

The first record of dermochelyid turtles in the Eocene of Tierra del Fuego: new insights on the evolution of the Weddellian faunas

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Abstract The Antarctic Paleogene marine fossil record has been the key to reconstructing the evolution of the Weddellian Sea and final dismemberment of Southern Gondwana. In this context, Eocene marine vertebrates from Seymour (Marambio) Island have provided valuable information. We present the first Eocene record of marine reptiles from the southern Atlantic Coast of South America. This corresponds to several postcranial turtle remains represented by a proximal end of the right humerus, three caudal and one thoracic vertebrae, a fragment of the left pubis, and ten ossicles of the dorsal carapace, coming from the Leticia Formation (late-mid Eocene) at Cabo Tiburones, Tierra del Fuego, Argentina. These materials show several features such as the size and general morphology of the humerus and vertebrae, and the presence of relatively small, irregular, smooth, and unkeeled ossicles, which allow us to assign them to Dermochelyidae indet. Dermochelyids are a cosmopolitan group of cryptodiran turtles, registered from the late Cretaceous up to the recent, with some physiological-biological peculiarities (e.g., endothermy and an exclusive jellyfish-based diet) and characterized by the presence of an osseous carapace formed by ossicles. The new finding from the Leticia Formation is an addition to the scarce and extremely fragmentary record of Eocene dermochelyids from the southern seas like those from the La Meseta and Submeseta formations (Antarctica) and the Waihao and Burnside formations (New Zealand). This new information allows us to discuss the presence of these turtles in such high latitudes in the past and its implication in the evolution of the Weddellian fauna.

Keywords marine reptiles, sea turtles, Dermochelyidae, Paleogene, La Meseta Formation, Submeseta Formation, Leticia Formation

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1 Introduction

Dermochelyids are a peculiar group of turtles in which their osseous carapace, contrary to all remaining turtles, is formed by hundreds of relatively small, irregular ossicles. In the fossil record, 16 species of dermochelyids (with up to 89 occurrences; Paleobiology Database: PBDB, accessed at 4 May 2022) are recognized from the late Cretaceous up to the Holocene. However, nowadays, dermochelyids are a relictual clade represented by only one extant species, *Dermochelys coriacea* (Turtle Taxonomy Working Group, TTWG, 2021). This species is cosmopolitan, being the extant species with a broader latitudinal range. The carapace of *Dermochelys coriacea* can reach up to 2 m in total length, their diet is based on jellyfish, and they can dive up to 1000 m (Bonin et al., 2006). Another peculiarity of *D. coriacea* is the development of “gigantothermy”, where the body temperature is regulated by a combination of large body size, insulative tissue, low metabolic rate, and changes in the blood flow (Paladino et al., 1990).

The Cenozoic dermochelyid record in Southern Gondwana (South America, Antarctica, Australia, and New Zealand) is scarce and represented by fragmentary remains. Dermochelyids are known from the Eocene of the La Meseta Formation (Seymour (Marambio) Island, Antarctica) where Dermochelyidae indet. and cf. *Psephophorus* sp. have been identified (Albright et al., 2003; de la Fuente et al., 1995). In addition to this published material, other dermochelyid ossicles that are currently under study were found in the overlying levels of the Submeseta Formation (Seymour (Marambio) Island, Antarctica). In the Southern Island of New Zealand, Köhler (1995a, 1995b) reported the presence of “*Psephophorus*” *terrypratchetti* from the Waihao and Burnside formations. Some years later, Karl and Tichy (2007), reassigned the humerus of *P. terrypratchetti* coming from the Burnside Formation to a new species: *Maorichelys wiffeni*. The Cenozoic record of dermochelyids is completed by the late Oligocene *Natemys peruvianus*, from the Pisco Formation (Peru, Pacific Ocean; Wood et al., 1996), the Early Miocene Dermochelyidae indet. from the Chilcatay Formation (Peru, Pacific Ocean; Bianucci et al., 2018), the Early Miocene Dermochelyidae indet. from the Gaiman Formation (de la Fuente and Vucetich, 1998; Sterli et al., 2021), and the Late Miocene Dermochelyidae indet. from the Pisco Formation (Peru, Pacific Ocean; Ochoa et al., 2021).

In this contribution, we present and describe new material of a dermochelyid coming from the Leticia Formation (late-mid Eocene) at the Atlantic Coast of South America, Tierra del Fuego Island, and we discuss its implications for the evolution of the Weddellian fauna.

Institutional abbreviations as follows.

AMNH, American Museum of Natural History, New York, United States of America.

BMNH R, British Museum of Natural History-Reptiles,

London, United Kingdom.

CADIC, Centro Austral de Investigaciones Científicas del Consejo Nacional de Investigaciones Científicas y Técnicas, Ushuaia, Argentina.

CMM V, Calvert Marine Museum-Vertebrates, Maryland, United States of America.

IRSNB R, Royal Belgium Institute of Natural Sciences-Reptiles, Brussels, Belgium.

LACM, Los Angeles County Museum, Los Angeles, United States of America.

OU, University of Otago, Geology Museum, Dunedin, New Zealand.

SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

2 Geological setting

The fossil-bearing Leticia Formation is part of the Austral foreland basin system that extends from northwestern Santa Cruz (Argentina) and eastern Magallanes-Última Esperanza (Chile) to Tierra del Fuego Island and the South Atlantic Ocean (Figure 1a), where it connects with the western Malvinas Basin (Biddle et al., 1986; Galeazzi, 1998; Torres Carbonell and Olivero, 2019). In Tierra del Fuego Island, the late Cretaceous to the Oligocene-earliest Miocene sedimentary fill of the foreland basin system includes four thick, unconformity-bounded, syntectonic clastic wedges dominated by deep-marine turbidite systems, which accumulated in successive elongated depocenters oriented subparallel to the Fuegian Andes. Within the thrust-fold belt, these depocenters comprise late Cretaceous–Danian turbidites, the Paleocene early to early-mid Eocene Río Claro Group, and the late-mid Eocene–Oligocene La Despedida Group. North of the thrust-fold belt, Cenozoic sedimentary rocks consist mostly of deep-marine subhorizontal turbidites of the Cabo Domingo Group (Figure 1b, Malumíán and Olivero, 2006; Olivero and Malumíán, 2008).

