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
ARTICLE

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Shell anatomy of the African Paleocene bothremydid turtle *Taphrosphys congolensis* and systematic implications within Taphrosphyini

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ABSTRACT

The bothremydid pleurodiran turtle *Taphrosphys congolensis* is a member of Taphrosphyina from the Paleocene of the Cabinda Province (Congo Basin, Angola). Very few specimens corresponding to elements of its shell have been so far figured. Abundant unpublished remains are analyzed in this paper. As a consequence, several regions of the shell are figured and characterized here for the first time, and intraspecific variability is recognized for several characters. Previous authors proposed some putative differences between the shells of *Taphrosphys congolensis* and the North American Paleocene *Taphrosphys sulcatus*. The increase in the knowledge about the shell of this African form allows us to refute most of them, the shell of both forms being recognized as more similar than previously identified. Thus, the identification of the genus *Taphrosphys* as restricted to three forms (i.e. the skull taxon *Taphrosphys ippolitoi*, and the skull and shell forms *T. congolensis* and *T. sulcatus*) is supported, and the record unquestionably attributable to this genus is modified from the Upper Cretaceous–Eocene lapse of time to the Paleocene exclusively.

Introduction

Taphrosphyina (sensu Gaffney et al. 2006) is a clade of pleurodiran bothremydid turtles known from the Upper Cretaceous to the Eocene, that is represented in several continents (i.e., North America, South America, Europe, Africa and the Middle East) (Bardet et al. 2000; Hay 1908; Zangerl 1947; Bergounioux 1952, 1956; Gaffney 1975; Wood 1975; de Broin 1977; de Lapparent de Broin and Werner 1998; de Lapparent de Broin 2000; Gaffney et al. 2006). The identification of a series of exclusive shell characters within Bothremydidae (including, among others, a well-developed ornamental pattern on the shell surface, composed by irregular polygons delimited by a network of deep furrows; and the presence of relatively small ischiac scars, located near the anal notch) allowed the attribution of isolated remains, and of several of the species currently included in Taphrosphyina, to the genus *Taphrosphys* Cope (1869) (e.g., Zangerl 1947; Wood 1975; De Broin 1977; Antunes and de Broin 1988; de Lapparent de Broin and Werner 1998). The recent study of several skulls that shared a unique combination of characters with the type species of the genus *Taphrosphys*, which is the North American Paleocene *Taphrosphys sulcatus* (Leidy 1856) (i.e., those of *Taphrosphys congolensis* (Dollo 1913), from the Selandian of Angola, and *Taphrosphys ippolitoi* Gaffney et al. (2006), from the Danian of Morocco), and the discovery of the skulls of other species also attributable to Taphrosphyina (i.e., those of Azabbaremys moragjonesi Gaffney, Moody and Walker 2001 and Acleistochelys maliensis Gaffney, Roberts, Sissoko, Bouaré, Tapanila and O'Leary 2007, from the

Paleocene of Mali; Labrostochelys galkini Gaffney, Tong and Meylan 2006 and Rhothonemys brinkmani Gaffney, Tong and Meylan 2006, from the Paleocene of Morocco; and Phosphatochelys tedfordi Gaffney and Tong 2003 and Ummulisani rutgersensis Gaffney, Tong and Meylan 2006, from the Ypresian of Morocco) allowed the recognition of a relatively wide diversity for this clade (see Gaffney et al. 2006 and references therein). In this way, the generic attribution of several forms of this clade to the genus *Taphrosphys* was questioned (i.e., 'Taphrosphys' ambiguum (Gaudry 1890), from the Upper Cretaceous of France; 'Taphrosphys' olssoni (Schmidt 1931), from the Eocene of Peru; and 'Taphrosphys' phosphaticus (de Stefano 1903), from the Eocene of Tunisia. See Zangerl (1947); de Broin (1977); Antunes and de Broin (1988); de Broin (1988); de Lapparent de Broin (2000)).

