The first Oligocene sea turtle (Pan-Cheloniidae) record of South America

Edwin Cadena¹, Juan Abella²,³ and Maria Gregori²

¹ Escuela de Ciencias Geológicas e Ingeniería, Yachay Tech, San Miguel de Urcuquí, Imbabura, Ecuador
² Universidad Estatal de la Península de Santa Elena, La Libertad, Santa Elena, Ecuador
³ Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Barcelona, Spain

ABSTRACT

The evolution and occurrence of fossil sea turtles at the Pacific margin of South America is poorly known and restricted to Neogene (Miocene/Pliocene) findings from the Pisco Formation, Peru. Here we report and describe the first record of Oligocene (late Oligocene, ∼24 Ma) Pan-Cheloniidae sea turtle remains of South America. The fossil material corresponds to a single, isolated and well-preserved costal bone found at the Montañita/Olón locality, Santa Elena Province, Ecuador. Comparisons with other Oligocene and extant representatives allow us to confirm that belongs to a sea turtle characterized by: lack of lateral ossification, allowing the dorsal exposure of the distal end of ribs; dorsal surface of bone sculptured, changing from dense vermiculation at the vertebral scute region to anastomosing pattern of grooves at the most lateral portion of the costal. This fossil finding shows the high potential that the Ecuadorian Oligocene outcrops have in order to explore the evolution and paleobiogeography distribution of sea turtles by the time that the Pacific and the Atlantic oceans were connected via the Panama basin.

INTRODUCTION

Sea turtles are iconic vertebrates that have inhabited Earth’s oceans for at least 125 Ma (See Cadena & Parham, 2015). However, their evolution and fossil record in South America during the Cenozoic (∼66 Ma to present) is still poorly explored and understood. At present, the South American fossil record of Cenozoic sea turtles (Chelonioida: Dermochelyidae + Pan-Cheloniidae, following Parham & Pyenson (2010) is restricted to the Paleocene (Danian) Pampaemys meridionalis De la Fuente & Casadio (2000), from the Roca and Jagüel Formations, Northern Patagonia, Argentina, later changed to Euclastes meridionalis (Lynch & Parham, 2003; De la Fuente et al., 2009), and currently attributed as Erquelinnesia meridionalis Parham & Pyenson (2010); the Miocene Pacificelys urbinai, represented by skulls, lower jaws, cervical vertebrae, a partial carapace and a few non-described plastron fragments, from the Pisco Formation, Department of Ica, Peru (Parham & Pyenson, 2010); and the dermochelyids: Natemys peruvianus also from the Pisco.
Formation, Peru (Wood et al., 1996), and undescribed remains from Chilcatay Formation (Oligocene to Miocene) of Peru (Brand et al., 2011).

Recently, a late Oligocene fossil site at the Pacific coast of Ecuador, Monteñita-Olón locality (Fig. 1) has shown being rich in marine vertebrates, including a new genus and species of dolphin *Urkudelphis chawpipacha* (Tanaka et al., 2017), abundant sharks and actinopterygian fish teeth (J Carrillo-Briceño et al., 2018, unpublished data) and isolated turtle remains. Here we describe an isolated costal bone belonging to a sea turtle from this site, which constitute the first record of Oligocene Pan-Cheloniidae sea turtles in South America. In addition, we discuss the importance of this fossil site for understanding the evolution and paleobiogeography of sea turtles in the American continent.

**MATERIALS AND METHODS**

**Fossil material**

The fossil costal bone described here is housed in the paleontological collection at the Universidad Estatal de la Península de Santa Elena (UPSE), La Libertad, Santa Elena Province, Ecuador. Specimen UPSE-T0036. Comparisons of this fossil was done with some extant representatives of Cheloniidae as follow: *Caretta caretta* NMW 31531 and 1858; *Eretmochelys imbricata* NMW 1853 and MTKD D 8295; and *Lepidochelys olivacea* YT-Ver-0002. Permit for paleontological exploration of the Monteñita/Olón locality was
granted to J Abella by the Instituto Nacional de Patrimonio Cultural (INPC) of Ecuador, permit No 0039-DR5.INPC.2015.

SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788  
Cryptodira Cope, 1868  
Chelonioid Baur, 1893  
Pan-Cheloniidae Joyce, Parham & Gauthier, 2004  
Gen. and Sp. Indet. (Fig. 2)

Locality and age

Montañita/Olón locality, between the towns of Montañita and Olón, Santa Elena Province, Ecuador (1° 48’ 50.64” S, −80° 45’ 24.18” W). Here, we provisionally identify the source horizon for UPSE-T0036 as the Zapotal Member of the Dos Bocas Formation following Whittaker (1988). However, the age of this horizon is well constrained based on the occurrence of fossil shark Carcharocles angustidens, indicating that it is late Oligocene in age (Bristow, 1975; Tanaka et al., 2017).

Description

UPSE-T0036 corresponds to a right costal 4 (14.5 cm length, 3.8 cm width as preserved) (Figs. 2A–2B). We use a specimen of the extant Eretmochelys imbricata MTKD D 8295 to indicate the anatomical position of UPSE-T0036 in a complete turtle carapace (Fig. 2C). UPSE-T0036 is a rectangular costal bone with almost the same medial and lateral regions width, lacking of fully ossified lateral region, which allows the exposure of the distal end of the costal rib. On its dorsal surface the bone exhibits a sculpturing pattern that varies along its width, being of dense vermiculation at the vertebral scute region (medial portion of the costal) (Fig. 2D), changing to anastomosing to almost parallel pattern of grooves at its lateral portion (Fig. 2E). The sulci between pleural and vertebral scutes are well defined, indicating that the vertebral scute covered 1/3 of the total surface of the bone, ending laterally in an acute tip. The sulcus between pleurals separates the bone in two almost equal portions. On its ventral surface (Figs. 2F–2G) the outline of the costal rib is defined along the length of the bone, showing a well-developed rib-head of the costal for the attachment with the thoracic vertebra.

DISCUSSION

Taxonomical attribution and comparisons

UPSE-T0036 costal bone is attributed as belonging to Pan-Cheloniidae by sharing with some of the fossil and extant representatives of this clade the following characteristics: lack of lateral ossification but keeping a considerable thickness (5–7 mm), allowing the dorsal exposure of the distal end of ribs; dorsal surface of bone scuptured, changing from dense vermiculation at the vertebral scute region to anastomosing pattern of grooves at the most lateral portion of the costal. Lateral reduction in ossification of costals allowing
Figure 2  Pan-chelonid (Gen. and Sp. Indt.) from Montañita/Olón locality compared with some extant marine turtles. (A–B). UPSE-T0036 right costal 6 in dorsal view. (C). Carapace of Eretmochelys imbricata MTKD D 8295, right costal 6 in yellow shadow. (D). Close-up of the medial region of UPSE-T0036 showing the pitted-vermiculated bone surface sculpturing (see circle (D) in (B)). (E). Close-up of the lateral region of UPSE-T0036 showing a bone surface sculpturing of anastomosing grooves (see circle (E) in (B)). (F–G). UPSE-T0036 right costal 6 in ventral view. (H–I). Right costal 6 of the extant Lepidochelys olivacea YT-Ver-0002 in dorsal view. (J–K). Right costal 6 of the extant Lepidochelys olivacea YT-Ver-0002 in ventral view. (L). Close-up of the medial region of Lepidochelys olivacea YT-Ver-0002 showing the pitted-vermiculated bone surface sculpturing (see circle (L) in (I)). (M). Close-up of the lateral region of Lepidochelys olivacea YT-Ver-0002 showing a bone surface sculpturing of anastomosing grooves (see circle (M) in (I)). Top scale bar applies for (A–B) and (F–G), bottom scale bar applies for (H–I) and (J–K). Abbreviations: co, costal bone; cr, costal rib; P, pleural scute; rh, rib head; V, vertebral scute.
Table 1  Comparison of the morphological characteristics of costal bones of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys*, with crown Cheloniidae (*Trachyaspis*, *Natator*, *Lepidochelys*, *Caretta*, *Chelonia*, *Eretmochelys*), with the addition of *Pacifichelys Parham & Pyenson (2010)* and UPSE-T-0036 Pan-Cheloniidae (Gen. and Sp. Indet.) described herein. Table taken and modified from *Weems & Sanders (2014)*.

