

The youngest known South American dyrosaurid (Late Paleocene of Colombia), and evolution of Dyrosauridae (Crocodyliformes: Tethysuchia)

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diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

The youngest known South American dyrosaurid (Late Paleocene of Colombia), and evolution of Dyrosauridae (Crocodyliformes: Tethysuchia)

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Submitted on 6 September 2023 | accepted on 3 March 2024 | published on 7 November 2024

urn:lsid:zoobank.org:pub:EA5E0619-A666-4BCC-8C3D-655106244A2E

Jouve S. & Rodríguez-Jiménez J. V. 2024. — The youngest known South American dyrosaurid (Late Paleocene of Colombia), and evolution of Dyrosauridae (Crocodyliformes: Tethysuchia). *Geodiversitas* 46 (17): 931-953. <https://doi.org/10.5252/geodiversitas2024v46a17>. <http://geodiversitas.com/46/17>

ABSTRACT

Here we describe a dyrosaurid vertebra recovered from the late Paleocene Cuervos Formation in the Llanos Foothills (Colombia), which was previously unknown to yield vertebrates. This is the third locality in Colombia with records of dyrosaurids. Until now, they were described in South America possibly from the Maastrichtian, but mainly from the Danian and the Selandian. The present specimen, dated from the Thanetian, is the youngest record of dyrosaurid remains on this continent, suggesting an incomplete knowledge on the history of this group in South America. Dyrosaurids diversified during the Maastrichtian, reached their golden age during the Paleocene, and declined from the lower Eocene. The reason why they seem to begin their decline during the Ypresian remains obscure, being incongruent with the Early Eocene Climatic Optimum that should have been favourable for this tropical crocodyliform. Their diversity is best known in Africa, where their apparent Ypresian decline in diversity could be related to their comparison with the Paleocene post K-Pg crisis recovery. The Paleocene shows a higher diversity and species turn-over compared to the more stable Ypresian fauna with a comparatively lower number of species. Similar evolution is observed for North American crocodylians, and strong correlation between the evolution of their diversity, and that of African dyrosaurids, suggests that they were impacted by the same factors. The real drop in dyrosaurid diversity would be Lutetian, as in North American crocodylians, more correlated with the middle-late Eocene climatic cooling. New exploration should be focused on South American Eocene fields to evaluate if the extinction of South American dyrosaurids at the end of the Paleocene was an artifact, or if their early extinction compared to African dyrosaurids was related to regional factors.

KEY WORDS
Crocodyliformes,
Dyrosauridae,
Colombia,
Paleocene.

RÉSUMÉ

Le dyrosauridé le plus récent découvert en Amérique du Sud, (Paléocène supérieur de Colombie), et évolution des Dyrosauridae (Crocodyliformes: Tethysuchia).

Nous décrivons une vertèbre de dyrosauridé découverte dans le Paléocène supérieur de la Formation Cuervos (Colombie), alors qu'elle n'avait fourni aucun vertébré dans les Llanos Foothills. Il s'agit de la troisième localité en Colombie à documenter la présence de dyrosaures. Jusqu'à présent, ils n'avaient été signalés que possiblement dans le Maastrichtien, mais aussi et surtout dans le Danien et le Sélandien ; les restes décrits ici provenant du Thanétien, ce sont les plus récents découverts sur ce continent. Cela souligne notre connaissance incomplète de l'histoire des dyrosauridés sud-américains. Les dyrosauridés se sont diversifiés durant le Maastrichtien, atteignent leur apogée au Paléocène, et déclinent à partir de l'Éocène inférieur. La raison pour laquelle leur diversité semble décroître à partir de l'Yprésien est obscure, incongruent avec l'optimum climatique de l'Éocène inférieur, qui aurait dû être favorable à ces crocodyliformes tropicaux. Leur diversité est mieux connue en Afrique, où leur déclin à l'Yprésien pourrait n'être qu'apparent, lié à une diversification plus faible par rapport à la restauration faunique post crise KPg du Paleocène. Au Paléocène, la diversité est bien plus élevée, avec un renouvellement des espèces important, contrastant avec la stabilité faunique de l'Yprésien, et un nombre d'espèces comparativement moins grand. Une évolution similaire est observée chez les crocodyliens nord-américains, et les fortes corrélations entre l'évolution de leur diversité et celle des dyrosaures africains suggèrent qu'ils auraient pu être impactés par les mêmes facteurs. La chute réelle de la diversité des dyrosaures pourrait être lutétienne, comme pour les crocodyliens nord-américains, plus logiquement corrélée au refroidissement climatique de l'Éocène moyen-supérieur. De nouvelles explorations devraient être conduites en Amérique du Sud dans les terrains éocènes pour évaluer si l'extinction des dyrosauridés à la fin du Paléocène y est un artéfact, ou si leur extinction précoce par rapport aux dyrosauridés africains est liée à des facteurs régionaux.

MOTS CLÉS
Crocodyliformes,
Dyrosauridae,
Colombie,
Paléocène.

INTRODUCTION

Dyrosauridae is an extinct family of neosuchian crocodyliforms that survived the Cretaceous-Palaeogene (K-Pg) extinction and thrived in marginal settings of the Tethys Ocean from the Late Cretaceous until their extinction during the early Eocene (Swinton 1950; Halstead 1975; Buffetaut 1976, 1978a, b, 1982; Brochu *et al.* 2002; Jouve 2005, 2007, 2021; Martin *et al.* 2019; Jouve *et al.* 2021). Occurrences of dyrosaurid species are known from North and South America, Africa, and Asia, with the most localities and most complete remains being found in Africa (e.g., Denton *et al.* 1997; Khosla *et al.* 2009; Sena *et al.* 2017; Jouve *et al.* 2021; Amoudji *et al.* 2021). The previous record of dyrosaurids in South America is essentially limited to seven regions (Cope 1886; Langston 1953, 1965; Buffetaut 1991; Barbosa *et al.* 2008; Hastings *et al.* 2010, 2011, 2015; Jouve *et al.* 2021). In Colombia (Fig. 1A), the published records of dyrosaurid remains are from the Cerrejon Mine and from Ortega, Tolima. In the former locality three species have been described from the middle Paleocene coal-bearing Cerrejon Formation (Hastings *et al.* 2010, 2011, 2015). From Ortega, six vertebral centra were described, recovered from red claystone that probably correspond to dyrosaurids of Maastrichtian age (?) (Langston 1953, 1965; Jouve *et al.* 2021). However, the colour of sediments cast doubt on the age assignment since the outcrops in the locality dominantly correspond to a Paleocene unit, especially the red sediments (Raasveldt 1956; Núñez *et al.* 1984a, b).