The studied area is located within the thrust-fold belt, along the Atlantic coast between Cabo Campo del Medio and Cerro Colorado, where an open anticline of 4–5 km in wavelength is exposed (Figures 1b–1c). To the south, a major transform fault, the Fagnano Transform System, active from the late Miocene (Torres Carbonell et al., 2008), separates the South American Plate from the Scotia Plate (Figure 1). At the Cabo Campo del Medio–Cerro Colorado anticline, a marked angular, high-relief unconformity separates the early-mid Eocene Punta Torcida Formation (Río Claro Group) from shallow-marine sandstones of the late-mid Eocene Leticia Formation (La Despedida Group) (Figure 1d). The intra Eocene unconformity marks a major change of sedimentary facies and sedimentary petrography, reflecting an important tectonic control on depositional environments. Beneath the unconformity, the Punta Torcida Formation consists of a deep-water turbidity system that

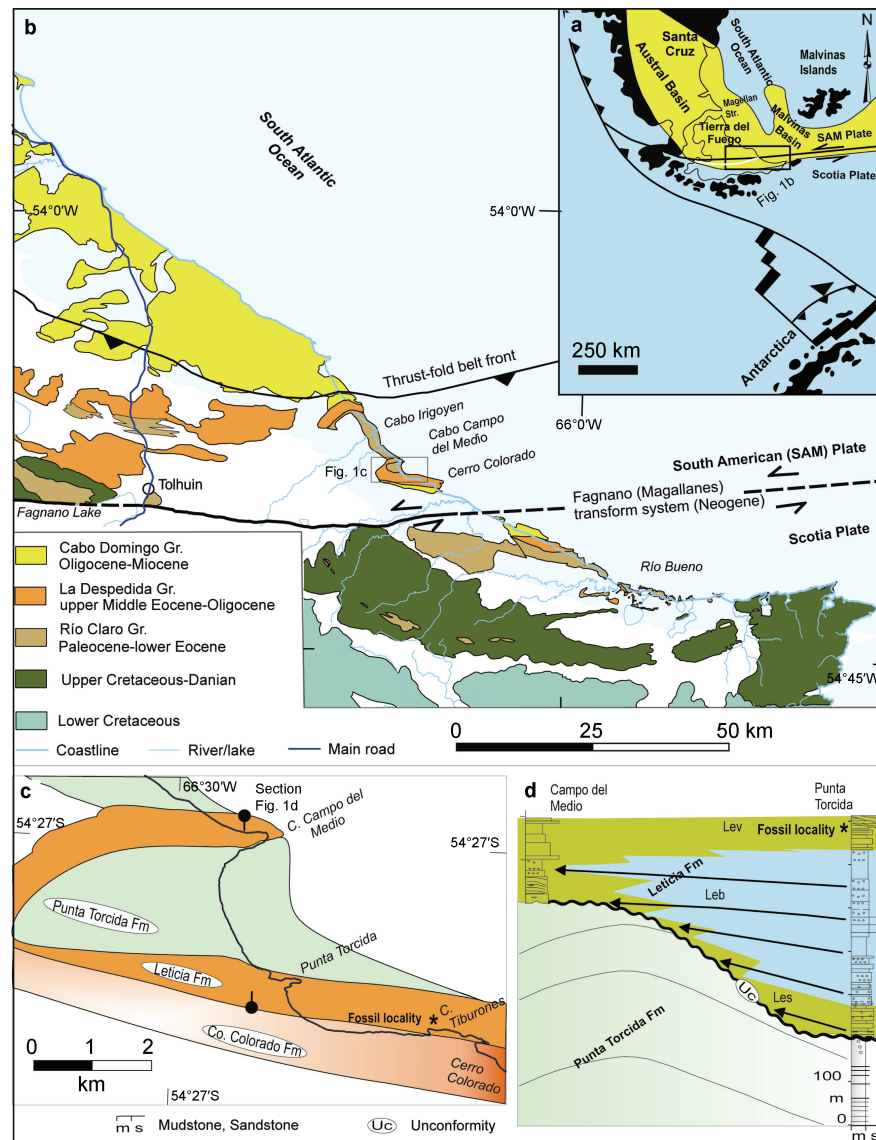


Figure 1 Location map and geology of the study area. **a**, location of the studied area within the Austral-Malvinas basin; **b**, geology of the southern Atlantic coast of Tierra del Fuego, showing areal distribution of the late Cretaceous–Miocene depocenters; **c** and **d**, detailed geological map (**c**) and section (**d**) of the Leticia Formation at the Cabo Campo del Medio anticline, showing the geographic and stratigraphic position of the dermochelyid fossil locality.

filled and elongated foredeep, the evolution of which is intimately related to the northward propagation of the thrust-fold belt during the early Eocene–early-mid Eocene (Torres Carbonell and Olivero, 2012, 2019). The sedimentary petrography of the Punta Torcida Formation is dominated by volcanoclastic components derived from the Fuegian–South Patagonian andesitic arc (Torres Carbonell and Olivero, 2019). Radiometric ages from circon grains recorded in one volcanoclastic package atop the Punta Torcida Formation gave a U–Pb age of 46.3 ± 0.4 Ma, early Lutetian (Olivero et al., 2020).

The Leticia Formation is characterized by shallow-water settings and both the base and top are marked by unconformities. Its base is the angular unconformity eroded into the Punta Torcida Formation and its top is defined by

the planar unconformity developed at the contact with the mid–late Eocene interval of the Cerro Colorado Formation (López Cabrera et al., 2008; Olivero and Malumián, 2008; Torres Carbonell and Olivero, 2012). The sedimentary petrography of the Formation is dominated by quartz-lithic components, mostly derived from older stratigraphic units of the Fuegian Andes (Olivero, 2002; Torres Carbonell and Olivero, 2019) that reflects a major orogenic exhumation of the southernmost Andes and deposition in a newly formed depocenter above the angular unconformity. This new depocenter was interpreted as a wedge-top depocenter denominated Maria Luisa sub-basin (Torres Carbonell et al., 2008, 2009). At the top of the Leticia Formation, an exceptional volcanoclastic package gave U–Pb ages of 41.9 ± 0.71 Ma (late Lutetian) to 39.6 ± 0.82 Ma (Bartonian)

ages (Olivero et al., 2020), which are consistent with the ages of the NP16 calcareous nannoplankton zone (Bedoya Agudelo, 2019; Olivero and Malumián, 2008) and dinocyst assemblages RTF 1 and RTF 2 (Amenábar et al., 2022), recorded in the Leticia Formation.

The Leticia Formation displays variable thicknesses and sedimentary facies on each limb of the Cabo Campo del Medio–Cerro Colorado anticline (Figures 1c–1d, Olivero et al., 2020). At the southern limb, the Formation is c. 520 m thick and consists of three main facies associations: a lower sandstone-dominated facies (Les); a middle very fine-grained totally bioturbated sandstone facies (Leb); and an upper volcanoclastic sandstone facies (Lev). At the northern limb of the anticline, the Leticia Formation, with a minimum thickness of 200 m, consists mostly of the Les and Lev facies associations. The package including the lower sandstone-dominated facies (Les) is recognized on both southern (80 m thick) and northern (100 m thick) limbs of the anticline (Figure 1b). The Les interval is dominated by thick, up to 2–3 m, fine massive fine-grained sandstone beds, with subordinated fine conglomerate lenses and normally graded fine-sandstone beds. This thick-bedded horizon is followed upwards by well-stratified, fine-grained, glauconite sandstones with parallel lamination, sometimes with dense concentrations of carbonaceous particles, current and wave-ripple cross-laminae, herringbone cross-stratification, and occasional large (1 m thick) dunes, with asymptotic cross-bedding. Some beds bear relatively abundant trace fossils, including the ichnogenera *Curvolithus*, *Diplocraterion*, *Euflabella*, *Gyrochorte*, *Macaronichnus*, *Ophiomorpha*, *Patagonichnus*, *Schaubcylindrichnus*, and *Tasselia* (López Cabrera et al., 2008; Olivero and López Cabrera, 2013). In the northern limb of the anticline, this lower sandstone-dominated package is characterized by large channels.