| Character                  | *Carolinochelys* | *Procolpochelys* | *Ashleychelys* | UPSE-T-0036 | *Pacifichelys* | Crown Cheloniidae |
|----------------------------|------------------|------------------|----------------|-------------|----------------|--------------------|
| Costal bones surface texture | Sculptured and uniform along the entire bone surface | Faintly sculptured to smooth | Strong sculptured and uniform along the entire bone surface | Strong sculptured, pitted-vermiculate medially, anastomosing grooves laterally | Sculptured and uniform along the entire bone surface | Faintly to strong sculptured, uniform or with variation from the medial to the lateral portions of the bones. |
| Carapace thickness         | Moderate         | Thick            | Moderate        | Moderate    | Moderate       | Moderate           |
| Vertebral scutes           | Narrow           | Narrow           | Wide            | Narrow      | ?              | Narrow to wide     |

the exposure of costal ribs occur also in some other turtles as for example Chelydridae (snapping and alligator turtles), however in these turtles the bone thickness is extremely reduced and the dorsal surface is smooth and developing ridges or knobs. Other groups of turtles that also exhibit reduction in lateral ossification of costals is the Tryionichidae (soft-shelled turtles), but in contrast to chelydrids and pan-cheloniids they develop a very distinct pitted dorsal bone sculpturing and absence of sulci from keratinous scutes.

Among pan-cheloniids UPSE-T0036 resembles the sculpturing pattern of other Cenozoic fossil forms from North and South America, as for example *Ashleychelys palmeri Weems & Sanders (2014)* from Charleston, South Carolina, USA, and the Miocene *Pacifichelys urbinai Parham & Pyenson (2010)* from Peru. However, it differs from the first one in having a narrower covering of the costal by the vertebral scute (as indicated by the sulcus). Unfortunately, the posterior region of the carapace is unknown for *P. urbinai*, avoiding to establishing if sculpturing pattern and scutes arrangement was similar as in UPSE-T0036. Other Oligocene sea turtles from South Carolina: *Procolpochelys charlestonensis Weems & Sanders (2014)* and *Carolinochelys wilsoni Hay (1923)* differ from UPSE-T0036 by having faintly sculptured to almost smooth dorsal carapacial bones. Table 1 shows the comparisons between UPSE-T0036 and Cenozoic taxa from American continent.

UPSE-T0036 resembles in geometry, sulci and medial to lateral sculpturing pattern variation of the posterior costals of some extant sea turtles, as for example *Lepidochelys olivacea* YT-Ver-0002 (Figs. 2H–2M), differing from this particular specimen by a wider covering of the vertebral scute on the costal surface. The width of vertebral scutes exhibit intraspecific variation as we observed in specimens of *Caretta caretta* NMW 31531 and 1858; and *Eretmochelys imbricata* NMW 1853 and MTKD D 8295 (Fig. 2C), for example in this last specimen the posterior vertebral scutes almost reach the most lateral portions of costal bones.
Importance of Montañita-Olón locality for South American sea turtle evolution understanding

The marine fossil vertebrates (cetaceans, sharks and turtles) recently discovered and described from the Oligocene, Montañita/Olón locality of Ecuador (Tanaka et al., 2017, J Carrillo-Briceño et al., 2018, unpublished data) represent the first occurrences of each of these groups in Paleogene (Oligocene) sequences of tropical South America; and for the particular case of turtles, the first Oligocene record of Pan-Cheloniidae marine turtles for the whole South America. Even though the material described herein corresponds to a single and isolated bone—reason why we avoid to formulate any further systematic or phylogenetic affinity hypotheses; it sets up a very promising scenario for future exploration and finding of new and more complete specimens that could elucidate if for instance the already known Oligocene sea turtle taxa from North America (Weems & Sanders, 2014; Weems & Sanders, 2017) inhabited also the tropical Pacific coast of South America; a hypothesis that it seems to be possible considering that during the Oligocene, the Pacific and the Atlantic oceans were connected via the Panama basin (Pindell, 1994; Boschman et al., 2014; Jaramillo, 2018) (Fig. 3A).

Thus, more complete sea turtle specimens from Montañita/Olón could shed light in establishing relationships with younger marine taxa from South America, as for example with the Miocene *Pacifichelys urbinai* Parham & Pyenson (2010) from Peru (Fig. 3B), or...
potentially being direct ancestors of any of the five extant representatives that inhabit the Pacific coast of tropical South America (Turtle Taxonomy Working Group et al., 2017) (Fig. 3C).

The fossil sea turtle material from Montaña/Olón also increases the knowledge on the fossil turtle paleobiodiversity of Ecuador, being the first record of a marine fossil turtle in the country and an addition to the already known occurrences of Pleistocene freshwater and terrestrial fossil turtles from Santa Elena Province (Cadena, Abella & Gregori, 2017).