Here, we describe a dyrosaurid vertebra collected by the second author in late 2013, in the Colombian Llanos Foothills

(Fig. 1A). The specimen was found in the Piñalerita Creek, north of Sabanalarga town (Casanare), in beds of the Cuervos Formation (Figs 1; 2; 3).

MATERIAL AND METHODS

STUDIED SPECIMEN

The vertebra described herein (UN-DG-Rp-1001) is held in the Reptile Collection, of the Departamento de Geociencias, Universidad Nacional de Colombia (Appendix 1).

The measurements were taken with a vernier digital caliper with an error of 0.01 mm and then rounded (Table 1). The following measurements were taken: centrum length, measured as the maximum anteroposterior dimension in the midline; anterior/posterior facet depth, measured as the maximum anteroposterior depth between exterior facet edge and the most interior part of the facet; anterior/posterior facet height, measured as the maximum dorsoventral diameter of the facet; anterior/posterior facet width, measured as the maximum horizontal diameter; centrum dorsal/ventral edge, measured as the length on each side of the centrum; hypapophysis height, measured as the maximum height between projected ventral margin of the centrum and the ventral base of the hypapophysis; and the centrum narrowest, measured as the minimum horizontal width of the centrum.

Additionally, a digital 3D point cloud reconstruction of the vertebra was created using photogrammetry to support observations (Fig. 4; Appendix 1), following the protocol of Mallison & Wings (2014). The 3D image was created using

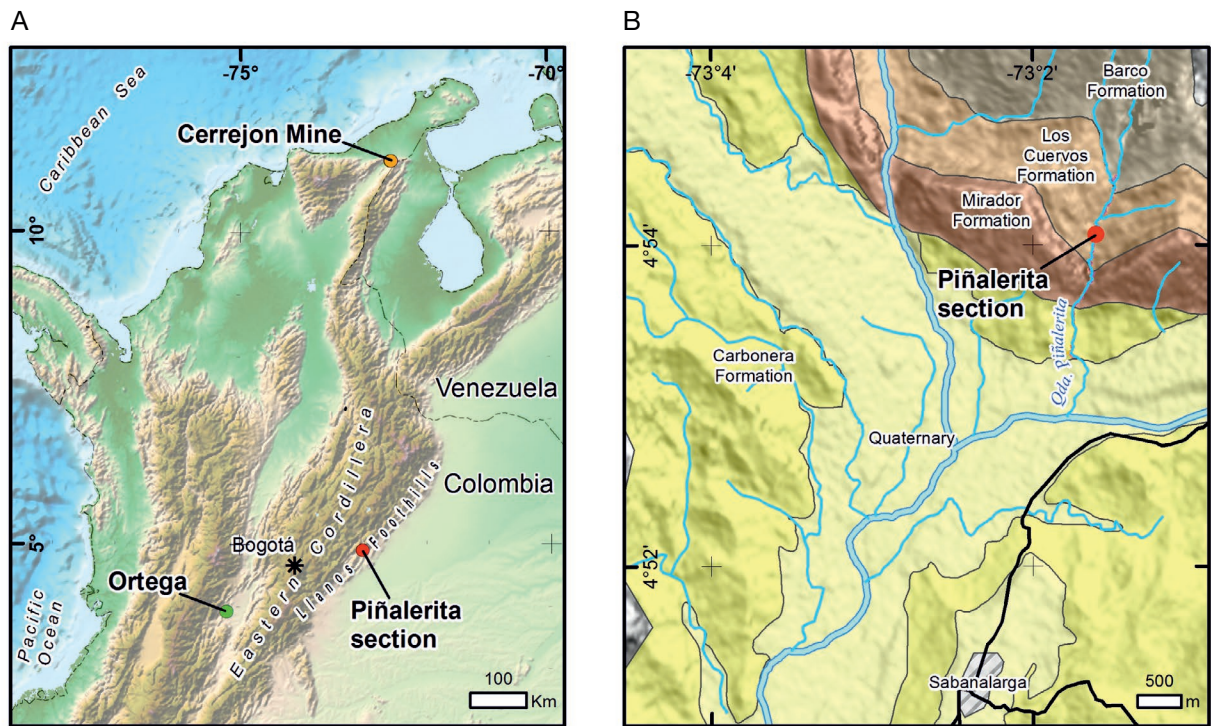


FIG. 1. — Geographical and geological context of the locality reported: **A**, localities with dyrosaurids in Colombia: Cerrejón Mine, Ortega (?) and Piñalierita Section (this study); **B**, geological map of the new locality, north of Sabanalarga town.

171 colours photos at 3648 × 2736 resolution acquired from a Canon PowerShot ELPH 190 IS digital camera. They were processed using VisualSFM (Wu 2011) and were edited using MeshLab (Cignoni *et al.* 2008).

BODY LENGTH ESTIMATIONS

In order to estimate the body size of the dyrosaurid UN-DG-Rp-1001, we tentatively used two different methods.

We used measurements from extant crocodylians and applied linear regression analyses to centrum lengths, then estimated the total body lengths of ancient crocodyliforms utilizing the work of Iijima & Kubo (2020; Appendix 2). The linear regression of centrum lengths versus body lengths of extant specimens is strongest between these two variables, with an R-squared above 0.960.

The second method does not use measurements from extant crocodylians. In previous papers, some estimation of the total body length of dyrosaurids have been proposed (Buffetaut 1978a; Jouve *et al.* 2005a; Hastings *et al.* 2015). These estimations were based on the comparison of the body length with the skull length for living species having different snout proportions. In dyrosaurids, the posterior part of the skull is particularly developed with anteroposteriorly elongated supratemporal fenestrae. In crocodylians, the supratemporal fenestrae are much shorter, so that, the skull is proportionally longer in dyrosaurids compared to the total body length. As a result, the estimation of the body length of dyrosaurids based on crocodylian data could be inadequate.