The thick Leb interval (350 m) is restricted to the southern limb of the anticline (Figure 1d) and consists mostly of very fine-grained glauconitic sandstones, with the original bedding obliterated by bioturbation, which is characterized by a dense mottling with few recognizable trace fossils (López Cabrera et al., 2008; Olivero and López Cabrera, 2013). Near the level of 410 m above the base of the Leticia Formation, the Leb interval records penguin fossil bones assigned to *Palaeudyptes gunnari* (Acosta Hospitaleche and Olivero, 2016; Clarke et al., 2003). This specimen was originally described by Clarke et al. (2003) and comes from Punta Torcida Locality (Figure 1).

The upper part of the Leticia Formation is dominated by volcanoclastic, coarse-grained sandstone and fine breccia (Lev facies), which are continuous across the Cabo Campo del Medio Anticline reaching nearly 40–50 m in the south and 60 m in the north (Figure 1d). Large channels sometimes nested in successive levels recording heterolithic bedding, epsilon cross-bedding, and trough cross-bedding are typical for this interval. The fossil dermochelyd material reported herein was found near the top of this interval (Figure 1d).

3 Systematic paleontology

Testudines Batsch, 1788
 Cryptodira Cope, 1868
 Durocryptodira Danilov and Parham, 2006
 Americhelydia Joyce et al., 2013
 Chelonioidea Baur, 1893
 Dermochelyidae Lydekker, 1889
 Dermochelyidae indet.

Referred specimens: CADIC 636, 10th thoracic vertebra; CADIC 637, 10 ossicles, caudal vertebra (?6th), caudal vertebra (8th or 9th), fragment of left pubis, and proximal end of the right humerus.

Horizon: leticia Formation, late-mid Eocene (Figures 1b–1d).

Location: all the postcranial material was found in different rock blocks coming from Cabo Tiburones Locality, at the Atlantic coast of Tierra del Fuego Province, Argentina (Figure 1a).

3.1 Description

Below we describe all postcranial materials here assigned to Dermochelyidae indet., coming from the same stratigraphic level of the Leticia Formation. These materials were not found articulated but rather associated, although they probably could correspond to the same individual. The thoracic vertebra CADIC P 636 was found in situ, while the other material CADIC P 637 was included in two blocks of rocks that had fallen from the original level (humerus vs. the other remains).

3.1.1 Ossicles

There are 10 ossicles preserved. They are relatively small (smaller than 35 mm) and thick (between 5.5 mm and 11.05 mm). They are irregular in shape, some more rounded and others with more straight borders. Their surface is mainly smooth with some small mammillae and pits. Most of them are isolated, except for two pairs that are connected by suture. None of the preserved ossicles are keeled (Figure 2).

3.1.2 Pubis

A fragment of the medial part of the left pubis is preserved (Figure 3). It is a flat element, which gets thicker towards the anterior.

3.1.3 Humerus

Only the proximal end of the right humerus is preserved (proximal epiphysis; Figure 4). As in other testudines, the general morphology of the humerus is somewhat different from other reptiles, given that the dorsal surface of the bone is directed slightly anteriorly (allowing the humerus to be protracted but limiting its retraction; Walker, 1971; Zangerl, 1953). This rotation of the longitudinal axis of the humerus in turtles is the result of the position of the humeral head and the arching of its shaft.

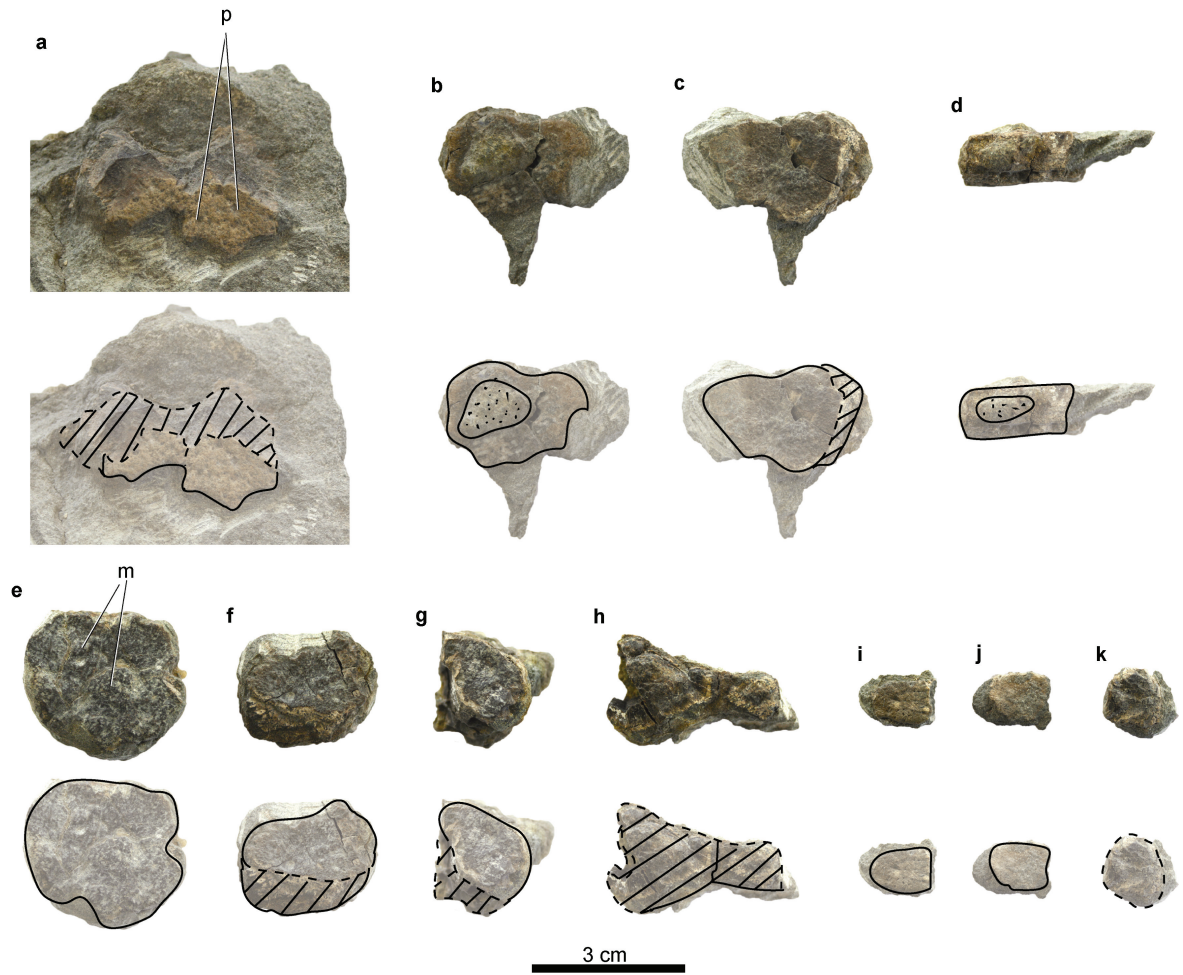


Figure 2 Dermostichia indet. CADIC 637, Leticia Formation, late-mid Eocene. Ossicles. **a**, two ossicles in dorsal (external) view; **b–d**, ossicle in dorsal (external) (**b**), ventral (internal) (**c**), and lateral views (**d**); **e**, ossicle in dorsal (external) view; **f**, ossicle in dorsal (external) view; **g**, ossicle in dorsal (external) view; **h**, two ossicles in dorsal (external) view; **i** and **j**, ossicle in dorsal (external) and ventral (internal) views; **k**, ossicle in dorsal (external) view. Abbreviations: m, mammilae; p, pits.



