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Cranial anatomy and holotype reconstruction of the Late Cretaceous turtle, *Australobaena chilensis* from the Quiriquina Formation, Chile

HANS-VOLKER KARL[1], AMTYAZ SAFI[2,*] & GOTTFRIED TICHY[3]
[1]*Department of Prehistory and Early History, Friedrich Schiller University, Löbdergraben 24a, Jena 07743, Germany*
[2]*Department of Zoology (Wildlife Section), University of Karachi 75270, Pakistan*
[3]*Department of Geography and Geology, Paris Lodron University of Salzburg, Hellbrunnerstrasse 34, 5020, Austria*
hvkarl@icloud.com; https://orcid.org/0000-0003-1924-522X
amtyaz.safi@gmail.com; https://orcid.org/0000-0002-4484-3224
schnuefferl@gmx.at
**Corresponding author: amtyaz.safi@gmail.com*

Abstract

Resolving the phylogeny of fossil turtles is uniquely challenging given the high potential for the unification of convergent lineages due to systematic homoplasy. Equivocal reconstructions of turtle evolution and biogeographic or palaeo-climatic data with phylogenetic hypotheses and new images of the holotype reconstructions of fossil turtles are important for prehistoric turtle fossil remains. Here we describe the cranial anatomy and holotype reconstruction of the Late Cretaceous turtle, *Australobaena chilensis* from the Quiriquina Formation of the Maastricht Ocean Horizon Chile, which was identified as a new genus and species of Baenidae (an extinct family of para-cryptodiran turtles) in 2002 by Karl and Tichy. The holotype is "SMF R 415", a partially destroyed skull without a lower jaw, and with a unique cranial plane. This taxon belongs to Baenidae, an extinct freshwater family from the Cretaceous period in North America. This is the first baenid fossil found outside of North America, and we re-describe and reconstruct it with new photographs and illustrations of the cranial anatomy of this material (Holotype).

Keywords: *Australobaena chilensis*, Cranial anatomy, Maastrichtian, Quiriquina Formation

Introduction

The first fossil turtle recorded from the latest Triassic was approximately 230 Ma (Rhodin *et al*., 2021), and while they have subsequently diversified and evolved, the general turtle Bauplan has remained remarkably constant. Their unique anatomical adaptations have allowed turtles to be quite evolutionary successful, even surviving the Cretaceous-Paleogene (K-Pg) mass extinction event that wiped out the non-avian dinosaurs (Smith & Laitman, 2023). Testudinata (turtles) as a clade have highly unusual, and therefore intrinsically fascinating, anatomy. From their iconic shell to a scapula that resides inside the equivalent of their ribcage to a lack of a muscular partition separating the thorax and abdomen, turtle anatomy is inherently remarkable (Smith & Laitman, 2023). The abundant record of marine turtles from the Late Cretaceous contrasts with the relatively poor record of contemporaneous terrestrial and freshwater species (Gentry *et al*., 2023). Baenidae is an extinct clade of fossil para-cryptodiran turtles known from the Early Cretaceous to the Eocene of North America. While during the Early Cretaceous, they were found across North America, during the Late Cretaceous they were only found in Laramidia, having disappeared from Appalachia. Most lineages survived the K-Pg Extinction, but the clade was extinct by the latest Eocene. They were primarily found in freshwater deposits and are considered to be aquatic, with a large generalist habit (Gaffney & Hyatt, 1971; Gaffney, 1972, 1979, 1982, 1983; Karl *et al*., 1998; Karl & Tichy, 2002; Brinkman, 2003a, 2005; Joyce, 2007; Joyce & Lyson, 2015). Baenidae is a diverse family of turtles with several recognized species from North America from the Upper Cretaceous to the Paleogene. They are trapped in different rocks, such as clastic sedimentary rocks, chemical rocks, biochemical sedimentary rocks, and organic sedimentary rocks (Hay, 1908; Gaffney, 1972; Karl & Tichy, 2002; Sterli & Joyce, 2007; Joyce & Lyson, 2015).

