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Authors: Mateus, Octávio, Jacobs, Louis, Polcyn, Michael, Schulp, Anne S., Vineyard, Diana, et al.

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The oldest African eucryptodiran turtle from the Cretaceous of Angola

OCTÁVIO MATEUS, LOUIS JACOBS, MICHAEL POLCYN, ANNE S. SCHULP, DIANA VINEYARD, ANDRÉ BUTA NETO, and MIGUEL TELLES ANTUNES



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A new Late Cretaceous turtle, *Angolachelys mbaxi* gen. et sp. nov., from the Turonian (90 Mya) of Angola, represents the oldest eucryptodire from Africa. Phylogenetic analysis recovers *Angolachelys mbaxi* as the sister taxon of *Sandownia harrisi* from the Aptian of Isle of Wight, England. An unnamed turtle from the Albian Glen Rose Formation of Texas (USA) and the Kimmeridgian turtle *Solnhofia parsonsi* (Germany), are successively more distant sister taxa. Bootstrap analysis suggests those four taxa together form a previously unrecognized monophyletic clade of marine turtles, herein named Angolachelonia clade nov., supported by the following synapomorphies: mandibular articulation of quadrate aligned with or posterior to the occiput, and basisphenoid not visible or visibility greatly reduced in ventral view. Basal eucryptodires and angolachelonians originated in the northern hemisphere, thus *Angolachelys* represents one of the first marine amniote lineages to have invaded the South Atlantic after separation of Africa and South America.

Key words: Chelonia, Eucryptodira, paleobiogeography, Cretaceous, Angola.

Octávio Mateus [omateus@fct.unl.pt], Departamento de Ciências da Terra (CICEGe-FCT), Universidade Nova de Lisboa, Lisbon, and Museu da Lourinhã, Rua João Luis de Moura, 2530-157 Lourinhã, Portugal;
Louis Jacobs [jacobs@mail.smu.edu], Michael Polcyn [mpolcyn@mail.smu.edu], and Diana Vineyard [vineyard@mail.smu.edu], Department of Earth Sciences, Southern Methodist University, Dallas, Texas 75275, USA;
Anne S. Schulp [anne.schulp@maastricht.nl], Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, NL-6211 KJ Maastricht, The Netherlands;
André Buta Neto [anbuneto@hotmail.com], Departamento de Geologia, Universidade Agostinho Neto, Luanda, Angola;
Miguel Telles Antunes [migueltellesantunes@gmail.com], Academia de Ciências de Lisboa, Rua da Academia das Ciências, 19. 1242-122 Lisboa, Portugal.

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Introduction

The Cretaceous fauna from Tadi, near the small coastal village of Iembe, Bengo Province, northern Angola was reported by Antunes (1964). In 2005 one of us (OM) found a turtle skull described herein in the same general area, but north of the type locality of the mosasaur *Angolasaurus bocagei*, which was located using Antunes (1964: pl. 1: 2). The turtle locality is separated from the *A. bocagei* locality by a normal fault (Fig. 1). The turtle locality is on the down-dropped side. Throw on the fault is on the order of a few tens of meters at most. The turtle was found in shallow marine sediments. The age of Iembe is regarded as Turonian (90 Mya) by Antunes (1964), Antunes and Cappetta (2002), and Jacobs et al. (2006) mainly based on sharks.

The African Mesozoic record of turtles was previously restricted to stem turtles (e.g., *Australochelys robustus*) and pleurodires, with the doubtful exception reported in 1855 of a "Chelonioidea or Dermochelyoidea indet." from the Albian–Cenomanian of South Africa by Baily (1855; see also Broin 2000; Gaffney et al. 2006, 2007). From Angola, Dollo (1913) described *Taphrosphys congolensis* from the Paleocene of Landana, in the Cabinda enclave of Angola, and Broin (2000) reported Bothremydidae indet. from the Late Senonian (ca. Campanian) of Ambrizete, in the northern littoral of Angola. Plates and skull fragments of chelonians were collected from Maastrichtian sediments at Bentiaba and the Giraul Valley (Antunes 1964: 135) in the 1960s and during recent expeditions. The most recent comprehensive phylogenetic analysis of Cretaceous non-pleurodiran turtles is provided by Joyce (2007) and is utilized here.

Institutional abbreviations.—MGUAN-PA, Museo Geológico da Universidade Agostino Neto, Luanda, Angola (Paleo-Angola Project Collection); SMU, Southern Methodist University, Dallas, USA.

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Systematic paleontology

Testudines Batsch, 1788

Eucryptodira Gaffney, 1975

Angolachelonia nov.

Definition.—Angolachelonia refers to the clade originating from the most recent common ancestor of *Angolachelys mbaxi* gen. et sp. nov. and *Solnhofia parsonsi* Gaffney, 1972.

Diagnosis.—Articulation of quadrate aligned with, or posterior to the occiput; basisphenoid absent or much reduced in ventral view; medial contact of palatines (convergent with Trionychia), expanded secondary palate (convergent with *Chelonia* and *Baptemys*).

Genus *Angolachelys* nov.

