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The first Paleogene (Oligocene) sea turtle record of South America

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The evolution and occurrence of fossil sea turtles at the Pacific margin of South America is poorly known and restricted to Neogene (Miocene) findings from Perú. Here we report and describe the first record of Paleogene (Late Oligocene, ~24 Ma) sea turtle remains. 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 belong 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 and changing to anastomosing pattern of grooves at the most lateral portion of the costal. This fossil finding shows the high potential that the Ecuadorian Paleogene 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.

1 The first Paleogene (Oligocene) sea turtle record of South America

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10

11 **Abstract**

12 The evolution and occurrence of fossil sea turtles at the Pacific margin of South America is
13 poorly known and restricted to Neogene (Miocene) findings from Perú. Here we report and
14 describe the first record of Paleogene (Late Oligocene, ~24 Ma) sea turtle remains. The fossil
15 material corresponds to a single, isolated and well-preserved costal bone found at the
16 Montañita/Olón locality, Santa Elena Province, Ecuador. Comparisons with other Oligocene and
17 extant representatives allow us to confirm that belong to a sea turtle characterized by: lack of
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22 evolution and paleobiogeography distribution of sea turtles by the time that the Pacific and the
23 Atlantic oceans were connected via the Panama basin.

24

25 **INTRODUCTION**

26 Sea turtles are iconic vertebrates that have inhabited Earth's oceans for at least 125 Ma (*Cadena*
27 *& Parham 2015*). However, their evolution and fossil record in South America during the
28 Cenozoic (~66Ma to present) is still poorly explored and understood. At present, the South
29 American fossil record of sea turtles (Pan-Chelonioidae) is restricted to the middle Miocene
30 *Pacifiquelys urbinai*; represented by skulls, lower jaws, cervical vertebrae, and a partial carapace
31 and a few non-descript plastron fragments, from the Pisco Formation, Department of Ica, Peru
32 (*Parham & Pyenson 2010*).

33 Recently, a fossil site at the Pacific coast of Ecuador (*Fig. 1*) has shown being rich in marine
34 vertebrates, including a new genus and species of dolphin *Urkudelphis chawpipacha* (*Tanaka et*
35 *al. 2017*), abundant sharks and fish teeth (*Carillo-Briceño et al., unpublished data*) and isolated
36 turtle remains. Here we describe an isolated costal bone belonging to a sea turtle, which

37 constitute the first record of Paleogene (Oligocene) sea turtles in South America. Thus, we
38 discuss the importance of this fossil site for understanding the evolution and paleobiogeography
39 of sea turtles in the American continent.

40 MATERIALS AND METHODS

41 Fossil material

42 The fossil costal bone described here is housed in the paleontological collection at the
43 Universidad Estatal de la Peninsula de Santa Elena (UPSE), La Libertad, Santa Elena Province,
44 Ecuador. Specimen UPSE-T0036. Comparisons of these fossils were done with some extant
45 representatives of Cheloniidae as follow: *Caretta caretta* NMW 31531 and 1858; *Eretmochelys*
46 *imbricata* NMW 1853 and MTKD D 8295; and *Lepidochelys olivacea* YT-Ver-0002. Permit for
47 paleontological exploration of the Montañita/Olón locality was granted to J. Abella by the
48 Instituto Nacional de Patrimonio Cultural (INPC) of Ecuador, permit N° 0039-DR5.INPC.2015.

49 SYSTEMATIC PALEONTOLOGY

50 Testudines *Batsch, 1788*

51 Cryptodira *Cope, 1868*

52 Pan-Chelonioida *Joyce, Parham, and Gauthier, 2004*

53 Gen. and Sp. Indet. (**Fig. 2**)

54

55 Locality and Age

56 Montañita-Olón locality, between the towns of Montañita and Olón, Santa Elena Province,
57 Ecuador (1°48'50.64" S, -80°45'24.18" W). Here, we provisionally identify the source horizon
58 for UPSE-T0036 as the Zapotal Member of the Dos Bocas Formation following Whittaker
59 (1988). However, the age of this horizon is well constrained based on the occurrence of fossil
60 shark *Carcharocles angustidens*, indicating that is late Oligocene in age (*Bristow 1975, Tanaka*
61 *et al., 2017*).