Figure 3 Dermostichia indet. CADIC 637, Leticia Formation, late-mid Eocene. Portion of left pubis. **a**, dorsal view; **b**, medial view; **c**, ventral view.

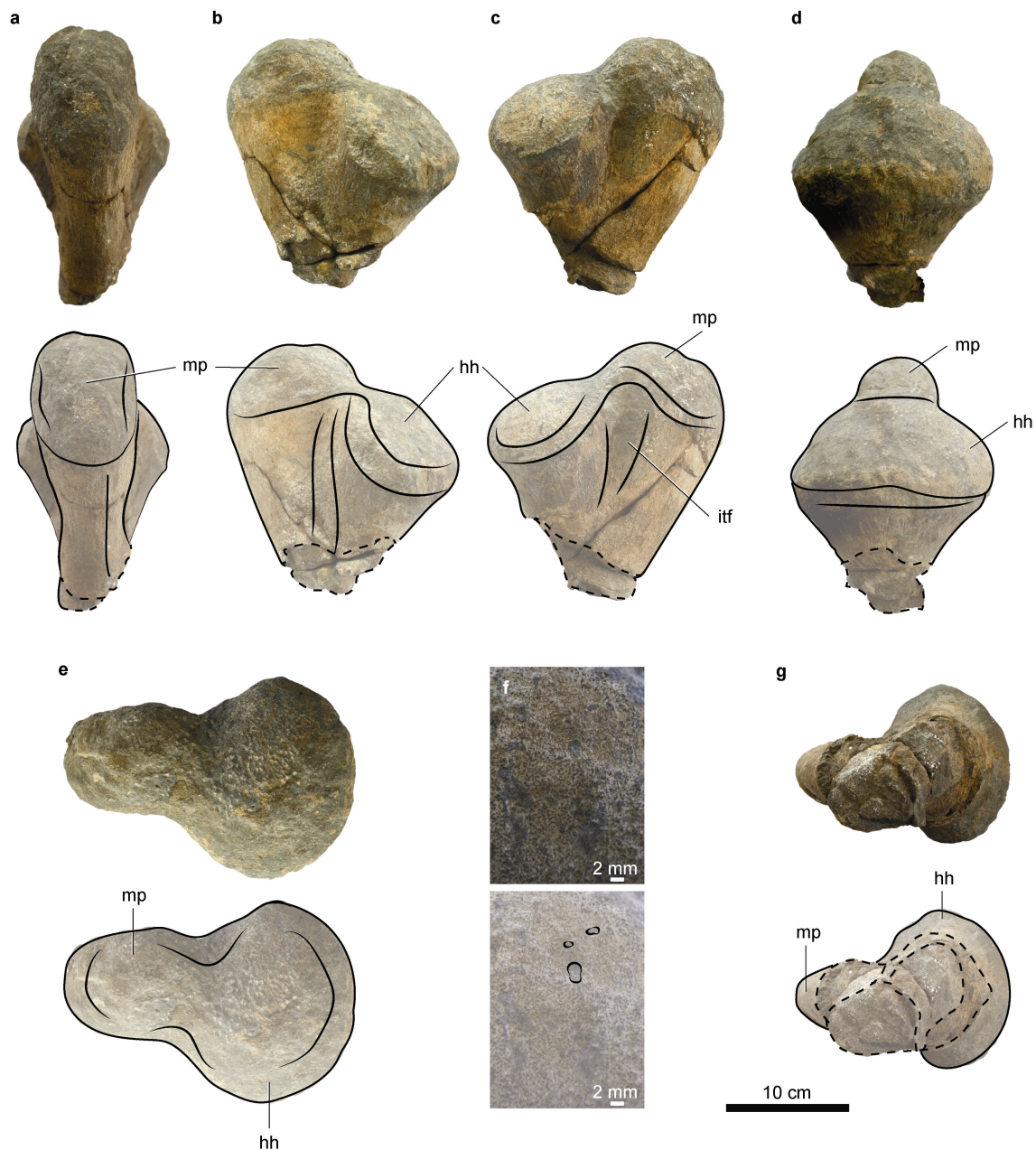


Figure 4 Dermochelyidae indet. CADIC 637, Leticia Formation, late-mid Eocene. Proximal end of right humerus. **a**, posterior view; **b**, dorsal view; **c**, ventral view; **d**, anterior view; **e**, proximal view; **f**, detail of the vascularization of the proximal end; **g**, distal view (diaphysis). Abbreviations: hh, humeral head; itf, intertubercular fossa; mp, medial process.

The fragment of the humerus preserves only the humeral head; as a consequence, it is not possible to estimate the angle between the epiphysis and the diaphysis of the bone. The articular surface of the humeral head is oval in proximal view, more developed towards the dorsal side. In the ventral view, the medial process and the intertubercular fossa are recognized. The medial process is higher than the head. Two muscles are attached to this process: the large *m. subscapularis* that is a strong fin protractor, and the *m. coracobrachialis magnus*, a ventral muscle, is seen extending from the shoulder posteriorly, toward its origin,

the coracoid (Walker, 1973; Wyneken, 2001).

The lateral process is not preserved in the humerus CADIC P 637 because in dermochelyids it has shifted distally onto the shaft. In *Dermochelys coriacea*, this lateral process is large and located about half away in the shaft (Figure 102 in Wyneken, 2001), forming a prominent transverse crest that receives the insertion of the *m. pectoralis* and *m. supracoracoid* (Figure 7A in Walker, 1973). The dorsal process is homologous to the deltopectoral crest of other reptiles (Walker, 1973). The intertubercular fossa is shallow and located between the medial process and the humerus

head. The humerus narrows distally to a sub-cylindrical shaft. The total length of the humerus is estimated at 36 to 40 cm.

In the proximal end, vascular foramina are seen (Figure 4f).

3.1.4 Vertebrae

Three vertebrae are preserved, one thoracic and two caudals.

Thoracic vertebra. The preserved thoracic vertebra (CADIC P 636) is identified as the last centrum, the 10th because its anterior articulation is flat and the posterior one is convex (Figures 5a–5f). Most of the left part of the centrum is missing. The centrum is antero-posteriorly elongated. Its anterior articulation has a subtriangular contour, while the posterior one is oval (being taller than wide). The base of the right transverse process is preserved and is located at the anterior half of the centrum. As it is also observed in the caudal vertebrae, the neural arches are not fused with the centra (as in the extant *Dermochelys coriacea*).