Etymology: *Angolachelys* means "Angola turtle" in classic Greek.

Type species: *Angolachelys mbaxi* gen. et sp. nov.; see below.

Diagnosis.—Same as for the type and only species.

Angolachelys mbaxi sp. nov.

Figs. 2, 3.

Etymology: Mbaxi means turtle in the Angolan Nyaneka-Nkumbi and Kimbundo languages.

Holotype: MGUAN-PA 002, a nearly complete skull, an ungual phalanx, two cervical vertebrae, proximal part of the ilium, shell parts, and a few uninformative fragments. It will ultimately be housed in the Geological Museum of the Universidade Agostinho Neto, in Luanda, Angola, and replicas will be kept in the participating institutions.

Type locality: Iembe, Bengo Province, Angola.

Type horizon: Tadi Beds (Itombe Formation) according to Antunes (1964) and Jacobs et al. (2006), Upper Turonian, Late Cretaceous.

Diagnosis.—Unambiguous autapomorphies include: divided external nares separated by an internarial process of the premaxilla; sub-circular rugosity on the dorsal surface of the squamosal; squamosal wings projected posteriorly, representing about 1/4 of the total length of the skull posterior to the quadrate, and frames the temporal fenestra both dorsally and laterally. *Angolachelys* also possesses an extremely derived secondary palate, extending posteriorly to a level well behind the orbits and an extensive skull roof with squamosal-parietal contact. *Angolachelys* appears to share with *Sandownia harrisi* a contribution of the jugal to the palate, small closely set eyes, and a unique trilobate outline of the rostrum.

Description.—The skull of *Angolachelys mbaxi* (Figs. 2, 3) is large and dorsoventrally flattened through crushing, although most of the damage is to the dorsal surface. The amount of crushing can be seen in posterior view as the supraoccipital collapsed onto the ventral margin of the foramen magnum. The right squamosal wing is broken away and the surface of the right quadrate condyle is eroded. The area anterior to the orbits is damaged, as is the postorbital region on each side. Even with crushing and damage taken into account, the skull appears dorsoventrally flat relative to its length. It is longer than broad with a narrow nasal region and extended squamosal wings (length from occipital condyle to tip of snout 179 mm; width across the articular surfaces of the quadrates 137 mm). The orbits are small, closely spaced, and oriented dorsally. The parietals form a slight medial bulge over the braincase, which is taken to be primary, as opposed to the result of crushing, because of the symmetry of the bulge. In lateral view, the lower margin of the skull has a sinuous outline for its entire length, from posterior to anterior, rising steeply from the quadrate condyle to the shallow cheek emargination, also rising gently both below the orbit and at the premaxilla. The premaxilla and the anterior part of the maxillae are well vascularized. The nasals of *A. mbaxi* are missing but were likely present and anteriorly placed, judging from the anterior extent of the prefrontals and internarial bar of the premaxilla. The prefrontals contact medially, are broad and unsculptured, and form the anteromedial margin of the orbit. The descending process of the prefrontal contacts both the vomer and the palatine within the orbit. There is no lacrimal bone.

The frontal forms the dorsal rim of the orbit, its anterior terminus roughly medial to the anterior orbital margin. The interorbital bar width is narrow. The parietal contacts the frontal posterior to the orbital margin. The parietal and squamosal have an extensive contact, as do the squamosal and postorbital. The descending process of the parietal closes off the anterior margin of the trigeminal foramen and contacts the palatine.

The maxilla extends from the posterolateral margin of the prefrontals to below the midpoint of the orbit where it contacts the jugal. The jugal forms the posteroventral rim of the orbit and extends posteriorly to form a suture with the quadratojugal. It does not contact the squamosal or participate in the upper temporal emargination. In palatal view, the jugal articulates with the maxilla anteriorly, the palatine medially, and the pterygoid posteromedially. It forms the anterior margin of the fossa temporalis inferior and contributes substantively to the secondary palate. The quadratojugal is longer than the jugal and outlines the anterior portion of a shallow cheek emargination. The quadratojugal contacts the squamosal high on the skull, but does not contact the maxilla to the anterior.

The long squamosals are superficially reminiscent of trionychids, but they roof the posterolateral portion of the temporal fossa, which is otherwise roofed by the parietal dorsomedially. A round, flat excrescence is found at the base of the squamosal wing on the dorsal surface, and there are abundant grooves on the surface of the skull. The squamosal is separated from the supraoccipital by the parietal. The postorbital is long but is damaged on both sides of the skull, although its posterior articulation with the squamosal is visible on the ventral surface of the skull roof above the quadrate. It does not contact the palatine. From the quadrate, the squamosal extends medially to the postorbital and parietal. Posteriorly the squamosal forms distinct protrusions. There is no supratemporal.

