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Oldest known sea turtle

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Reptiles constitute a primarily terrestrial assemblage, but several groups returned to the marine environment after the first appearance of reptiles in the late Palaeozoic era¹. Successful diversification of the chelonoid sea turtles, particularly during the Cretaceous period, was perhaps one of the most important events in the history of turtles (and marine reptiles)^{2–4}. The fossil record of chelonoids before the Late Cretaceous has been poorly documented. Here I report the discovery of an exceptionally well-preserved skeleton of the oldest known chelonoid, from the Early Cretaceous stage (about 110 million years before the present)^{5–7} of eastern Brazil. This specimen represents a new taxon, extending the history of chelonoids by 10 million years,

and it sheds new light on the early evolution of the group. The limb of the specimen is a relatively primitive paddle, which still possesses movable digits as in freshwater turtles. However, the skull is specialized in the manner of later chelonoids, with large interorbital foramina that are indicative of huge lachrymal salt glands surrounding the eyes^{8,9}. This discovery supports the idea that the establishment of the salt-excreting system, and the occupation of a marine habitat, may have preceded the formation of rigid paddles in the history of chelonoids.

Testudines Linnaeus 1766

Cryptodira Gray 1825

Eucryptodira Gaffney 1975

Chelonioidea Agassiz 1857

Protostegidae Cope 1873

Santanachelys gaffneyi, gen. et sp. nov.

Etymology. Santana, for the locality; chelys (Greek): turtle; gaffneyi, in honour of Eugene S. Gaffney, an authority on fossil turtles.

Holotype. THUG1386 (Teikyo Heisei University, Ichihara, Chiba, Japan), a nearly complete skeleton (Fig. 1).

Locality. Near Santana do Cariri, Ceara State, Brazil.

Horizon. Romualdo Member, Santana Formation (Early Cretaceous: Late Aptian or Early Albian)^{5–7}.

Diagnosis. Scute sulci on the dermal roofing elements of skull and the carapace are present; the nasal is much smaller than the prefrontal; the prefrontal–postorbital contact at the orbital rims is absent; the foramen palatinum posterius opens laterally; the lingual ridge of the maxilla is low, and not exposed from lateral ridge; the first thoracic rib is elongated, reaching to the distal end of the first costal; the lateral process of the humerus lacks a medial concavity; the articulations of the first and second metacarpals and



Figure 1 Holotype of *Santanachelys gaffneyi*, gen. et sp. nov. (THUG1386). The median length of the preserved carapace is 145 mm. **a**, Dorsal view. **b**, Ventral view. **c**, Left lateral view.

digits are movable; the xiphiplastra are as long as they are broad, and are medially attached along their entire length (Figs 1–3).

Santanachelys differs from all other chelonoids in its possession of an unusually elongate first thoracic rib. It differs from all other protostegids in its possession of large xiphiplastra and movable articulations of first and second metacarpals and digits, and in lacking a medial concavity of the lateral process of the humerus^{2,4}. It differs from *Rhinochelys*, a protostegid known primarily from isolated skulls, in possessing much smaller nasal bones^{2,10} and also in lacking an antero-dorsal bulge (Fig. 3a) (refs 2, 10).

The discovery of a chelonoid in the Santana Formation of Brazil extends the range of this group from the Late Albian (where species such as *Rhinochelys* and *Notochelone* have been found) back to the Early Albian or Late Aptian^{2,4}. The relationships of *Santanachelys* to other chelonoids and eucryptodires (Fig. 4) show that this is the most primitive member of the protostegid family of Cretaceous sea turtles^{2,4,10,11}. This result also implies that chelonoids had diversified into the three families (Protostegidae, Dermochelyidae and Cheloniidae) by the Early Albian or Late Aptian, and that the origin of chelonoids might be traced back much further, possibly to the Neocomian¹². *Santanachelys* is also the first known protostegid from South America. Despite its small body size (200-mm long as preserved), the highly ossified skeleton, particularly in the carapace and manus, indicates that this individual may have reached at least sub-adult size.

One of the major questions about the chelonoid adaptation to marine environments has concerned the timing of the modification of its limbs into paddle-like, propulsive organs, involving the immobilization of the manus and pes^{11,13,14}. The more primitive stage of paddle morphology was hitherto known only in some primitive cheloniids such as *Toxochelys*¹¹ (in the Late Cretaceous and *Tasbacka*¹⁵ (in the Paleocene), in which movable first and second metacarpals and (short) digits were retained. The discovery of this primitive grade of paddle in *Santanachelys* (Fig. 3e) indicates that the complete formation of paddles, consisting of immobile metacarpals and elongate digits, may have been independently acquired in each of the three families of chelonoids.