Caudal vertebrae. Both caudal vertebrae (CADIC P 637) are procoelous, have transverse processes located in the anterior half of the centrum, and have articulations for chevron bones. One caudal vertebra is identified as the 6th caudal (Figures 5g–5l) based on its relative size, shape, proportions, and structures. The centrum of this vertebra is slightly longer than the height. The cotyle seems to be triangular and faces anteroventrally. The condyle is more oval with the main axis located horizontally. The neural arch is missing in this vertebra. The other caudal vertebra is identified as the 8th or 9th in the series (Figures 5m–5r). The centrum of this vertebra is much elongated than the previously described vertebra, being longer than height. The cotyle seems to be triangular and faces anteroventrally. The condyle is more oval with the main axis located horizontally. Most of the neural arch of this vertebra is missing, but the base of the right prezygapophysis and the left prezygapophysis are preserved.

3.2 Comparisons

The only known humerus from a Paleogene dermochelyid from the southern latitudes, besides the one from the Leticia Formation (Figure 6a), is *Maorichelys wiffeni* (Karl and Tichy, 2007) from the Burnside Formation (mid-late Eocene) near the city Dunedin in New Zealand (Köhler, 1995a; Figure 6b). Only the proximal end and part of the shaft of the humerus of *Maorichelys wiffeni* (OU 22021) is preserved. If we compare both humeri, their morphology is similar regarding the shape and proportions of the head and the medial process, being the medial process taller than the head and forming a shallow V between them; however, the humerus of *Maorichelys wiffeni* is 25% smaller than the one from the Leticia Formation. Besides, the humeral head in *Maorichelys* is a bit tilted to the ventral side. Other dermochelyid humeri from the fossil record are known from the northern hemisphere such as *Eosphargis gigas*, *E. breineri*,

Egyptemys eocaenus, *Psephophorus polygonus*, *P. calvertensis*, and *P. rupeliensis*. The humerus of *Eosphargis gigas* (BMNH R 2717) from the early Eocene (Ypresian) of England (Figure 6c) also preserves the proximal and part of the shaft (including the displaced lateral process and the deltopectoral crest). The head and the medial process of *E. gigas* is also robust as in *Maorichelys* and the new fragmental humerus CADIC 637 here described, however its medial process is not as tall as in *M. wiffeni* and CADIC 637. The humerus of *E. breineri* from the early Eocene (Ypresian) of Denmark (Nielsen, 1963) is complete, but only seen in ventral view (Figure 6d). The angle between the medial process and the head is around 160°, much wider than in CADIC 637 and *M. wiffeni*. The humerus of *Egyptemys eocaenus* (BMNH R 3017 and SMNS 11243) from the late Eocene of Egypt (Figure 6e) has a more gracile proximal end with a much taller medial process than in CADIC 637 and *M. wiffeni*. Besides, the humerus of *P. eocaenus* is smaller (19 cm long) than CADIC 637. Unfortunately, the comparison of CADIC 637 with *Psephophorus rupeliensis* (IRSNB R 14) from the Oligocene of Belgium is not possible because both specimens do not preserve parts in common (Figure 6f). The humerus of *P. ?rupeliensis* (IG 8638) from the Oligocene of Belgium is almost complete, however the surface is eroded (Figure 46 in Köhler, 1996), consequently, the general shape is obscured. There is one humerus from *P. polygonus* (IRSNB R 15) from the Miocene of Belgium that is complete (Figure 6g). Compared to CADIC 637 and *M. wiffeni*, the outline between the head and the medial process is U-shaped instead of a shallow V as in the former two. The same outline between the medial process and the humeral head is present in *P. calvertensis* (CMM V 12) from the Miocene of the United States of America (Figure 6h), however in this specimen, the medial process is taller making the outline deeper. The outline between the medial process and the humeral head in *Psephophorus* sp. (LACM 6688/44596) from the Miocene of the United States of America (Figure 6i) and the extant *Dermochelys coriacea* (Figure 6j) is an inverted shallow V.

On the other hand, ossicles are a bit more abundant in the Paleogene fossil record from the southern hemisphere. In this regard, the Leticia Formation ossicles can be compared with “*Psephophorus*” *terrypratchetti* found in the late Lutetian–early Bartonian Waihao Greensand Formation in New Zealand and with cf. *Psephophorus* sp. and *Dermochelyidae* indet., both from the La Meseta Formation (Seymour (Marambio) Island, Antarctica; de la Fuente et al., 1995). “*Psephophorus*” *terrypratchetti* (Waihao Formation), cf. *Psephophorus* sp. (La Meseta Formation), the *Dermochelyidae* indet. (La Meseta Formation), and CADIC 637 (Leticia Formation) share the absence or paucity of ossicle external sculpturing and the lack of keels (at least in the preserved parts). These features are also similar to that of the ossicles coming from the Antarctic Submeseta Formation. *Natemyx peruvianus* from the Oligocene of Peru