Few complete dyrosaurid specimens are known, but several specimens of *Dyrosaurus maghribensis* Jouve *et al.*,

TABLE 1. — Centrum measurements (in mm) of UN-DG-Rp-1001.

UN-DG-Rp-1001	Measurements
Centrum Length mid-height	54.55
Anterior face depth	9.75
Posterior face depth	2.82
Anterior face greatest width	56.31
Anterior face height	61.52
Posterior face greatest width	56.47
Posterior face height	61.82
Centrum dorsal edge	54.95
Centrum ventral edge	55.60
Hypapophysis	11.02
Centrum narrowest	39.80

2006 are relatively well preserved. Specimens OCP DEK-GE 254 and OCP DEK-GE 255 enable the reconstruction and estimation of the length from the tip of the snout to the second sacral vertebra (Appendix 3). Unfortunately, no tail is completely preserved, and its length is estimated on observations made on thalattosuchians, another group of marine longirostrine crocodyliforms for which numerous complete specimens are known (Appendix 3) (cervical + dorsal length = 59% of tail length in *Steneosaurus bollensis* Re 1193/1 (Tübingen)). Thalattosuchians are recognized as the sister taxon to tethysuchians (including dyrosaurids) in some phylogenetic analyses (e.g. Andrade *et al.* 2011; Leardi *et al.* 2018). To estimate the total body length of the specimen described here we thus used the proportions of the centrum length in the reconstructed *D. maghribensis* (Jouve *et al.* 2006) (Appendix 3).

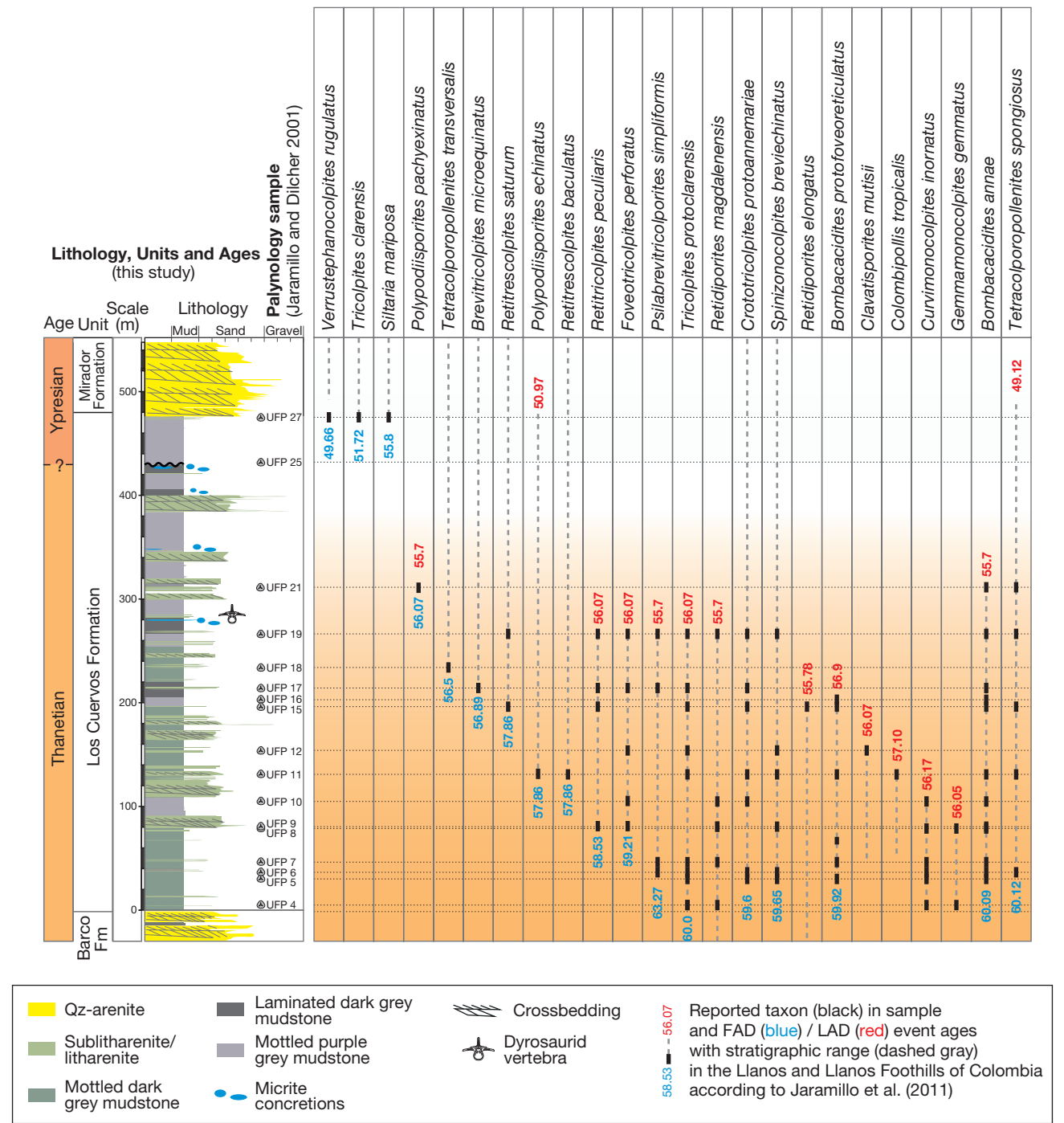


FIG. 2. — Stratigraphical section at the Piñalerita Creek with position of the vertebra and palynological results of some key taxa in the transition Paleocene-Eocene (after Jaramillo & Dilcher 2001; Jaramillo et al. 2011).

DIVERSITY ESTIMATE

The number of recognised dyrosaurid species is low, with less than 25 species from the Campanian to the Late Eocene (Appendix 4). In consequence, no complex and reliable statistical analysis can be conducted with this current sample. We compared dyrosaurid data with various proxies for temperature and sea level, using δO^{18} data and mean for temperatures from Cramer et al. (2009) (Appendix 5), mean temperatures from Grossman & Joachimski (2022)

(Appendix 6), δO^{18} data and mean as proxies for sea surface temperatures from the PhanSST global database (Judd et al. 2022; Appendix 7), and sea level from Miller et al. (2005) (Appendix 8). We tested their correlation with both corrected and uncorrected diversity using Past 3.10 (Hammer et al. 2001).

