

A NEW DUROPHAGOUS STEM CHELONIID TURTLE FROM THE LOWER PALEOCENE OF CABINDA, ANGOLA

by TIMOTHY S. MYERS¹ , MICHAEL J. POLCYN¹, OCTÁVIO MATEUS^{2,3}, DIANA P. VINEYARD¹, ANTÓNIO OLÍMPIO GONÇALVES⁴ and LOUIS L. JACOBS¹

¹Roy M. Huffington Department of Earth Sciences, Southern Methodist University, 3225 Daniel Ave, Dallas, TX 75275, USA; smyers@smu.edu, mpolcyn@smu.edu, vineyard@smu.edu, jacobs@smu.edu

²CICEGe-Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Caparica, 2829-516, Portugal; omateus@fct.unl.pt

³Museu da Lourinhã, Rua João Luis de Moura 95, Lourinhã, 2530-158, Portugal

⁴Departamento de Geologia, Faculdade de Ciências, Universidade Agostinho Neto, Avenida 4 de Fevereiro 7, Luanda, Angola; antonio.goncalves@geologia-uan.com

Typescript received 20 June 2017; accepted in revised form 11 October 2017

Abstract: A new stem cheloniid turtle, *Cabindachelys landanensis*, gen. et sp. nov., is represented by a nearly complete skull and partial hyoid collected in lower Paleocene shallow marine deposits, equivalent to the offshore Landana Formation, near the town of Landana in Cabinda, Angola. A partial chelonioid carapace previously reported from this locality is referred here to *C. landanensis*. *Cabindachelys landanensis* possesses clear synapomorphies of Pan-Cheloniidae, including a rod-like rostrum basisphenoidale, V-shaped basisphenoid crest, and secondary palate, but also retains a reduced foramen palatinum posterius, unlike most other pan-cheloniids. Phylogenetic analysis suggests that *C. landanensis* forms a weakly-supported clade with *Erquelinnesia gosseleti*, *Euclastes acutirostris*, *Euclastes wielandi* and *Terlinguachelys fischbecki*, although a close relationship between the protostegid *T. fischbecki* and these durophagous pan-cheloniids is unlikely. The Paleocene–Eocene strata near Landana have

produced a number of turtle fossils, including the holotype specimen of the pleurodire *Taphrosphys congolensis*. A turtle humerus collected c. 1 m above the holotype skull of *C. landanensis* differs from humeri of chelonioids and *Taphrosphys*, indicating that a third turtle taxon is present at Landana. Cheloniid fossil material is rare in the Landana assemblage, in comparison with the abundant remains of *Taphrosphys congolensis* found throughout the stratigraphic section. This disparity implies that *C. landanensis* preferred open marine habitats, whereas *Taphrosphys congolensis* spent more time in nearshore environments. The appearance of new durophagous species such as *C. landanensis* in the early Paleocene reflects the rapid radiation of pan-cheloniids as they diversified into open niches following the K–Pg extinction.

Key words: Testudines, Cheloniidae, Cryptodira, Paleocene, phylogeny, Africa.

Fossil turtle remains were first recovered in Palaeogene strata exposed in coastal cliffs west of the town of Landana in the Angolan province of Cabinda in 1895. These specimens, comprising several carapace fragments (MRAC uncat.), were formally assigned to *Podocnemis congolensis*, a new species of *Podocnemis* (Dollo 1912, 1913). Additional material collected from the Landana area in 1913 (including a skull, mandible, cervical vertebra, pelvic elements and more carapace fragments) led Dollo to erect the new genus *Bantuchelys* for these pleurodire fossils (Dollo 1924). Based on his assessment of the turtle assemblage, including indeterminate and fragmentary material, Dollo concluded that there was evidence for at least three turtle taxa (including *Bantuchelys*) at Landana. Nearly 50 years later, reanalysis of the Landana turtle assemblage determined that only two

taxa were present (Wood 1973, 1975). Wood (1975) referred the cranial and carapace material originally described as *Bantuchelys* to the genus *Taphrosphys* and tentatively identified the mandible described by Dollo (MRAC 3090) and a more recently collected partial carapace (MRAC 4796) as belonging to a toxochelyid sea turtle (Wood 1973). Gaffney *et al.* (2006), in their review of Pleurodira, asserted that the mandible identified by Wood as toxochelyid is better interpreted as belonging to *Taphrosphys congolensis*, a conclusion with which we concur. Recent fieldwork in Cabinda, conducted under the auspices of Projecto PaleoAngola, has led to the discovery of additional fossil turtle material near Landana. This study examines the taxonomy and phylogenetic relationships of these new specimens and explores their relationship to



FIG. 1. Map of Cabinda showing the locality for *Cabindachelys landanensis* gen. et sp. nov., holotype MGUAN-PA 298. The area around Landana (marked with letter A) is enlarged at upper right. Colour online.

previously-collected material. The data presented here offer insight into the palaeoecology of turtles living in the early Paleocene nearshore environments of Cabinda and illustrate the rapid expansion of marine turtles into empty niches following the K–Pg extinction event.

AGE AND GEOLOGICAL SETTING

The new specimens described here were collected in June 2012 from the coastal cliffs just west of the town of Landana in the Angolan province of Cabinda (Fig. 1). An isolated, mostly complete skull and associated partial hyoid (MGUAN-PA 298) were removed from a 90 cm thick, very fine grained, light yellowish-brown sandstone. The heavily bioturbated and laterally continuous unit contains relict ripple cross-laminations and is bounded by fossiliferous, bioturbated limestones. Other fossil material collected from this unit includes shark and ray teeth and shell fragments that are attributable to *Taphrosphys congolensis* based on their surface ornamentation. The coastal outcrops near Landana, first described by Bequaert (1923), were further explored in the 1930s by Dartevelle & Casier (1943). These beds are stratigraphically equivalent to deep-water marine strata of the Paleocene–Eocene Landana Formation that are

located in the subsurface of the offshore Lower Congo Basin (Brownfield & Charpentier 2006). Organic-rich shales and turbidites in this offshore unit compose a thick regressive sequence that was deposited during the terminal subsidence phase in the development of the Lower Congo Basin, which formed in response to opening of the South Atlantic (Brice *et al.* 1982; Da Costa *et al.* 2001). Deposition of the interbedded sandstones and limestones exposed along the Cabinda coast was contemporaneous with deep-water deposition of the Landana Formation, but the coastally-exposed strata represent shallow marine and marginal marine environments.

Nautiloid biostratigraphy (Miller 1935; Miller & Carpenter 1955) suggests that the Landana Formation and its onshore equivalents are lower Paleocene (Danian) to lower Eocene (Lutetian), *c.* 66–41 Ma (Gradstein *et al.* 2012). During field operations in June 2012, an *in situ* specimen of *Cimomia landanensis* (Miller 1935) was documented *c.* 3 m above MGUAN-PA 298, confirming that strata lower in the stratigraphic section are Danian (*c.* 66–62 Ma). Most, if not all, of the fossil turtle material recovered from the Landana locality, including specimens collected early in the twentieth century, is early Paleocene in age (Fig. 2).

Institutional abbreviations. I.R.Sc.N.B., Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MGUAN-PA, Museo geológico da Universidade Agostino Neto, Luanda, Angola (PaleoAngola Project Collection); MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; NJSM, New Jersey State Museum, Trenton, New Jersey, USA; OCP, Office Chérifien des Phosphates, Casablanca, Morocco; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA.

SYSTEMATIC PALAEOLOGY

TESTUDINES Batsch, 1788
 CRYPTODIRA Cope, 1868
 CHELONIOIDEA Baur, 1893
 PAN-CHELONIIDAE Joyce *et al.*, 2004

Genus CABINDACHELYS nov.

LSID. urn:lsid:zoobank.org:act:1960322C-D22F-4649-BD5B-42EA378D919E

Derivation of name. Named for the Angolan province of Cabinda and *chelys*, Greek for turtle.

Type species. *Cabindachelys landanensis* sp. nov.

Diagnosis. As for type and only species.