These medium-to-large terrapins had different shapes of skulls, for example, long, triangular and rounded with latticed surfaces, as well as narrow to very large or elongated surfaces, indicating their feeding habits and diet (Sterli & Joyce, 2007; Lyson & Joyce, 2009a, b). Baenid turtles inhabit rivers, lakes, and other freshwater reservoirs. The limbs were only partially known. Hay

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(1908) already noted that they were adapted for swimming. Although baenids are common in the fossil record, only the holotypes of *Cedrobaena putorius* and *Eubaena hatcheri* (*Baena longicauda*) preserve partial limbs (Gaffney & Hyatt, 1971). Most species of this family were found in sandstone and riverine deposits; some species were more commonly found in fine-grained over bank deposits nearby. The excellent fossil record of baenids is due to either: (a) most representatives of this group were found in freshwater reservoirs and therefore have a high potential for preservation (Sterli & Joyce, 2007); or (b) many species from this clade fused their shells into adult forms, and so complete preserved shells are commonly found. Pieces and fragmented shells of baenid species are one of the most common fossils found in the latest Cretaceous and Paleogene sediments (Gaffney & Hiatt, 1971; Gaffney, 1972, 1979, 1982, 1983; Karl *et al*., 1998; Karl & Tichy, 2002; Sterli & Joyce, 2007). However, complete crania and skull shells are not commonly recorded from North America. Only 11 fossil taxa have complete crania and skull shells, out of 29 previously discovered baenid taxa from the Early Cretaceous to the Eocene in North America (Sterli & Joyce, 2007; Joyce & Lyson, 2015).

Fossils collected from Chile provide new insights into the biogeography of fossil testudines from the Late Cretaceous. The ancient reptiles from these areas were plesiosaurs of the family Plateosauridae and some mosasaurs (Gasparini *et al*., 2003; Otero *et al*., 2015; Frey *et al*., 2016; Otero, 2017; Otero, 2021), and very few sea turtles (Gasparini & Biró-Bagóczky, 1986; Karl *et al*., 1998; Karl & Tichy, 2002, Parham et al, 2014; Jiménez-Huidobro *et al*., 2015, 2019). Parham *et al*. (2014) assigned a skull to the stemcheloniid, *Euclastes* (Previously designated as *Osteopygis*), using open nomenclature for this fossil specimen of the genus *Euclastes.* The Alpha taxonomy of the previously discovered and described turtle's skull of the Quiriquina Formation (The holotype of *Australobaena chilensis* described here for cranial anatomy) is plausible due to its preservation. The identification, reconstruction, and description of these fossils allow new comparisons with other fossil collections from many regions in the Southern and Western Hemisphere of the Pacific basin. Late Cretaceous fossils from Chile, provide important data about archaeo-zoological features of fossil reptiles, global comparisons, and a broad latitudinal pattern of reptiles of similar age in the Campania-Maastricht case (Parham *et al*., 2014). Previous reports of turtles from the Quiriquina Formation include some specimens, *viz*., the *Durophagous* chelonioidean mandible (Q/377) (Gasparini & Biró-Bagóczky, 1986) and a *Durophagous* turtle skull (Karl *et al*., 1998), initially considered chelonioidean and later assigned to an extinct taxon, otherwise purely a North American freshwater clade (Karl & Tichy, 2002). The authors described the skull of a *Durophagous* (Hard-shelled) chelonioid, a sea turtle from the Late Cretaceous (Maastrichtian) Quiriquina Formation of Quiriquina (SMF R4151). The current studied fossil and that of the Parham *et al*. (2014) specimen from the Quiriquina Formation provide an opportunity to discuss some new taxonomic questions about *Durophagous* chelonioidean sea turtles in general and the turtles from the Quiriquina Formation in particular. The description of these skulls also highlights emerging diversity patterns and the biogeography of stem-cheloniid dispersal across the K/Pg boundary. Leidy (1871a, b) described the first baenid fossils from a newly discovered rich Eocene fossil bed near Fort Bridger in western Wyoming from Eocene basins.