The raw diversity data were corrected with the most recent phylogenetic results (Jouve et al. 2021). The phylogenetic relationships are thus superimposed on the stratigraphy,



FIG. 3. — Outcrop, greenish gray mudstone where the vertebra UN-DG-Rp-1001 was collected, near the base of the Jacob's staff.

and ghost lineages of species are filled, considering also unidentified species following the method proposed by Jouve (2021). We also compared the evolution of dyrosaurids with those of crocodylians. We used the raw and sub-sampled diversity provided in De Celis *et al.* (2020). To test the impact of the incompleteness of our knowledge on South American dyrosaurid diversity, we evaluated the regional variations in comparing the best known African dyrosaurid diversity with global and North American crocodylian diversity.

ABBREVIATIONS

NTM	Museum and Art Gallery of the Northern Territory, Darwin (= MAGNT);
OCP DEK-GE	Office Chérifien des Phosphates, Direction de l'Exploitation de Khouribga, Geologie-Exploitation, Khouribga;
UF	Florida Museum of Natural History, Gainesville, FL;
USNM	Smithsonian National Museum of Natural History, Washington DC;
UN-DG-Rp	Reptile Collection, Departamento de Geociencias, Universidad Nacional de Colombia.

GEOLOGICAL SETTING

The vertebra was collected on the Piñalerita Creek, 6 km north of Sabanalarga town, Casanare (Fig. 1A, B). It was collected from rocks of the late Paleocene-early Eocene Cuervos Formation (Jaramillo & Dilcher 2001; Jaramillo *et al.* 2005) (Fig. 2). The Cuervos Formation is sandwiched between two dominant quartz arenite successions with cross-bedded beds, the Barco Formation (below) and the Mirador Formation (above) (Figs 1B; 2). The Cuervos Formation is around 475 m in thickness, it consists dominantly of gray and greenish gray mudstone mottled by rhizoliths), with intercalations of thick beds of slightly carbonaceous shale and greenish gray sub/litharenites with crossbedding (Fig. 2). The vertebra described here was collected 276 meters above the base of the unit. The bed containing the vertebra is greenish gray, massive with rhizoliths, has calcareous concretions and is locally thinly laminated (Fig. 3).

The vertebra is assigned to a possible Thanetian age based on the stratigraphic ranges of the palynologic taxa in the Llanos Basin. Previous palynologic studies of the Cuervos Forma-

tion in the Piñalerita section and in the basin showed rich and diverse pollen/spore assemblages, which are considered the most reliable biostratigraphic tool in the Paleogene succession of Colombia (Jaramillo & Dilcher 2001; Jaramillo *et al.* 2005; Jaramillo *et al.* 2011). Between the samples UFP 8 to UFP 27 of Jaramillo & Dilcher (2001), there is a last appearance datum (LAD) and first appearance datum (FAD) for several markers, where the model ages by Jaramillo *et al.* (2011) suggest a possible stratigraphic position below the Thanetian-Ypresian boundary (Fig. 2).

Palynofacies and lithofacies analyses from this locality by Jaramillo & Dilcher (2001), indicate that the Los Cuervos Formation represents coastal plain/fluvial floodplain deposits incised by discrete meander rivers and eventual lacustrine deposits. The palynoflora is dominated by palms with intermittent presence of damp tropical forest. The depositional environment of the vertebra-bearing bed corresponds to coastal plain muddy deposits.

SYSTEMATIC PALEONTOLOGY

Super Order CROCODYLOMORPHA Walker, 1970
Clade CROCODYLIFORMES Hay, 1930
Clade TETHYSUCHIA Buffetaut, 1982
Family DYROSAURIDAE de Stefano, 1903

Dyrosauridae indet.
(Fig. 4)

DESCRIPTION

The centrum is weakly amphicoelous with both facets concave (Fig. 4A, C, D), and shield-shaped (larger dorsally and pointed ventrally) (Table 1). The anterior facet is deeper (9.75 mm) than the posterior facet (2.82 mm). In lateral views (Figs 4B, E, F), the centrum has a sub-quadrangular outline, being slightly higher (facet heights 61.52 and 61.82 mm) than wide (facet greatest widths 56.31 and 56.47 mm). The ventral margin of the centrum is faintly concave and bears a short hypapophysis on its anterior half. The anterior margin of the hypapophysis is much more vertical than its gently convex posterior portion, so that its lowest part is in the anterior quarter of the hypapophysis. The neurocentral suture is visible and runs transversally along the lateral margin of the centrum and remains ventral to the parapophysis. In the right lateral view (Figs 4B, E), the centrum presents a rounded parapophysis, located dorsal to the level of the ventral margin of the neural canal, and just posterior to the midlength of the centrum. The basal part of the diapophysis is preserved, dorsal to the parapophysis, and its location suggests that both apophyses were grouped on the same lateral peduncle of the neural arch, and that the diapophysis projected more laterally than the parapophysis. The parapophysis seems to have been ventral or slightly anteroventral to the diapophysis in lateral view. A small part of the right prezygapophysis is preserved. In dorsal view, the apophyses of the neural arch are broken, which only preserved the basal parts of the neural spine and apophyses (Fig. 4G). In lateral view, its anterobasal margin

is located at the level of the parapophysis, at the level of the centrum midlength. In ventral view (Fig. 4H), the centrum appears constricted, hourglass-shaped, and with the centrum narrowest (39.80 mm) at ~71% of the margins (facet greatest widths 56.31 and 56.47 mm).

TAXONOMICAL ATTRIBUTION

The known diversity of the late Paleocene-early Eocene crocodyliforms is restricted to three taxa: sebecosuchians, crocodylians and dyrosaurids. The amphicoelous articular surface of the centrum excludes that the specimen was a crocodylian. The shape of the articular surface of the centrum being dorsoventrally slightly ovoid and almost as high as wide, combined with the centrum being almost as long as high, plus the poorly concave ventral margin of the centrum in lateral view are characteristics observed in dyrosaurids (Buffetaut 1982; Jouve *et al.* 2006). These differ from the centrum of sebecosuchians, which is wider than high and longer than high, and has a strongly dorsally concave ventral margin (Pol *et al.* 2012).