Information corresponding to elements of the shell is only available in two of the three species here supported as belonging to the genus *Taphrosphys*: *T. sulcatus* and *T. congolensis*. Wood (1975) reviewed some of the specimens used by Dollo (1912, 1913, 1924)) to propose and describe, in a preliminary way, the species 'Podocnemis' congolensis; and he also examined other unpublished specimens, reassigning this species to the genus *Taphrosphys*. As a consequence, Wood (1975) proposed some differences between the shells of *T. congolensis* and *T. sulcatus*. However, he indicated that since at least some of these characters were subject to individual variation in some pelomedusoid species, their validity as diagnostic characters could be questioned. He pointed out that the provisional validity of both species could be justified considering that they were not only from different continents but also of different ages. Thus,
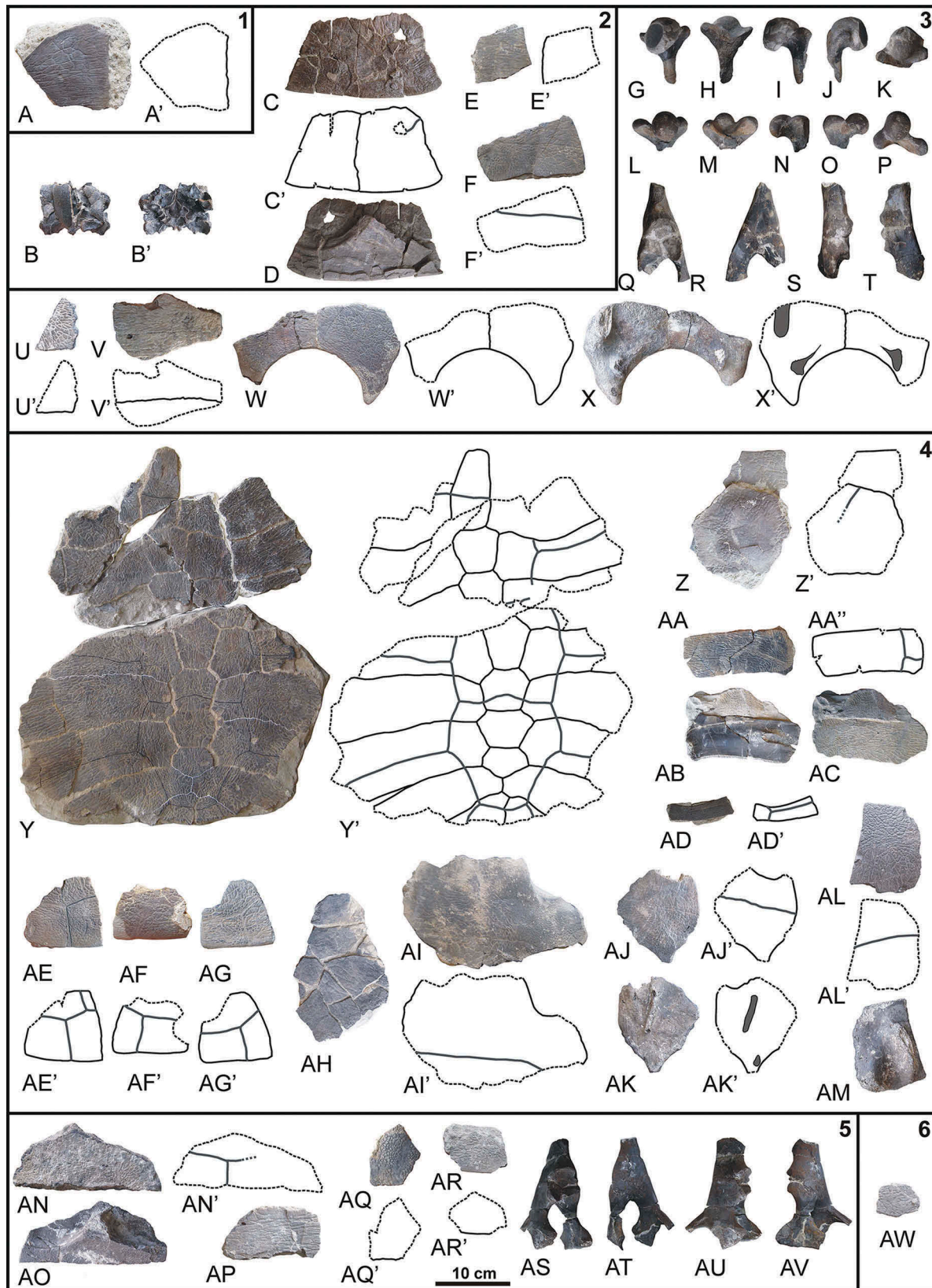
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Figure 1. Specimens of *Taphrosphys congolensis*, from the Paleocene of Landana (Cabinda Province, Angola). A, MRAC 6313, partial hyoplastron or hypoplastron. B, MRAC 13,525, skull. C–D, MRAC 3086A, two articulated peripherals. E, MRAC 6314, partial plate. F, MRAC 6315, partial plate. G–K, MRAC 16,011, proximal region of a left femur. L-P, MRAC 16,010, proximal region of a left humerus. Q–T, MRAC 16,012, partial right hemipelvis. U, MRAC 6319, partial plate. V, MRAC 13,722, two articulated partial plates. W–X, MRAC 6320, posterior half of a pair of xiphiplastra. Y, MRAC 13,725, partial carapace, including the complete neural series and the medial area of the costals. Z, MRAC 13,721, partial first right costal and partial plate. AA–AC, MRAC 13,529, fifth left costal. AD, MRAC 13,528, second right costal. AE, MRAC 13,527, peripheral. AF, MRAC 13,723, peripheral. AG, MRAC 13,724, peripheral. AH, MRAC 6321, partial plate or plates. AI, MRAC 13,727, partial left hyoplastron. AJ–AK, MRAC 6322, left xiphiplastron. AL–AM, MRAC 6323, partial right xiphiplastron. AN–AO, MRAC 6325, partial peripheral. AP, MRAC 6331, partial plate. AQ, MRAC 6326, partial plate. AR, MRAC 6329, partial peripheral. AS-AV, MRAC 6295, left hemipelvis. AW, MRAC 6332, partial plate. The layers from which they come are indicated in the figure by numbers. Layer 1 could correspond to the Selandian. Layers 2 to 6 are Selandian.
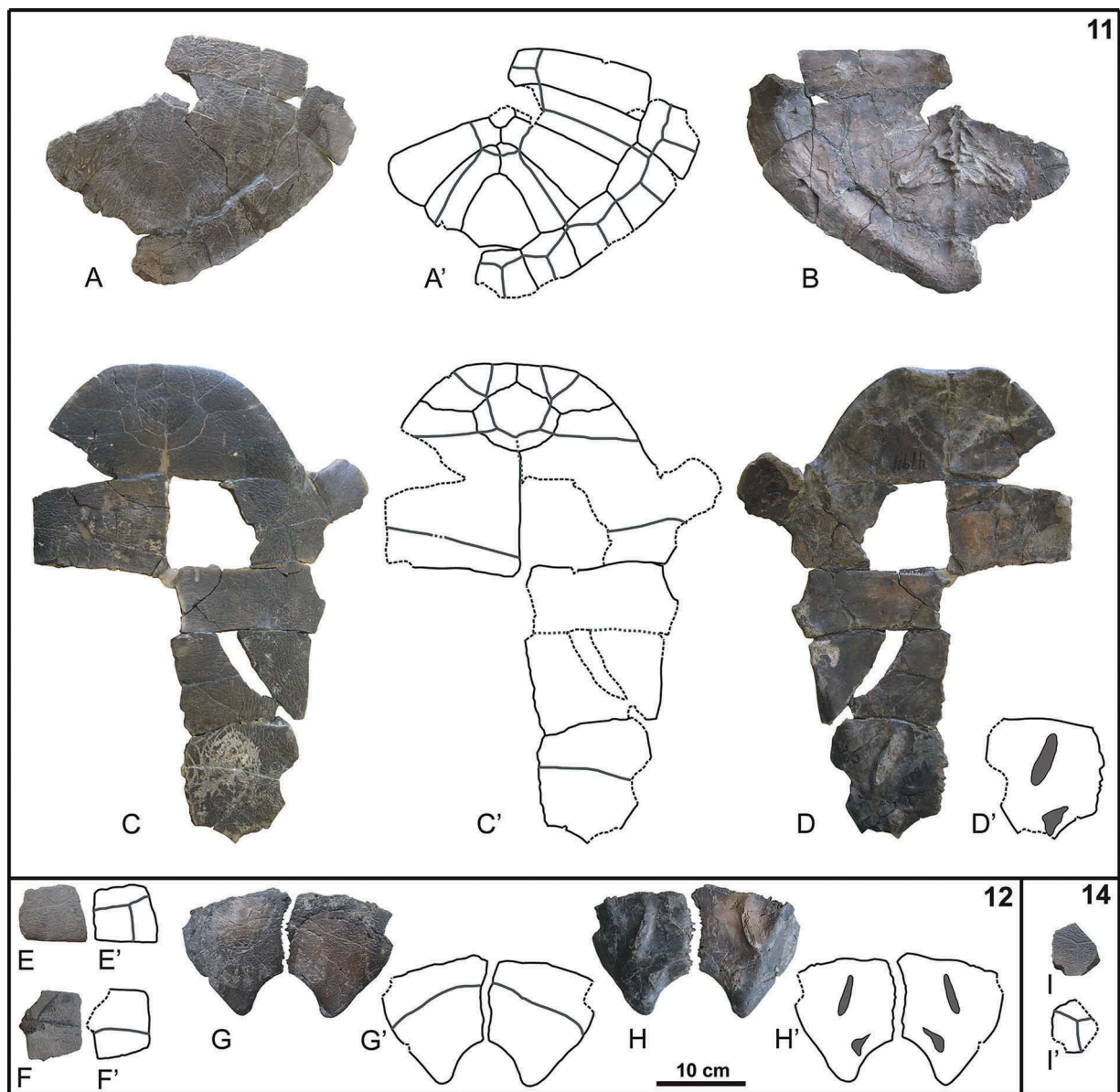
Figure 2. Specimens of *Taphrosphys congolensis*, from the Paleocene of Landana (Cabinda Province, Angola). A–B, MRAC 4795, posterior region of a carapace, including the partial last neural, the suprapygal, the pygal, the seventh and eighth left costals, the fifth to eighth right costals, and the four posterior right peripherals. C–D, MRAC 4794, partial plastron, including the entoplastron, both epiplastra, both hyoplastra, the left hypoplastron, and the partial left xiphiplastron. E, MRAC 13,714, peripheral. F, MRAC 6338, partial right hypoplastron. G–H, MRAC 6337, xiphiplastra. I, MRAC 6340, partial peripheral. The layers from which they come are indicated in the figure by numbers. Layers 11 and 12 are Selandian. Layer 14 is middle Selandian to middle Thanetian.