The present article is focused on the reconstruction and re-description of a turtle of the Late Cretaceous of the Senonian of Chile, Western South America [which was identified as a new genus and a new species of baenid, *Australobaena chilensis* by Karl & Tichy (2002)], aided by new images of the cranium of a partially damaged skull without a lower jaw. This was the first occurrence outside of North America.

Material and methods

The collection for this article was recorded in the Quiriquina Formation, a geological formation in Chile whose strata date back to the Late Cretaceous (about 70.6–66.0 Ma) (Parham *et al*., 2014) (Figs 1, 2).

The type specimen comes from the former private collection of Dr K. Falke (1949) and then came to the palaeontological collection of the Senckemberg Natural History Museum and Research Institute. For the comparative study, measurements and photographs were taken (photography, X-rays, 3D scans). These data were compared with available original skulls of fossil and extant sea turtles and with relevant published data. The state of preservation of the skull surface does not allow viewing of all areas because large parts of the posterior edge of the tectum are missing and surface areas on the sides have also been eroded. Therefore, a phylogenetic comparison was not possible. It was decided to carry out a description in alpha taxonomy with particular attention to the palatal and facial skulls.

Systematic palaeontology

Testudinata Klein, 1760
Cryptodira Cope, 1868
Chelonioidea Baur, 1893

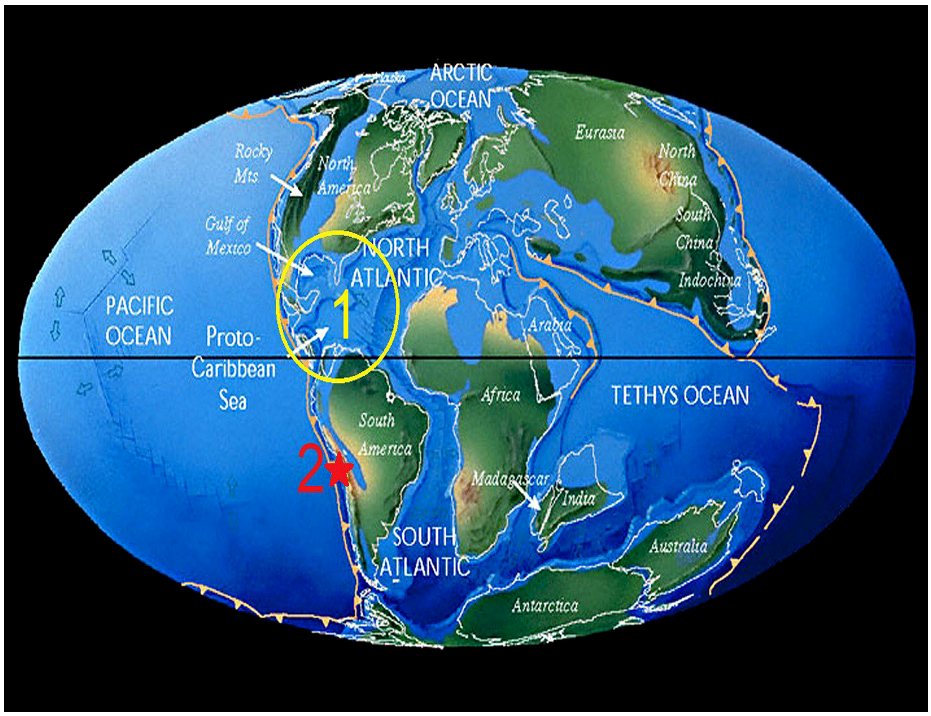

FIGURE 1. The World map during the Cretaceous Period showing Proto-Caribbean Sea (Period showing the Proto-Caribbean Sea (1) and the Site of fossils (2) originating from Senonian deposits in Chile, Western South America) (Retrieved from Google).

