is separated from the septa and might rather represent the coeval *Protochelonibia submersa*.

Another plate consisting of a fused rostrum with rostro-laterals from the Late Miocene of Gran Canaria was described by Rothpletz & Simonelli (1890) as *Chenolobia* [sic] *hemisphaerica*. It is clearly distinguished from *Protochelonibia submersa* by its convex shape, the narrow and short alae and the sheath which covers half of the plate. The species from Gran Canaria is treated herein as *Chelonibia hemisphaerica* (Rothpletz & Simonelli, 1890). *Chelonibia? duvergieri* De Alessandri, 1922 from the Burdigalian of France develops a very similar interior sculpture, with numerous septa and a sheath that covers about one half of the inner side of the parietes, but differs from the new species in its much smaller size and the rugose outer surface.

The new genus *Protochelonibia* possesses eight parietal plates, a feature which has been considered plesiomorphic since Darwin (1854), and which is typically found in members of the pachylasmatids, chthamalids and chelonibiids (Krüger 1940; Newman & Ross 1976), and the archaeobalanids (Buckeridge 1983, 1995). As far as chelonibiids are concerned, an important feature is the retention of the triangular outline of the rostrum of *Protochelonibia* throughout life.

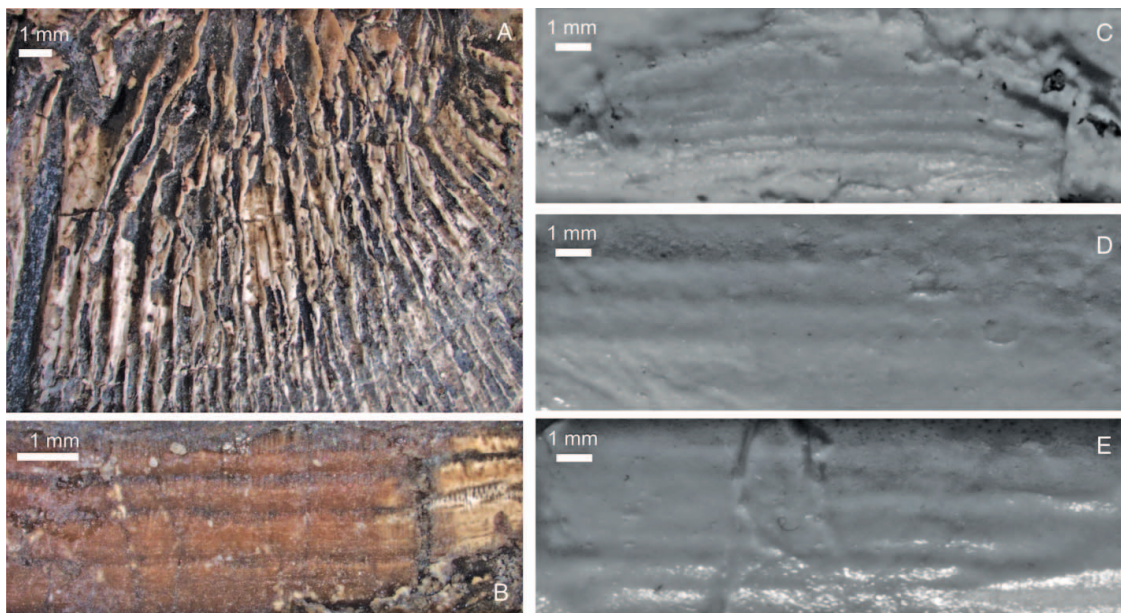


Figure 5. *Protochelonibia submersa* Harzhauser & Newman sp. nov. **A**, interior view of the carino-lateral CL2 of specimen D showing the longitudinal ribs or septa; **B**, imprint of a straight object against which CL1 of specimen A abutted; **C**, silicone mould of the imprint shown in Fig. 5B; **D**, **E**, silicone moulds of the surface sculpture of the carapace area above the ribs of two extant *Caretta* from the collection of the NHMW.

