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

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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 thecranial 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...
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).

**SYSTEMATIC PALAEONTOLOGY**

**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 Dartevelle & 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), Dartevelle & 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 Dartevelle & Casier (1943). Abbreviations: c, clay; ss, sandstone (vf, fine; f, fine; m, medium; c, course); co, conglomerate; ls, limestone. 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
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.
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, basisphenoid 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 aperture narium externa. The anterior margin of the prefrontals is fractured, and the dislocated pieces of bone have been pushed into the aperture 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 quadrate/jugal (Figs 3E, 4E). The jugal contacts the quadrate/jugal 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 posteroomedially. The foramen palatinum posterius is located at the junction of the jugal, pterygoid and palatine (Figs 3D, 4D).

The quadrate/jugal 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 quadrate/jugal shares a small contact with the postorbital, and the ventral margin forms the posterior portion of the...
check 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 quadrate/jugal. The preserved portion of the squamosal articulates with the quadrate/jugal anteriorly and the postorbitobitals dorsally, but its contribution to the upper temporal emargination is uncertain.

The large postorbitobital compose 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 postorbitobital, exposed on the lateral side of the skull, contacts the jugal, quadrate/jugal and squamosal. The postorbitobital contacts with the jugal and the preserved portion of the right squamosal are similar in length, whereas the suture between the postorbitobital and the dorsal projection of the quadrate/jugal 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 praepalatinum 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 median 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 posterodorsally. 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 posteriorius (most easily viewed in dorsal aspect) is located at the junction of the pterygoid, the palatine and the jugal.
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 clinoideus and emerging from the pterygoid via the foramen anterius canalis carotici interni, at which point it bifurcates into the palatine artery and cerebral artery.

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 anteroventrally, 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 cerebrali.

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.

**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; facc, foramen anterius canalis carotici cerebralis; faccp, foramen anterius canalis carotici palatinum; fpcci, foramen posterius canalis carotici interni; ica, internal carotid artery; oc, occipital complex; paa, palatine artery; pc, processus clinoideus; pt, pterygoid; rb, rostrum basisphenoidale.
c. 90°. A semilunate articular surface. The processes are thin, oriented at 3.6 cm wide mediolaterally and 2.7 cm wide dorsoventrally, with beyond the processes, which are subequal in size. The head is width of 3.8 cm. The prominent humeral head projects anteriorly processes measures 5.8 cm, and the distal end has a maximum difference is not pronounced. A U-shaped fossa separates the shaft, with neither one shifted distally. The medial process is holotype skull of Cabindachelys landanensis a bed 1 recovered during the 2012 Projecto PaleoAngola field season, from A complete left humerus (MGUAN Humerus. were broad and hexagonal. Sulci forming the lateral boundaries of the vertebral scutes are located near the distal ends of the costals (Wood 1973). 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 Chelonioidea. 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-Chelonioidea (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 Chelonioidea, 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-Chelonioida (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 Erquilinnesia gosseleti, Euclastes acutirostris, Euclastes wielandi and Terlinguachelys fischbecki (Fig. 9). Another analysis of Pan-Chelonioida, 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 Chelonioidea is defined as the crown clade comprising the most recent common ancestor of Chelonia mydas and Dermochelys coriacea and all its descendants. Pan-Chelonioidea refers to the clade containing crown Chelonioidea and all the fossil species located along the stem of Chelonioidea. 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 secondary palate indicates that Cabindachelys landanensis is a pan-cheloniid (Parham 2005). Cabindachelys landanensis differs from many other cheloniids in the presence...
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 acutirostris* 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 similar to *Itilocheles rasstrigin*, a stem chelonid 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.
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 repositioned at the Musée 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 taxa like *Erquelinnesia gosseleti* and the palatine forms a much smaller triturating surface (similar to other taphrosphyine jaws) and large processus retroarticularis, which is absent in chelonioids. 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 repositioned at the Musée 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 taxa like *Erquelinnesia gosseleti* and the palatine forms a much smaller 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-osseified 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*, is currently known, 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 *Cabinachelys 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 *Cabinachelys 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 durophy (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 durophy evolved independently at least three times within Pan-Cheloniidae (Parham & Pyenson 2010). Phylogenetic analyses indicate that chelonioids 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 Cabinachelys 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 Palaeocene (Parham et al. 2014). Durophagous chelonioids (e.g. Alienochelys seloumi, Brachyopsemys tingitana, Cabinachelys landanensis, Euclastes acutirostris, Euclastes sp.) are particularly abundant and diverse in the Palaeogene of Africa (Jalil et al. 2009; Tong & Meylan 2013; Lapparent de Brion 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 Palaeocene shallow marine strata exposed west of the town of Landana represent a new genus of durophagous, stem cheloniid turtle, Cabinachelys 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 Erquelimesia 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.

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**DATA ARCHIVING STATEMENT**

Data for this study, including character codings for Cabinachelys 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/47F23BBF-E4EC-4136-B02F-2D08CD4D7EFD.

**Editor.** Roger Benson

**REFERENCES**

Ministério do Ultramar, Junta de investigações do Ultramar, Lisbon.


— 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.