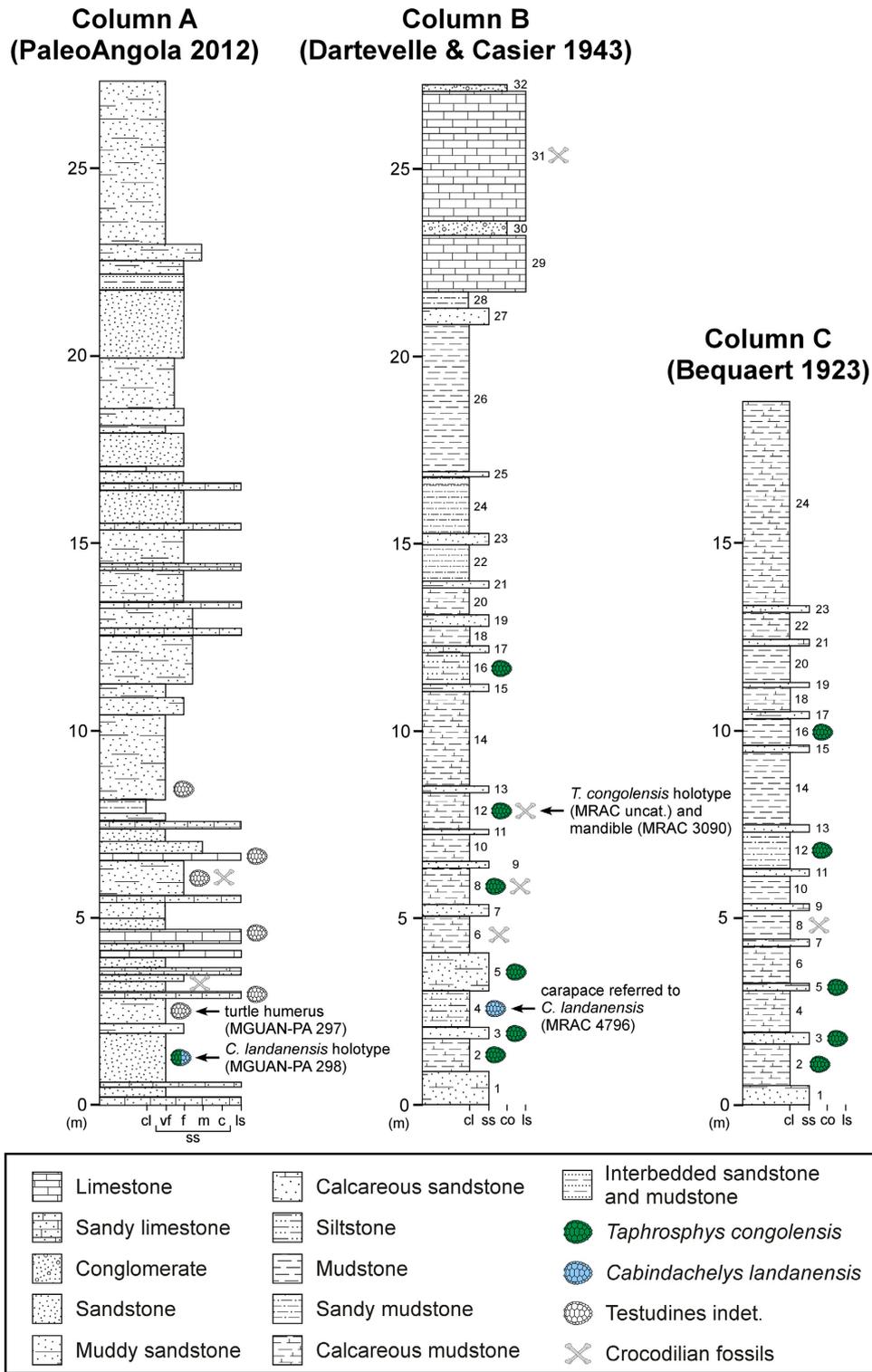


FIG. 2. Composite stratigraphic columns measured at Landana locality showing the stratigraphical position of fossil turtle material. Column A was measured in June 2012 by participants in Projecto PaleoAngola; column B was constructed from measurements and descriptions given by Darteville & Casier (1943); and column C was drafted using information from Bequaert (1923). The fossil turtle material in column A was collected in 2012 by Projecto PaleoAngola, and placement of turtle fossils in columns B and C is based on information from Bequaert (1923), Dollo (1924), Darteville & Casier (1943) and Wood (1973, 1975). The numbers to the right of the beds in columns B and C correspond to the bed numbers assigned by Bequaert (1923) and Darteville & Casier (1943). *Abbreviations:* c, clay; ss, sandstone (vf, fine; f, fine; m, medium; c, coarse); co, conglomerate; ls, limestone. Colour online.



FIG. 3. Photos of the skull of *Cabindachelys landanensis* gen. et sp. nov., holotype MGUAN-PA 298 in: A, anterior; B, posterior; C, dorsal; D, ventral; E, right lateral; and F, left lateral views. Scale bar represents 5 cm. Colour online.

Cabindachelys landanensis sp. nov.

Figures 3–5

LSID. urn:lsid:zoobank.org:act:65589F4D-CECB-498C-8C2E-09F30E6D1B83

Derivation of name. Named for the town of Landana, near the locality where the type specimen was collected.

Holotype. MGUAN-PA 298; almost complete skull (Figs 3, 4) and left first branchial horn of the hyoid (Fig. 5).

Referred material. MRAC 4796; partial carapace.

Type horizon and locality. Coastal cliffs near Landana, Cabinda, Angola (PaleoAngola locality Landana 1). Collected from a shallow marine, very fine grained, light

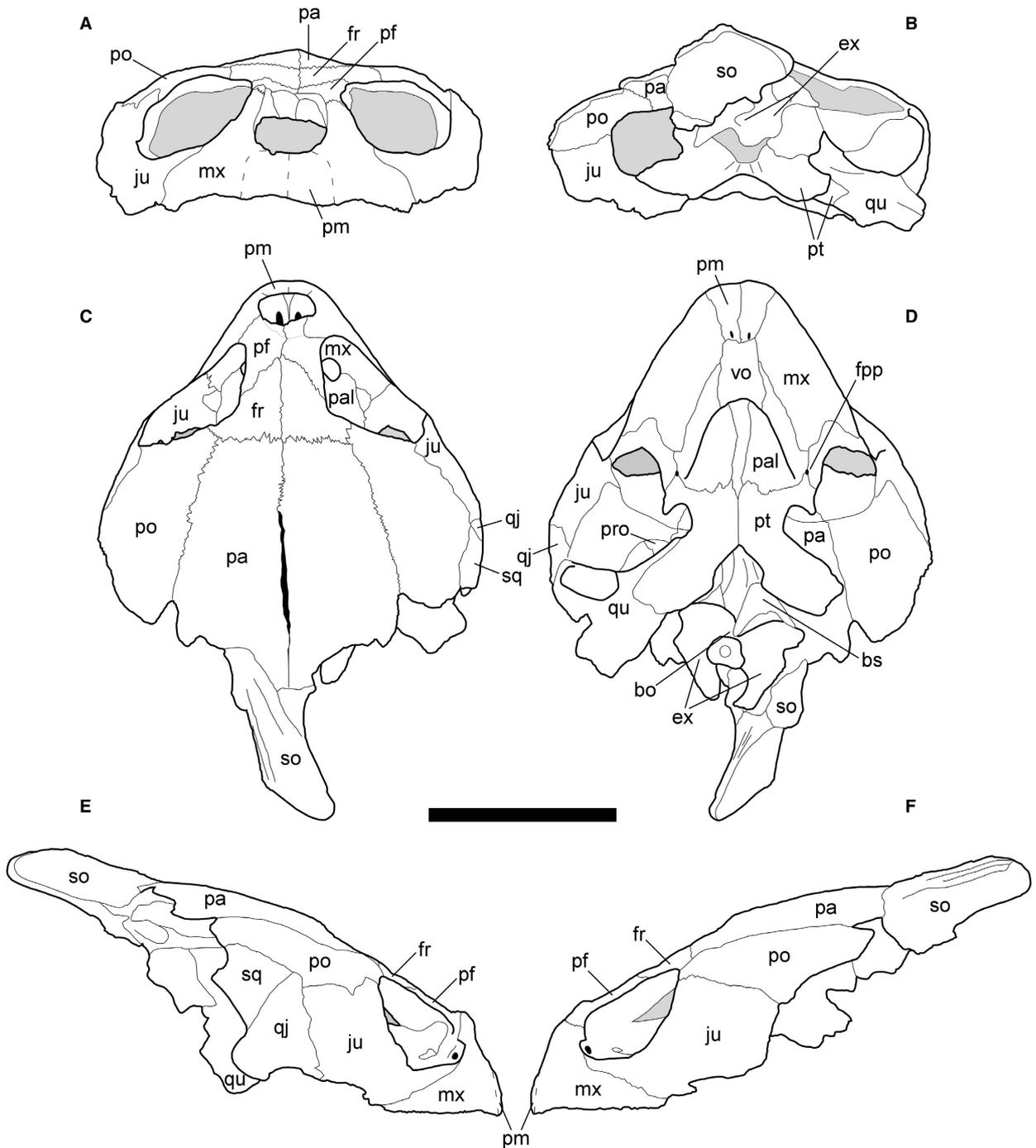


FIG. 4. Line drawings of the skull of *Cabindachelys landanensis* gen. et sp. nov., holotype MGUAN-PA 298 in A, anterior; B, posterior; C, dorsal; D, ventral; E, right lateral; and F, left lateral views. *Abbreviations:* bo, basioccipital; bs, basisphenoid; ex, exoccipital; fpp, foramen palatinum posterius; fr, frontal; ju, jugal; mx, maxilla; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pro, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar represents 5 cm.

yellowish-brown sandstone equivalent to the Landana Formation, lower Paleocene (Danian).

Diagnosis. Diagnosed as a pan-cheloniid turtle based on the presence of a rod-like rostrum basisphenoidale

(Character (Ch.) 86), which is not found in protostegids, and a V-shaped crest on the ventral plate of the basisphenoid (Ch. 88), which is absent in both protostegids and dermochelyids. Distinguished from other pan-cheloniids by the presence of a foramen palatinum

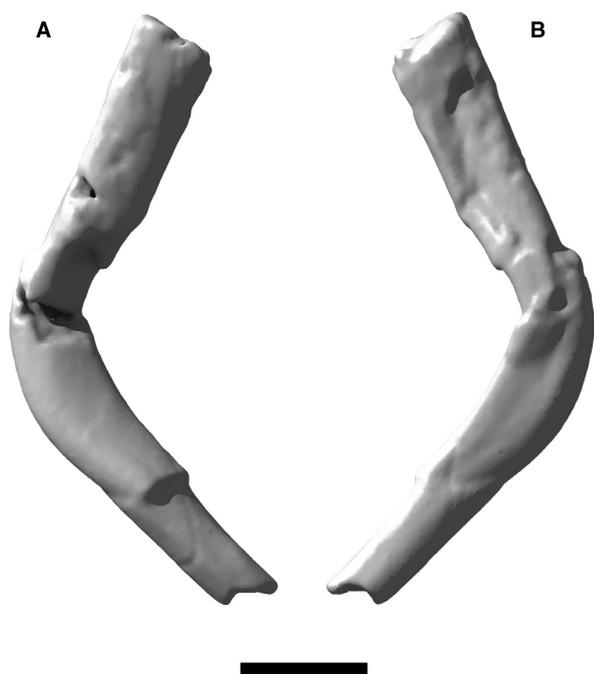


FIG. 5. CT rendering of the left first branchial horn of the hyoid of *Cabindachelys landanensis* gen. et sp. nov., holotype MGUAN-PA 298 in: A, dorsal; and B, ventral view. Scale bar represents 1 cm.