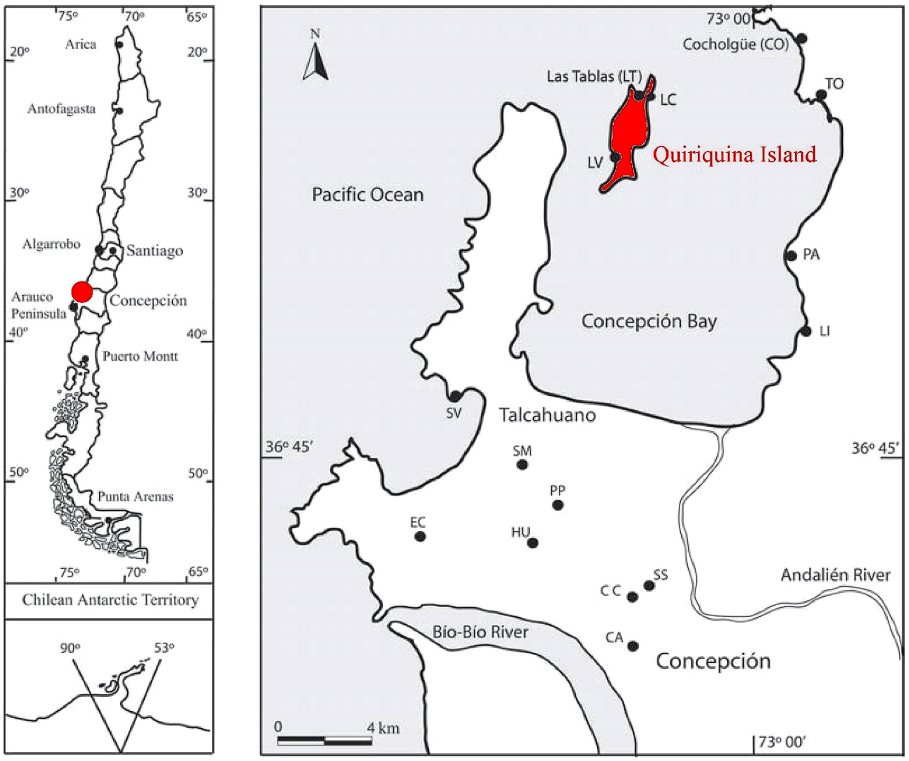

FIGURE 2. Map of the Chilean territory showing the location of outcrops of the Quiriquina Formation in the Concepción area in a more highlighted sketch (Courtesy by Salazar *et al*., 2010).

Pancheloniidae Parham *et al*., 2014
***Australobaena* Karl & Tichy, 2002**
***Australobaena chilensis* Karl & Tichy, 2002**

Material. The type specimen is SMF R 4151, a partially damaged skull without a mandible, a 3-D body fossil, 1949 exchanged with Dr K. Falke. It is stored in the