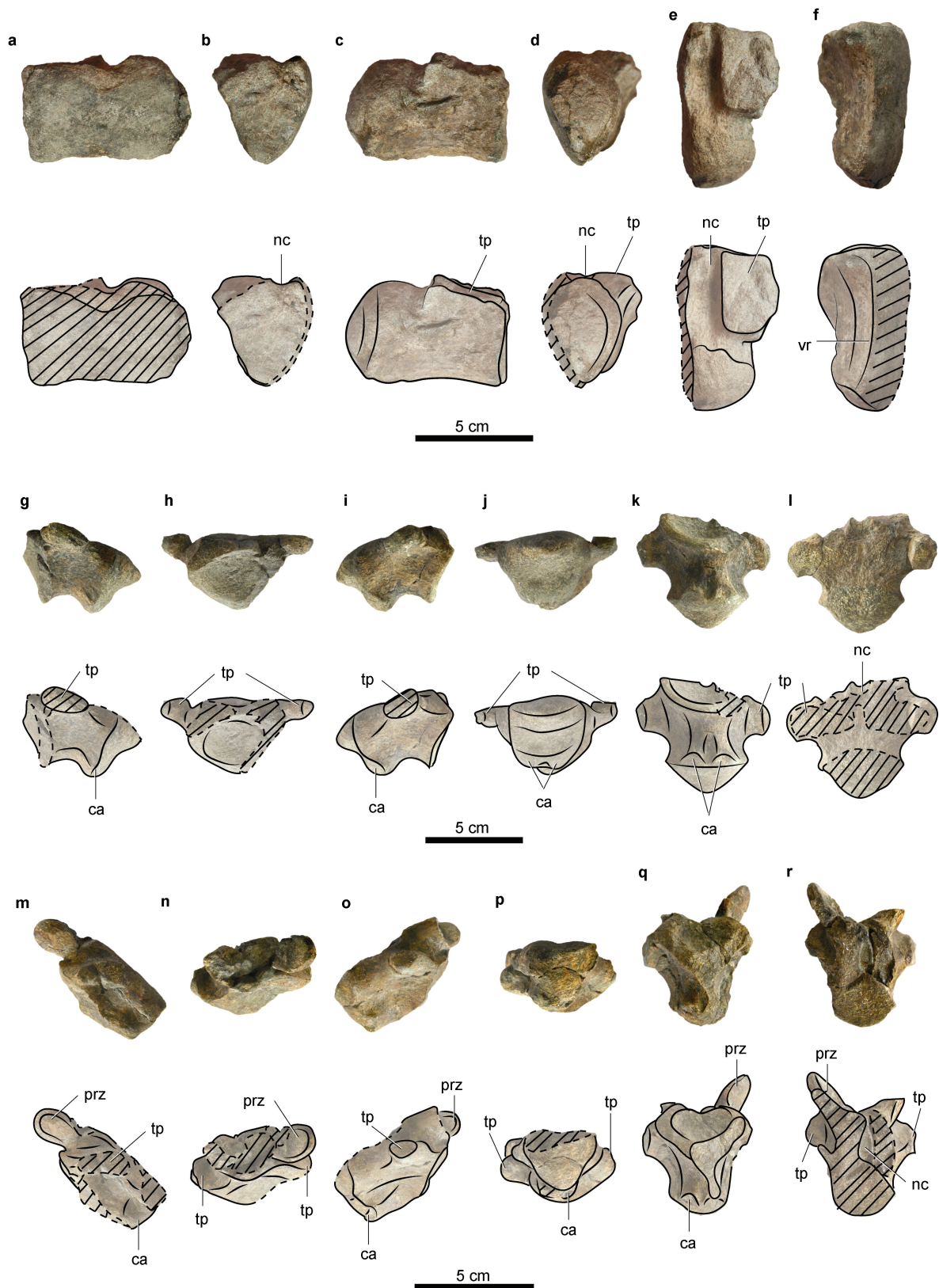


Figure 5 Dermochelyidae indet. CADIC 636 and 637, Leticia Formation, late-mid Eocene. Thoracic and caudal vertebrae. **a–f**, thoracic vertebra, CADIC 636; **g–l**, caudal vertebra (6th; CADIC 636); **m–r**, caudal vertebra (8th to 9th; CADIC 636). **a, g, m**, left lateral view; **b, h, n**, anterior view; **c, i, o**, right lateral view; **d, j, p**, posterior view; **e, k, q**, ventral view; **f, l, r**, dorsal view. Abbreviations: ca, chevron articulation; nc, neural canal; prz, prezygapophysis; tp, transverse process; vr, ventral ridge.

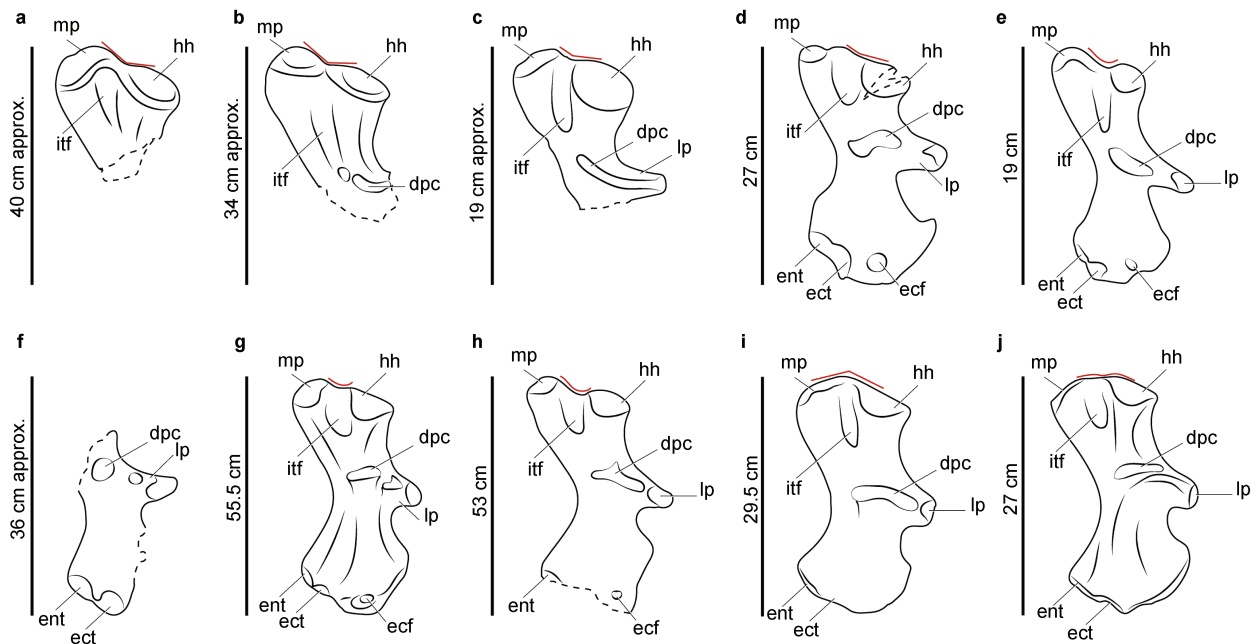


Figure 6 Comparison of left humeri in ventral view of different dermochelyid specimens since the Eocene until recent times. **a**, *Dermochelyidae* indet., CADIC 637 (the image was reflected to make the comparison easier), Eocene, Tierra del Fuego, Argentina; **b**, *Maorichelys wiffeni* OU 22021 (reflected), Eocene, New Zealand; **c**, *Eosphargis gigas* BMNH R 2717 (reflected), Eocene, England; **d**, *Eosphargis breinerii*, Eocene, Denmark; **e**, *Egyptemys eocaenus* SMNS 11243 and BMNH R 3017, Eocene, Egypt; **f**, *Psephophorus rupeliensis* sensu Dollo IRSNB R 14 (reflected), Oligocene, Belgium; **g**, *Psephophorus polygonus* IRSNB R 15, Miocene, Belgium; **h**, *Psephophorus calvertensis* CMM V 12, Miocene, United States of America; **i**, *Psephophorus* sp. LACM 6688/44596, Miocene, United States of America; **j**, *Dermochelys coriacea* AMNH 7161 (reflected), extant, United States of America. Abbreviations: dpc, delto-pectoral crest; ecf, ectepicondylar foramen; ect, ectepicondyle; ent, entepicondylar; hh, humeral head; itf, intertubercular fossa; lp, lateral process; mp, medial process.

has relatively large ossicles arranged in a sunflower pattern (Wood et al., 1996). As the external surface suffered abrasion in the field, the eroded external surface makes it difficult to interpret its external ornamentation.

The occurrence of humeri of a similar morphology in the Leticia (Tierra del Fuego) and the Burnside (New Zealand) formations and fragments of dermal ossicle mosaics similar in the La Meseta/Submeseta (Antarctica) and the Whaihao Greensand (New Zealand) formations (Albright et al., 2003; Köhler, 1995b) suggest the presence of at least one dermochelyid lineage (Wood et al., 1996) as a member of the Weddellian fauna. This Weddellian dermochelyid can be characterized by having the shell composed by a mosaic of relatively small bony ossicles. There are no keels or ridges, no linear arrangements of enlarged ossicles, and no obvious differentiation in the size or shape of individual ossicles.