posterius (Ch. 66), a vomer with a dorsal plate longer than the ventral plate, and a deep posterior emargination of the secondary palate/triturating surface that extends well anterior of the subtemporal fenestrae. Differentiated from *Carolinohelys wilsoni*, *Eochelone brabantica*, *Procolpochelys grandaeva* and *Toxochelys latiremis* by presence of a secondary palate (Ch. 40); *Erquelinnesia gosseleti*, *Euclastes acutirostris* and *Euclastes wielandi* by less extensive secondary palate and long, slender dorsal plate of vomer; *Allopleuron hoffmanni*, *Puppigerus camperi*, *Tasbacka ouledabdounensis* and *Tasbacka aldabergeni* by lack of elongated skull and pointed snout; *Itilochelys rasstrigin* by shallow cheek emargination, vomer with a shorter ventral plate, and a larger palatine contribution to triturating surface; *Ctenochelys stenoporus* by a fully-developed secondary palate; *Argillochelys africana* by frontal contribution to orbital margin (Ch. 10); *Argillochelys africana*, *Argillochelys cuneiceps*, *Ashleychelys palmeri*, *Carolinohelys wilsoni* and *Pacificchelys* spp. by dorsolateral orientation of the orbits (Ch. 12); and from *Argillochelys africana*, *Argillochelys cuneiceps*, *Ctenochelys stenoporus*, *Euclastes acutirostris*, *Euclastes platyops*, *Euclastes wielandi*, *Itilochelys rasstrigin*, *Mexichelys coahuilaensis* and *Pacificchelys* spp. by a palatine contribution to the triturating surface that is less than 30% of the width of the triturating surface (Ch. 39).

Description of holotype

Skull. The nearly complete skull of *Cabindachelys landanensis* is preserved in three dimensions, but displacement of several ventral and posterior elements indicates that it has undergone some dorsoventral compression. The braincase is partially disarticulated, and the supraoccipital, exoccipitals, basioccipital and basisphenoid have been displaced from their original locations. The left quadrate, left prootic, left squamosal, most of the right squamosal, and both opisthotics are missing, but the remainder of the skull is complete and well-preserved. The maximum length of the skull along the midline from the anterior margin of the premaxilla to the posterior tip of the crista supraoccipitalis is 14.4 cm, although this measurement is affected by dislocation of the supraoccipital. The midline measurement from the anterior border of the premaxilla to the posterior edge of the parietal-supraoccipital suture is 10.9 cm, and the maximum skull width is 10.3 cm.

Skull roof elements. The prefrontal, which is only slightly smaller in dorsal area than the frontal, forms the anterodorsal margin of the orbit and the dorsal margin of the apertura narium externa. The anterior margin of the prefrontals is fractured, and the dislocated pieces of bone have been pushed into the apertura narium externa, giving the appearance of dislocated nasals (Figs 3C, 4C). A triangular process of the prefrontal extends posteriorly along the orbital margin and forms an extensive contact with the frontal medially. The prefrontal descends ventrally to form the anterior wall of the orbit. Within the orbit, the prefrontal contacts the vomer, but a palatine contact is absent. The contribution of the frontal to the posterodorsal orbital margin is similar in extent to the orbital contribution of the prefrontal. Posteriorly, the frontal contacts both the parietal and the postorbital. The frontals project anteromedially to form a triangular process in anterolateral contact with the prefrontals.

The parietal is the largest of the skull roof elements in terms of dorsal exposure. It contacts the frontal anteriorly, the postorbital laterally, and the parietal posteriorly. The relationship between the parietal and the squamosal is unclear because neither squamosal is preserved in its entirety. The jugal, which is best exposed in lateral view, forms the posterior floor and posterolateral margin of the orbit. The contribution of the jugal to the floor of the orbit is similar in size to those of the maxilla and palatine. The ventral margin of the jugal slopes dorsally, creating a shallow cheek emargination in concert with the quadratojugal (Figs 3E, 4E). The jugal contacts the quadratojugal posteriorly and the postorbital dorsally. There is no jugal-squamosal contact and no possibility that the jugal participates in the upper temporal emargination. In ventral view, the jugal contacts the maxilla anteriorly, the palatine medially, and the pterygoid posteromedially. The foramen palatinum posterius is located at the junction of the jugal, pterygoid and palatine (Figs 3D, 4D).

The quadratojugal is smaller than the jugal and roughly triangular in shape. It has broad contacts with the jugal anteriorly, the squamosal posteriorly, and the quadrate medially. The dorsal apex of the quadratojugal shares a small contact with the postorbital, and the ventral margin forms the posterior portion of the

cheek emargination. The left squamosal is missing, and the right squamosal is only partially preserved. The remnant of the right squamosal is roughly triangular in shape and slightly smaller than the quadratojugal. The preserved portion of the squamosal articulates with the quadratojugal anteriorly and the postorbital dorsally, but its contribution to the upper temporal emargination is uncertain.

The large postorbital composes a significant portion of the skull roof and shares a long medial contact with the parietal and a much smaller contact with the frontal. The anterior border forms the posterior margin of the orbit. The ventral margin of the postorbital, exposed on the lateral side of the skull, contacts the jugal, quadratojugal and squamosal. The postorbital contacts with the jugal and the preserved portion of the right squamosal are similar in length, whereas the suture between the postorbital and the dorsal projection of the quadratojugal is much shorter. The width and depth of the temporal emargination are unclear because neither squamosal is complete.

Palatal elements. The premaxilla contacts the maxilla and the vomer. Viewed anteriorly, the sutures with the maxilla are not well defined, but contacts with the maxilla and the vomer on the ventral surface are clear. The presence of a foramen praepalatium is equivocal. In ventral view, two small pores are visible on the posterior portion of the premaxillae, just anterior to the contact with the vomer (Figs 3D, 4D); however, canals connecting these features to the fossa nasalis are not visible in the CT imagery. The premaxilla, which widens anteriorly, forms the anterior part of the upper triturating surface and the anterior margin and floor of the apertura narium externa. There is no premaxillary hook on the tomial ridge, but the ridge is sharp and well defined along its entire length. The labial ridge, which is low and rounded, disappears as it reaches the posterior portion of the maxilla. The maxilla composes the majority of the triturating surface. The dorsal process of the maxilla defines the lateral margin of the apertura narium externa and forms the anterior border and anterior floor of the orbit. The posteroventrally oriented suture between the maxilla and jugal is located beneath the orbit. The ventral margin of the maxilla does not participate in the cheek emargination. There is a small maxillary contact with the prefrontal at the terminus of the slender dorsal process. The anteromedial contact of the maxilla with the premaxilla is not well defined, but the ventral suture between these elements is clear. In anteroposterior order on the ventral surface, the maxilla has medial contacts with the premaxilla, the vomer and the palatine.

The ventral plate of the vomer, located just posterior to the premaxilla, is narrow and trapezoidal in shape. The apertura narium interna is bounded medially by the vomer and laterally by the palatine. The vomer, with minor contributions from the palatines, forms a modest secondary palate that separates the internal nares from the oral cavity. Posteriorly, the dorsal plate of the vomer narrows to a thin strip that separates the palatines, with the posterior tip contacting the pterygoids (Figs 3D, 4D). In ventral view, the palatine abuts the vomer medially, the maxilla and the jugal laterally, and the pterygoid posteriorly. Medial to the maxilla, the palatine composes *c.* 15% of the area of the triturating surface (measured with ImageJ). The palatine also

forms the medial part of the orbital floor, where it contacts the maxilla and jugal.

Palatoquadrate elements. The left quadrate is missing, but the right element is well preserved. The quadrate constricts posterodorsally to form the anterior border of the antrum postoticum, which is roofed by the squamosal. There is no precolumellar fossa, and the incisura columellae auris opens posteroventrally. The dorsal process of the quadrate forms the floor of the cavum acustico-jugulare, with the pterygoid covering the prootic. The pterygoids have an extensive medial contact, with a long posterior process that extends back to overlap the quadrate. Anteriorly, the pterygoid articulates with the vomer and the palatine, and the processus pterygoideus externus forms a small suture with the jugal. There is a small hook-like projection on the posterior edge of the processus pterygoideus externus, bordering the fossa temporalis inferior. Posteriorly, there is also contact between the pterygoids and both the basioccipital and the exoccipitals. The relatively small foramen palatinum posterius (most easily viewed in dorsal aspect) is located at the junction of the pterygoid, the palatine and the jugal.

Braincase elements. The crista supraoccipitalis extends posteriorly far beyond the occipital condyle. A horizontal crest runs its entire length, lending this element a T-shaped cross-section. The supraoccipital forms the dorsal border of the foramen magnum, but does not contribute significantly to the skull roof. Although the braincase is collapsed, and some of the original relationships of the component elements are difficult to discern, the CT data may be used to reconstruct of this part of the skull (e.g. Fig. 6). The exoccipitals form the majority of the occipital condyle and most of the margin of the foramen magnum, although they do not meet dorsally. The exoccipitals articulate with the basioccipital, pterygoids and supraoccipital. Two foramina nervi hypoglossi are visible on either side of the neck of the occipital condyle. The basicranial elements have been displaced, and the basioccipital is largely obscured by the basisphenoid. However, the shape of the posterior margin of the basisphenoid and analysis of CT imagery indicate that the anterior border of the basioccipital is convex (Fig. 6B). The basioccipital forms the ventral portion of the occipital condyle, and it is broadly fan-like in shape. It articulates laterally with the pterygoids, posterolaterally with the exoccipitals, and anteriorly with the basisphenoid.

The left prootic is missing, and the right element is visible only in anterior view, at the back of the orbit. Neither the left nor the right opisthotic is present. The ventral surface of the basisphenoid resembles a transversely oriented boomerang, tapering anteriorly to meet the medial suture between the pterygoids and forming a concave contact with the basioccipital posteriorly (Fig. 6B). The basisphenoid forms a low V-shaped crest where the anterolateral margins of the ventral plate contact the pterygoids. Anteriorly, the rostrum basisphenoidale is narrow, rod-like and tapered (Fig. 6). CT data indicate that the paired processus clinoides is prominent, and the dorsum sellae is relatively high, overhanging the sella turcica posteriorly (Fig. 6D). The lateral margins of the sella turcica converge anteriorly to form a shallow sulcus on the posterodorsal portion of the rostrum basisphenoidale.