The rostral region of the skull is of unusual shape in that the triturating surface of the premaxilla is dorsally more ele-

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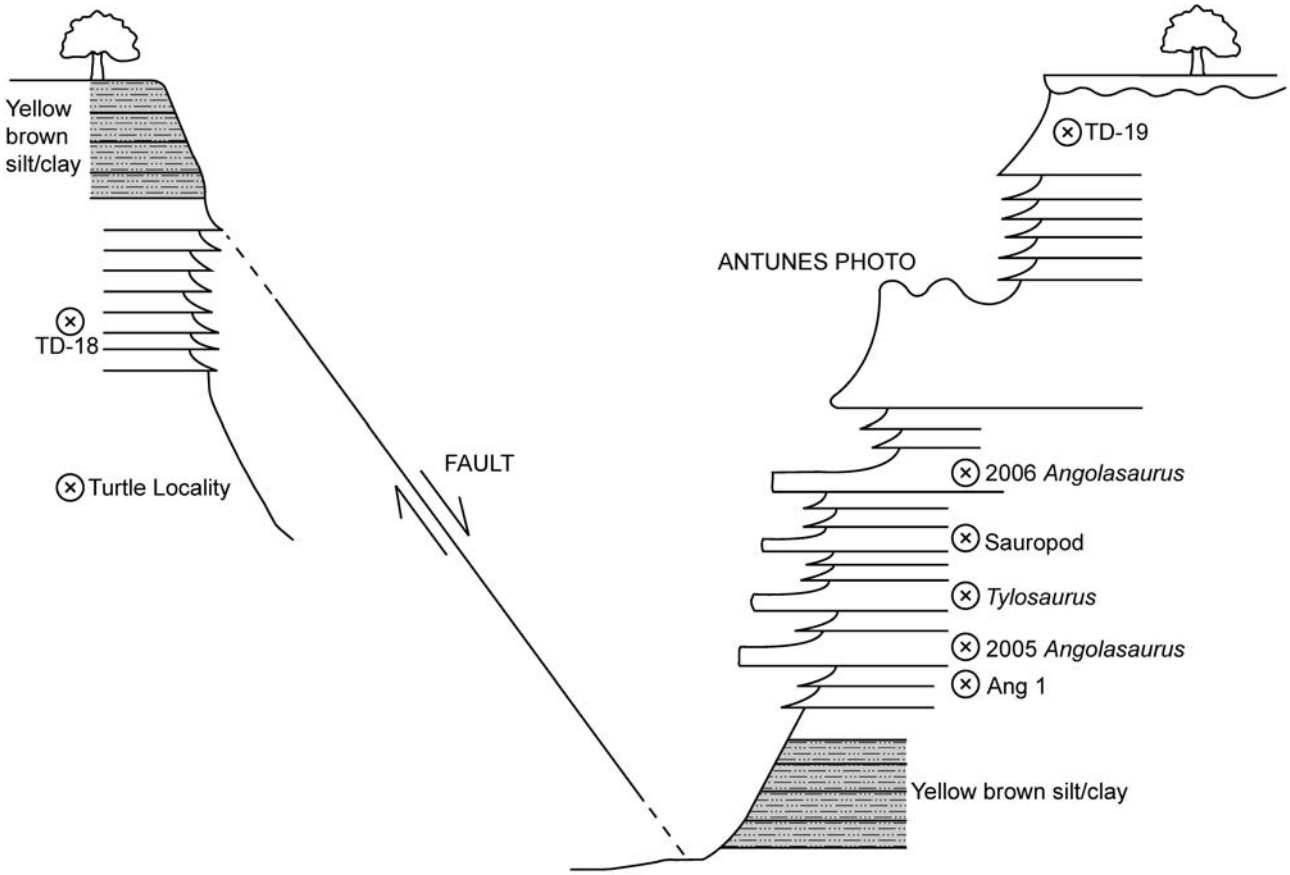


Fig. 1. Stratigraphic distribution of fossils at Tadi Beds of Iembe, Angola. Antunes photo refers to Antunes (1964: pl. 1: 2), which shows the locality from which the holotype of *Angolasaurus bocagei* was collected. Note fault separating the type locality of *Angolachelys* from that of *Angolasaurus*. Not to scale. TD-18, TD-19, and Ang 1 refer to mosasaurs.

vated than that of the maxillae, and in dorsal view the premaxilla forms an anterior prominence. The elevation at the premaxillary-maxillary suture on either side of the premaxilla causes the anterior margin of the jaw to present a trilobed appearance, but there is no premaxillary hook along its ventral margin. The labial ridge of the premaxilla and the anterior portion of the maxilla is rounded, rather than sharp, and it is broadly flattened on the posterior portion of the maxilla. The dorsal process of the premaxilla subdivides the external nares and forms the anteriomedial margin of the external nares, causing them to be directed somewhat anterolaterally. The premaxillae are fused and form the ventral margin of the external nares. There is a smooth, shallow, ventrolateral scallop to the ventral surface of each external naris. Divided nares are primitive for amniotes generally but not for eucryptodires; therefore, the divided nares of *Angolachelys* represent a derived state. No suture is visible on the dorsal process to delineate the nasal-premaxilla contact. In palatal view, the fused premaxilla is small and roughly triangular. A foramen praepalatinum appears to be present along the broken posterior margin of the premaxilla.