Studies of the living chelonoids have revealed another important adaptation to marine life among sea turtles^{8,9}. Most marine vertebrates must continuously confront the problem of water loss and salt gain; however, the kidneys of reptiles are unable to handle a large salt influx. Marine reptiles are unique in the variety of cephalic organs that can be used as salt glands. Salt excretion in sea turtles mainly occurs in salt-gland fluids secreted by highly modified lachrymal glands, which are much larger than the brain. The chelonoids are unique among the casichelydian turtles (turtles

descended exclusively from *Proganochelys*, the most primitive turtle from the Late Triassic) in that they possess a large foramen interorbitale formed by a relatively narrow processus inferior parietalis^{16–18}. The processus is completely lost in living *Dermochelys coriacea*¹⁷, which has particularly large lachrymal glands¹⁹. The enlargement of the posterior portion of the foramen interorbitale seems to be related to the development of the large lachrymal gland, which lies postero-medial to the eye of sea turtles^{19,20}. This portion of the foramen interorbitale is limited by a much broader processus inferior parietalis in most turtles^{16,17}. The Jurassic plesiochelyids, primitive eucryptodires once considered to be ancestral chelonoids¹⁶ but later regarded as more basal animals^{14,21} (Fig. 4), have a processus that is intermediate in size between those of the chelonoids and those of the other casichelydians¹⁶. A large foramen interorbitale with a narrow processus inferior parietalis like that in *Santanachelys* (Fig. 3d) is also seen in primitive chelonoids such as *Toxochelys*² (Cheloniidae) and *Corsochelys*²² (Dermochelyidae). This suggests that the large, salt-excreting lachrymal glands were already developed in this primitive sea turtle, and that the evolutionary appearance of the lachrymal gland preceded the formation of rigid paddles in the history of chelonoids. The function of the gland in excreting salt indicates that *Santanachelys* may have lived in a marine habitat (as

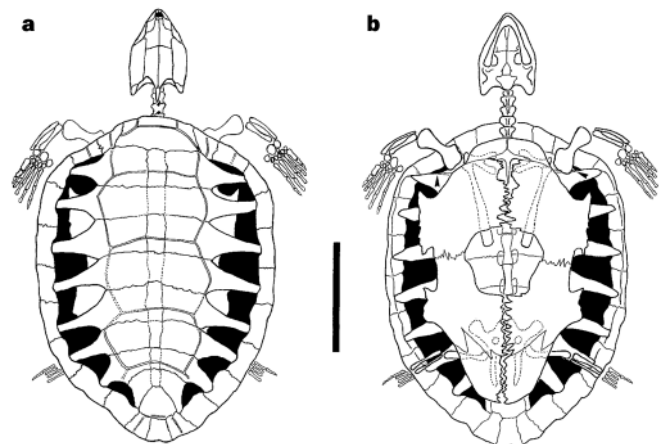


Figure 2 Skeletal reconstruction of *Santanachelys gaffneyi*, (THUG1386). **a**, Dorsal view. **b**, Ventral view, with appendicular skeleton overlying plastron shown by dotted lines. Arrowheads in **b** indicate the distal end of first thoracic ribs. Scale bar, 5 cm.