CONCLUSIONS

The costal bone described herein is the first undisputable record of Oligocene (late Oligocene, ∼24 Ma) marine turtles Pan-Cheloniidae of South America. This fossil finding shows the high potential that the Ecuadorian Oligocene outcrops have in order to explore the evolution and paleobiogeography distribution of sea turtles by the time that the Pacific and the Atlantic oceans were connected via the Panama basin. More complete specimens will have to be found in the Montaña/Olón in order to establish in detail the taxonomy and phylogenetic relationships of the Oligocene sea turtles that inhabited this part of South America. We hope this finding will encourage more paleontological expeditions and support for this type of studies in Ecuador and northern South America.

Institutional abbreviations

| Abbreviation | Institution |
|--------------|-------------|
| MTKD         | Senckenberg Museum of Natural History, Dresden collections, Germany. |
| NMW          | Natural History Museum of Vienna, Austria. |
| UPSE         | paleontological collection, Universidad Estatal de la Península de Santa Elena La Libertad, Santa Elena Province, Ecuador. |
| YT           | Yachay Tech paleontological collection, San Miguel de Urcuquí, Ecuador. |

ACKNOWLEDGEMENTS

Thanks to K Guerrero for assistance in the logistics during the visit of the first author (E Cadena) to Santa Elena Province. JA thanks the Marine Biology students and staff from UPSE, who actively participated in the fieldwork, and the “Comuna de Montaña” and “Comuna de Olón” for their support. We thank the Instituto Nacional de Patrimonio Cultural (INPC) for the prospection and excavation permits. We thank the three reviewers (J Parham, I Danilov, and R Hirayama) for their comments and suggestions to improve this manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Funding for this work was provided by the Alexander von Humboldt Foundation of Germany under a return fellowship given to the first author and funds from the School of Geological Science and Engineering of Yachay Tech. “Proyecto Prometeo” of the “Secretaria de Educación Superior, Ciencia Tecnología e Innovación”, Republic of Ecuador.
The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures
The following grant information was disclosed by the authors:
Alexander von Humboldt Foundation of Germany.
School of Geological Science and Engineering of Yachay Tech.

Competing Interests
The authors declare there are no competing interests.

Author Contributions
- Edwin Cadena conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Juan Abella and Maria Gregori conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Field Study Permissions
The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):
The permit for paleontological exploration of the Montañita/Olón locality was granted to J Abella by the Instituto Nacional de Patrimonio Cultural (INPC) of Ecuador, permit No 0039-DR5.INPC.2015.

Data Availability
The following information was supplied regarding data availability:
Specimen UPSE-T0036 is stored at Universidad Estatal de la Península de Santa Elena (UPSE), La Libertad, Santa Elena Province, Ecuador.

REFERENCES
Alroy J. 2009. Taxonomic occurrences of Chelonioidea recorded in the Paleobiology Database. Fossilworks. Available at http://fossilworks.org (accessed on 08 February 2018).
Batsch AJ. 1788. Versuch einter Anleitung, zur Künntniss und Geschichte der Thiere und Mineralien. Jena: Akademie Buchhandlung, 22.
Baur G. 1893. Notes on the classification of the Cryptodira. American Naturalist 27:672–675.
Blakey R. 2016. Paleomaps. Available at https://www2.nau.edu/rcb7/globaltext2.html (accessed on 08 February 2018).
Boschman LM, Van Hinsbergen DJJ, Torsvik TH, Spakman W, Pindell JL. 2014. Kinematic reconstruction of the Caribbean region since the Early Jurassic. Earth-Science Reviews 138:102–136 DOI 10.1016/j.earscirev.2014.08.007.
Brand L, Urbina M, Chadwick A, DeVries TJ, Esperante R. 2011. A high resolution stratigraphic framework for the remarkable fossil cetacean assemblage of the Miocene/Pliocene Pisco Formation, Peru. Journal of South American Earth Sciences 31:414–425 DOI 10.1016/j.jsames.2011.02.015.

Bristow CR. 1975. On the age of the Zapotal Sands of Southwest Ecuador. Newsletter Stratigraphy 4:119–134 DOI 10.1127/nos/4/1975/119.

Cadena EA, Abella J, Gregori M. 2017. New findings of Pleistocene fossil turtles (Geemydidae, Kinosternidae and Chelydridae) from Santa Elena Province, Ecuador. PeerJ 5:e3215 DOI 10.7717/peerj.3215.