4 Discussion

4.1 Size, metabolism, and paleobiological/paleoenvironmental implications of the Weddellian dermochelyids

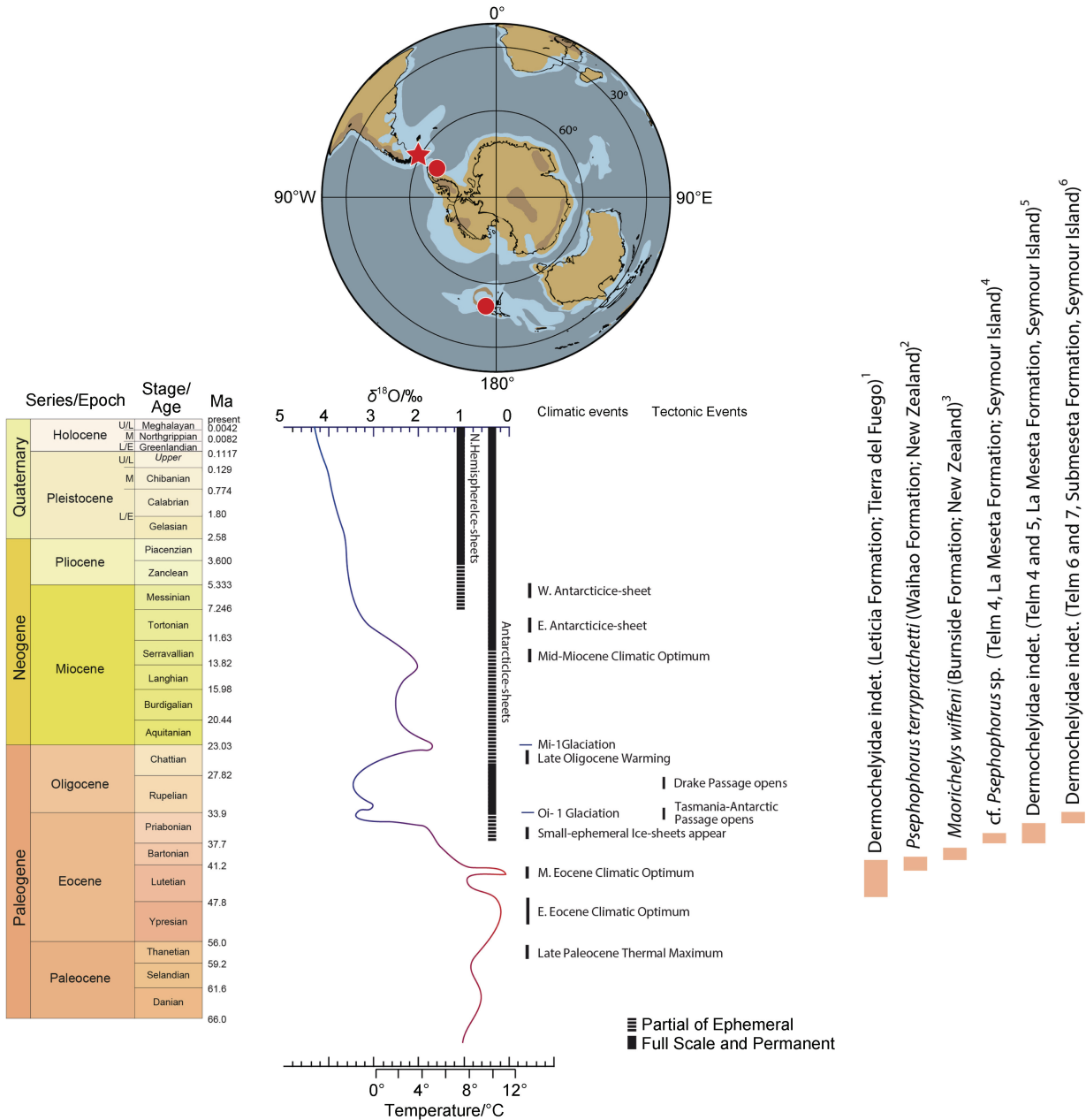
The extinct Eocene dermochelyids seem to have

similar unique anatomical and likely physiological adaptations as the leatherback extant species. In *Dermochelys coriacea* these include the absence of a primary “thecal” shell, possession of an extensive layer of peripheral of adipose tissue (Davenport et al., 1990), proportionally larger fore flippers than other species of Chelonioidea (Joyce and Gauthier, 2004). On this basis the skeleton of *Dermochelys coriacea* remains extensively cartilaginous even in adults (Pritchard, 1980; Pritchard and Trebbau, 1984). The epiphyses are vascularised perichondrially and transphyseally, and the medullary bone is not remodeled, features that are unique among extant reptiles (Figure 20.2 in Rhodin et al., 1981). These features may reflect adaptation to a marine diving lifestyle, because they occur also in cetaceans and sirenians, and to some extent in extinct marine reptiles such as ichthyosaurs and plesiosaurs (Rhodin et al., 1981). *Dermochelys coriacea* is the largest living sea turtle in the world, reaching a length of 2.3 m and a weight of more than 600 kg (e.g., Fontanes, 2003). According to their fossil record, dermochelyids would have reached similar or bigger sizes in the past. For example, Köhler (1995b) estimated body lengths of 2.3 to 2.5 m for “*P.* terrypratchetti”. Skeletal growth in tetrapods is allometric, so it is not correct to make linear extrapolations when estimating the total size of a specimen

with respect to the total size of the humerus. However, if we assume that in dermochelyids the relationship between limbs proportion with respect to total body size would have been similar in the past, then we could propose that several extinct forms of dermochelyids, with estimated humerus lengths of 36– 40 cm (e.g., CADIC 637; Figure 6a) or up to 53 cm (e.g., *Psephophorus calvertensis* CMM V 12; Figure 6h), would have been much bigger than the living *Dermochelys coriacea*.

As noted above the horizons where dermochelyid

fossils were discovered in Tierra del Fuego Island, Seymour (Marambio) Island (Antarctica), and New Zealand are referred to as late–mid Eocene in age. According to Porebski (2000), near the early middle Eocene boundary the major sea-level low stand was recorded, and Southern Ocean surface temperature had declined to about 10–11 °C. The climatic deterioration was perceptible by the late–mid Eocene (Figure 7) because of major changes in ocean circulation (with the opening of the Drake Passage and the consequent development of the circum-Antarctic



current, see below) as well as the onset of deep water between Antarctica and Australia, and the closure of the Tethyan seaway (Lawver and Gaghan, 1998; Lawver et al., 1992). However, in contrast to Porebski (2000), and based on seasonally resolved temperature and precipitation data from the latest Lutetian (~42 Ma) from the eastern Antarctic Peninsula, Judd et al. (2019) proposed warmer climatic conditions for austral high-latitudes during the late-mid Eocene. These authors also conclude that their results match with the existence of closed or shallow Drake and Tasman passages with middle Eocene austral high-latitude oceans non-contiguous and suggest that the eastern margin of the middle Eocene Antarctic Peninsula may have been kept warmer than the rest of the Weddell basin by a subtropical derived branch current, from either the South Atlantic Gyre or frictional flow across a shallow Drake Passage. However, whatever the paleoclimatic reconstructions are, the record of dermochelyid fossils in high latitudes as a component of the Weddellian fauna is compatible with a sea turtle that can live in waters with a wide temperature gradient due to anatomical and likely physiological adaptations, as occurs with the extant *Dermochelys coriacea* (e.g., Frair et al., 1972; Greer et al., 1973; Mrosovsky and Pritchard, 1971).