T. sulcatus was recognized as a form from the Late Cretaceous and *T. congolensis* as a Paleocene taxon. However, *T. sulcatus* is now identified as a Danian species (Gaffney et al. 2006). The recent description of a skull of *T. congolensis* confirmed that these African and North American forms were to two differentbut closely related species (Gaffney et al. 2006). Gaffney et al. (2006) identified other putative differences comparing the shells of both taxa, based on information from the relatively scarce material of *T. congolensis* published by Dollo (1912, 1913, 1924)) and Wood (1975).

Wood (1975) indicated that abundant material found after the studies of Dollo (1912, 1913, 1924)) was deposited in the Royal Museum for Central Africa (Tervuren, Belgium). However, most of these specimens remained hitherto unpublished. Only six specimens attributable to the shell of *T. congolensis* had been figured so

far: a fragment of a carapace corresponding to the lectotype (Figures 1–2 in the plate 7 of Dollo 1913; and Figure 1 of Wood 1975. See Figure 3(b–c)); a fragment of an indeterminate plate (Figures 3–4 in the plate 7 of Dollo 1913); a fragment of a carapace corresponding to the posterior half (plates 1–2 in Wood 1975. See Figures 2(a–b)); a relatively complete plastron (plates 3–4 in Wood 1975. See Figure 2(c–d)); and two pairs of xiphiplastra (plate 6 in Wood 1975. See Figure 1(w–x), 2(g–h)). In addition, an almost complete left hemipelvis (plate 5 in Wood 1975. See Figure 1(as–av)), and the only known skull (Figures. 187–189 in Gaffney et al. 2006. Figure 1(b)) and lower jaw of this taxon (Figure 1 in Dollo 1924; plate 3 in Wood 1973; Figure. 250 in Gaffney et al. 2006) were figured. The MRAC houses elements preserving regions of the shell not analyzed so far, as is the case of the nuchal plate. All the remains attributable to *T. congolensis* of
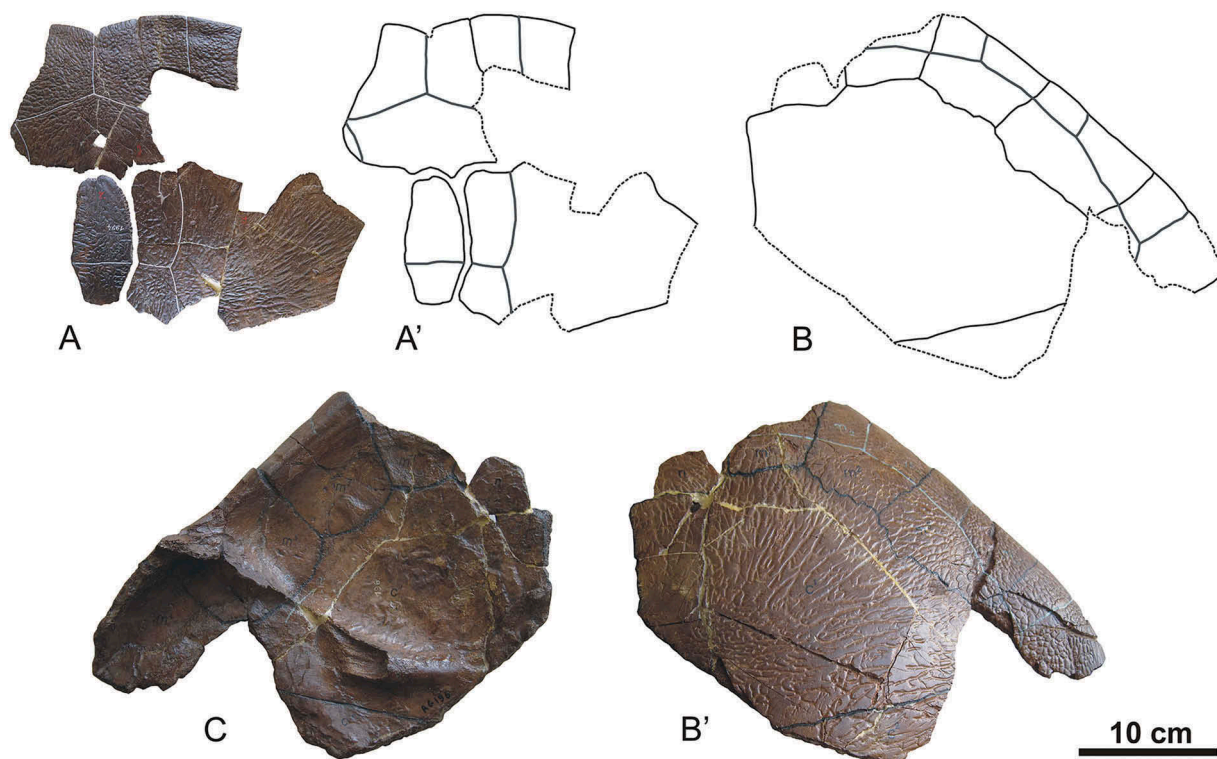
Figure 3. Partial anterior region of two carapaces of *Taphrosphys congolensis*, from the Paleocene of Landana (Cabinda Province, Angola), of which the precise Selandian or Thanetian layers where they were found are unknown. A, MRAC 3067, nuchal and partial first right peripheral; MRAC 1974, first neural; MRAC 3071, first right costal. B–C, MRAC 196, lectotype of *T. congolensis*, composed by the right postero-lateral margin of the nuchal, the partial first right peripheral, the second to fourth right peripherals, the almost complete first right costal, and the partial second right costal.

which the precise stratigraphic level in which they have been found is known (i.e., a total of 34 specimens) are figured here (Figures 1–2). In addition, two other relevant specimens for which the exact layers from which they come cannot be specified, are also figured (Figures 3(a–c)). The detailed study of all the remains of Bothremydidae so far recognized in the Paleocene levels of Landana (Cabinda, Angola) allows us to completely characterize the carapace of this species (Figure 4).