So, the present vertebra can be considered to be from a dyrosaurid.

DISCUSSION

POSITIONING OF THE LLANOS FOOTHILLS VERTEBRA ALONG THE AXIAL SKELETON

The axial skeleton has been poorly studied in extant species, and its inter and intraspecific variability have been evaluated recently. Variations exist between alligatoroids and crocodylids (Chamero *et al.* 2014), and if some morphometric analyses have been conducted (Chamero *et al.* 2014; Iijima & Kubo 2019), no complete morphological descriptions and comparisons have been published. So, morphological characters distinguishing extant species as to their intraspecific variability remains poorly documented. This is much truer for dyrosaurids. Only few axial materials of identified species have been published, and most of them are isolated and fragmentary vertebrae of unknown or unclear position (e.g. Amoudji *et al.* 2021; Troxell 1925; Argollo *et al.* 1987; Denton *et al.* 1997; Scavezzoni & Fischer 2021). Axial skeletons from Saudi Arabia (*Rhabdognathus* sp.), including a fairly complete individual, and an almost complete vertebral column from Pakistan have been described, but they are mostly represented by illustrations, thus their incomplete descriptions exclude their use for comparative work (Storrs 1986; Langston 1995).

In the end, only few works can be used that include detailed description and/or clear figures, with the knowledge of their exact position in the axial skeleton. They concern *Hyposaurus natator* Troxell, 1925 (= *Hyposaurus rogersii*), *Congosaurus bequaerti* Dollo, 1914, and *Dyrosaurus maghribensis* (Jouve & Schwarz 2004; Jouve *et al.* 2006; Schwarz *et al.* 2006; Callahan *et al.* 2015). This makes evaluation of the interspecific variability difficult. Moreover, as almost complete axial skeletons from several individuals are only known for one species (Jouve & Jalil 2020), distinction between intra- and interspecific variability is difficult.

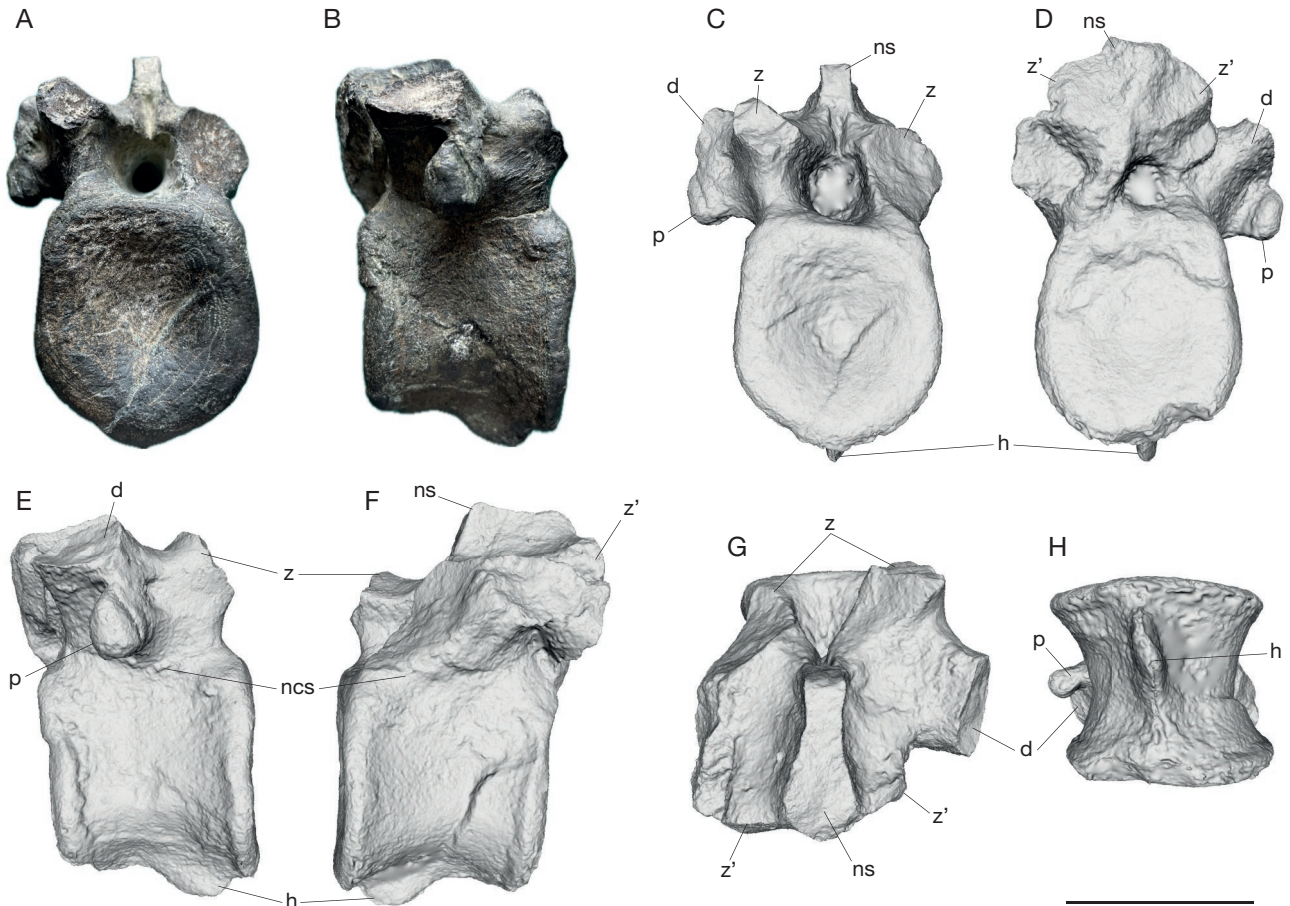


FIG. 4. — Actual (A, B) and 3D model (C–H) pictures of anterior dorsal (D4 or D5) vertebra UN-DG-Rp-1001 of the Piñalera Section, Cuervos Formation (Thanetian–Ypresian). Views: A, anterior; B, right lateral; C, anterior; D, posterior; E, right lateral; F, left lateral; G, dorsal; H, ventral. Abbreviations: d, diapophysis; z, prezygapophysis; z', postzygapophysis; ns, neural spine; p, parapophysis; h, hypapophysis; ncs, neurocentral suture. The 3D model of the vertebra is provided in Appendix 1.