The subfamily Chelonibiinae presently includes 12 species-group taxa, and these can be divided into three species groups. The transfer of *Chelonibia capellini* De Alessandri, 1895 to the new genus *Protochelonibia* reduces the number of species groups within *Chelonibia* to two: those of *Chelonibia patula* (Ranzani, 1818) and *Chelonibia testudinaria* (Linnaeus, 1758). The former is more closely related to *C. manati* (Gravel, 1903) *sensu lato* than to the latter and therefore its group could readily be given generic status. However, while such a revision would likely prove acceptable, it is beyond the scope of the present paper. On the other hand, *Protochelonibia* stands well apart from members of Chelonibiinae and Emersoniinae by virtue of its rostrum being not only triangular but free of the rostralaterals, and by its longitudinal septa forming disorderly rather than orderly radial basal ribs. In fact, *Protochelonibia* could be ancestral to both subfamilies, and therefore we propose that *P. submersa* and *P. capellini* are recognized as representing a subfamily of their own.

Distribution. Known so far only from the Early Miocene (Aquitanean) of the North Alpine Foreland Basin, which was part of the Paratethys Sea. A further record from the Burdigalian of the proto-Mediterranean Sea might be represented by an isolated plate from the Turin Mountains.

Multiple origins of tripartite and compound rostra

The most primitive known balanomorph, the extant *Eochionelasmus* Yamaguchi & Newman, 1990, has a six-plated wall consisting of the rostrum, paired rostro-laterals and carino-laterals, and the carina plus numerous whorls of imbricating plates (R-RL-CL-C+IPs). This configuration was derived from the brachylepdomorph wall, R-C+IPs (Newman 1987; Newman & Yamaguchi 1995), by transfer of a pair of CLs and subsequently of RLs from the imbricating whorls to the primary wall. There must have been an intermediate configuration, R-CL-C+IPs, which has not yet been found in the fossil record. Once the RLs were transferred from the imbricating whorls to the primary wall, the order in which the whorls of imbricating plates were added could be reversed from their junction with the primary wall, as in brachylepdomorphs, to the basal margin contacting the substratum, as in balanomorphs such as *Eochionelasmus* (Yamaguchi & Newman 1990; Newman & Yamaguchi 1995).

This basal six-plated configuration (R-RL-CL-C+IPs) gave way to an eight-plated wall (R-RL-CL1-CL2-C+IPs) by the addition of the second pair of carino-laterals (CL2), not by transfer of imbricating plates to the primary wall, but by replication of the CL1s, a process that persists in the ontogeny of higher balanomorphs (cf. Costlow &

Bookhout 1956; Yamaguchi & Newman 1990). This eight-plated configuration is seen in *Waikalasma* Buckeridge, 1983 (cf. Buckeridge & Newman 1992) and *Catophragmus sensu lato* (Darwin 1854; Buckeridge 1995; Ross & Newman 2001). Instructively, while the RLs were transferred to the wall before the replication of the CLs, they did not become fully integrated; that is, they were not incorporated into the sheath until the *Catophragmus* level of organization was achieved.

The eight-plated configuration without imbricating whorls underwent various reductions to six, four and even one plate (Newman & Ross 1976; Ross & Newman 1996, 2001). The first step in reduction involved the 'rostral complex' consisting of the rostrum flanked by the rostralaterals (RL-R-RL). The parietes of the most primitive balanomorphs lack radii, and so if the wall plates diverge with growth, the alae of the rostrum are exposed. However, if for some reason the parietes do not diverge with growth, as is the case with the rostral complex in *Protochelonibia*, then the parietes of rostro-laterals about the paries of the rostrum and thereby conceal the rostral alae. In the present case, the sutures are still visible and the complex is referred to as a tripartite rostrum. It does not become a compound rostrum until no trace of the sutures is to be seen.