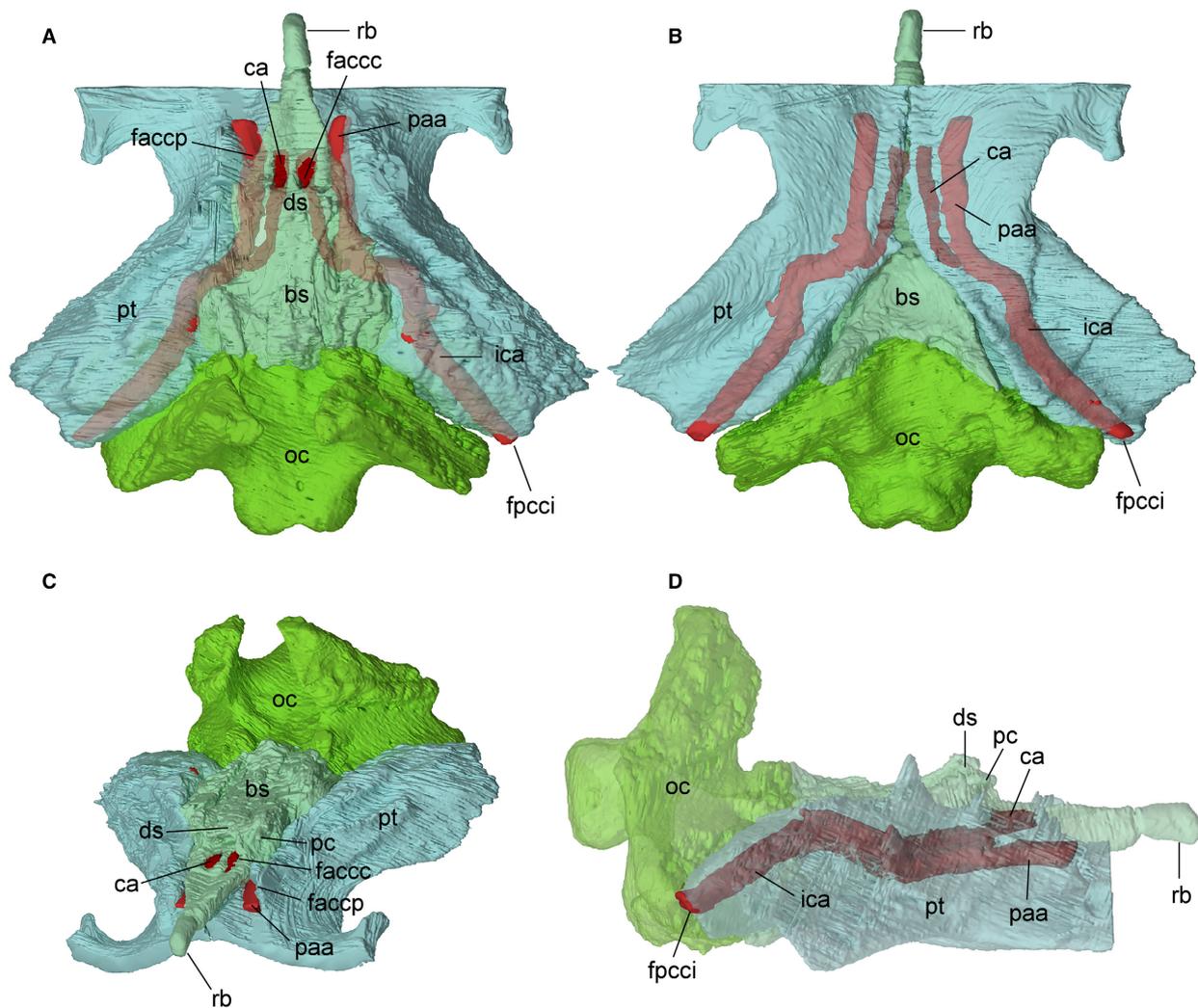


FIG. 6. CT rendering showing relationships of basicranial elements and pathways of the internal carotid artery and its branches. A, dorsal; B, ventral; C, anterolateral; and D, right lateral view. Note the slender, rod-shaped rostrum basisphenoidale. *Abbreviations:* bs, basisphenoid; ca, cerebral artery; ds, dorsum sellae; faccc, foramen anterius canalis carotici cerebri; faccp, foramen anterius canalis carotici palatinum; fpcci, foramen posterius canalis carotici interni; ica, internal carotid artery; oc, occipital complex; paa, palatine artery; pc, processus clinoides; pt, pterygoid; rb, rostrum basisphenoidale.

Carotid circulation. The terminology in this section follows the nomenclature presented by Rabi *et al.* (2013). CT imagery shows that the internal carotid artery enters the pterygoid posteriorly, just lateral to the tuberculum basioccipitale, via the foramen posterius canalis carotici interni. The artery traces an anterodorsal and slightly medial path relatively deep within the posterior part of the pterygoid, roughly following the medial margin of the pterygoid (Fig. 6). Just anterior to the dorsal aspect of the basioccipital-basisphenoid suture, the path of the internal carotid becomes almost longitudinal, and dips anteroventrally before turning sharply medially at about the level of the processus clinoides and emerging from the pterygoid via the foramen anterius canalis carotici interni, at which point it bifurcates into the palatine and cerebral arteries.

The palatine artery is of the same diameter as the internal carotid, and lies within a deep sulcus on the medial side of the

pterygoid. The pterygoid composes the majority of the palatine canal, with the remainder formed by the medial contribution of the basisphenoid. The palatine artery follows a roughly longitudinal path and slopes only modestly anterodorsally. It is exposed anterodorsally, emerging from the palatine canal via the foramen anterius canalis carotici palatinum at a position nearly even with the anterior margin of the foramen anterius canalis carotici cerebri.

The cerebral artery branches from the dorsomedial part of the internal carotid artery, trending sharply anteromedially for a short distance, then angling gently dorsomedially. The cerebral artery lies within a deep sulcus that is exposed ventrolaterally on the basisphenoid, but originally would have been fully enclosed by the pterygoid both ventrally and laterally. The artery completely enters the basisphenoid anteriorly, emerging a short distance ahead within the floor of the sella turcica via the foramen anterius canalis carotici

cerebralis (Fig. 6). Thus, the canalis caroticus cerebralis is formed by both the basisphenoid and pterygoid for most of its distance.

Hyoid. The left first branchial horn was found beneath the skull when it was prepared. The horn is mostly complete (Fig. 5), with some portion (possibly cartilaginous) missing distally. It has been somewhat distorted by crushing, so the measurements given here are approximate. The total length of the element along the midline is 5.3 cm, with a 2.5 cm proximal part and a 2.8 cm distal portion. The proximal diameter is 0.8 cm, and the angle between the proximal and distal segments is 115°.

Other relevant turtle specimens from the Landana locality

Carapace. A partial carapace (MRAC 4796) was figured and described in detail by Wood (1973, fig. 1, plates 1–2). The original description is summarized here. This specimen, which was collected from a bed *c.* 1 m above MGUAN–PA 298 in the Landana stratigraphy (Fig. 2), comprises the posterior half of the carapace and is characterized by prominent costo-peripheral fontanelles. The maximum preserved length of MRAC 4796 is 46 cm (43 cm along the midline), although the total length of the carapace is likely to have been more than a metre (Wood 1973). The specimen includes at least portions of neurals four to eight, and left and right costals five to eight. The fourth neural, and the fifth and sixth right costals are incomplete. The neurals are hexagonal and anteroposteriorly elongate, with a coffin-shaped outline. A single, mid-dorsal ridge is present, tapering posteriorly until it disappears altogether on the eighth neural, and a single epineural ossification is located dorsal to the suture between the fourth and fifth neurals (Wood 1973). The costals are short and wide, separated by large fontanelles (Wood 1973, fig. 1, plate 1).

The presence of sulci crossing the fifth neural, left sixth costal, and right sixth and seventh costals indicates that the dorsal surface of the carapace was covered by keratinous scutes. These sulci define the boundary between the third and fourth vertebral scutes. Sulci forming the lateral boundaries of the vertebral scutes are located near the distal ends of the costals (Wood 1973). Orientation of the sulci suggests that the vertebral scutes were broad and hexagonal.

Humerus. A complete left humerus (MGUAN–PA 297) was recovered during the 2012 Projecto PaleoAngola field season, from a bed 1–2 m above the stratigraphic level of MGUAN–PA 298, the holotype skull of *Cabindachelys landanensis*. The humerus measures 14.8 cm in length, with a strongly curved, flattened shaft (Fig. 7). Proximally, the distance between the medial and lateral processes measures 5.8 cm, and the distal end has a maximum width of 3.8 cm. The prominent humeral head projects anteriorly beyond the processes, which are subequal in size. The head is 3.6 cm wide mediolaterally and 2.7 cm wide dorsoventrally, with a semilunate articular surface. The processes are thin, oriented at *c.* 90° to each other, and located at similar positions relative to the shaft, with neither one shifted distally. The medial process is slightly larger and broader than the lateral process, but the size difference is not pronounced. A U-shaped fossa separates the

processes and wraps around the ventral side of the humeral head. Ridges arising from each process form the lateral margins of this fossa, but do not meet at the midline of the shaft. The condyles at the distal end are only weakly differentiated by the entepicondylar groove on the ventral surface.