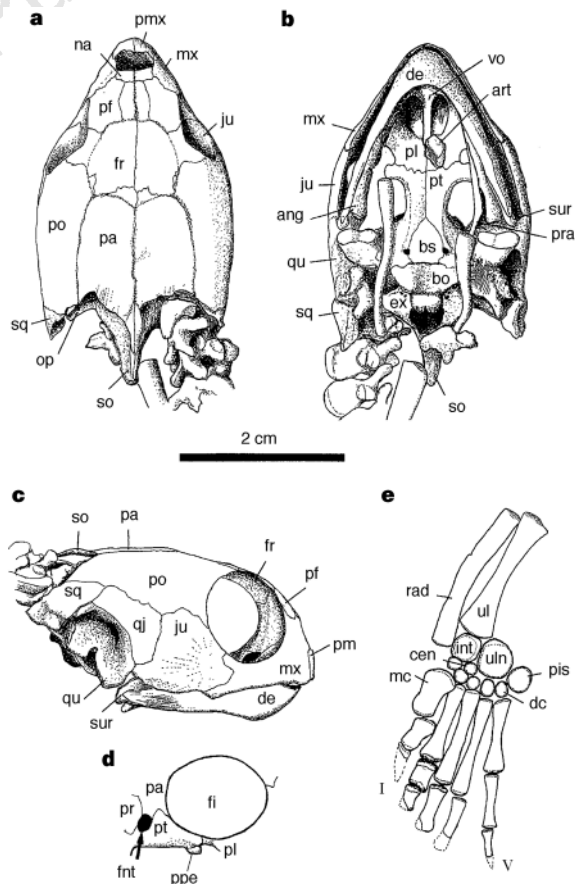


Figure 3 *Santanachelys gaffneyi* (THUG1386). The skull in **(a)** dorsal, **(b)** ventral and **(c)** right lateral views is shown, as is **(d)** the right ethmoid region of the skull. **e**, Left forelimb, dorsal view. Abbreviations: ang, angular; art, articular; bo, basioccipital; bs, basisphenoid; cen, centrale; dc, distal-carpal; de, dentary; ex, exoccipital; fi, foramen interorbitale; fr, frontal; fnt, foramen nervi trigemini; int, intermedium; ju, jugal; mc, metacarpal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pf, prefrontal; pis, pisiform; pl, palatine; pmx, premaxilla; po, postorbital; ppe, processus pterygoideus externus; pr, pro-otic; pra, prearticular; pt, pterygoid; qj, quadrato-jugal; qu, quadrate; rad, radius; so, supraoccipital; sq, squamosal; sur, surangular; ul, ulna; uln, ulnare; vo, vomer.

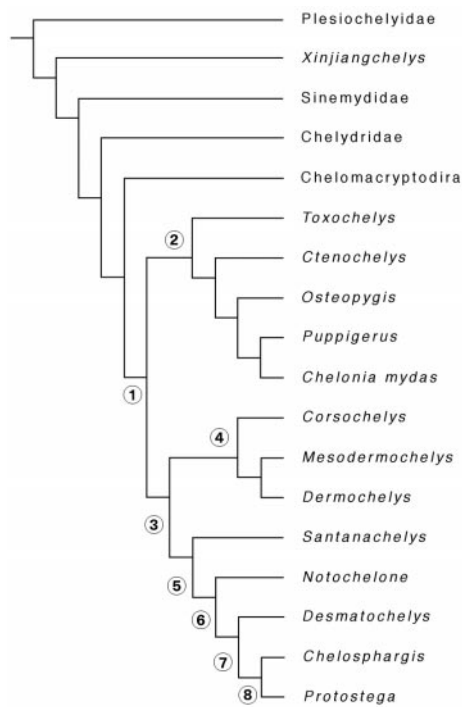


Figure 4 Cladogram showing relationships among selected eucryptodiran turtles. Chelonioida is the ingroup; other taxa are outgroups. The analysis is based on 104 characters; the tree length is 208; the consistency index is 0.567; and the retention index is 0.720. Circle numbers indicate nodes or branching points of chelonioids (see Methods).

also indicated by the depositional environment of the fossil)^{5,6}, and that the shift in environment preceded the evolution of paddles. □

Methods

Cladistic analysis was based on the implementation of the software package PAUP (phylogenetic analysis using parsimony) version 3.0, developed by D. L. Swofford. Terminal taxa included in the analysis are the Plesiochelyiidae, *Xinjiangchelys*, Sinemydiidae, Chelydridae (including *Platysternon*), Chelomacryptodira (Testudinoidea and Trionychoidea), and Chelonioida, including Cheloniidae (*Toxochelys*, *Ctenochelys*, *Osteopygis*, *Puppigerus* and *Chelonia mydas*), Dermochelyiidae (*Corsochelys*, *Mesodermochelys* and *Dermochelys*), and Protostegidae (*Santanachelys*, *Notochelone*, *Desmatochelys*, *Chelosphargis* and *Protostega*). For the list of the 104 osteological characters and the data matrix for the analysis, see Supplementary information. A single tree was obtained by a branch-and-bound search option (Fig. 4).

All characters were coded as reversible, and multistate characters were coded as unordered to avoid *a priori* assumptions of transformation vectors. When one or more taxa are coded as having multiple states, I interpret multiple states as uncertainty rather than polymorphism. Synapomorphies for the numbered nodes of chelonioids (Fig. 4) follow DELTRAN character optimization, because it is slightly more conservative in terms of assigning synapomorphies to clades in a data matrix with a substantial amount of missing data. Synapomorphies also shared unequivocally by ACCTRAN character optimization are italicized. For the complete list of synapomorphies of both DELTRAN and ACCTRAN character optimizations, see Supplementary information.