62

63 **Description.** UPSE-T0036 corresponds to a right costal 4 (14.5 cm length, 3.8 cm width as
64 preserved) (**Fig. 2 A-B**). We use a specimen of the extant *Eretmochelys imbricata* MTKD D
65 8295 to indicate the anatomical position of UPSE-T0036 in a turtle carapace (**Fig. 2 C**). UPSE-
66 T0036 is a rectangular costal bone with almost the same width at the anterior and posterior
67 margins, lacking of fully ossified lateral region, which allows the exposure of the distal end of
68 the costal rib. On its dorsal surface the bone exhibits a sculpturing pattern that varies along its
69 length, being of dense vermiculation at the vertebral scute region (medial portion of the costal)
70 (**Fig. 2 D**), changing to anastomosing to almost parallel pattern of grooves at its lateral portion
71 (**Fig. 2 E**). The sulci between pleural and vertebral scutes are well defined, indicating that the
72 vertebral scute covered 1/3 of the total surface of the bone, ending laterally in an acute tip. The
73 sulcus between pleurals separates the bone in two almost equal portions. On its ventral surface
74 (**Fig. 2 F-G**) the outline of the costal rib is define along the length of the bone, showing a
75 protuberant ventrally projected process for the attachment with the thoracic vertebra.

76

77 DISCUSSION

78 Taxonomical attribution and comparisons

79 UPSE-T0036 costal bone is attributed as belonging to Pan-Chelonioidea by sharing with some of
80 the fossil and extant representatives of this clade the following characteristics: lack of lateral
81 ossification but keeping a considerable thickness (5-7 mm), allowing the dorsal exposure of the
82 distal end of ribs; dorsal surface of bone sculptured, changing from dense vermiculation at the
83 vertebral scute region and changing to anastomosing pattern of grooves at the most lateral
84 portion of the costal. Lateral reduction in ossification of costals allowing the exposure of costal
85 ribs occur also in some other turtles as for example Chelydridae (snapping and alligator turtles),
86 however in these turtles the bone thickness is extremely reduced and the dorsal surface is smooth
87 and developing ridges or knobs. Other group of turtles that also exhibit reduction in lateral
88 ossification of costals is the Tryionichidae (soft-shelled turtles), but in contrast to chelydrids and
89 pan-chelonoidids they develop a very distinct pitted dorsal bone sculpturing and absence of sulci
90 from keratinous scutes.

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

102 UPSE-T0036 resembles in geometry, sulci and medial to lateral sculpturing pattern variation
103 of the posterior costals of some extant sea turtles, as for example *Lepidochelys olivacea* YT-Ver-
104 0002 (Fig. 2 H-M), differing from this particular specimen by a wider covering of the vertebral
105 scute on the costal surface. The width of vertebral scutes exhibit intraspecific variation as we
106 observed in specimens of *Caretta caretta* NMW 31531 and 1858; and *Eretmochelys imbricata*
107 NMW 1853 and MTKD D 8295 (Fig. 2 C), for example in this last specimen the posterior
108 vertebral scutes almost reach the most lateral portions of costal bones.

109

110 **Importance of Montañita-Olón locality for South American sea turtle evolution** 111 **understanding**

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

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

129 The fossil sea turtle material from Montañita-Olón also increases the knowledge on the
130 fossil turtle paleobiodiversity of Ecuador, being the first record of a marine fossil turtle in the
131 country and an addition to the already known occurrences of Pleistocene freshwater and
132 terrestrial fossil turtles from Santa Elena Province (*Cadena et al. 2017*).

133

134

135 CONCLUSIONS

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

145

146 Institutional abbreviations

147 MTKD, Senckenberg Museum of Natural History, Dresden collections, Germany; NMW,
148 Natural History Museum of Vienna, Austria; UPSE, paleontological collection, Universidad
149 Estatal de la Península de Santa Elena La Libertad, Santa Elena Province, Ecuador. YT, Yachay
150 Tech paleontological collection, San Miguel de Urcuquí, Ecuador.

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156 prospection and excavation permits.

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Table 1 (on next page)

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-Chelonioidea (Gen. and Sp. Indet.) described herein. Table taken and modified from Weens & Sanders (2014).

1 **Table 1.** Comparison of the morphological characteristics of costal bones of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys*, with
 2 crown Cheloniidae (*Trachyaspsis*, *Natator*, *Lepidochelys*, *Caretta*, *Chelonia*, *Eretmochelys*), with the addition of *Pacificchelys* *Parham*
 3 & *Pyenson* (2010) and UPSE T-0036 Pan-Chelonioida (Gen. and Sp. Indet.) described herein. Table taken and modified from *Weens*
 4 & *Sanders* (2014).
 5

Character	<i>Carolinochelys</i>	<i>Procolpochelys</i>	<i>Ashleychelys</i>	UPSE-T-0036	<i>Pacificchelys</i>	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

6

Figure 1

Map of Ecuador showing Santa Elena Province.