Cadena EA, Parham JF. 2015. Oldest known marine turtle? A new protostegid from the Lower Cretaceous of Colombia. PaleoBios 32:1–42.

Cadena EA, Rincon A, Bourque J, Jaramillo C, Montes C, Bloch J, MacFadden B. 2012. New Turtles (Chelonia) from the Late Eocene Through Late Miocene of the Panama Canal Basin. Journal of Paleontology 86:539–557 DOI 10.1666/11-106.1.

Cope E. 1868. On the origin of genera. Proceedings of the Academy of Natural Sciences of Philadelphia 20:242–300.

De la Fuente MS, Casadío SE. 2000. Un nuevo osteopigino (Chelonii: Cryptodira) de la Formación Roca (Paleoceno inferior) de Cerros Bayos, provincia de La Pampa, Argentina. Ameghiniana 37:235–246.

De la Fuente MS, Fernández M, Parras A, Herrera Y. 2009. Euclastes meridionalis (De la Fuente & Casadío) (Testudines: Pancheloniidae) from Danian levels of the Jagüel Formation at Cerro Azul, Northern Patagonia, Argentina. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 253:327–339 DOI 10.1127/0077-7749/2009/0253-0327.

Hay OP. 1923. Oligocene sea turtles of South Carolina. Pan-American Geologist 40:29–31.

Jaramillo CA. 2018. Evolution of the Isthmus of Panama: biological, paleoceanographic and paleoclimatological implications. In: Hoorn K, Perrigo A, Antonelli A, eds. Mountains, climate and biodiversity. Oxford: Wiley Blackwell, 323–338.

Joyce WG, Parham JF, Gauthier JA. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78:989–1013 DOI 10.1666/0022-3360(2004)078<989:DAPFTC>2.0.CO;2.

Lynch SC, Parham JF. 2003. The first report of hard-shelled sea turtles (Cheloniidae sensu lato) from the Miocene of California, including a new species (Euclastes hutchisoni) with unusually plesiomorphic characters. PaleoBios 23:21–35.

Parham JF, Pyenson ND. 2010. New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. Journal of Paleontology 84:231–247 DOI 10.1666/09-077R.1.

Pindell JL. 1994. Evolution of the Gulf of Mexico and the Caribbean. In: Donovan SK, Jackson TA, eds. Caribbean geology: an introduction. Kingston: University of the West Indies Press, 13–39.
Tanaka Y, Abella J, Aguirre-Fernández G, Gregori M, Fordyce RE. 2017. A new tropical Oligocene dolphin from Montañita/Olón, Santa Elena, Ecuador. *PLOS ONE* 12:e0188380 DOI 10.1371/journal.pone.0188380.

Turtle Taxonomy Working Group, Rhodin AGJ, Iverson JB, Bour R, Fritz U, Georges A, Shaffer HB, Van Dijk PP. 2017. In: Rhodin AGJ, Iverson JB, Van Dijk PP, Saumure RA, Buhlmann KA, Pritchard PCH, Mittermeier RA, eds. *Turtles of the world, 8th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC tortoise and freshwater turtle specialist group*, Vol. 7. New York: Chelonian Research Foundation, 1–292 DOI 10.3854/crm.7.checklist.atlas.v8.2017.

Weems RE, Sanders AE. 2014. Oligocene pancheloniid sea turtles from the vicinity of Charleston, South Carolina, U.S.A. *Journal of Vertebrate Paleontology* 34:80–99 DOI 10.1080/02724634.2013.792826.

Weems RE, Sanders AE. 2017. More-complete remains of *Procolpochelys charlestonensis* (Oligocene, South Carolina), an occurrence of *Euclastes* (upper Eocene, South Carolina), and their bearing on Cenozoic pancheloniid sea turtle distribution and phylogeny. *Journal of Vertebrate Paleontology* 34:80–99.

Whittaker JE. 1988. *Benthic Cenozoic foraminifera from Ecuador: taxonomy and distribution of smaller benthic foraminifera from Coastal Ecuador (late Oligocene—late Pliocene)*. London: British Museum (Natural History).

Wood RC, Johnson-Gove J, Gaffney ES, Maley KF. 1996. Evolution and phylogeny of Leatherback turtles (Dermochelyidae), with descriptions of new fossil taxa. *Chelonian Conservation and Biology* 2:266–286.