The maxilla is extensive, forming a large portion of an expanded secondary palate. The palatal opening of the temporal fossa is narrow anteriorly and extends to a level anterior to that of the internal nares, approximately at the level of the frontoparietal suture.

The vomer is a single robust unit, forming a substantial portion of the secondary palate, including the median portion of its posterior margin. It appears to be separated from the pterygoids by the palatines. The palatine does not contribute to the lateral braincase wall. There are no vomerine, palatine, or pterygoid teeth.

The quadrate constricts around the columella to divide the middle ear into the lateral cavum tympani and the medial cavum acustico-jugulare. The cavum tympani is fully developed and there is no precolumellar fossa. The quadrate arcs posterodorsally to its curved contact with the elongate squamosal. The antrum postoticum is only weakly developed, but the quadrate does not fully enclose its anterior perimeter. The incisura columellae auris is closed.

The epipterygoid is apparently present on the lateral wall of the braincase. The pterygoids contact each other medially and extend posterolaterally. The posterior pterygoid process extends posteriorly to the back of the skull. The cavum acustico-jugulare and recessus scalae tympani are floored by a posterior process of the pterygoid. The basipterygoid articulation is fused and there is no interpterygoid vacuity. The pterygoids contact the basioccipital. There is no processus

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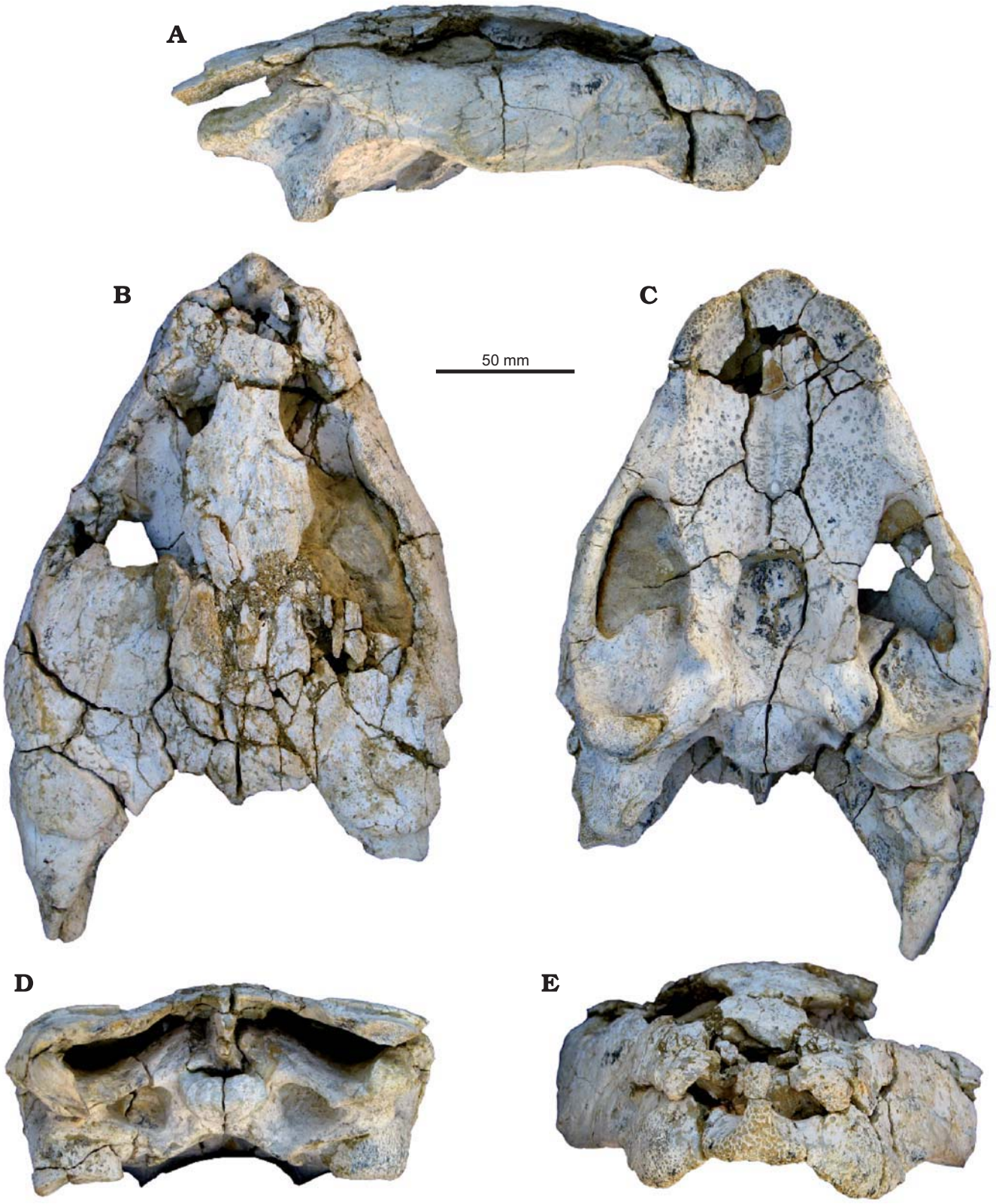