In dyrosaurids, several characters can help to locate the position of the vertebrae along the axial skeleton. The most important are the shape of the neural spine, the shape and position of the diapophyses and parapophysis on the centrum, and length/height of the hypapophysis, but the important intraspecific variability in the hypapophysis shape has been noted at least for the last cervicals and first dorsals (Jouve & Jalil 2020).

UN-DG-Rp-1001 has a short parapophysis located on the same peduncle with the diapophysis and located ventral and slightly anterior to it. The neurocentral suture passes ventral to the base of the parapophysis-diapophysis peduncle. This is observed in the vertebrae posterior to the second dorsal in *C. bequaerti*, *H. natator*, and *D. maghribensis* (Jouve & Schwarz 2004; Jouve *et al.* 2006; Jouve & Jalil 2020; Schwarz *et al.* 2006; Callahan *et al.* 2015). The hypapophysis is very short. Compared with what is observed in *D. maghribensis* (OCP DEK-GE.254), the size and relative location of the lateral apophyses resemble what is seen in the third and fourth dorsals, but the short height of the hypapophysis more closely corresponds to what is observed in the fifth dorsal. Compared with *H. natator*, the parapophysis-diapophysis relationships could correspond to the condition found in the third cervi-

cal, where the short hypapophysis was probably present in the fifth dorsal. In extant species, the posteriormost vertebra in which the hypapophysis is present, and short, is the third or fourth dorsal depending on the species. So, if the shortest hypapophysis is in the dorsal 5 in one known dyrosaurid individual, *D. maghribensis*, and probably in *H. natator*, it cannot be asserted that it is the case in all dyrosaurids. We thus consider that the vertebra is probably the fourth or the fifth dorsal.

TOTAL BODY SIZE ESTIMATION

Traditionally, crocodylomorph bones from the axial skeleton have been used infrequently as proxies for body size compared to skulls and limbs bones (e.g., Sereno *et al.* 2001; O'Brien *et al.* 2019). Recently, Iijima & Kubo (2020) presented a dataset of extant crocodylians and proposed a vertebrae-based method to estimate absolute and species-specific body lengths in crocodylians. We have used this dataset (Appendix 2) to estimate the total length of the dyrosaurid UN-DG-Rp-1001 at around 4.4 m (Fig. 5).

In the reconstructed skeleton of *D. maghribensis*, the fourth and fifth dorsal vertebrae have a respective length of 7 and 6.5 cm. The total body length of this reconstructed

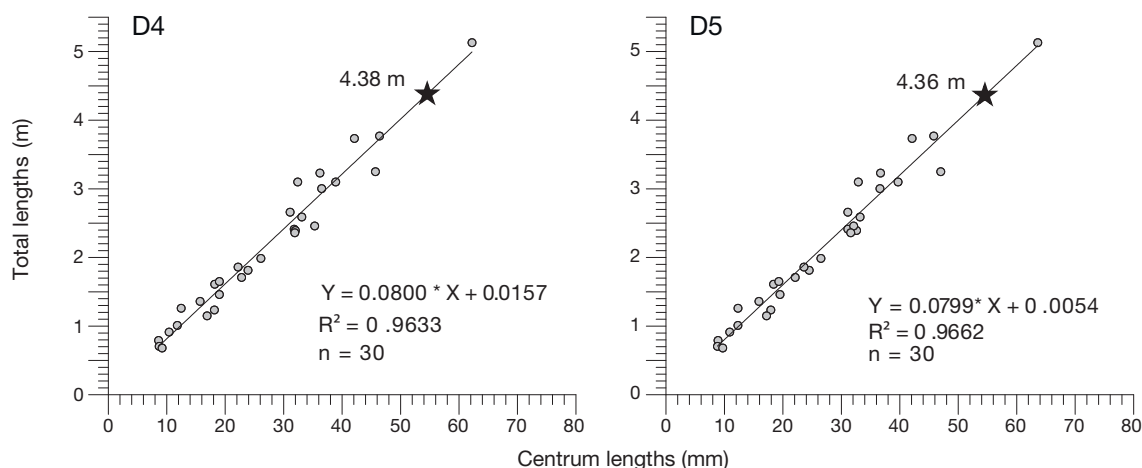


FIG. 5. — Estimated length (star) based on measurements of centrum lengths and total lengths of 30 crocodylians (gray dots) by Iijima & Kubo (2020) (Appendix 2).

specimen is 5.40m, and following this, the estimated length of UN-DG-Rp-1001 is 4.20–4.53m. An estimation close to what is obtained above using crocodylians. Also, this does not consider the variation in the snout proportion, which can change the total length by a few centimeters or by decimeters.

Dyrosaurids show a wide range in size, from 2 meters for the small *Cerrejonisuchus improcerus* Hastings, Bloch, Cadena & Jaramillo, 2010 to eight meters for *Phosphatosaurus gavialoides* Bergounioux, 1956 (Jouve *et al.* 2005a; Hastings *et al.* 2011). UN-DG-Rp-1001 was probably a medium-sized dyrosaurid.

PALEOBIOGEOGRAPHIC IMPLICATIONS

South American dyrosaurids

This material represents the first record of vertebrates in the Paleogene succession of the Colombian Llanos Foothills. The morphology of the vertebra indicates that it is a dyrosaurid crocodyliform. At least seven dyrosaurid species have been recognised in South America, three Bolivian early Danian species, one late Danian species in Brazil (following Jouve *et al.*, 2021, *Guarinisuchus munizi* Barbosa *et al.*, 2008 is considered as a junior synonym to *Hyposaurus derbianus* Cope, 1885), and three Selandian species in Colombia (Fig. 6). Additional isolated remains have also been identified from Bolivia and Colombia with an age tentatively attributed to Maastrichtian, but this age is uncertain, and both remains could be Danian in age (see Jouve *et al.* 2021 and above). So, until the present described remains, dyrosaurids were known from possibly Maastrichtian, or Danian, to Selandian in South America. The remains described herein are the youngest known record of a dyrosaurid in South America (Fig. 6). Dyrosaurids are known from the same interval of time in North America, with the last recognised dyrosaurids from the Thanetian (Denton *et al.* 2014), but an isolated caudal vertebra attributed to dyrosaurids has been noted from the Priabonian of Alabama. Its formal description has not yet been published (Ehret & Hastings 2013), and it is potentially the youngest known dyrosaurid ever described.