PHYLOGENETIC ANALYSIS

Phylogenetic analyses were conducted to determine the placement of *Cabindachelys landanensis* within Chelonioida. We used a modified version of the matrix presented by Cadena & Parham (2015) that contains 155 taxa (fossil and extant) and 256 characters. Analyses were performed with TNT version 1.1 (Goloboff *et al.* 2008), using the same, molecular-based, constraint tree for extant taxa as Cadena & Parham (2015). *Cabindachelys landanensis* was scored using both the holotype cranial material (MGUAN–PA 298) and referred carapace material (MRAC 4796). Additionally, 26 character codings for *Angolachelys mbaxi* were changed, based on data published by Mateus *et al.* (2009), observations of the holotype specimen (MGUAN–PA 002), and examination of newly-discovered and as-yet-unpublished cranial material referable to *A. mbaxi* (MGUAN–PA 296). Corrected character codings for *A. mbaxi* and the new codings for *C. landanensis* are detailed in Myers *et al.* (2017). Character numbering here and elsewhere in the text, tables, and figures reflects the numbering scheme in the original matrix of Cadena & Parham (2015), starting with Character 1. However, TNT character numbers begin with 0, so all characters in the archived TNT file (Myers *et al.* 2017) are numbered *n*–1 for any given character *n*. The coding of Character 135 (costal 9: present/absent) was changed from 0 to 1 for *Rhinochelys nammourensis* based on the

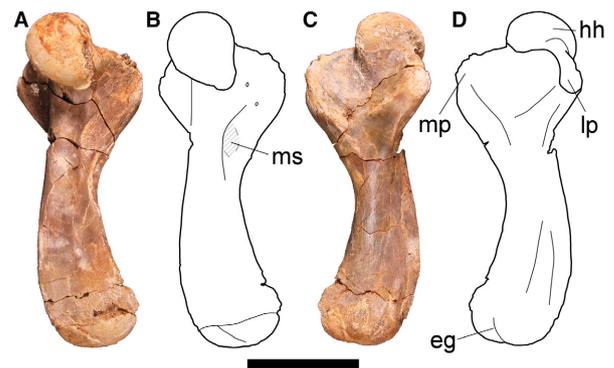
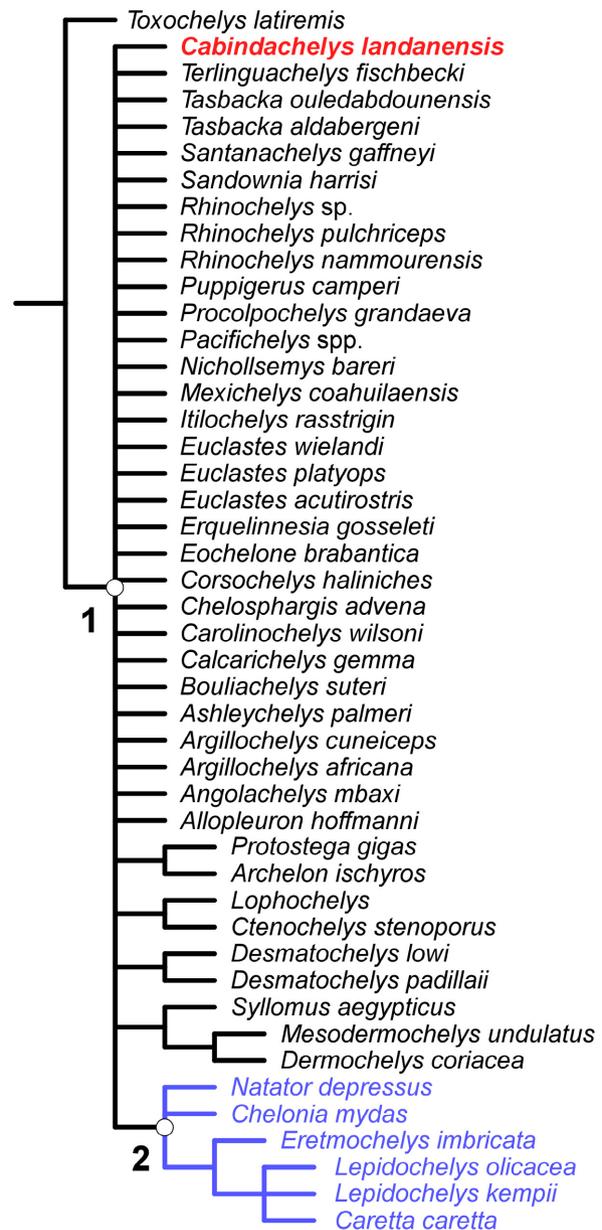


FIG. 7. Photographs and line drawings of unidentified left humerus MGUAN–PA 297. A–B, dorsal; C–D, ventral view. This specimen is referable to neither *Taphrosphys congolensis* nor Pan-Chelonioida (*sensu* Joyce *et al.* 2004). Abbreviations: eg, entepicondylar groove; hh, humeral head; lp, lateral process; mp, medial process; ms, muscle scar. Scale bar represents 5 cm. Colour online.

description by Tong *et al.* (2006), and Character 10 (frontal contribution to orbit: absent/present) was switched from 1 to 0 for *Argillochelys africana* based on the information in Tong & Hirayama (2008). Phylogenetic analyses were run using traditional (heuristic) tree searches with 1000 replicates of random addition sequences, followed by tree-bisection reconnection (TBR) branch swapping, saving 10 trees per replicate. Trees were collapsed after the search, and maxtrees was set to 50 000. For analysis of Testudinata (all 155 OTUs, outgroup = *Proganochelys quenstedti*) some replications overflowed in the first analysis, so a second search was run on trees in RAM. The tree buffer overflowed during the second round of searching, yielding 50 000 equally parsimonious trees of 1225 steps. *Cabindachelys landanensis* falls into a large polytomy at the base of Chelonioidae, leaving the relationships within this clade largely unresolved, especially with respect to stem cheloniids (Fig. 8). In order to improve the resolution of the analysis and attempt to better ascertain the phylogenetic relationships of *C. landanensis*, a second set of analyses was run including only the 46 taxa identified as pan-chelonioids (*sensu* Joyce *et al.* 2004) in the initial analysis of Testudinata (see full tree in Myers *et al.* 2017). In the analysis of Pan-Chelonioidae (46 OTUs, outgroup = *Toxochelys latiremis*), some replications overflowed in the first search, and a subsequent search using trees in RAM produced 9630 equally parsimonious trees with 291 steps. In the resultant strict consensus tree, *C. landanensis* forms a poorly-supported clade with *Erquelinnesia gosseleti*, *Euclastes acutirostris*, *Euclastes wielandi* and *Terlinguachelys fischbecki* (Fig. 9). Another analysis of Pan-Chelonioidae, performed without coding for the partial carapace (MRAC 4796) referred to *C. landanensis*, yields 9630 equally parsimonious trees of 290 steps, and the topology of the strict consensus tree remains unchanged.

DISCUSSION

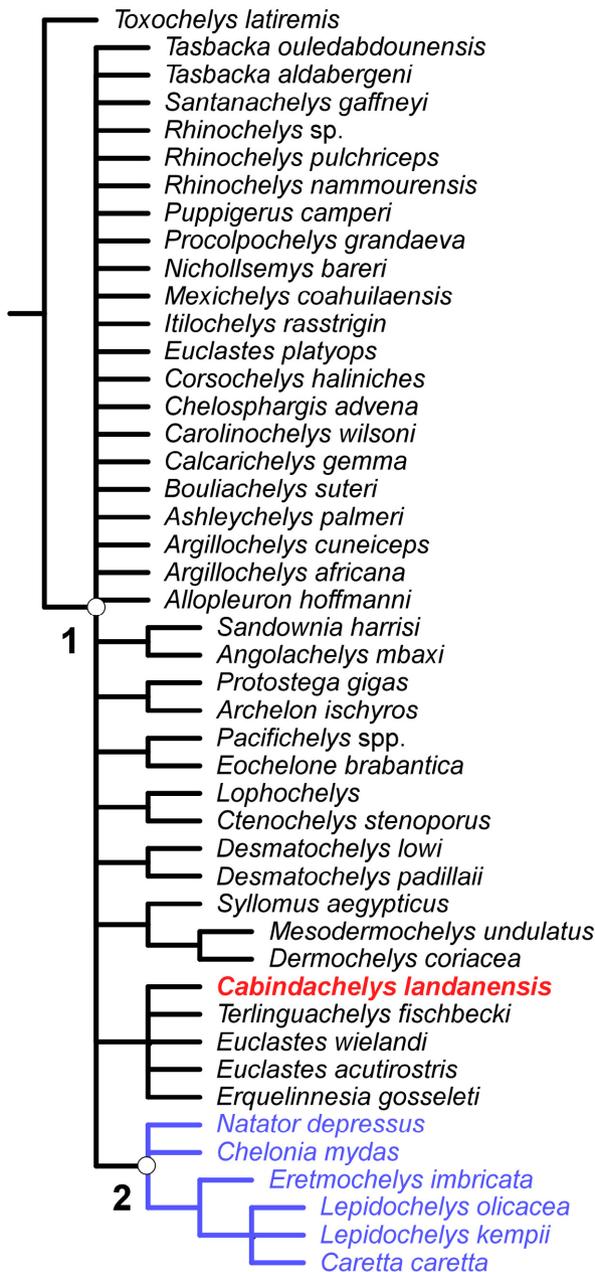
This paper follows the phylogenetic taxonomy of Joyce *et al.* (2004), wherein Chelonioidae is defined as the crown clade comprising the most recent common ancestor of *Chelonia mydas* and *Dermochelys coriacea* and all its descendants. Pan-Chelonioidae refers to the clade containing crown Chelonioidae and all the fossil species located along the stem of Chelonioidae. Similarly, Cheloniidae is the crown clade composed of the most recent common ancestor of *Chelonia mydas* and *Caretta caretta* and all its descendants, and Pan-Cheloniidae is the most inclusive stem-based clade that contains Cheloniidae and does not overlap with stems of extant non-cheloniid taxa (Joyce *et al.* 2004). Presence of a thin, rod-like rostrum basisphenoidale, V-shaped basisphenoid crest, and



1 Chelonioidae 2 Cheloniidae

FIG. 8. Strict consensus of 50 000 MPTs, showing the phylogenetic position of *Cabindachelys landanensis* gen. et sp. nov. (MGUAN-PA 298) within Testudinata. 26 codings for *Angolachelys mbaxi* (Mateus *et al.* 2009) were updated, and single characters were recoded for both *Argillochelys africana* and *Rhinochelys nammourensis*. Only pan-chelonioids are shown here. The TNT file and full strict consensus tree are available in Myers *et al.* (2017). Colour online.

secondary palate indicates that *Cabindachelys landanensis* is a pan-cheloniid (Parham 2005). *Cabindachelys landanensis* differs from many other cheloniids in the presence



1 Chelonioidae 2 Cheloniidae

FIG. 9. Strict consensus of 9630 MPTs, depicting relationships within Pan-Chelonioidae (*sensu* Joyce *et al.* 2004) including *Cabindachelys landanensis* gen. et sp. nov. (MGUAN-PA 298). This analysis included only taxa identified as pan-chelonioids in the analysis of Testudinata. The consensus tree topology remains unchanged when the analysis is run without coding for the referred carapace material (MRAC 4796). Colour online.

of the foramen palatinum posterius, which is primitive within Pan-Cheloniidae. This foramen is greatly reduced in *C. landanensis* compared to the large foramina present

in primitive stem chelonioids such as *Toxochelys latiremis* (e.g. Matzke 2009).