Location and outcrop of Montañita/Olón locality from where UPSE-T0036 described herein was found.

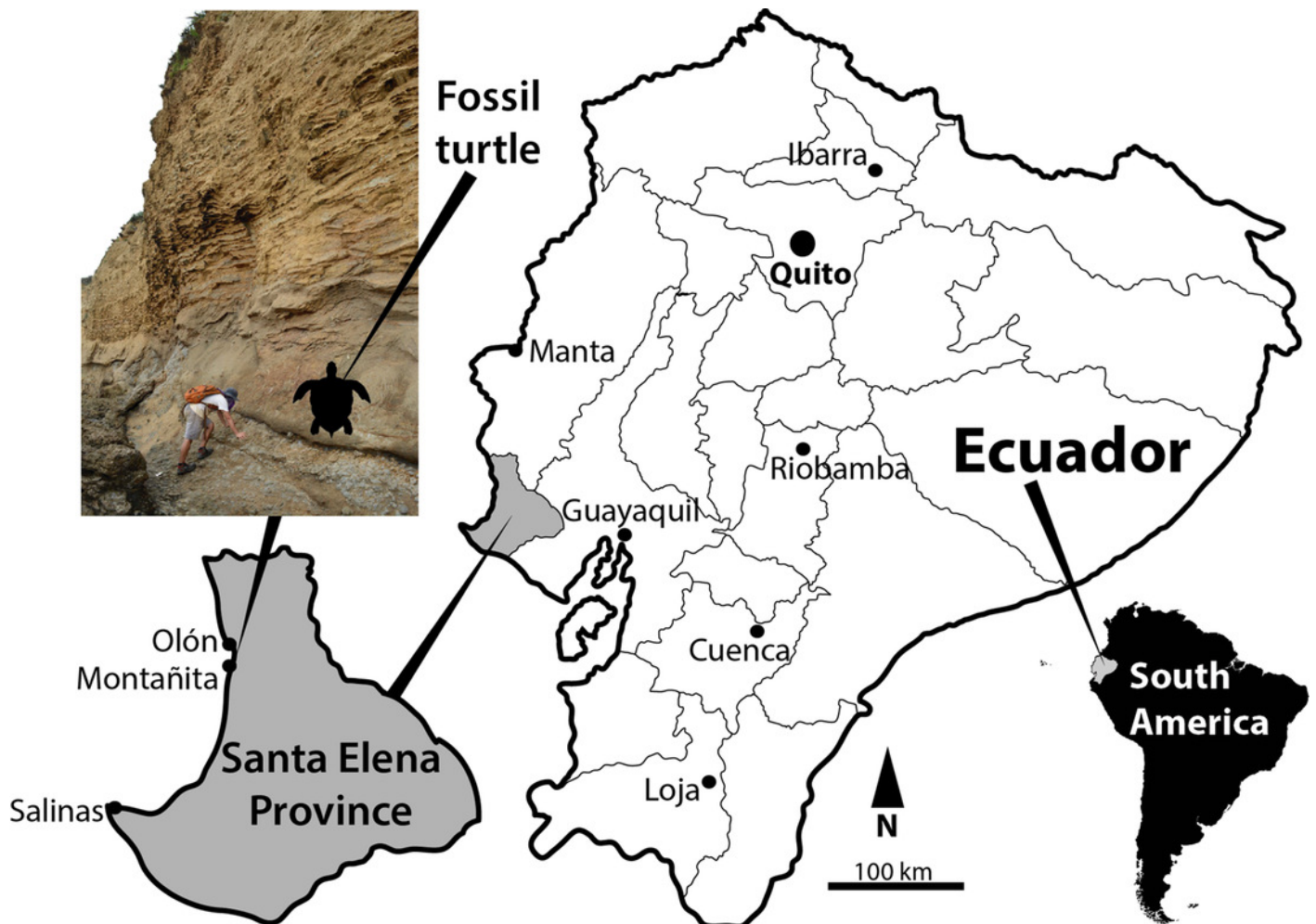


Figure 2

Pan-chelonoidid (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 shadows. (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.