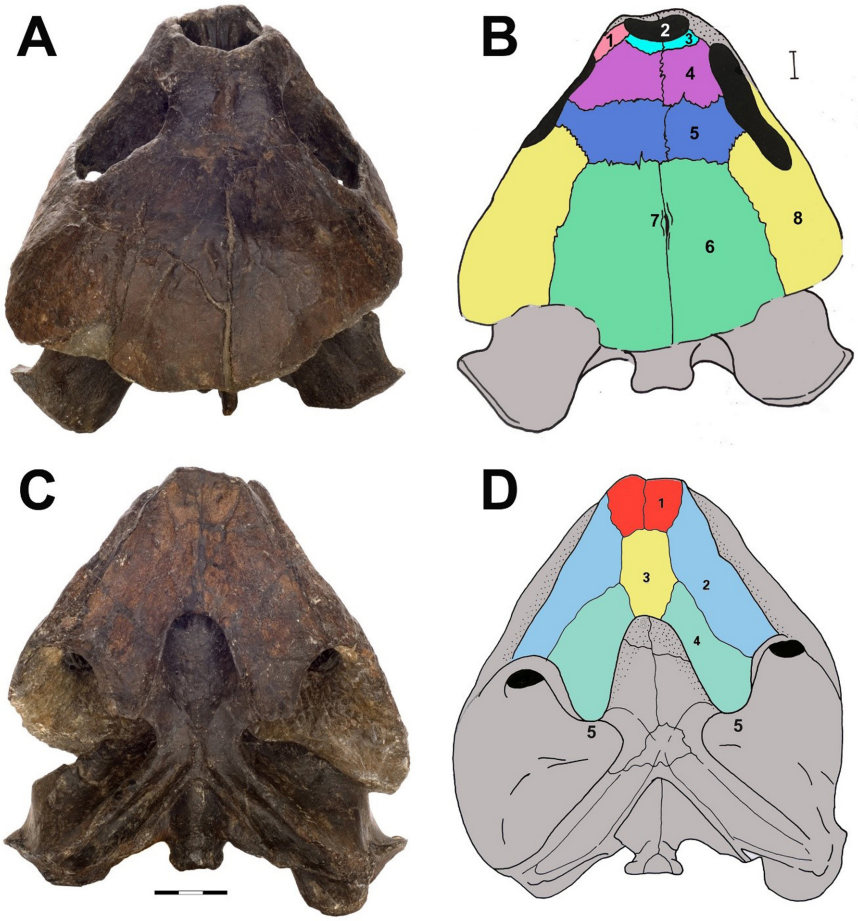

FIGURE 3. *Australobaena chilensis*, (Holotype, No. R4151), skull roof. **A**, Dorsal view. **B**, Interpretive drawing of dorsal view. Abbreviations: 1. pm, Premaxilla; 2. cn, cavum nasale; 3. na, nasal; 4. pf, prefrontal; 5. f, frontal; 6. t, temporal; 7. ep, eminentia parietalis; 8. qj, quadratojugal. **C**, Ventral view. **D**, Interpretive drawing (artificial model) of ventral view. Abbreviations: Abbreviations: 1. pm, premaxillar; 2. m, maxillar; 3. v, vomer; 4. spal, secondary palatine; 5 ppt, processus pterygoideus (compare with figure 4). Scale bar = 5 cm.

Palaeontological Collection of the Senckenberg, Museum in Frankfurt am Main (SFMF), Germany. *Australobaena* was named by Karl & Tichy (2002). Its type is *Australobaena chilensis.* It was assigned to Baenidae by Karl & Tichy (2002); and to Pancheloniidae by Parham *et al*. (2014).

Diagnosis. Anatomical terms of the shell follow those of Zangerl (1969). This preserved skull shows a clear relationship with the baenid turtles, as it shows very well-developed secondary palatine completely built by premaxillae, the secondary vomer, maxillae, and palatines; posterior parts of palatines fused with pterygoid processes; nasals present; nasal passage shorter than in Osteopygidae; skull longer than wide (Figs 3–6). This new genus, *Australobaena* is close to the genus *Eubaena*, concerning the primary palatine as described by Karl & Tichy (2002).

Type locality and horizon. Its type locality is Quiriquina, which is in a Maastrichtian marine horizon in the Quiriquina Formation in Quiriquina Island of central Chile. Quiriquina Island, Chile is located at the entrance to the Bay of Concepción, 11 km north of Talcahuano. (Quiriquina is a Mapuche word meaning "many True thrushes") (Figs 1, 2); Upper Cretaceous; Maastrichtian.

Discussion

Karl & Tichy (2002) and Parham *et al*. (2014) described that *Durophagous,* stemcheloniid Sea turtles have various taxonomic histories. Many species were assigned for decades to the genus *Osteopygis* (Cope, 1869), or erroneously to the clade *Osteopyginae* (Zangerl, 1969). Parham (2005) described *Osteopygis* as a chimera that showed a carapace fragment belonging to a basal cryptodiren "*Macrobaenid*" freshwater turtle. The skulls of *Durophagous* sea turtles have usually been assigned to *Osteopygis* because of the extensive secondary palatine Parham (2005); Parham *et al*. (2014). The Maastrichtian record of baenids is rich but unfortunately

FIGURE 4. *Australobaena chilensis*, Holotype, No. R4151, x-ray photo from Karl *et al*. (1998, 2002). Abbreviations: 1, cavum nasale; 2, apertura narium interna; 3, meatus choanae; 4, vomer butress; 5, processus pterygoideus; 6, ethmyoidal fissura (compare with fig. 3). Scale bar = 5 cm.