1. Chelonioida. *Processus inferior parietalis* as narrow as the foramen nervi trigemini or absent; foramen stapedio temporale concealed from dorsal by dermal roofing elements; *foramen premaxillae* absent; *paired foramina arterius canalis carotici interni* lie close together; *dorsum sellae* high and separated from *sella turcica* and *anterius canalis carotici interni*; symphyseal ridge of dentary present; first thoracic ribs limited within nuchal width; coracoid as long as or much longer than humerus; humerus longer than femur; lateral process of the humerus located distal to caput humeri; *flat carpal and tarsal elements*; *Third to fifth digits without movable articulations*; *distal portion of costals reduced*; scute

sulci on plastron rudimentary or absent; *entoplastron not tightly sutured with hypoplastron*.

2. Cheloniidae. Orbital direction dorsolateral; *parietal–squamosal contact present*; *upper triturating surface involving palatines*; *apertura narium interna entirely formed by vomer and palatines*, excluding maxillae; *ventral surface of basisphenoid with V-shaped crest emerginated from posterior*; ventral thin keel at posterior cervical centra present; *ulna–radius contact through prominent distal rugosities*; cervical scute overlying more than half width of nuchal; *neural number nine by splitting of eighth or seventh neurals*.

3. Dermochelyioidae (Dermochelyiidae and Protostegidae). *Medial process of jugal absent*; jugal–pterygoid contact absent; *proportion of cervical centra as high as wide*; eighth cervical centrum longer than seventh; *first thoracic vertebra with its anterior articulation facing anteriorly*; *scapular angle formed by scapular prong and acromion about 110° or more*; *thyroid fenestra small, subdivided*; *lateral process of ischium small*; *shoulder of caput humeri absent*; *femoral trochanters connected by bony ridge*; *neural bones rectangular*; *plastral index larger than 100*; *entoplastron T-shaped, with distinct lateral wings*.

4. Dermochelyiidae. Cranial scute sulci on dermal roofing elements absent; *processus trochlearis oticum formed by prootic reduced*; *ossification of rostrum basisphenoidale reduced*; *foramen caroticum laterale larger than foramen arterius canalis carotici interni*; *scute sulci on carapace absent or rudimentary*; *plastral fontanelles between hyo–hypoplastra as large as or much larger than hypoplastron, or hypoplastron*; *medial contact of xiphoplastra absent*.

5. Protostegidae. *Nasal present*; *jugal–quadrate contact, excluding quadrado–jugal from lower cheek margin*; *lower cheek emargination absent*; *vomer–palatine contact lost, palatines medially meeting*; *foramen palatinum posterius open postero–laterally*; *pterygoid extending onto mandibular articular surface of quadrate*; *foramen posterius canalis carotici interni between pterygoid and basisphenoid*; *rodlike rostrum basisphenoidale*; *third (or second) cervical centrum biconvex*; *lateral process of pubis extending anteriorly beyond midline portion of pubis*; *lateral process of humerus enlarged within the anterior portion of shaft, not easily visible from ventral view*; *radius with middle portion bent toward anterior*; cervical scute overlying more than half the width of nuchal; *thick neurals with median keel*.

6. Unnamed taxon (protostegids excluding *Santanachelys*). Upper triturating surface involving vomer; *high lingual ridge of maxilla exposed from lateral*; *lateral process of humerus with a medial concavity*; first and second digits modified into paddle without movable articulations; *xiphoplastra much broader than long, curved medially, with large midline fontanelle*.

7. Unnamed taxon. *Foramen palatinum posterius absent*; *pterygoid narrow, C-shaped*; *large processus trochlearis oticum involving deep notch of quadrate*; first suprapygial absent.

8. Unnamed taxon. Prefrontal–postorbital contact present; scar for *M. latissimus dorsi* and *teres major* located at middle of shaft; *star-shaped, hyo–hypoplastra*.

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from Mary Sheehan at the editorial office of Nature.

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Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current

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The Southern Ocean surrounds the Antarctic continent and supports one of the most productive marine ecosystems. Migratory and endemic species of whales, seals and birds benefit from the high biomass of their principal prey, krill (*Euphausia superba*) and cephalopods, in this area. Most species of baleen whales and male sperm whales in the Southern Hemisphere migrate between low-latitude breeding grounds in winter and highly productive Antarctic feeding grounds in summer. Here I show the importance of the southernmost reaches of the strongest ocean current, the Antarctic Circumpolar Current (ACC), to a complex and predictable food web of the Southern Ocean. The circumpolar distributions of blue, fin and humpback whales from spring to midsummer trace the non-uniform high-latitude penetration of shoaled, nutrient-rich Upper Circumpolar Deep Water, which is carried eastward by the ACC. The poleward extent of this water mass delineates the Southern Boundary¹ of the ACC and corresponds not only to the circumpolar distributions of baleen whales, but also to distributions of krill and to regions of high, seasonally averaged, phytoplankton biomass. Sperm whales, which feed on cephalopods², also congregate in highest densities near the Southern Boundary. The association of primary production, Krill, and whales with the Southern Boundary, suggests that it provides predictably productive foraging for many species, and is of critical importance to the function of the Southern Ocean ecosystem.