The best knowledge about the anatomy and variability of the shell of *T. congolensis* allows us to evaluate here the putative differences relative to *T. sulcatus* indicated in previous papers, as well as to analyze the similarity of the shell of these two forms for characters hitherto unknown or not compared. Thus, the close phylogenetic relationship between both species recognized by the study of the skulls (see Gaffney et al. 2006) is also confirmed by the comparative analysis of the shells. The shell of this genus, which
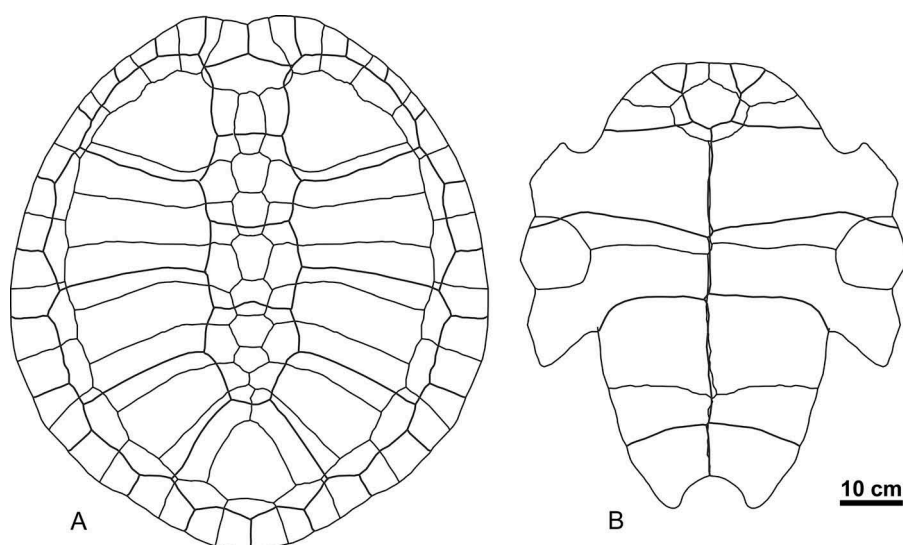

Figure 4. Reconstruction of the shell of *Taphrosphys congolensis*, from the Paleocene of Landana (Cabinda Province, Angola). A, caparace, in dorsal view. B, plastron, in ventral view.

had not been characterized in the most recent diagnosis proposed for it (see Gaffney et al. 2006), is here compared with that of the other members of Taphrosphyina. As a result, the identification of 'Tretosternum' ambiguum Gaudry (1890), 'Podocnemis' olssoni Schmidt (1931) and Gafsachelys phosphatica de Stefano (1903) as species belonging to the genus Taphrosphys is evaluated.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, United States; MRAC, Royal Museum for Central Africa, Tervuren, Belgium; YPM VPPU, Princeton University collection in the Division of Paleontology, Yale Peabody Museum, New Haven, United States.

Systematic paleontology

Testudines Batsch (1788)
Pleurodira Cope (1864)
Pelomedusoides Cope (1868)
Bothremydidae Baur (1891)
Bothremydodda Baur (1891)
Taphrosphyini Gaffney et al. (2006)
Taphrosphyina Gaffney et al. (2006)
Taphrosphys Cope (1869)
Taphrosphys congolensis (Dollo 1913)
(Figures 1–4)

Synonymy: Podocnemis congolensis Dollo (1912) (*nomen nudum*); *Podocnemis congolensis* Dollo (1913) (new species); *Bantuchelys congolensis* Dollo (1924) (new generic attribution).

Type specimen: The lectotype, MRAC 196, several articulated elements of the right antero-lateral area of a carapace (Figure 3 (b–c)). Its precise stratigraphic position in the Selandian to Thanetian Landana Section (Cabinda Province, Congo Basin, Angola), between the layers 1 and 18, is unknown.

Other specimens recognized here as attributable to this taxon: 34 specimens of which the layer of origin in the Landana Section (Cabinda Province, Congo Basin, Angola) is known. Layer 1: MRAC 6313, partial hyoplastron or hypoplastron (Figure 1(a)). Layer 2: MRAC 13,525, skull (Figure 1(b)); MRAC 3086A, two articulated peripherals (Figure 1(c–d)); MRAC 6314, partial plate (Figure 1(e)); MRAC 6315, partial plate (Figure 1(f)). Layer 3: MRAC 16,011, proximal region of a left femur (Figure 1(g–k)); MRAC 16,010, proximal region of a left humerus (Figure 1(l-p)); MRAC 16,012, partial right hemipelvis (Figure 1(q–t)); MRAC 6319, partial plate (Figure 1(u)); MRAC 13,722, two articulated partial plates (Figure 1(v)); MRAC 6320, posterior half of a pair of xiphiplastra (Figure 1 (w–x)). Layer 4: MRAC 13,725, partial carapace, including the complete neural series and the medial area of the costals (Figure 1(y)); MRAC 13,721, partial first right costal and partial plate (Figure 1(z)); MRAC 13,529, fifth left costal (Figure 1 (aa–ac)); MRAC 13,528, second right costal (Figure. 1(ad)); MRAC 13,527, peripheral (Figure 1(ae)); MRAC 13,723, peripheral (Figure 1(af)); MRAC 13,724, peripheral (Figure 1(ag)); MRAC 6321, partial plate or plates (Figure 1(ah)); MRAC 13,727, partial left hyoplastron (Figure 1(ai)); MRAC 6322, left xiphiplastron (Figure 1(aj–ak)); MRAC 6323, partial right xiphiplastron (Figure 1(al–am)). Layer 5: MRAC 6325, partial peripheral (Figure 1(an–ao)); MRAC 6331, partial plate (Figure 1(ap)); MRAC 6326, partial plate (Figure 1(aq));

MRAC 6329, partial peripheral (Figure 1(ar)); MRAC 6295, left hemipelvis (Figure 1(as-av)). Layer 6: MRAC 6332, partial plate (Figure 1(aw)). Layer 11: MRAC 4795, posterior region of a carapace, including the partial last neural, the suprapygal, the pygal, the seventh and eighth left costals, the fifth to eighth right costals, and the four posterior right peripherals (Figure 2 (a–b)); MRAC 4794, partial plastron, including the entoplastron, both epiplastra, both hyoplastra, the left hypoplastron, and the partial left xiphiplastron (Figure 2(c–d)). Layer 12: MRAC 13,714, peripheral (E); MRAC 6338, partial right hypoplastron (Figure 2(f)); MRAC 6337, xiphiplastra (Figure 2(g–h)). Layer 14: MRAC 6340, partial peripheral (Figure 2(i)). Other specimens, whose precise stratigraphic position in the sequence, between the layers 1 and 18, is unknown, are also part of the MRAC collection. Two of these specimens are considered here of special relevance considering their systematic value: the partial anterior region of a carapace (i.e., the specimen in Figure 3(a), composed by the collection numbers MRAC 3067, MRAC 1974 and MRAC 3071), and the only lower jaw recognized for this species (MRAC 3090. See Figure 1 in Dollo 1924; plate 3 in Wood 1973; Figure. 250 in Gaffney et al. 2006).

Locality and horizon: Landana Section, South Atlantic shoreline of the Cabinda Province, Congo Basin, Angola. Dollo (1912, 1913, 1924)) identified the presence of this form in the layers 2, 3, 5, 12 and 16 of the Landana Section, the first four now being recognized as Selandian, and the last layer as corresponding to an age spanning from the middle Selandian to the middle Thanetian (Solé et al. in press). Dartevelle and Casier (1959) also reported the presence of this form in the Selandian layer 8. Wood (1975) recognized remains that he attributed to this species from the layers 1 (possibly Danian); 4, 6, 11 (Selandian); 14 (middle Selandian to middle Thanetian) and 18 (middle to latest Thanetian). The specific specimens had not previously been assigned to specific levels. The review of the collection deposited in the MRAC allows us to identify abundant specimens from the Selandian (layers 2, 3, 4, 5, 6, 11, 12, and maybe 1; see Figures 1, 2(a-h)), and one specimen coming possibly from the Thanetian (layer 14; Figure 2(i)), in addition to other specimens whose information on their precise levels of origin is unknown, but that, based on the information provided by the previous authors (Dollo 1912, 1913, 1924; Dartevelle and Casier 1959; Wood 1975), are interpreted as collected between the layers 1 and 18. Therefore, *Taphrosphys congolensis* is identified as a Selandian to Thanetian form.