The overall shape of the skull in *Cabindachelys landanensis* is comparable to the dorsoventrally low skull profile and flat skull roof of *Toxochelys latiremis* (Matzke 2009), which contrasts markedly with the highly vaulted skull roofs of pan-chelonioids such as *Chelonia mydas* and *Euclastes wielandi* (Hirayama 1994). In dorsal view, the posterior portion of the skull formed by the parietal and postorbital is broad, as in *Erquelinnesia gosseleti* and *Euclastes wielandi*, but anteriorly there is a medial constriction beneath the orbit where the jugal and maxilla meet (Figs 3C, 4C), such that the lateral margins of the skull are stepped inward, making the snout appear pinched. *Cabindachelys landanensis* has a moderately expanded secondary palate, similar in extent to that of *Chelonia mydas* (Hirayama 1997), with the internal nares surrounded by the vomer and the palatines (Figs 3, 4). The secondary palate of *C. landanensis* is not as extensive as in *Euclastes wielandi* or *Erquelinnesia gosseleti* (Zangerl 1971; Lynch & Parham 2003; Parham 2005), as reflected by differences in: (1) the exposure of the vomer; and (2) the relative positions of the secondary palate and subtemporal fenestrae. In *C. landanensis*, the vomer possesses a slender dorsal plate that is longer in ventral aspect than the ventral plate on the palatal surface. In contrast, the dorsal plates of the vomers in *Euclastes wielandi* and *Erquelinnesia gosseleti* are almost entirely obscured by the posterior portion of the secondary palate, and in *Euclastes acutirostris*, the exposed portion of the dorsal plate is clearly shorter than the ventral plate (Fig. 10). *Cabindachelys landanensis* is also distinguished from *Euclastes wielandi* and *Erquelinnesia gosseleti* by the position of the posterior edge of the secondary palate relative to the anterior margin of the subtemporal fenestrae. In *Erquelinnesia gosseleti*, the posterior palatal margin at the centerline is closer to the posterior edge of the subtemporal fenestrae than it is to the anterior margin, whereas in *Euclastes acutirostris* and *Euclastes wielandi* the posterior edge of the secondary palate at the centerline is either slightly posterior to or roughly even with the anterior-most projection of the subtemporal fenestrae (Fig. 10). Conversely, the posterior edge of the secondary palate (at centerline) of *C. landanensis* is clearly anterior to the anterior projection of the subtemporal fenestrae in ventral view. *Cabindachelys landanensis* appears quite similar to *Itilochelys rasstrigin*, a stem cheloniid from the lower Paleocene (Danian) of Russia (Danilov *et al.* 2010). Both *C. landanensis* and *I. rasstrigin* possess expanded secondary palates, and in dorsal view, both have 'pinched' snouts characterized by medially-stepped margins beneath the orbits, near the contact between the jugal and maxilla. However, the skull of *I. rasstrigin* is dorsoventrally tall with a deep cheek emargination and is more elongated

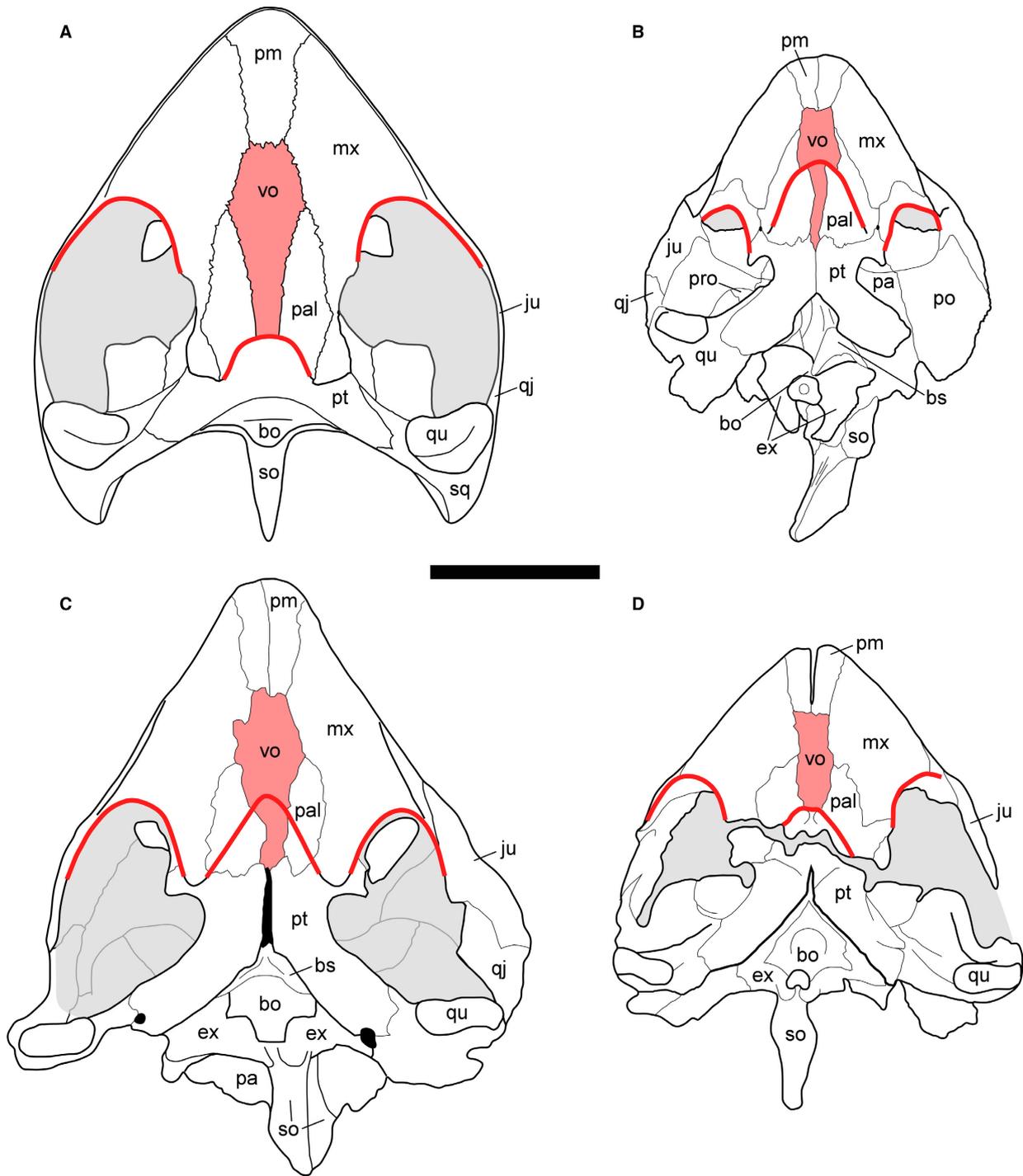


FIG. 10. Line drawings of skulls of durophagous stem cheloniids in ventral view. A, *Erquelinnesia gosseleti* (I.R.Sc.N.B. No. 1563) after Zangerl (1971). B, *Cabindachelys landanensis* gen. et sp. nov. (MGUAN-PA 298). C, *Euclastes acutirostris* (OCP.DEK/GE 408) after Jalil *et al.* (2009). D, *Euclastes wielandi* (NJSM 11872) after Fastovsky (1985) and Parham (2005). The vomers are shaded, and the posterior palatal margins and anterior margins of the subtemporal fenestrae are traced with thick lines. *Abbreviations:* bo, basioccipital; bs, basisphenoid; ex, exoccipital; ju, jugal; mx, maxilla; pa, parietal; pal, palatine; pm, premaxilla; po, postorbital; pro, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar represents 5 cm. Colour online.

anteroposteriorly than that of *C. landanensis*. The ventral plate of the vomer is considerably longer anteroposteriorly in *I. rasstrigin*, and the palatine forms a much smaller portion of the area of the triturating surface.

Wood (1973) initially suggested a toxochelyid affinity for the partial carapace (MRAC 4796) and mandible (MRAC 3090) that were collected from the Landana locality sometime prior to the 1970s and deposited at the Musee Royal de l'Afrique Centrale in Tervuren, Belgium. Gaffney *et al.* (2006) subsequently referred the mandible to *Taphrosphys congolensis* due to its narrow triturating surface (similar to other taphrosphyine jaws) and large processus retroarticularis, which is absent in chelonioids. The width of the dentary triturating surface on MRAC 3090 is certainly much narrower than in durophagous pan-cheloniids that have expanded secondary palates and large upper triturating surfaces (e.g. *Euclastes acutirostris*, *Euclastes wielandi*, *Erquelinnesia gosseleti*). The triturating surface on MRAC 3090 is similar in area to that of *Ctenochelys stenoporus*, which lacks a fully-developed secondary palate (Matzke 2007); therefore, even if MRAC 3090 was not referable to *T. congolensis*, its morphology would still be inconsistent with the palatal characteristics of *C. landanensis*. In contrast, the poorly-ossified costals and well-developed costal fontanelles of MRAC 4796 indicate clear chelonioid affinities that, in conjunction with its close stratigraphic proximity to the holotype skull of *C. landanensis* (MGUAN-PA 298) in the Landana section (Fig. 2), support referral of this carapace material to *C. landanensis*.