Fig. 2. Photographs of the skull of eucryptodiran turtle *Angolachelys mbaxi* gen. et sp. nov. (MGUAM-PA 002) from the Turonian of Iembe, Angola; in left lateral (**A**), dorsal (**B**), ventral (**C**), posterior (**D**), and anterior (**E**) views.

trochlearis pterygoideus nor is there a foramen palatinum posterius that can be discerned. The supraoccipital forms the dorsal margin of the foramen magnum, preventing the exoccipitals from having a dorsal contact. It protrudes well posterior to the foramen magnum, but it lacks a large dorsal exposure. The opisthotic is tightly fused to the squamosal and

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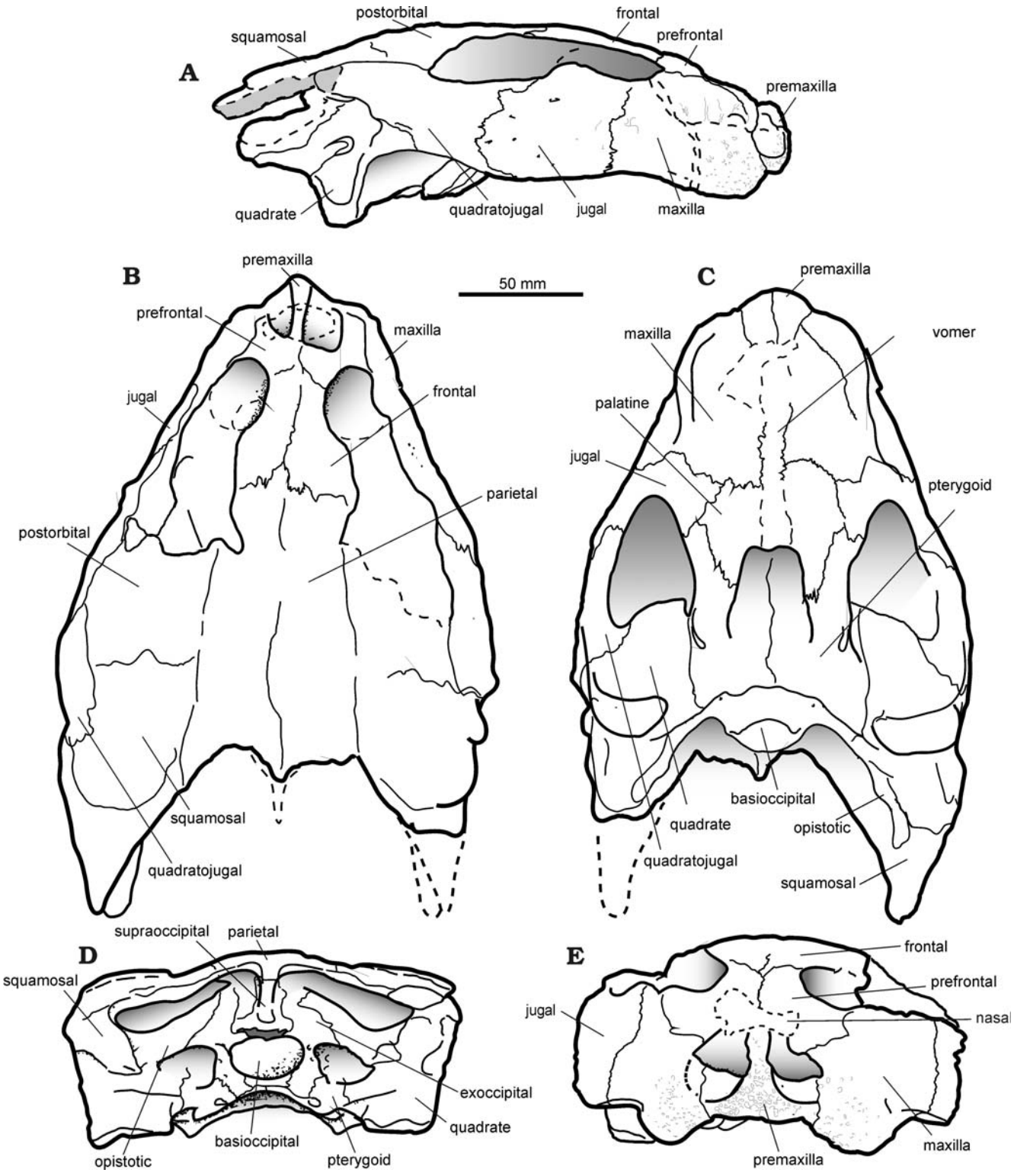


Fig. 3. Interpretative drawings of the skull of eucryptodiran turtle *Angolachelys mbaxi* gen. et sp. nov. (MGUAM-PA 002) from the Turonian of Iembe, Angola; in left lateral (**A**), dorsal (**B**), ventral (**C**), posterior (**D**), and anterior (**E**) views.

quadrate. The basisphenoid is not exposed in palatal view due to the ventro-medial contact of the pterygoids.