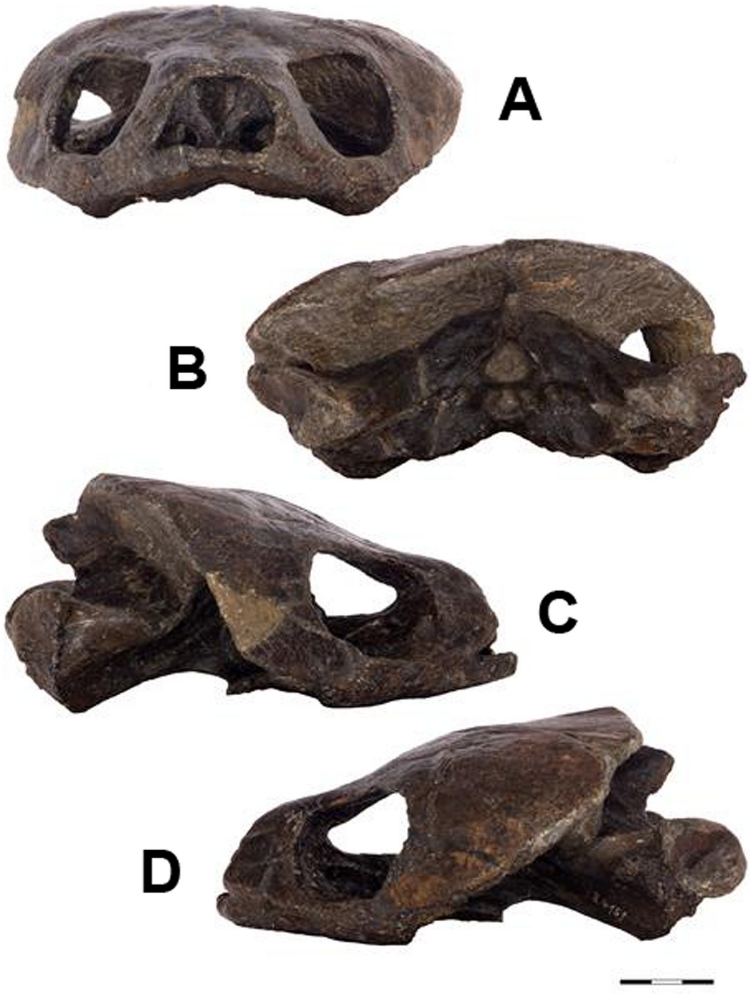

FIGURE 5. *Australobaena chilensis*, Holotype, No. R4151, Cranium. **A**, Front view. **B**, Back view. **C**, Right view. **D**, Left view. Scale bar = 5 cm.