The ACC is dominated by a thick layer of warm, saline, oxygen-poor and macronutrient-rich water, Circumpolar Deep Water (CDW), which originates at low latitudes, shoals southwards, and is eventually entrained in the surface mixed layer^{1,3}. Upper Circumpolar Deep Water (UCDW)^{1,3} is the only water mass that is found exclusively in the ACC¹. At its poleward edge, UCDW lies at depths near 200–500 m, where wind-induced divergence and upwelling bring high concentrations of phosphate, nitrate, and silicate to the Antarctic Surface Water³. The southern end of the characteristic signal of UCDW is a water-mass boundary which constitutes a reasonable poleward extent of the ACC; this feature has been named the Southern Boundary¹.

The upward flux and entrainment of high concentrations of

macronutrients or trace metals into the surface mixed layer from UCDW at the Southern Boundary should increase regional primary production, enhance secondary production (that is, production of krill) and attract cetaceans and other foraging apex predators. In general, nutrients are not considered to be limiting for phytoplankton growth in Antarctic waters⁴ and local iron enrichment may be an important factor that determines the spatial variability in phytoplankton production⁵. However, the concentrations of iron and other trace elements in UCDW and near the Southern Boundary

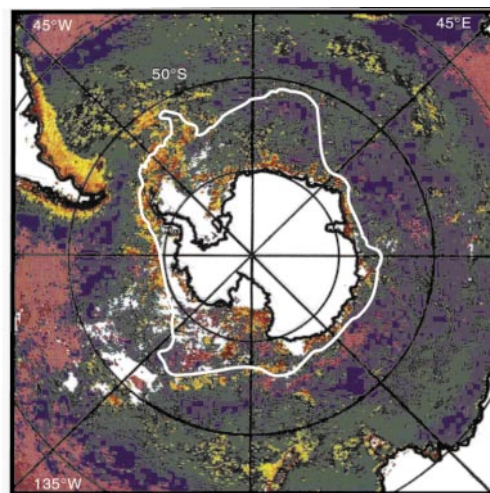


Figure 1 Annual coastal zone colour scanner (CZCS) pigment concentration, averaged from data from October 1978 to June 1986 (ref. 4), in relation to the location of the Southern Boundary of the ACC¹ (white line).

Figure 2 Distribution of principal concentrations of krill⁶ in relation to the East Wind Drift and Weddell Drift (dashed lines), Polar Front (black line) and Southern Boundary¹ (red line). Principal concentrations of krill are shown as encircled black circles.

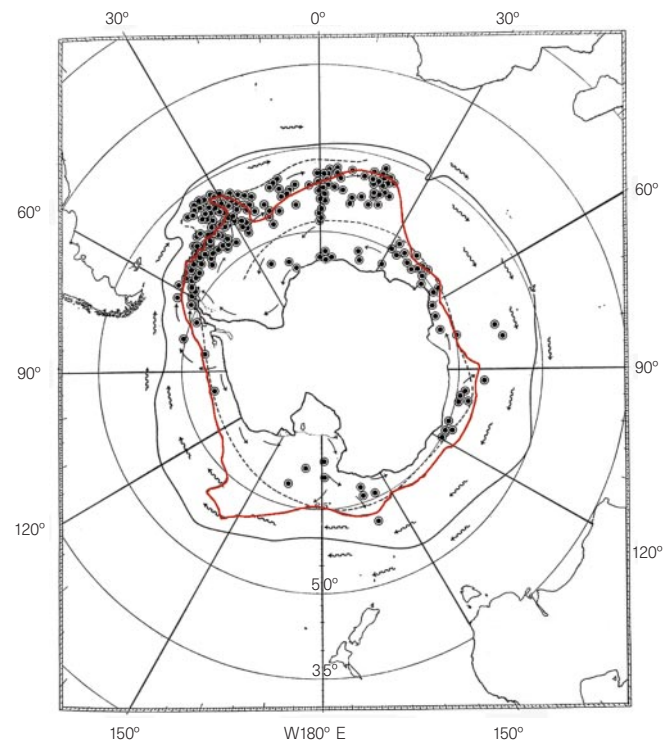


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