Crushing prevents determining whether the course of the hyomandibular branch of the facial nerve is parallel to the vena capitis lateralis. This character is poorly known in many taxa but its distribution would suggest that it probably passes through the cranio-quadrate space parallel to the vena capitis lateralis. The stapedio-temporal canal is anterior to the fenestra ovalis between the quadrate and prootic and the foramen stapedio-temporale is relatively large. The jugular foramina

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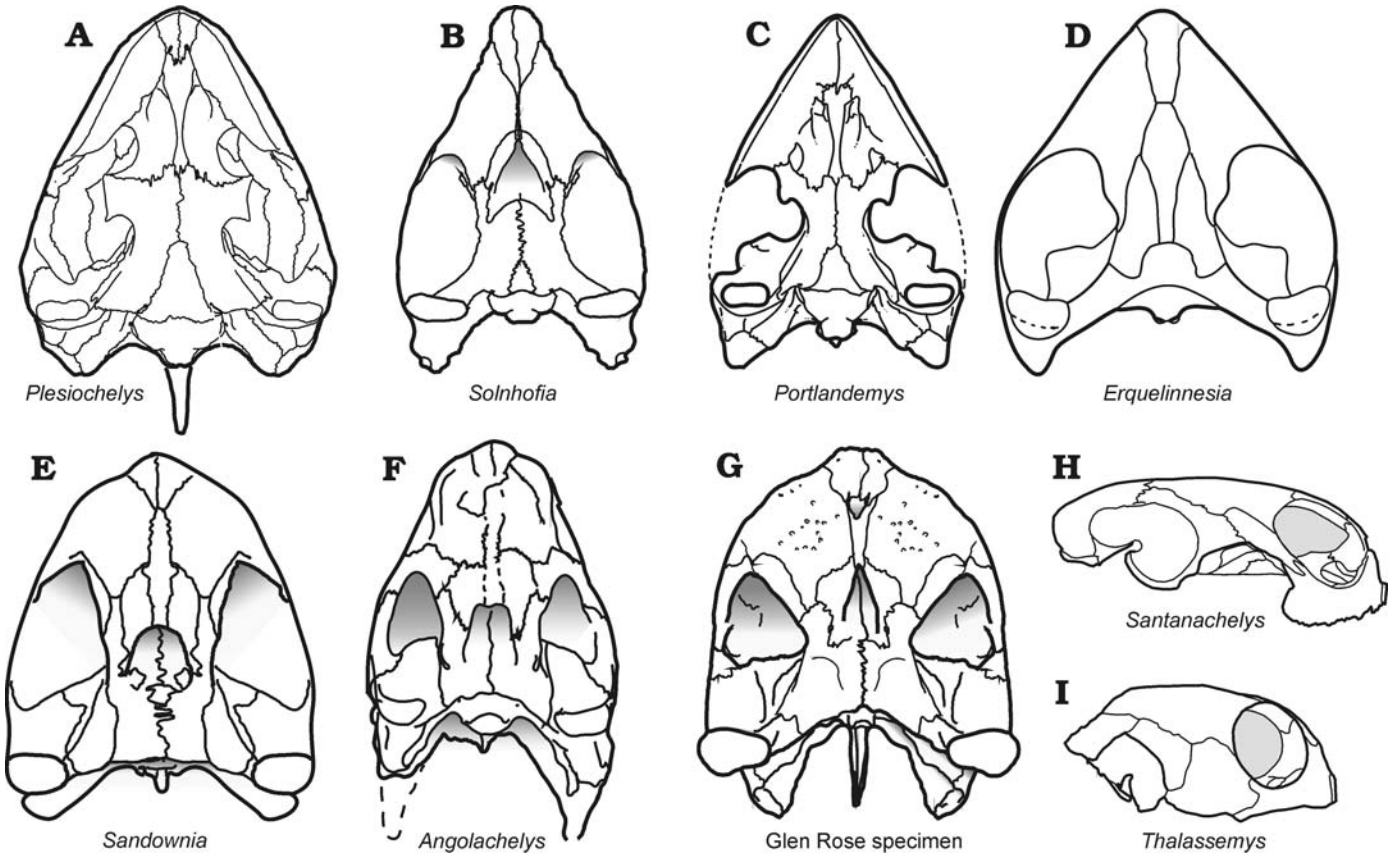


Fig. 4. Skulls of basal eucryptodires in ventral view (except *Santanachelys* and *Thalassemys* depicted in right lateral view). **A**. *Plesiochelys etalloni* SM 135 Late Jurassic of Switzerland (Gaffney 1976). **B**. *Solnhofia parsonsi* from Late Jurassic of Germany and Switzerland (after Gaffney 1975). **C**. *Portlandemys mcdowelli* BM (NH) R 2914 from the Late Jurassic of England (Gafney 1976). **D**. *Erquelinnesia gosseleti* from the Upper Paleocene (Thanetian) of Belgium (Zangerl 1971). **E**. *Sandownia harrisi* from the Early Cretaceous of England (Meylan et al. 2000). **F**. *Angolachelys mbaxi* from the Turonian of Angola (this study). **G**. Glen Rose SMU is an unnamed taxon from the Albian of Glen Rose, Texas (SMU specimen). **H**. *Santanachelys gaffneyi* from the Late Aptian or Early Albian of Brazil (Hirayama 1998). **I**. *Thalassemys marina* from the Late Jurassic of Germany (Billon-Bruyat et al. 2005, after Rieppel 1980).

are well defined by bone. The foramen posterius canalis caroticus internus is positioned near the posterior end of the skull and the fenestra perilymphatica is quite likely large.