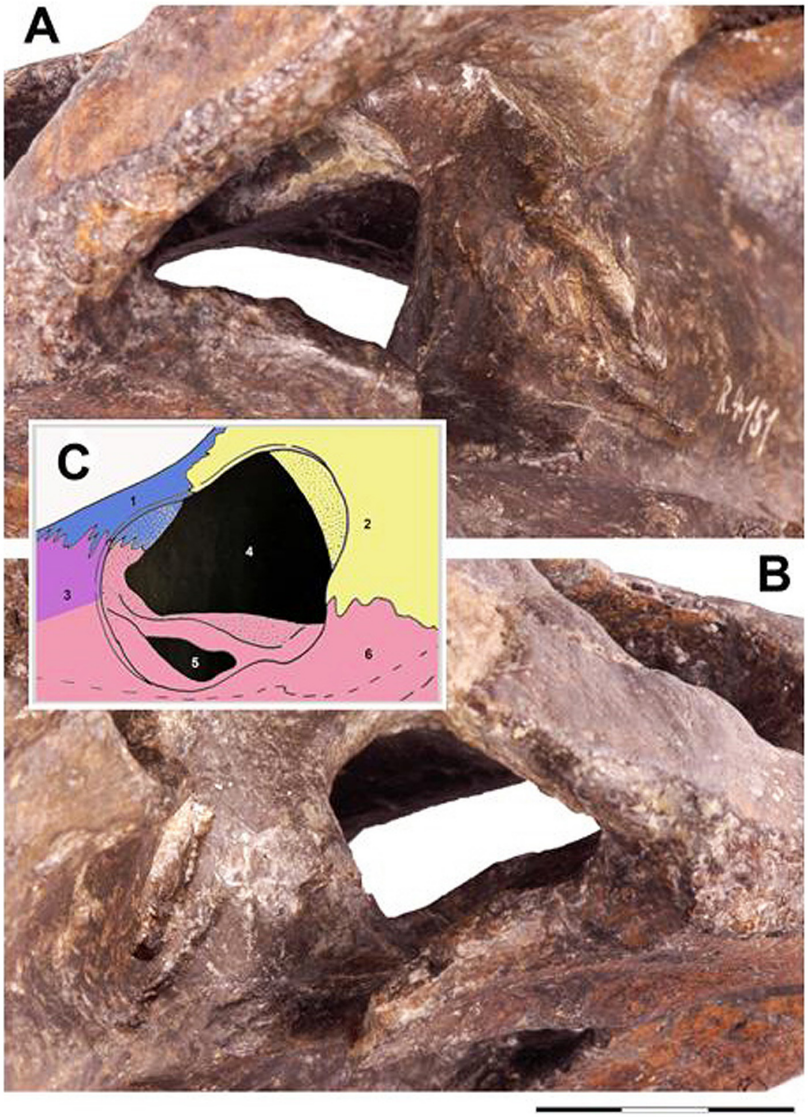

FIGURE 6. *Australobaena chilensis*, Holotype, No. R4151, Optic region of the skull. **A**, Left side. **B**, Right side. **C**, Interpretive drawing of the optic region. 1. fr, Frontal; 2. pofr, post orbital; 3. Prob, pre-orbital; 4. orb, Orbital; 5. fo, foramen orbitale; 6. j, jugal. Scale bar = 2 cm.

restricted entirely to the northern basins of Alberta, Colorado, Montana, Wyoming, North Dakota, South Dakota, and Saskatchewan. Joyce & Lyson (2015) recognized nine valid baenid taxa and one lineage from this region but note, that number is likely inflated by para taxonomy, as four taxa are known from skulls only *(Gamerabaena sonsalla, Eubaena cephalica, Hayemys latifrons and Stygiochelys estesi*), four from shells only (*Boremys sp.*, *Eubaena hatcheri*, *Baena hayi and Thescelus insiliens*), but only two from skull and shells (*Palatobaena cohen* and *Cedrobaena brinkman*).

The Late Cretaceous baenid record starts in the Santonian of Canada with the appearance of *Neurankylus lithographicus* (Larson *et al*., 2013). The Early Cretaceous to Eocene of North America has yielded a lot of rich fossil terrapin material, indicating that baenids were a diverse group throughout this period and were only slightly affected by the K–Pg mass extinction event (Sterli & Joyce, 2007). However, very little is known about the early evolution of this group. The discovery of new fossil records of baenid turtles over the last two decades has spawned much research on Baenidae, like the discovery of new species *Boremys Pulchra* (Testudines: Baenidae) from the Early Cretaceous in Maryland, the discovery of a new baenid species from the Santonian bed in Canada, the re-description of Campanian taxa from Canada and *Neurankylus eximius* (Brinkman & Nicholls, 1991, 1993; Brinkman, 2003a); the description of abundant material from the Maastrichtian of North Dakota, including the description of three new species; the description of a turtle fauna from the Campanian of Utah, including one new species and the description of new Paleogene taxa from

Paleocene of California (Hutchison, 2004), and from the Eocene of Wyoming (Archibald & Hutchison, 1979). The stratigraphic range of various baenid species was further investigated based on shell pieces (Lillegraven & Eberle, 1999; Holroyd *et al*., 2001, 2014; Holroyd & Hutchison, 2002; Lyson *et al*., 2011). Although the para-taxonomy of the family largely remains unresolved, it is related to phylogenetic and stratigraphic methods potentially based on shell and cranium, which in turn permits a more realistic assessment of diversification (Lyson & Joyce, 2010, 2015).