Description of the shell: The carapace of *Taphrosphys congolensis* can reach a length greater than 90 cm. Both the external surfaces of its carapace and its plastron show a well-developed ornamental pattern, composed by irregular polygons delimited by a network of deep furrows (Figures 1–3). The carapace is longer than wide, being cordiform (Figure 4). A shallow nuchal notch is identified (Figure 3 (a)). It is restricted to the nuchal plate. This plate is recognized as almost as wide as it is long. The neural series is composed of seven plates (Figure 1(y)). The first one is rectangular, noticeably longer than wide. It is in contact with the nuchal plate. The second to sixth neurals are hexagonal, relatively wide for their length, especially the posterior

ones, which are as wide as they are long. The antero-lateral margins of these plates are shorter than the postero-lateral ones. The last neural is pentagonal. The neural series does not contact the suprapygal plate. Therefore, the last two pairs of costals show a medial contact (Figure 2(a)). The suprapygal is longer than wide. The axillary processes reach almost the lateral half of the first pair of costals (Figure 3(c)). The inguinal processes overlaps more than a quarter of the width of the fifth costals (Figure 2(b)). The scars of the ilium are well-developed on the last pair of costals, but they also overlap the posterior margin of the seventh costals, and the antero-lateral border of the pygal plate.

This taxon lacks a cervical scute (Figure 3(a)). The antero-lateral margins of the first vertebral are located on the nuchal plate in some specimens (Figure 3(a)), but this scute is wider than the nuchal in others (Figure 1(z)). The remaining vertebrals are relatively narrow (Figures 1(y), 2(a)). In this sense, the last vertebral is noticeably longer than wide. The marginal scutes reach the peripheral series (Figure 4(a)). The first pair of marginals is at least as wide as it is long (Figure 3(a)).

The plastral lobes of *Taphrosphys congolensis* are relatively wide (Figure 4(b)). So, the anterior one is more than twice as wide as it is long (Figure 2(c)). This lobe is subtrapezoidal, with a substraight anterior margin, perpendicular to the axial plane, but with subrounded lateral borders. It is noticeably shorter than both the posterior lobe and the plastral bridge, which are subequal in length. The epiplastral symphysis is relatively short, being less than a quarter of the length of the entoplastron. The entoplastron is rhombic. It is wider than long in ventral view. The lateral margin of the xiphiplastra are convex in some specimens (Figure 2(g)), but anteriorly convex and posteriorly concave in others (Figure 1(aj)). The anal notch is relatively deep, reaching the anterior tip of the scars of the ischia in some specimens (Figure 1(ak)). This notch is at least 1.5 times wider than long (Figure 2(g)). It shows rounded lateral margins. The pubic scars are tangential in relation to the axial plane (Figure 2(d,h). They are relatively narrow, although specimens in which they are noticeably narrower than others are also recognized (Figure 2(d,h)). The ischial scars are relatively small (Figure 2(h)). They are located near the anal notch. A thin ridge of this scar, running antero-medially towards the midline but not reaching it, is present, being more developed in some specimens than in others (Figure 1 (x)). The morphology of these scars is generally subtriangular (Figures 1(x), 2(d,h)), but it is identified as suboval in some individuals (Figure 1(ak)).

The intergular scute is slightly longer than wide (Figure 2(c)). This heptagonal scute shows a long overlap on the entoplastron, but it does not reach the posterior margin of this plate. The gular scutes reach the anterior margin of the entoplastron. They are slightly narrower than the intergular. The humeral-pectoral sulci are well away from the epiplastra. The distance between the entoplastron and the pectoral-abdominal sulci is greater than the length of this plate. The pectoral-abdominal sulci overlap the mesoplastra. The femorals are identified as the longest scutes in the medial plane.

Discussion

Evaluating the putative differences between the shells of Taphrosphys congolensis *and* Taphrosphys sulcatus

Gaffney et al. (2006) proposed amended diagnoses for the members of Taphrosphyina. Although these authors did not
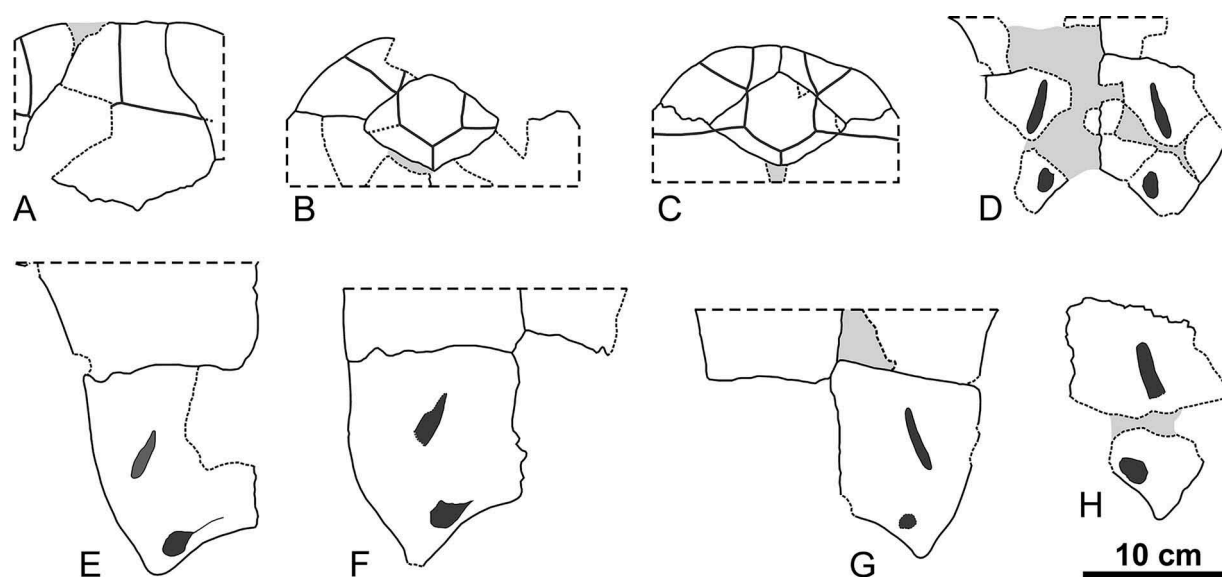

Figure 5. Schematic drawings corresponding to the sutures, sulci and of pelvis scars of some regions of several specimens of *Taphrosphys sulcatus*, from the Danian of North America A, AMNH 1347, dorsal view of the nuchal and medial region of the first pair of peripherals. B, AMNH 1472, ventral view of the medial area of the anterior plastral lobe. C, YPM VPPU 18,706, ventral view of the medial area of the anterior plastral lobe. D, AMNH 1125, dorsal view of the posterior plastral lobe. E, YPM VPPU 18,707, dorsal view of the posterior plastral lobe. F, AMNH 1474, dorsal view of the posterior plastral lobe. G, YPM VPPU 18,706, dorsal view of the posterior plastral lobe. H, AMNH 1472, dorsal view of the right xiphiplastron. The light gray surfaces correspond to the areas covered by sediment. Those in dark gray represent the pelvis scars.