Tripartite and compound rostra first appear in the pachylasmatines, a sister group of the chelonibiines. A clear difference between these groups is the presence of radii in chelonibiines. The eight-plated ancestors of the pachylasmatines also gave rise to the chthamaloids and they too develop compound rostra in higher forms. The former also gave rise to the balanoids which also include an eight-plated form, *Palaeobalanus* Buckeridge, 1983, albeit its rostrum is nearly compound. Thus it appears the rostral complex gave rise to compound rostra, by way of a tripartite rostrum, several times in the evolution of the balanomorphs.

The earliest hint of sea-turtle fouling in barnacles?

The oldest records of the family of the Chelonibiidae range back to the Eocene (Ross & Newman 1967) and first true *Chelonibia* appear in Miocene strata (Buckeridge 1995). Nevertheless, nothing is known about the preferred substratum of these early chelonibiid species. Modern species of this family are mainly attached to sea-turtles, although other substrata such as blue crabs have been documented (Williams & Porter 1964). No fossil chelonibiids still attached to their host substratum are known to the authors. Due to the membranous base, no traces of the host are usually preserved on isolated colonies or plates. Therefore, the moment when chelonibiids started to choose sea turtles as favoured substrata remains enigmatic but the

newly described colony may be a hint to at least an Early Miocene starting point.

The colony of *Protochelonibia* must have been attached to a free-swimming or pelagic object because, due to the anoxic bottom conditions, an attachment to benthic organisms such as decapods or molluscs can be ruled out. An interesting feature of the colony is a straight line along the right side of specimen A. This indicates growth along a solid straight structure which caused a significant angular deformation largely of CL2. This structure is also documented in basal view: three plates trace the surface of the object to which the colony was attached (Fig. 5B, C). The preserved part suggests a surface consisting of several low, slightly wavy ridges of *c.* 0.2 mm width with rounded backs which are separated by shallow grooves of *c.* 0.3 mm width. This sculpture cannot be clearly identified. A comparison with modern Cheloniidae, however, revealed a similar sculpture on the carapace of *Caretta* along the ribs where low and narrow longitudinal threads occur (Fig. 5D, E). The dimensions are not fully identical as the ribs of modern *Caretta* are generally slightly broader and larger. Nevertheless, the occurrence of such structures in sea-turtles may support the hypothesis that *Protochelonibia submersa* was attached to a cheloniid turtle. A potential host of the chelonibiids might have been *Trachyaspis lardy* Meyer, 1843. This was a widespread sea-turtle species in the Miocene of the Mediterranean and the Paratethys seas that developed narrow longitudinal threads on its carapace (Chesi *et al.* 2007). Unfortunately, the sculpture of the organic scutes of *Trachyaspis* is poorly known and an attribution of the imprints to *Trachyaspis* remains hypothetical.

Conclusions

Protochelonibia submersa is the earliest representative of the chelonibiid subfamily Protochelonibiinae, if not the Chelonibiidae. It appeared during the Early Miocene in the European Paratethys Sea and probably also the proto-Mediterranean Sea where it persisted into the Late Pliocene. Morphologically, the newly described subfamily is closely related to Chelonibiinae, which are the dominant sea-turtle fouling barnacles in modern oceans. Protochelonibiinae differ from Chelonibiinae in their triangular rostrum with distinct sutures on the external wall that contributes to diametric growth throughout life.

The sculpture of the host substratum is preserved as imprints along the carino laterals of one specimen. Although the pattern of ridges and furrows cannot be identified with certainty, the similarities with the sculpture of the carapace of modern *Caretta* and fossil *Trachyaspis* suggest that *Protochelonibia submersa* is the earliest record of sea-turtle fouling in balanids. The co-existence of members of both subfamilies during the Miocene and Pliocene docu-

ments a higher diversity of chelonibiids in pre-Pleistocene times and indicates that Chelonibiinae were able to outcompete their supposed sister-group with the onset of the glacial cycles.

Acknowledgements

We thank Peter Dworschak and Richard Gemel (both NHMW) for help with literature and for providing access to modern Cheloniidae. The constructive reviews of John Buckeridge (RMIT University, Melbourne) and Michael Frick (Caretta Research Project, Georgia) helped to improve the quality of the paper.

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