The dentary is unusual in that the symphysis is long, similar to *Erquelinnesia gosseleti*, a taxon we consider valid (contra Lynch and Parham 2003). The posterior portion of the lower jaw is missing and it is unknown whether a splenial was present. The symphysis is fused and the labial ridge is rounded, rather than sharp. The symphyseal region is highly vascularized. The lateral wall of the dentary, where it thickens relative to the anterior portion, is slightly convex and bordered by a ventral ridge.

Two incomplete cervical vertebrae were collected (22 and 28 mm long). The wide centrum is strongly procoelous with a conspicuous middle ventral ridge. The prominent transverse process is positioned at the anterior half of the centrum.

The ungual phalanx (30 mm long) from the right autopodium is curved lateraly. Unlike modern marine turtles like *Chelonia mydas*, the articular facet in *Angolachelys mbaxi* is divided by a ridge. The mid cross section is transversely expanded, the width being about twice the height. There is a small constriction between the main body and the articular expansion. The ventral tubercle is short. The small plate fragments that were recovered are not informative except by the absence of any notable ornamentation.

Phylogenetic analysis.—*Angolachelys mbaxi* is referred to Eucryptodira based on the path of the internal carotid artery through the pterygoid and on possession of paired prefrontals. To further ascertain relationships amongst eucryptodires, the new taxon was included in a phylogenetic analysis based on the data set of Joyce (2007).We included two additional taxa and five new or adapted characters (Gaffney 1979; Parham and Fastovsky 1997). A number of Joyce's (2007) taxa were excluded from the analysis including all members of Pleurodira and Paracryptodira as they are uninformative as ingroup members in our analysis based on Joyce's (2007) previous results. *Proganochelys* was used as the outgroup. The matrix was run with a total of 28 taxa and 141 characters using a heuristic search with equal weighting. The characters were optimized using the DELTRAN setting.

Results.—The analysis produced 60 equally parsimonious trees with a length of 246 steps and with a consistency index of 0.515 and a rescaled consistency index of 0.685. We se-

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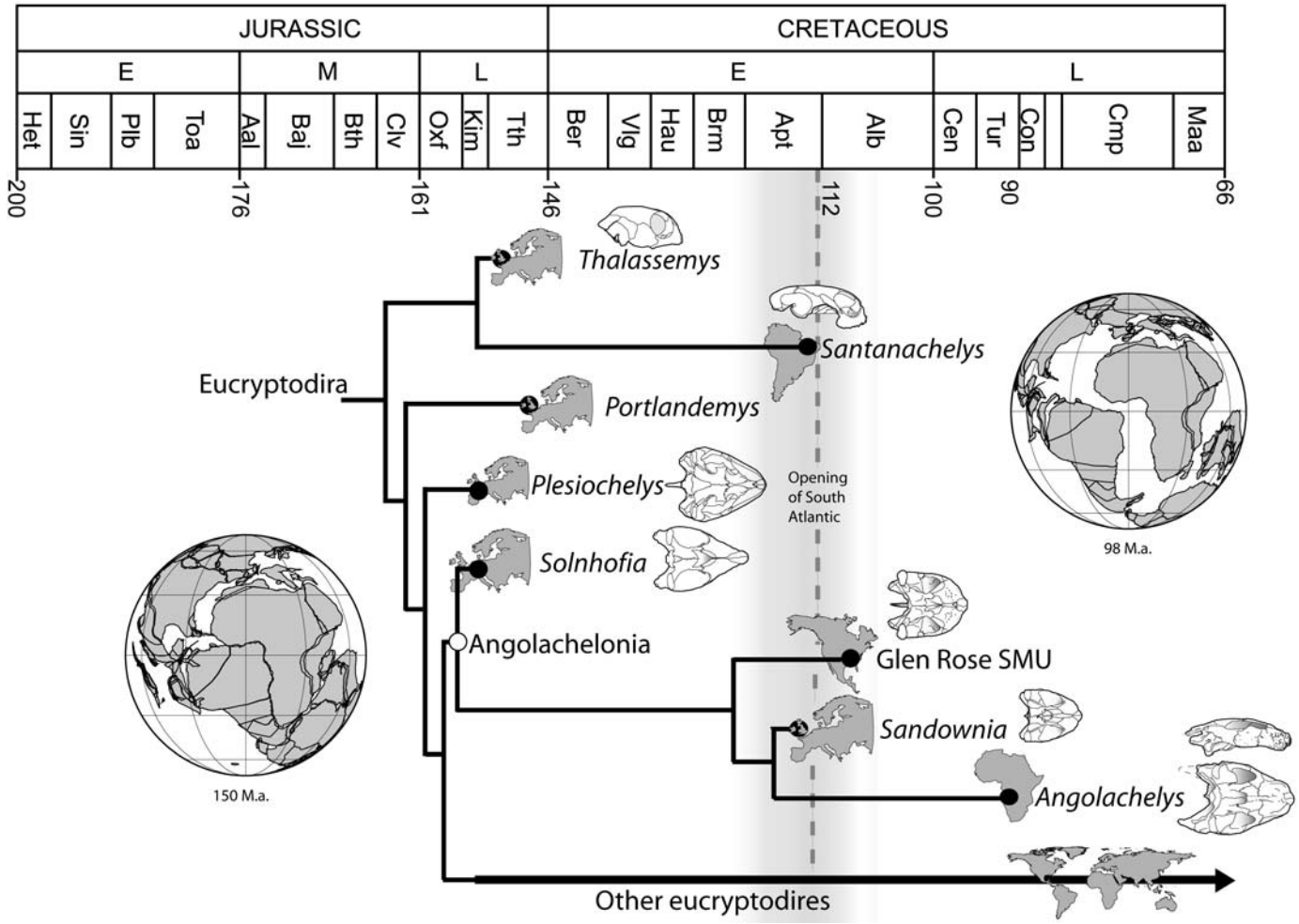