Phylogenetic analyses suggest several migrations from Africa to South America, and several independent lineages are found from Bolivia's and Colombia's best known dyrosaurids (Jouve 2021; Jouve *et al.* 2021). The fragmentary nature of the present specimen does not permit a clear determination of its affinities, but its age and location are closer to previously described remains from the Selandian Cerrejon Formation rather than from the Danian Bolivian and Brazilian species.

Since the sample and the number of species do not allow the use of statistical methods to evaluate the evolution of dyrosaurids (less than 25 species are formally recognized), an empirical analysis of their spatial and temporal distribution provides some information, in particular, on the orientation for future researches.

A strong disparity exists between the observed dyrosaurid diversity on the various continents (Fig. 7). The global apparent diversity is largely driven by the best known African and South American diversity. The known South American diversity is the highest during the Danian and Selandian, while the Selandian and Thanetian are the stages with the highest number of identified species in Africa (Fig. 8; Table 2). At least 15 dyrosaurid species have been described in Africa from the Maastrichtian to the Paleocene. The new dyrosaurid remains described in Colombia allows us to draw a quite similar scenario in South America, with also a maximal diversity during the Paleocene (Table 2; Figs 7, 8; Appendix 4), represented by at least seven species. Contrary to what is known in Africa, few Thanetian remains are known, with a maximum during the Danian. Could this be due to poor availability of Thanetian sediments? The same is true for the Ypresian Age, for both South American and African continents, and much more for the Lutetian, for which the number of available sites with crocodyliforms is low.

The new remains suggest that our evaluation of the South American dyrosaurid diversity is probably biased by our poor knowledge of post Selandian fossiliferous sites. More effort should be conducted to evaluate if they really became extinct at the end of the Paleocene.

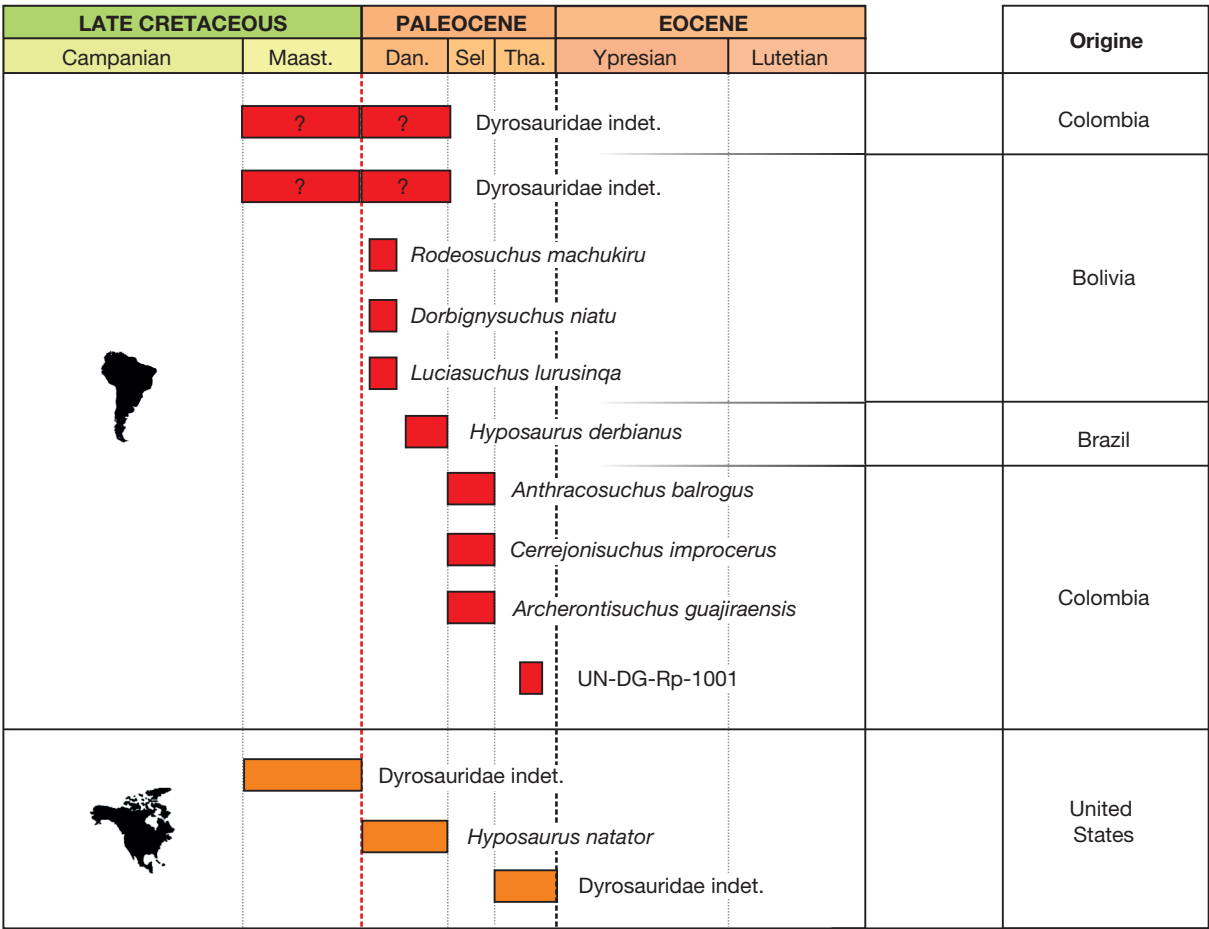


Fig. 6. — Stratigraphical distribution of South and North American dyrosaurids. The possible Priabonian North American dyrosaurid is not figured.