Riabinin (1938) reported the possible presence of baenids from Late Cretaceous sediments exposed in Kazakhstan, but he did not substantiate this claim with any specimens. All current reviews on the turtle fauna of Asia agree that baenids never occurred on this continent (Sukhanov, 2000). The present baenid turtle's fossil, a partial skull from the Late Cretaceous of Chile, was previously described by Karl *et al*. (1998) and Karl & Tichy (2002) from the Late Cretaceous of Chile as a new taxon of baenid, *Australobaena chilensis*. Parham *et al*. (2014) highlighted the surprising nature of this identification. Still, they were reluctant to provide an authoritative reassessment of this taxon, as the holotype is fragmentary and demands a better description. Joyce & Lyson (2015) described that all baenids, even fully molluscivorous forms such as *Palatobaena* spp., lack true secondary palates and never exhibit a vomerine contribution to the triturating surfaces, in contrast to various radiations of testudines and stated that all baenids are only restricted to North America. We here reassess the anatomy of the skull of this taxon, as the holotype is incomplete and we here agree with the second initial description by Karl & Tichy (2002) with confidence that this partially damaged skull from the Late Cretaceous of Chile is a new genus and a new species of baenid, *Australobaena chilensis*. This baenid possesses two distinct external nares almost completely separated by a dorsal projection of the premaxillae and a ventral extension of the nasals, an autapomorphic feature among known baenid taxa. The skull is wedge-shaped with a broad rostrum and laterally expanded nasals. However, the descriptive analysis of baenidae indicates that the character states exhibited by those taxa represent plesiomorphic status within baenidae, and its relationships within this clade need re-evaluation.

Conclusion

Studies of the taxonomy of *Durophagous* stem-cheloniids (Parham & Pyenson, 2010; Parham *et al*., 2014) reveal an emerging pattern of *Euclastes* biogeography, with *Euclastes* dominating the stem-cheloniid localities in the Maastrichtian, crossing the K/Pg boundary, and finally becoming extinct at the end of the Paleocene as the stem-cheloniid radiation accelerates. *Australobaena* (SMF R4151) fits a different character to *Euclastes* and appears to correspond to a highly evolved status and is owned by nasals. Even though baenids were not documented in modern South America before the discovery of *Australobaena* and other researchers have identified the species as a pancheloniid, the presence of the Nasalia and the constellation of the continental masses of the Americas at the time of the Late Cretaceous contradict this. Western Interior Sea between the two land masses created Laramidia to the west and Appalachia to the east during the Late Cretaceous. The Western Interior Seaway divided across the Dakotas and retreated south towards the Gulf of Mexico, the Proto-Caribbean Sea, and the shelves (*e.g.*, Conceptión Bay) and island areas (*e.g.*, Quiriquina island) of South America (see Fig. 1). In this connected sea area, the exchange of aquatic creatures was possible. Baenidae was an extinct family of para-cryptodiran turtles from the Early Cretaceous to the Eocene of North America. While during the Early Cretaceous, they are found across North America, during the Late Cretaceous they are discovered in Laramidia and Quiriquina island, having disappeared from Appalachia. Most lineages survived the K-Pg mass extinction, but the family was extinct by the latest Eocene. They are primarily found in freshwater deposits and are considered aquatic, with a large generalist habit and seawater. The glauconitic sandstones and conglomerates of the Quiriquina Formation were deposited in a marine environment.

Acknowledgments

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