Fig. 5. Relationship and chronopaleogeography of basal eucryptodires. The paleogeographic maps were generated by the models available at www.odsn.de and based on Hay et al. (1999). See caption of Fig. 4 for locations and age of the taxa. The grey bar represents the time for the opening of South Atlantic.

lected one of the 60 trees that was largely consistent with that recovered by Joyce (2007) with the exception of a new monophyletic group, herein named Angolachelonia nov., that includes ([*Angolachelys mbaxi* + *Sandownia harrisi*] + GlenRoseTurtle + *Solnhofia parsonsi*). Tree stability was tested using 240 bootstrap replicates and indicates poor support for most basal taxa with retention of three of Joyce's (2007) clades (e.g., an unnamed clade that includes *Sinemys* + *Ordosemys*; Chelonioidea; and Kinosternoidea + Trionychia). Bootstrap analysis supports Angolachelonia in 75% of the replicates in the preferred cladogram (Fig. 5) and the clade consisting of ([*Angolachelys mbaxi* + *Sandownia harrisi*] + unnamed taxon from Glen Rose) is retained in greater than 75% of the trees using majority rule test.

Discussion.—The most obvious apomorphy of *Angolachelys mbaxi* is the extensive secondary palate with the apertura narium interna lying at a level well posterior to the orbits. In addition, the structure of the squamosal wing with a distinct excrescence at its base is unique (Figs. 2, 3). The flat posterior triturating surface of the maxilla is also unique, so far as we are aware. The expansion of the jugal onto the secondary palate is shared with *Sandownia harrisi* (Fig. 4) and is unique among turtles (Meylan et al. 2000), as is the peculiar premaxillary prominence. *A. mbaxi* is more derived than *S. harrisi* in the extensive development of the palate, the squamosal wings, and the triturating surface, and in having divided nares. *S. harrisi* has been reported to lack an epipterygoid, and if so, is more derived than *A. mbaxi* in that character. Karl and Tichy (2002) addressed the homology of the secondary palate noting it independently occurs in four clades, including Plesiochelydae, Cheloniidae, Baenids, and Osteopygidae, a taxon now considered invalid (Parham 2005). Karl and Tichy (2002) suggested the development of an extensive secondary palate may have been both an adaptation to enlarge the narial passages, thus allowing pre-warmed air to enter the lungs, and also a feeding adaptation, facilitating a durophagous habit. Given the distribution of this character within turtles, we interpret this character as uniquely derived within Angolachelonia. The unique combination of features in *Angolachelys mbaxi* include the presence of separate external nares, minor temporal emargination, expanded palate, squamosal excrescences, flattened triturating surface of posterior maxilla, sweeping squamosal wings that cover the temporal fossa, and orbits narrowly placed.

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Conclusions

Figure 5 illustrates the temporal and geographic distribution of the Angolachelonia. We conclude that: (i) This new taxon represents the oldest record for Eucryptodira in Africa and the first in the Mesozoic of that continent; (ii) *Angolachelys mbaxi* is a member of a new clade, Angolachelonia, that includes *Sandownia harrisi*, *Solnhofia parsonsi*, and an unnamed taxon from Glen Rose, Texas, and that is diagnosed by the anterior position of the occiput relative to the quadrate and by the reduction or absence of the basisphenoid in ventral view. Angolachelonians have a narrow interorbital bar, medial contact of the palatines, and an expanded secondary palate; and (iii) Angolachelonians and basal eucryptodires were among the first marine turtles. This clade originated in the Northern Hemisphere, and represents the first marine turtle lineage that crossed from the North to South Atlantic during the Aptian and post-Aptian opening of the South Atlantic seaway (Jacobs et al. 2009). The Cretaceous marine turtles of Australia (Kear 2003) cannot have passed through the Atlantic gateway because their Early Cretaceous occurrence pre-dates the opening of the Atlantic Ocean.

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