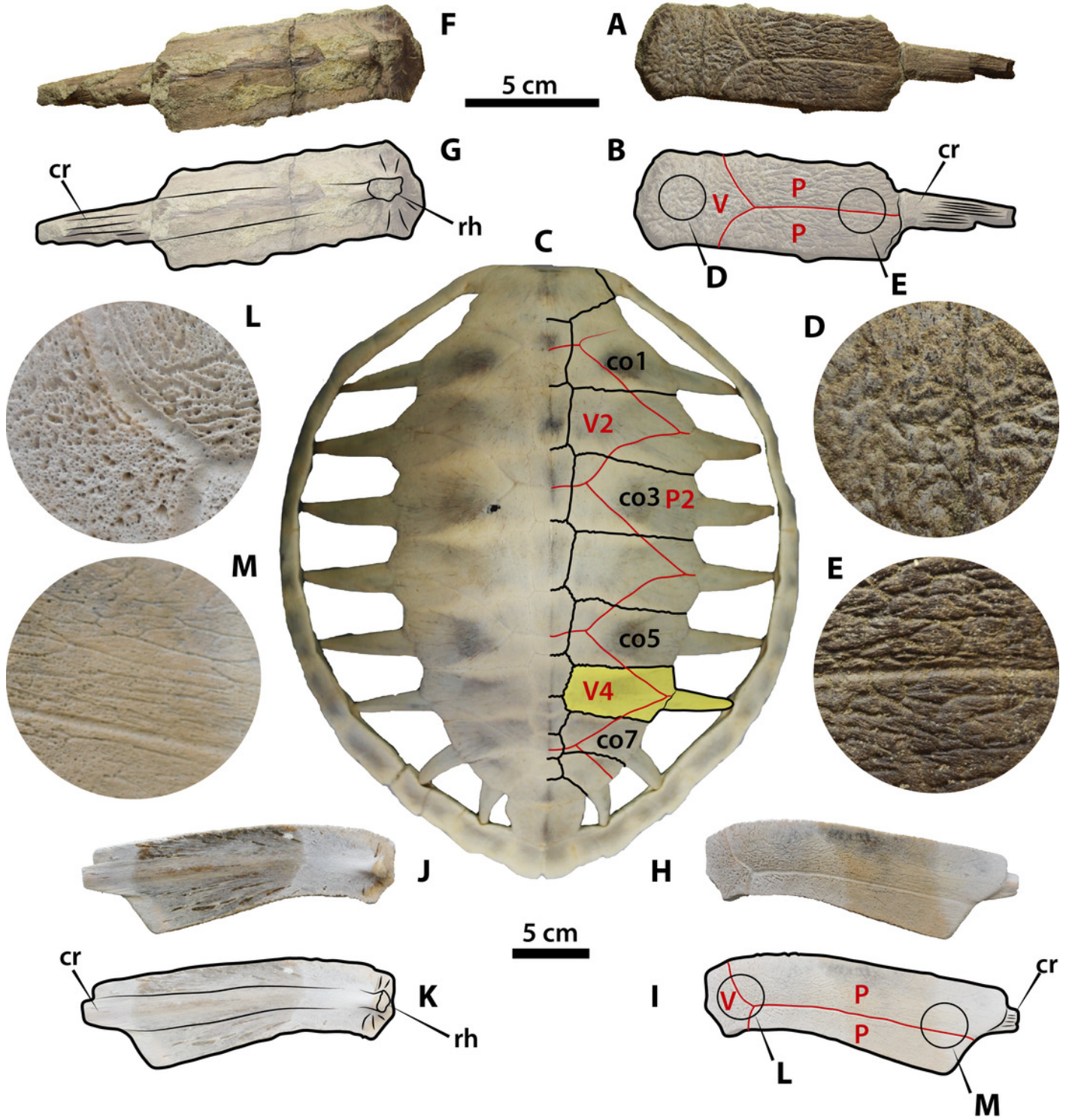


Figure 3

Paleogeographic reconstruction of South America and the fossil and extant distribution of chelonioidid marine turtles.

(A). Oligocene fossil occurrences of chelonioidid turtles, including the first record of South America described here (UPSE-T0036). (B). Miocene, fossil occurrences of chelonioidid turtles, adding the record from Panama basin (*Cadena et al. 2012*). (C). Present biogeographic distribution of marine turtles (Chelonioidia) based on *Turtle Taxonomy Working Group (2017)*. Red dots indicate fossil occurrences based on Fossilworks paleobiology database (*Alroy 2009*). Paleogeography taken and modified from *Bakley (2016)*. Abbreviations: F, Foraging., N, Nesting., V, Vagrant.