include shell characters in the comparative diagnoses between *Taphrosphys congolensis* and *Taphrosphys sulcatus*, they recognized several putative differences. Thus, they characterized the plastron of *T. sulcatus* as narrow, that of *T. congolensis* being wider. As in other turtles, variability is recognized in the width/length ratio of the plastron of both species, the ratio observed here for the plastra of both forms being similar. In fact, specimens of *T. sulcatus* with a wider plastron than others of *T. congolensis* are also recognized. Thus, the ratio corresponding to the width of the anterior plastral lobe/ medial plastral length, from the anterior end to the anterior region of the anal notch, of the most complete plastron of *T. congolensis* shows that it is narrower than that interpreted for the plastron of the specimen of *T. sulcatus* AMNH 1125 (see Figure. 102 in Hay 1908), that of *T. congolensis* being 0.59, but that of *T. sulcatus* 0.65.

Gaffney et al. (2006) indicated, with doubts, that the plastral bridge of *T. congolensis* could be narrower than that of *T. sulcatus*. The available evidences do not support this hypothesis.

Wood (1975) indicated that the plastral bridge of *T. congolensis* had approximately the same length as the posterior lobe or that its length was slightly greater, the length of the posterior lobe of *T. sulcatus* being greater than that of bridge. The material of *T. congolensis* recognized here demonstrates variability in the length of the posterior plastral lobe, due to the variation in the length of the xiphiplastra, considering both the medial suture and the maximum length of these plates. A similar range of variability is identified for *T. sulcatus*, with specimens with some xiphiplastra being notably shorter relative to the length than others (e.g., compare AMNH 1125, Figure 5(d), with YPM VPPU 18,707, Figure 5(e)). Therefore, this character cannot be recognized as different between the species.

Gaffney et al. (2006) recognized several differences when comparing the morphology of the posterior lobe of both species. Thus, they indicated that the lateral margins of the posterior lobe of *T. congolensis* were different from those of *T. sulcatus*, being tapering in the African species but parallel in the North American one; the anal notch being wider in *T. sulcatus*. In this sense, Wood (1975) characterized the broad anal notch of *T. sulcatus* as shallow and parabolic, that of *T. congolensis* being recognized as fairly deep and semi-circular. The identification of several xiphiplastra of *T. congolensis* allows us to recognize variability in that region. Thus, the notch is recognized as approximately 1.5 times wider than long in the specimen MRAC 6337 (Figure 2(g-h)), but it is almost twice as wide as it is long in MRAC 6320 (Figure 1(w-x)). The width/length ratio of the anal notch of this second specimen is compatible with that of some known specimens of *T. sulcatus* (e.g., the aforementioned specimen AMNH 1125, Figure 5(d)). The different ratio between these two specimens of *T. congolensis* implies different morphologies of the notches. The notch of MRAC 4794 (Figure 2(c-d)) is interpreted as shallower than that of MRAC 6337 (Figure 2(g-h)). The notch reaches the anterior tip of the scars of the ischia, or even exceeds this structure, in other specimens (e.g., Figure 1(x,ak)). Considering the very small number of xiphiplastra known for *T. congolensis*, with only two specimens in

which the anal notch can be well characterized, a clear difference with *T. sulcatus* cannot be established. Thus, the characterization of the lateral margins of the posterior plastral lobe of *T. sulcatus* as parallel but those of *T. congolensis* as tapering is not supported by the study of the collection of *T. congolensis* performed here. The posterior region of the lateral margin of the hypoplastron of the specimen of *T. congolensis* MRAC 6338 (Figure 2(f)) has a subparallel margin, similar to that recognized in the hypoplastra of specimens of *T. sulcatus* as AMNH 1474 (Figure 5(f)) and YPM VPPU 18,706 (Figure 5(g)). This region is markedly tapered towards the posterior area in specimens of *T. sulcatus* such as YPM VPPU 18,707 (Figure 5(e)), an intermediate state being recognized in the specimen of *T. congolensis* MRAC 4794 (Figure 2(c-d)). The lateral margin of the xiphiplastra of *T. congolensis* does not correspond to that of a form with tapering borders, but its morphology is also subject to variability, being convex in some specimens (e.g., Figure 2(g-h)), but anteriorly convex and posteriorly concave in others (e.g., Figure 1(aj-ak)). Thus, this last morphology is similar to that of the specimen of *T. sulcatus* AMNH 1474 (Figure 5(f)), the variability recognized for both species being similar.

Wood (1975) indicated that ischial scars of both forms were relatively small, those of *T. sulcatus* being smaller. Intraspecific variability is identified for both species, individuals of *T. congolensis* with smaller scars than others being recognized (e.g., see Figure 2(h) versus Figure 2(d)), as also occurs for *T. sulcatus* (e.g., see Figure 5(d) and G, versus Figure 5(f)). Thus, the recognized size range for both species is compatible. Wood (1975) notified the presence of a thin ridge of this scar running antero-medially towards the midline of *T. congolensis*, not reaching it. He indicated that it is absent in *T. sulcatus*. This structure is here recognized as more developed in some specimens of *T. congolensis* than in others (e.g., it is well developed in MRAC 6320, Figure 1(x)), and a well development is also identified in some specimens of *T. sulcatus* (e.g., Figure 5(e)). Wood (1975) characterized the ischial scars of *T. congolensis* as triangular in outline, those of *T. sulcatus* being oval to rounded. Although the morphology of the ischial scars of *T. congolensis* is generally subtriangular (Figures 1(x), 2(d,h)), it also shows other morphologies, being suboval in other specimens (e.g., Figure 1(ak)). The morphology of this scar is here recognized as variable in *T. sulcatus*, not only being subcircular (Figure 5(g)) or suboval, longer than wide (Figure 5(d)) or wider than long (Figure 5(h)), but also subtriangular (Figure 5(f)). Therefore, the variability here recognized for the ischial scars of both species is high, and clear differences between *T. congolensis* and *T. sulcatus* cannot be characterized by this element. In the same way, the morphology and thickness of the pubic scars of both species is also subject to intraspecific variability, and specimens of both *T. congolensis* and *T. sulcatus* in which they are noticeably narrower than others are recognized (e.g., compare the specimens in Figures 1(ak), 2(h) with whose in Figures 1(x), 2(d) for *T. congolensis*; and those in Figure 5(d,g) with those in 5F, H for *T. sulcatus*).