4.2 Eocene Weddellian fauna

The Weddellian Zoogeographic Province conceived by Zinsmeister (1979, 1982) on marine molluscan, echinoderm and arthropod faunas existed from the late Cretaceous through the Eocene, when Australia, Antarctica, and southernmost South America were in proximity (Woodburne and Zinsmeister, 1984; Zinsmeister, 1979, 1982). This Province is characterized as cool temperate, shallow waters extending from southern South America (Austral-Magallanes Basin: Tierra del Fuego and Santa Cruz provinces in Argentina and the Magallanes Region in Chile), along the Antarctic Peninsula and West Antarctica, to New Zealand, Tasmania, and southeastern Australia (Figure 4 in Acosta Hospitaleche et al., 2013). It is worth mentioning that Case (1988) expanded this concept to a “biogeographic province” with the inclusion of terrestrial plants and mammals. During the late Cretaceous the Antarctic Peninsula and the rest of Western Antarctica land masses were probably formed by a series of discrete microcontinental blocks that formed a single southern landmass extending from southern South America (Figure 4 in Acosta Hospitaleche et al., 2013) to Antarctica. At that time, the western sector of Gondwana was apparently divided into a few distinct tectonic units: South America, West Antarctica (comprising the Antarctic Peninsula, Marie Byrd and Ellsworth lands), and Ellsworth and Whitmore mountains (Dalziel and Elliot, 1982). Although the Antarctic Peninsula has been at almost the same paleolatitude (60°S–65°S) since the late early Cretaceous (Lawver et al., 1992), the northern tip of the Antarctic Peninsula and southernmost end of South America (the Magallanes Region) were connected

facilitating both floristic and faunal interchange (Marenssi and Santillana, 1994; Olivero et al., 1991; Reguero et al., 1998, 2002; Reguero and Goin, 2021; Reguero and Marenssi, 2010; Shen, 1995).

Assemblages of Eocene marine vertebrates registered in different areas of the Weddellian Province (e.g., fishes, whales, birds including penguins) show strong affinities in their taxonomic composition. Although the remains of dermochelyids described here have not been found associated with other taxa, there are records of fossil vertebrates from nearby locations that come from comparable marine levels of the Leticia Formation. Among these, the presence of penguins in the Eocene (Bartonian) in Tierra del Fuego Province can be mentioned (e.g., Acosta Hospitaleche and Olivero, 2016; Clarke, 2003). Particularly, the species *Palaeudyptes gunnari* (Wiman, 1905), was redescribed by Acosta Hospitaleche and Olivero (2016) on the basis of several postcranial elements coming from Punta Torcida locality in the Leticia Formation (Figure 1). *Palaeudyptes* is widely recorded in the Eocene of Antarctica (Seymour (Marambio) Island, Telm 7, Submeseta Formation, late Eocene; Acosta Hospitaleche and Reguero, 2014; Jadwiszczak, 2006), and Chile (Sierra Dorotea, Puerto Natales, southernmost Chile, Río Turbio Formation, mid to late Eocene; Sallaberry et al., 2010), reinforcing the idea that at high southern latitudes, the Eocene was a time of diversification and abundance among penguins, with Antarctic species likely dispersing northwards along the South American coast (e.g., Acosta Hospitaleche and Olivero, 2016; Acosta Hospitaleche and Reguero, 2014; Acosta Hospitaleche et al., 2013). In this sense, it has been mentioned that major Eocene penguin speciation resulted in a diverse Antarctic assemblage that probably expanded its range towards the South American coasts (Acosta Hospitaleche et al., 2013).

4.3 Drake Passage opening and Antarctic Circumpolar Current

The opening of the Drake Passage is probably one of the most important events in the history of the actual global oceanic and atmospheric circulation, given that its presence is categorical for the existence of the Antarctic Circumpolar Current (ACC). Since the breakup of Gondwana, this gateway has been responsible for the free transfer of water masses between the Atlantic and Pacific oceans. The timing and manner of the opening of the central Scotia Sea, responsible for the opening of the ocean floor of Drake Passage, are still under discussion (e.g., Acosta Hospitaleche et al., 2013; Eagles et al., 2006). Some authors sustain that this opening and expansion of the ocean floor would have occurred between 50 Ma and 41 Ma, causing for the first time a shallow ocean circulation between the Pacific and Atlantic oceans (e.g., Eagles et al., 2006). Geophysical and paleontological data indicate that the Antarctic Peninsula and southern South America (Patagonia

+ Magallanes Region) disconnected probably before the end of the early Eocene, and that by the mid-late Eocene the continents were already separated by several hundred-kilometer-wide marine gaps (e.g., Ksepka et al., 2006). Unfortunately, age estimates for the onset of a seaway through the Drake Passage between the Antarctic Peninsula and southern South America range from the middle Eocene (Livermore et al., 2005; Scher and Martin, 2006) to the Oligocene (Lawver and Gahagan, 2003) or even the Early Miocene (Barker, 2001), complicating interpretations of the relation between ocean circulation and global cooling.

The subsequent development of a deep-water sea route between southernmost South America and the Antarctic Peninsula generated not only the final isolation of South America during the Paleogene, but also accentuated the development of different marine ecosystems characteristic of the Weddellian Biogeographic Province. These marine ecosystems show affinities in the taxonomic composition of their vertebrate assemblages (Zinsmeister, 1979), as is the case of sea turtles and penguins. Even more, in the case of penguins, Acosta Hospitaleche et al. (2013) pointed out that the evolution of the group was influenced by the opening of the Drake Passage with the consequent development of the ACC.

5 Conclusions

The dermochelyid turtle from the Leticia Formation (Tierra del Fuego Island, Argentina), together with *Maorichelys wiffeni* (Burnside Formation, New Zealand; Karl and Tichy, 2007) is one of the most complete materials known for the Eocene of the southern hemisphere. The Leticia dermochelyid record is composed by caudal vertebrae, a thoracic vertebra, ossicles and a proximal humerus that could correspond to the same individual, probably adult, with a forelimb stylopodium of an estimated length of 36–40 cm. The morphology of the proximal humerus fragment is more similar to *Maoricheys wiffeni*, from the mid-late Eocene of New Zealand, than to the extant dermochelyid *Dermochelys coriacea*, and other extinct (e.g., *Eosphargis gigas*, *Egyptemys eocaenus*) dermochelyids. However, the humerus from the Leticia Formation presents certain differences with respect to *Maoricheys wiffeni*, such as the size of the bone and the position of the proximal head, which is inclined more ventrally in the New Zealand species (although these differences could be related with ontogenetic variation). The ossicles recovered in the Leticia Formation resemble those found at different levels of the late-middle Eocene of the La Meseta Formation and the uppermost Eocene/? Oligocene Submeseta Formation (Antarctica), and “*Psephophorus*” *terrypratchetti* from the Waihao Greensand Formation (New Zealand). Weddellian dermochelyids could be characterized by having the shell composed by a mosaic of relatively small bony ossicles,

without keels or ridges, no linear arrangements of enlarged ossicles, and with no obvious differentiation in the size or shape of individual ossicles. The presence of dermochelyids as components of the Weddellian fauna of the middle to late Eocene/? Oligocene in such high latitudes, is compatible with both paleoclimatic scenarios proposed for the opening of the Drake Passage (e.g., Judd et al., 2019; Porebski, 2000), since the possible anatomical and likely physiological adaptations of these turtles would allow them to inhabit waters with a wide temperature gradient, just as it occurs with the living *Dermochelys coriacea*.

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