The phylogenetic analyses presented here suggest that *Cabindachelys landanensis* forms a poorly-supported clade with *Erquelinnesia gosseleti*, *Euclastes acutirostris*, *Euclastes wielandi* and *Terlinguachelys fischbecki* within Chelonioida (Fig. 9). The synapomorphies uniting this clade are dorsolaterally facing orbits (Ch. 12), vomerine pillar obscured by triturating surface (Ch. 50), large processus trochlearis oticum with a well-defined muscularity facet (Ch. 57), small contribution of the quadrate to the muscularity facet of the processus trochlearis oticum (Ch. 58), dentary without symphyseal ridge (Ch. 111) and pygal posterior notch present (Ch. 140). Analyses of durophagous pan-cheloniids are often confounded by homoplasy (e.g. Parham & Pyenson 2010), but with the exception of Character 50, the synapomorphies of this clade are not palatal characters related to feeding specialization. However, it is unlikely that the Campanian-age protostegid *Terlinguachelys fischbecki* is closely related to the four other taxa in this clade. The mandible of *T. fischbecki*, which constitutes the only known cranial material of this taxon, has a relatively narrow triturating surface. The lower triturating surface is especially small compared to durophagous taxa like *Erquelinnesia gosseleti*, *Euclastes acutirostris* and *Euclastes wielandi*; *T. fischbecki* may lack a

secondary palate altogether (Lehman & Tomlinson 2004). Approximately 79% of the characters in this analysis are coded as missing for *T. fischbecki*, and this high percentage of missing (mostly cranial) data probably explains why this protostegid appears in a clade with durophagous stem cheloniids. Although this analysis, like that of Cadena & Parham (2015), recovers protostegids within crown-Chelonioida (Figs 8, 9), stratigraphical and biogeographical complications cast doubt on this phylogenetic relationship (Cadena & Parham 2015), as do other phylogenetic analyses (Joyce 2007; Joyce *et al.* 2013). The fact that protostegids do not form a monophyletic group in the strict consensus trees, and the general lack of resolution in these analyses, is most likely due to homoplasy.

The humerus (MGUAN-PA 297) collected from the Landana locality is not referable to either *Cabindachelys landanensis* or *Taphrosphys congolensis*. Humeral material belonging to *Taphrosphys congolensis* is currently unknown, but MGUAN-PA 297 clearly differs from the humerus of *Taphrosphys sulcatus* from the Paleocene of New Jersey, USA, which has a prominent medial process and a wide distal end (Gaffney 1975). Pan-chelonioid humeri are characterized by a distally shifted lateral process and a high angle between the humeral head and shaft (Lynch & Parham 2003; Parham & Pyenson 2010). The medial and lateral processes of MGUAN-PA 297 are subequal in size and occupy similar positions on either side of the humeral head. The angle between the humeral head and the shaft is *c.* 19°, compared to 29° for *Toxochelys latiremis* and 11° for *Chelydra serpentina* (Zangerl 1953). Collectively, these features suggest that MGUAN-PA 297 does not belong to a marine turtle and is therefore not referable to *Cabindachelys landanensis*.

The presence of MGUAN-PA 297 indicates that at least three different turtle species are represented in the Landana assemblage, as originally suggested by Dollo (1924). Most of the specimens collected from the onshore exposures of the Landana Formation belong to the pleurodire *Taphrosphys congolensis* (see Gaffney *et al.* 2006 for a list of specimens from this locality referred to *T. congolensis*). Carapace and plastron fragments with the anastomosed surface texture characteristic of *T. congolensis* are abundant in the lower half of the Landana stratigraphic section. A much smaller number of specimens, including MGUAN-PA 298 and MRAC 4796, are attributable to *Cabindachelys landanensis*, and MGUAN-PA 297 belongs to a third, as yet unidentified, non-marine turtle species. The relative rarity of material referable to *C. landanensis* at the Landana locality is consistent with a preference for open marine habitats, and the broad skull and expanded secondary palate suggest that *C. landanensis* fed primarily on hard-shelled organisms. Reduction of the bony shell through development and expansion of costo-peripheral fontanelles, as seen in the carapace referred here to

C. landanensis, is a chelonioid adaptation to open marine habitats. In contrast, *T. congolensis* probably preferred nearshore and marginal marine environments such as those represented by the Landana strata.

Adaptations for durophagy (i.e. large triturating surfaces on an expanded secondary palate) evolved multiple times in marine turtles, beginning with protostegids in the Cretaceous, and there is evidence that durophagy evolved independently at least three times within Pan-Chelonioidea (Parham & Pyenson 2010). Phylogenetic analyses indicate that cheloniids diverged from dermochelyids in the Western Interior Seaway of North America in the Cretaceous (Joyce *et al.* 2013; Parham *et al.* 2014). With the extinction of protostegids in the Late Cretaceous, stem cheloniids such as *Mexichelys coahuilaensis* and *Euclastes wielandi* (Brinkman *et al.* 2009; Parham & Pyenson 2010; Parham *et al.* 2014) filled this niche. The genus *Euclastes* is widespread in the latest Cretaceous, with definitive occurrences in the Maastrichtian of North America, South America, and Africa (Parham *et al.* 2014). Currently available fossil evidence indicates that *Euclastes wielandi* was the only durophagous pan-chelonioid to cross the Cretaceous–Palaeogene boundary (Parham 2005; Parham *et al.* 2014) with other durophagous taxa presumably succumbing to unfavourable conditions connected to the K–Pg extinction event. The loss of many marine turtle species in the Late Cretaceous allowed new taxa to fill the empty niche space as pan-cheloniids diversified in the early Palaeogene. The phylogenetic analysis presented here implies that *Cabindachelys landanensis* belonged to a clade of durophagous stem cheloniids that survived the K–Pg extinction and began to radiate soon thereafter. By the Eocene, some chelonioid genera again achieved global distributions that contrast with the more regional endemism observed in the Paleocene (Parham *et al.* 2014). Durophagous chelonioids (e.g. *Alienochelys selloumi*, *Brachyopsemys tingitana*, *Cabindachelys landanensis*, *Euclastes acutirostris*, *Euclastes* sp.) are particularly abundant and diverse in the Palaeogene of Africa (Jalil *et al.* 2009; Tong & Meylan 2013; Lapparent de Broin *et al.* 2014; Strganac *et al.* 2015), although the concentration of occurrences in Morocco and Angola is probably the result of preservational and/or sampling bias.

CONCLUSION

The fossil turtle skull and partial hyoid (MGUAN–PA 298) reported here from lower Paleocene shallow marine strata exposed west of the town of Landana represent a new genus of durophagous, stem cheloniid turtle, *Cabindachelys landanensis*. A partial carapace collected from this same locality and originally described by Wood (1973) is referred to this new taxon. An isolated left

humerus (MGUAN–PA 297), probably the remains of a non-marine turtle that were washed into the nearshore environment, is not attributable to either *C. landanensis* or *Taphrosphys congolensis*. These new specimens demonstrate that at least three different species of turtles are preserved in the coastal outcrops near Landana, as originally suggested by Dollo in 1924. The relative rarity of chelonioid fossil material attributable to *C. landanensis* at the Landana locality compared to the abundance of specimens identifiable as *Taphrosphys congolensis* suggests that *T. congolensis* frequented nearshore habitats, whereas *C. landanensis* spent relatively little time foraging in paralic environments, instead preferring open marine habitats. Phylogenetic analysis indicates that *C. landanensis* forms a weakly-supported clade with *Erquelinnesia gosseleti*, *Euclastes acutirostris*, *Euclastes wielandi* and *Terlinguachelys fischbecki*, although it is unlikely that *T. fischbecki* is closely related to these durophagous stem cheloniids. This clade of pan-cheloniid durophages crosses the K–Pg boundary and illustrates the radiation and diversification of pan-cheloniids in the early Palaeogene as marine ecosystems recovered from this global extinction event.

Acknowledgements. This research was conducted under the auspices of Projecto PaleoAngola, an international cooperative research effort among the contributing authors and their institutions, funded by the National Geographic Society, the Petroleum Research Fund of the American Chemical Society, Sonangol E.P., Esso Angola, Fundação Vida of Angola, LS Films, Maersk, Damco, Safmarine, Catoca Diamond Mine, Kwanza Lodge, ISEM at SMU, The Royal Dutch Embassy in Luanda, TAP Airlines, KLM Royal Dutch Airlines, and The Saurus Institute. We thank Maria Luísa Morais, Margarita Ventura, and André Buta Neto for assisting our team in the field. Tako and Henriette Koning provided valuable support in Angola. We thank the handling editor Roger Benson and two anonymous referees for their helpful suggestions on an earlier draft of this paper.

DATA ARCHIVING STATEMENT

Data for this study, including character codings for *Cabindachelys landanensis* and *Angolachelys mbaxi*, TNT file for analysis of Testudinata, and cladogram from analysis of Testudinata, are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n618q>.

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/47F23B-BF-E4EC-4136-B02F-2D08CD4D7EFD>.

Editor. Roger Benson

REFERENCES

- BATSCH, A. J. G. K. 1788. *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. Akademische Buchhandlung, Jena, 528 pp.