Although Gaffney et al. (2006) indicated that the intergular of *T. congolensis* is not longer than it is wide, the only specimen in which the complete morphology and arrangement of

this scute can be observed shows that this assertion is not correct, the length/width ratio being approximately 1.1 (Figure 2(c)). The intergular of *T. sulcatus* was characterized by Wood (1975) as nearly twice as long as broad. However, this ratio is recognized as close to 1.6 in AMNH 1472 (Figure 5(b)), but close to 1.4 in YPM VPPU 18,706 (Figure 5(c)). Although the limited number of specimens allows us to refute the putative remarkable difference in this ratio recognized by Wood (1975) when both species were characterized, it is not enough to confirm if the intergular of *T. sulcatus* is always longer, in relation to the width, than that of *T. congolensis*. In this sense, the ratio between the length of the entoplastron in which the intergular extends on this plate, and the maximum length of the plate, is similar comparing the specimen of *T. congolensis* MRAC 4794 (about 0.85; Figure 2(c)) and that of *T. sulcatus* YPM VPPU 18,706 (about 0.85; Figure 5(c)), being lower in AMNH 1472 (about 0.75; Figure 5(b)).

Wood (1975) characterized the intergular of *T. congolensis* as hexagonal, that of *T. sulcatus* being described as pentagonal. However, the intergular of both forms is here recognized as heptagonal (Figures 2(c), 5(b-c)).

Wood (1975) interpreted a maximum midline plastral length for *T. congolensis* of 51 cm, that of *T. sulcatus* being recognized as 37 cm. These measures were considered as correct by Gaffney et al. (2006). That plastral length of *T. congolensis* is approximately equivalent to that of MRAC 4794, measured from the anterior border to the anterior margin of the anal notch (Figure 2(c-d)). The xiphiplastral symphysis of this specimen measures 10.5 cm. The length of *T. sulcatus* may be greater than that so far interpreted, being similar or even greater than that of this specimen of *T. congolensis*. Thus, specimens of *T. sulcatus* with a xiphiplastral symphysis similar to that of the mentioned specimen of *T. congolensis*, and others in which it is greater, are recognized: that of the specimen AMNH 1474 (Figure 5(f)) is 9.3 cm (the morphology of the adjacent plates shows that the medial length of the not preserved xiphiplastron of this specimen was greater), that of YPM VPPU 18,706 (Figure 5 (g)) is 10.6 cm, and that of YPM VPPU 18,707 (Figure 5(e)) is 11.2 cm. In fact, these specimens are not the largest here identified for this genus. Thus, the length of the carapace of the specimen of *T. congolensis* MRAC 196 (Figure 3(b-c)) is interpreted as greater than 90 cm, being probably close to 1 m. Specimens of *T. sulcatus* in which a carapace length close to that of specimen MRAC 196 are also recognized. For example, the length of the nuchal plate of AMNH 1347 (Figure 5(a)), close to 13 cm, would be slightly less than that of MRAC 196 (Figure 3(b-c)).

A shallow nuchal notch is identified in the only nuchal of *T. congolensis* in which the anterior margin is known (Figure 3(a)). Gaffney et al. (2006) pointed out that this structure is absent in Taphrosphyini. However, some variability is recognized here in this region for *T. sulcatus*. Thus, although a nuchal notch is generally absent in this species (e.g., AMNH 1470, AMNH 2524), a shallow notch is observed in specimens such as AMNH 1125 and YPM VPPU 18,706. Therefore, this character cannot be used either to establish differences between the shells of both forms.

The first vertebral scute of the specimen of *T. congolensis* MRAC 3067 (Figure 3(a)) is relatively narrow, the anterolateral corners being in contact with the lateral margins of the nuchal plate. The margin between the first vertebral and the first right pleural shows that this vertebral of MRAC 13,721 was noticeably wider (Figure 1(z)). A similar variability is observed in *T. sulcatus* (see specimens whose first vertebral are almost as wide as the nuchal plate in the Figures. 101 and 103 of Hay 1908; but others in which this scute is wider than the nuchal in the Figure. 112 of, 1908; and, especially, in the Figure. 265 of Gaffney et al. 2006).

As a result of these comparisons, no character allows us to establish robust differences between the shell of *T. congolensis* and *T. sulcatus*. Therefore, the shell of the representatives of *Taphrosphys* is recognized as similar, and the characterization of each of its species is identified as restricted to the skull characters (see Gaffney et al. 2006).

Comparisons of the shell of the genus *Taphrosphys* with those of the other members of Taphrosphyina

Several representatives of Taphrosphyina are exclusively known by the skull. However, shell remains of some species of Taphrosphyina not attributable to the genus *Taphrosphys* are known: scarce and poorly preserved elements of the carapace of *Acleistochelys maliensis*, a plastron of *Ummulisani rutgersensis*, a plastron corresponding to the holotype and only known specimen of '*Tretosternum*' ambiguum, the poorly preserved internal cast of the carapace and the relatively well-preserved plastron of the holotype and only known specimen of '*Podocnemis*' olssoni, and several shells of *Gafsachelys phosphatica* (Zangerl 1947; Bergounioux 1952, 1956; De Broin 1977; Gaffney et al. 2006, 2007). The representatives of the genus *Taphrosphys* here recognized by the shell (i.e., *Taphrosphys sulcatus* and *Taphrosphys congolensis*) differ from *U. rutgersensis* in which the ischiac scars are well separated from the anal notch margins. The epiplastral symphysis of the *U. rutgersensis* specimen is considerably longer than that of *Taphrosphys*, its length being almost half of that of the entoplastron. In addition, the intergular scute of that specimen is very long, reaching the posterior margin of the entoplastron, and the gular scutes are also long, overlapping the entoplastron.

The close phylogenetic relationship between *T. sulcatus* and *T. congolensis* pointed out by Gaffney et al. (2006) from the study of their skulls is supported here thanks to the comparative analysis of the shells of both forms. The shells of '*Tretosternum*' ambiguum, from the Maastrichtian of France, '*Podocnemis*' olssoni, from the Eocene of Peru, and *Gafsachelys phosphatica*, from the Eocene of Tunisia, share characters traditionally recognized as exclusive to the genus *Taphrosphys* (e.g. the ornamental pattern of the external surface of the plates, the morphology of the plastron, the proximity of the scar of the ischium to the anal notch). For that reason, some authors considered that they could all belong to this genus (Zangerl 1947; De Broin 1977, 1988; Antunes and De Broin 1988; De Lapparent De Broin 2000). However, the subsequent discovery of new taxa allowed to recognize that these characters are shared by all members of Taphrosphyina

of which the shell is known (Gaffney et al. 2006), which is supported here. The study carried out here allows to confirm previous differences between the members of *Taphrosphys* and those species, as well as to identify additional characters. Thus, 'P.' *olssoni* differs from the members of *Taphrosphys* in several character states exclusive for this member of Taphrosphyina, such as: the presence of a rounded anterior lobe; its deep and almost as long as wide anal notch, with rounded margins; the presence of short gular scutes, well away from the entoplastron. In addition, as in *U. rutgersensis*, the gulars of this species are noticeably narrower than the intergular scute.

As de Broin (1977) indicated, '*Tretosternum*' *ambiguum* shows a short distance between the entoplastron and the pectoral-abdominal sulcus, equivalent to the length of this plate. This character is exclusively recognized as shared with *U. rutgersensis* within Taphrosphyina. As in *U. rutgersensis*, the gular scutes of '*Tr.*' *ambiguum* show a well-developed superposition on the entoplastron. This species presents the longest anterior plastral lobe in Taphrosphyina, being almost as long as the bridge. In addition, this lobe is more tapered than in the other forms. '*Tretosternum*' *ambiguum* is the only representative of the clade with a mesoplastra that is wider than long.