- BAUR, G. 1893. Notes on the classification of the Cryptodira. *American Naturalist*, **27**, 672–675.
- BEQUAERT, J. 1923. Observations géologiques faites au cours d'un voyage dans l'enclave de Cabinda et le bas-Congo. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, **33**, 18–28.
- BRICE, S. E., COCHRAN, M. D., PARDO, G. and EDWARDS, A. D. 1982. Tectonics and sedimentation of the South Atlantic rift sequence: Cabinda, Angola. 5–18. In WATKINS, J. S. and DRAKE, C. L. (eds). *Studies in continental margin geology*. AAPG Memoir, **34**.
- BRINKMAN, D., AQUILLON-MARTINEZ, M. C., DE LEON DÁVILA, C. A., JAMNICZKY, H., EBERTH, D. A. and COLBERT, M. 2009. *Euclastes coahuilaensis* sp. nov., a basal cheloniid turtle from the late Campanian Cerro del Pueblo Formation of Coahuila State, Mexico. *PaleoBios*, **28**, 76–88.
- BROWNFIELD, M. E. and CHARPENTIER, R. R. 2006. Geology and total petroleum systems of the West-Central Coastal Province (7203), West Africa. *US Geological Survey Bulletin*, **2207-B**, 1–52.
- CADENA, E. A. and PARHAM, J. F. 2015. Oldest known marine turtle? A new protostegid from the Lower Cretaceous of Colombia. *PaleoBios*, **32**, 1–42.
- COPE, E. D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **20**, 242–300.
- DA COSTA, J. L., SCHIRMER, T. W. and LAWS, B. R. 2001. Lower Congo Basin, deep-water exploration province, offshore west Africa. 517–530. In DOWNEY, M. W., THREET, J. C. and MORGAN, W. A. (eds). *Petroleum provinces of the twenty-first century*. AAPG Memoir, **74**.
- DANILOV, I. G., AVERIANOV, A. O. and YARKOV, A. A. 2010. *Itilochelys rasstringin* gen. et sp. nov., a new hard-shelled sea turtle (Cheloniidae *sensu lato*) from the Lower Paleocene of Volgograd Province, Russia. *Proceedings of the Zoological Institute RAS*, **314**, 24–41.
- DARTEVELLE, E. and CASIER, E. 1943. Les poissons fossiles du Bas-Congo et des régions voisines. *Annales du Musée du Congo Belge, Série A. Minéralogie, géologie, paléontologie*, **2**, 1–200.
- DOLLO, L. 1912. Sur les premiers restes de Tortues fossiles recueillis au Congo. *Bulletin de L'Académie Royale de Belgique (Classe des Sciences)*, **1**, 8–9.
- 1913. *Podocnemis congolensis*, tortue fluviatile nouvelle du montien (Paléocène inférieur) du Congo et l'évolution des chéloniens fluviatiles. *Annales du Musée du Congo Belge, A. Minéralogie, géologie, paléontologie*, **3**, 49–65.
- 1924. *Bantuchelys*, genre nouveau de Tortues, découvert dans le Paléocène du Congo. *Bulletin de L'Académie Royale de Belgique (Classe des Sciences)*, **10**, 613–635.
- FASTOVSKY, D. E. 1985. A skull of the Cretaceous chelonioid turtle *Osteopygis* and the classification of the Osteopyginae. *New Jersey State Museum, Investigation*, **3**, 1–28.
- GAFFNEY, E. S. 1975. A revision of the side-necked turtle *Taphrosphys sulcatus* (Leidy) from the Cretaceous of New Jersey. *American Museum Novitates*, **2571**, 1–24.
- TONG, H. and MEYLAN, P. A. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, **300**, 1–698.
- GOLOBOFF, P. A., FARRIS, J. S. and NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.
- GRADSTEIN, F. M., OGG, J. G., SCHMITZ, M. D. and OGG, G. M. 2012. *The geologic time scale 2012*. Elsevier, 720 pp.
- HIRAYAMA, R. 1994. Phylogenetic systematics of chelonioid sea turtles. *The Island Arc*, **3**, 270–284.
- 1997. Distribution and diversity of Cretaceous chelonioids. 225–241. In CALLAWAY, J. M. and NICHOLLS, E. L. (eds). *Ancient marine reptiles*. Academic Press.
- JALIL, N.-E., DE BROIN, F., BARDET, N., VACANT, R., BOUYA, B., AMAGHZAZ, M. and MESLOUH, S. 2009. *Euclastes acutirostris*, a new species of littoral turtle (Cryptodira, Cheloniidae) from the Palaeocene phosphates of Morocco (Oulad Abdoun Basin, Danian-Thanetian). *Comptes Rendus Palevol*, **8**, 447–459.
- JOYCE, W. G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*, **48**, 3–102.
- PARHAM, J. F. and GAUTHIER, J. A. 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.
- — LYSON, T. R., WARNOCK, R. C. M. and DONOGHUE, P. C. J. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. *Journal of Paleontology*, **87**, 612–634.
- LAPPARENT DE BROIN, F., BARDET, N., AMAGHZAZ, M. and MESLOUH, S. 2014. A strange new chelonioid turtle from the latest Cretaceous phosphates of Morocco. *Comptes Rendus Palevol*, **13**, 87–95.
- LEHMAN, T. M. and TOMLINSON, S. L. 2004. *Terlinguachelys fischbecki*, a new genus and species of sea turtle (Chelonioida: Protostegidae) from the Upper Cretaceous of Texas. *Journal of Paleontology*, **78**, 1163–1178.
- LYNCH, S. C. and PARHAM, J. F. 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.
- MATEUS, O., JACOBS, L., POLCYN, M., SCHULP, A. S., VINEYARD, D., BUTA NETO, A. and ANTUNES, M. T. 2009. The oldest African eucryptodiran turtle from the Cretaceous of Angola. *Acta Palaeontologica Polonica*, **54**, 581–588.
- MATZKE, A. T. 2007. An almost complete juvenile specimen of the cheloniid turtle *Ctenochelys stenoporus* (Hay, 1905) from the Upper Cretaceous Niobrara Formation of Kansas, USA. *Palaeontology*, **50**, 669–691.
- 2009. Osteology of the skull of *Toxochelys* (Testudines, Chelonioida). *Palaeontographica Abteilung A*, **288**, 93–150.
- MILLER, A. K. 1935. The “Paleocene” nautiloid cephalopods of Landana, Portuguese West Africa. *Journal of Paleontology*, **9**, 167–173.
- and CARPENTER, L. B. 1955. *Cretaceous and Tertiary nautiloids from Angola*. Estudos, Ensaios e Documentos, **21**.

- Ministério do Ultramar, Junta de investigações do Ultramar, Lisbon.
- MYERS, T. S., POLCYN, M. J., MATEUS, O. M., VINEYARD, D. P., GONÇALVES, A. O. and JACOBS, L. L. 2017. Data from: A new durophagous stem cheloniid turtle from the lower Paleocene of Cabinda, Angola. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.n618q>
- PARHAM, J. F. 2005. A reassessment of the referral of sea turtle skulls to the genus *Osteopygis* (Late Cretaceous, New Jersey, USA). *Journal of Vertebrate Paleontology*, **25**, 71–77.
- and PYENSON, N. D. 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.
- OTERO, R. A. and SUÁREZ, M. E. 2014. A sea turtle skull from the Cretaceous of Chile with comments on the taxonomy and biogeography of *Euclastes* (formerly *Osteopygis*). *Cretaceous Research*, **49**, 181–189.
- RABI, M., ZHOU, C.-F., WINGS, O., GE, S. and JOYCE, W. G. 2013. A new xinjiangchelyid turtle from the Middle Jurassic of Xinjiang, China and the evolution of the basiptyergoid process in Mesozoic turtles. *BMC Evolutionary Biology*, **13**, 203.
- STRGANAC, C., JACOBS, L. L., POLCYN, M. J., MATEUS, O., MYERS, T. S., SALMINEN, J., MAY, S. R., ARAÚJO, R., FERGUSON, K. M., OLÍMPIO GONÇALVES, A., MORAIS, M. L., SCHULP, A. S. and DE SILVA TAVARES, T. 2015. Geological setting and paleoecology of the Upper Cretaceous Bench 19 marine vertebrate bonebed at Bentiaba, Angola. *Netherlands Journal of Geosciences – Geologie en Mijnbouw*, **94**, 121–136.
- TONG, H. and HIRAYAMA, R. 2008. A new species of *Argillochelys* (Testudines: Cryptodira: Cheloniidae) from the Ouled Abdoun phosphate basin, Morocco. *Bulletin de la Société Géologique de France*, **179**, 623–630.
- and MEYLAN, P. 2013. Morphology and relationships of *Brachyopsemys tingitana* gen. et sp. nov. from the early Paleocene of Morocco and recognition of the new eucryptodiran turtle family: Sandownidae. 187–212. In BRINKMAN, D. B., HOLROYD, P. A. and GARDNER, J. D. (eds). *Morphology and evolution of turtles*. Springer.
- HIRAYAMA, R. and MAKHOUL, E. 2006. *Rhinochelys* (Chelonioidea: Protostegidae) from the Late Cretaceous (Cenomanian) of Nammoura, Lebanon. *Atti Della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **147**, 113–138.
- WOOD, R. C. 1973. Fossil marine turtle remains from the Paleocene of the Congo. *Annales du Musée Royal du Congo Belge, Tervuren (Belgique). Série in-8°, Sciences Géologiques*, **75**, 1–35.
- 1975. Redescription of “*Bantuchelys*” *congolensis*, a fossil pelomedusid turtle from the Paleocene of Africa. *Revue de Zoologie Africaine*, **89**, 127–144.
- ZANGERL, R. 1953. The vertebrate fauna of the Selma Formation of Alabama. Part IV. The turtles of the family Toxochelyidae. *Fieldiana: Geology Memoirs*, **3**, 137–277.
- 1971. Two toxochelyid sea turtles from the Landenian sands of Erquelinnes (Hainaut), of Belgium. *Institut Royal des Sciences Naturelles de Belgique, Mémoires*, **169**, 1–32.