The discontinuous neural series of *Gafsachelys phosphatica* differs from the condition for all *Taphrosphys* specimens, which always show the presence of seven neurals, only the last two pairs of costals displaying a medial contact.

Conclusions

Taphrosphys congolensis is a bothremydid turtle exclusively identified in the Paleocene (Selandian to possibly Thanetian levels) of the Cabinda Province (Congo Basin, Angola). It is a member of Taphrosphyina. Very few elements of the shell of this taxon were figured in previous publications. Abundant unpublished specimens are analyzed here. This study allows us to describe hitherto unknown regions of the shell of this taxon, to better characterize poorly represented areas, and to recognize intraspecific variability for several characters.

Only one other species of the genus *Taphrosphys* is known by the shell: *Taphrosphys sulcatus*, from the Danian of North America. Despite the limited knowledge about the shell of *T. congolensis*, several previous authors proposed putative differences between the shells of both species. However, the additional knowledge of the shell of *Taphrosphys congolensis* allows us to refute most of them, the shell of this African form being recognized as very similar to that of the North American representative. Therefore, the identification of the genus *Taphrosphys* as restricted to three forms (i.e. the skull taxon *Taphrosphys ippolitoi* and the skull and shell forms *T. congolensis* and *T. sulcatus*) is supported by this study. As a consequence, the identification of the French Maastrichtian '*Tretosternum*' *ambiguum*, the Peruvian Eocene '*Podocnemis*' *olssoni*, and the Tunisian Eocene *Gafsachelys phosphatica* as members of Taphrosphyina not attributable to the genus *Taphrosphys* is here supported. Thus, the detailed revision of these first two species is necessary in order to define

those two new genera of Taphrosphyina. In this way, the record unquestionably attributable to the genus *Taphrosphys* is restricted here from the Upper Cretaceous–Eocene time span to the Paleocene.

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References

Antunes MT, de Broin F. 1988. Le Crétacé terminal de Beira Litoral, Portugal: remarques stratigraphiques et écologiques, étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). Ciênc Terra. 9:153–200.

Bardet N, Capetta H, Pereda Suberbiola X, Mouty M, al Maleh AK, Ahmad AM, Khrata O, Gannoum N. 2000. The marine vertebrate faunas from the late cretaceous phosphates of Syria. Geol Mag. 137:269–290.

Batsch GC. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Akad. (Ed). Jena: Buchhand.

Baur G. 1891. Notes on some little known American fossil tortoises. P Acad Nat Sci Phila. 43:411–430.

Bergounioux F-M. 1952. Les chéloniens fossiles de Gafsa. Serv Géol Protectorat de la République Française au Maroc: Notes Mém. 92:377–396.

Bergounioux F-M. 1956. Les reptiles fossiles des dépôts phosphatés sud tunisiens. Ann des Mines et de la Géol. 15:1–105.

Cope ED. 1864. On the limits and relations of the Raniformes. P Acad Nat Sci Phila. 16:181–183.

Cope ED. 1868. On the origin of genera. P Acad Nat Sci Phila. 20:242–300.

Cope ED. 1869. Synopsis of the extinct reptilia found in the mesozoic and tertiary strata of new jersey. In: Cook GH, editor. Geology of new jersey, new jersey geological survey, appendix B. Newark: State Geologist; p. 733–738.

Dartevelle E, Casier E. 1959. Les poisons fossiles du Bas-Congo et des régions voisines (troisième partie). Ann Mus Congo Belge A. 2:201–256.

de Broin F. 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. Memoir Mus Natl Hist. 38:1–366.

de Broin F. 1988. Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondawana et la dispersion géographique des tortues pleurodires à partir du Crétacé. Studia Geol Salmanticensia, Studia Palaeocheloniologica. 2:103–142.

de Lapparent de Broin F. 2000. African chelonians from the jurassic to the present: phases of development and preliminary catalogue of the fossil record. Palaeontol Afr. 36:43–82.

de Lapparent de Broin F, Werner C. 1998. New late cretaceous turtles from the western desert, Egypt. Ann Paleontol. 84:131–214.

de Stefano G. 1903. Nuovi Rettili degli strati a fosfato della Tunisia. B Soc Geol Ital. 22:51–80.

Dollo L. 1912. Sur les premiers restes de tortues fossiles recueillis au Congo. Bull Acade R Belg. 1:8–9.

Dollo L. 1913. *Podocnemis congolensis*, tortue fluviatile nouvelle du Montien (Paléocène inférieur) du Congo et l'évolution des chéloniens fluviatiles. Ann Mus Congo Belge A. 3:49–65.

Dollo L. 1924. *Bantuchelys*, genre nouveau de tortues découvert dans le Paléocène du Congo. Bull Acade R Belg. 10–12:613–635.

Gaffney ES. 1975. A revision of the side-necked turtle *Taphrosphys sulcatus* (Leidy) from the cretaceous of New Jersey. Am Mus Novit. 2571:1–24.

Gaffney ES, Moody RTJ, Walker CA. 2001. *Azabbaremys*, a new side-necked turtle (Pelomedusoides: bothremydidae) from the Paleocene of Mali. Am Mus Novit. 3320:1–16.

Gaffney ES, Roberts E, Sissoko F, Bouaré ML, Tapanila L, O'Leary MA. 2007. *Acleistochelys*, a new side-necked turtle (pelomedusoides: bothremydidae) from the Paleocene of Mali. Am Mus Novit. 3549:1–24.

Gaffney ES, Tong H. 2003. *Phosphatochelys*, a new side-necked turtle (Pelomedusoides: bothremydidae) from the Paleocene of Morocco. B Am Mus Nat Hist. 279:644–659.

Gaffney ES, Tong H, Meylan PA. 2006. Evolution of the side-necked turtles: the families bothremydidae, euraxemydidae, and araripemydidae. B Am Mus Nat Hist. 300:1–700.

Gaudry A. 1890. Les enchainements du monde animal dans les temps géologiques. Fossiles secondaires. Paris: F. Savy.

Hay OP. 1908. The fossil turtles of North America. Carnegie Inst Wash Publ. 75:1–568.

Leidy J. 1856. Notices of remains of extinct turtles of new jersey, collected by prof. cook, of the state geological survey, under the direction of Dr. W. Kitchell. P Acad Nat Sci Phila. 8:303–304.

Schmidt KP. 1931. A fossil turtle from Peru. Field Mus Nat Hist, Geol Ser. 4:251–254.

Solé F, Noiret C, Desmares D, Adnet S, Taverne L, De Putter L, Mees F, Yans J, Steeman T, Louwye S, et al. in press. Reassessment of historical sections from the Paleogene marine margin of the Congo Basin reveals an almost complete absence of Danian deposits. Geosci Front. doi: 10.1016/j.gsf.2018.06.002

Wood RC. 1973. Fossil marine turtle remains from the Paleocene of the Congo. Ann Mus R Afr Centrale. 8:1–28.

Wood RC. 1975. Redescription of 'Bantuchelys' congolensis, a fossil pelomedusid turtle from the Paleocene of Africa. Rev De Zool Afr. 89:127–144.

Zangerl R. 1947. Redescription of *Taphrosphys olssoni* a fossil turtle from Peru. Fieldiana. 10:29–40.