HISTORY OF DYROSAURID DIVERSITY

The dyrosaurids are distributed worldwide, except in Europe and ancient Eurasia (India not included), with a temporal range extending from the late Cretaceous to the middle or late Eocene (e.g. Buffetaut 1982; Hastings *et al.* 2015; Jouve 2021)(Appendix 4). They began their apparent diversification during the Maastrichtian, reaching their maximum diversification during the Paleocene, and declined from the Ypresian (Fig. 8A). Only one species is known during each stage from the Lutetian and later, the taxic dyrosaurid diversity seems to have been dwindling from the Lutetian to their extinction during the Bartonian or Priabonian. On the contrary, the Paleocene seems to be the dyrosaurid golden age. Phylogenetic correction of the taxic diversity does not consistently change the global patterns of the curves, increasing the diversity in older time bins, because the phylogenetic estimate only constructs backward-extending ghost lineages (Tennant 2016). Post Selandian South American dyrosaurid diversity is almost unknown while, as demonstrated by the remains described herein, it existed. The intervals with the worst known dyrosaurid diversity are mainly those from the Eocene, those that remain uncorrected by the phylogenetic corrections. For these reasons, the phylogenetically

corrected diversity could be less relevant and reliable than the uncorrected one.

Crocodylians show a similar evolution to their diversity through time, but an opposite geographical distribution. Whereas the Late Cretaceous to Eocene crocodylian sampling comes essentially from Europe, North America, and Asia, where dyrosaurids are absent or very poorly diversified (De Celis *et al.* 2020; Jouve 2021), the evolution of their diversity follows those observed for dyrosaurids. Crocodylian diversity rose during the Maastrichtian-Paleocene, reached its maximal speciation during the Thanetian (Solórzano *et al.* 2019), as did the African dyrosaurids, and was followed by an Ypresian-Lutetian drop. A strong correlation is observed between dyrosaurid and crocodylian diversity (Table 3), with high Pearson coefficients of correlation reaching 0.98 (p: 0.00028). Spearman's correlation is only high and relevant when taxic dyrosaurid diversity is compared to sub-sampled crocodylian diversity (Appendix 9). This suggests that dyrosaurid and crocodylian evolution follows a globally similar pattern from the Late Cretaceous to the Eocene and could have been impacted by the same biotic and abiotic factors, even if crocodylians are mainly found in the northern hemisphere, and dyrosaurids in former Gondwana.

TABLE 2. — Species diversity data used in curves (Fig. 8A) and the correlation analyses (Tables 3; 4) (data from Appendix 4).

Raw dyrosaurid diversity		Campanian	Maastrichtian	Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian
Taxic diversity number of species	Africa	1	4	5	12 7 9		5	1	0	0
	North America	0	1	1	1	?	?	?	1?	1?
	South America	0	1	4	7 3 1		0	0	0	0
	India	0	1	1	1	?	1	?	1	0
	total	1	7	11	21 10 11		6	1	1-2	1?
Dyrosaurid diversity corrected with phylogeny										
Species diversity corrected with phylogeny	Africa	2	6	9	17 11 11		5	1	0	0
	North America	0	2	1	2	?	?	?	1?	1?
	South America	0	6	7	8 3 1		0	0	0	0
	India	0	1	1	1	?	1	?	1	0
	total	2	15	18	28 14 13		6	1	1-2	1?
Crocodylia										
Raw		13	23	29		19	22	17		
Sub-sampled		2.36	7.15	13.8		6.48	3.85	4.22		

Comparison of dyrosaurid diversity with several abiotic factors is interesting and has previously been attempted. Martin *et al.* (2014) did not find a clear correlation between dyrosaurid extinction and sea surface temperature evolution, but the inconsistent sampling for the sea surface temperatures for the key period in dyrosaurid evolution, Paleocene-Eocene, is strongly biased and questions the reliability of the results (Jouve *et al.* 2017). Forêt *et al.* (2024) did not find clear correlation between temperature and tethysuchian evolution, like Mannion *et al.* (2015) for marine crocodyliiforms. Jouve & Jalil (2020) did not find a global correlation between temperature proxies (δO^{18} from Prokoph *et al.* 2008) and tethysuchian diversity, but a positive correlation for the Late Jurassic-earliest Cretaceous (Oxfordian-Cenomanian) interval, and on the contrary, an inverse correlation with the same proxy for the Turonian-Thanetian and a strong positive correlation with sea level. So, the signal provided by dyrosaurids or tethysuchians is not clear and correlation of their evolution with biotic and abiotic factors is also unclear.

Mean temperatures (Grossman & Joachimski 2022) and temperature proxy (δO^{18} ; Cramer *et al.* 2009) from two different datasets used herein show a clear rise in the global temperature during the Ypresian, corresponding to the Early

Eocene climatic optimum (EECO) (Fig. 8B, C). The mean δO^{18} (Cramer *et al.* 2009), also shows three other temperature rises, one during the Danian, at the boundary between Thanetian and Ypresian (corresponding to the Paleocene-Eocene Thermal Maximum, PETM), another during the early Bartonian (Middle Eocene climatic optimum, MECO) (Fig. 8B). The Maastrichtian seems to correspond to a period of a strong drop in temperature (Fig. 8C). δO^{18} proxy for the sea surface temperatures also shows a strong rise during the Thanetian-Ypresian (Judd *et al.* 2022; Fig. 8D). Both global and sea surface temperatures show a similar highest level during the Ypresian, but while the lowest temperature values were obtained for the latest Cretaceous period, the lowest sea surface temperatures seem to be middle Paleocene (Fig. 8). Neither of these highest or lowest temperature values correspond to highest or lowest dyrosaurid diversity values. Sea level from Miller *et al.* (2005) data follows more or less the sea surface temperatures with a maximal rise during the Ypresian (Fig. 8E). Jouve & Jalil (2020) found a strong correlation between both proxies for the Turonian-Thanetian time interval.

As discussed in previous papers (Hastings *et al.* 2015; Barbosa *et al.* 2008; Jouve & Jalil 2020; Jouve *et al.* 2008, 2021; Jouve 2021), dyrosaurids diversified at the end of the Late Cretaceous and the beginning of the Paleocene, a time interval of strong drop in temperatures. To the contrary, in the Ypresian the Early Eocene Climatic Optimum (EECO) corresponds to an apparent drop in dyrosaurid diversity (Fig. 8; Table 2). A similar drop is observed in the Northern hemisphere for crocodylian diversity (De Celis *et al.* 2020), with a high extinction rate during the Lutetian-Bartonian (Solórzano *et al.* 2019). Also, could the Paleocene-Eocene Thermal Maximum (PETM) have had an impact on the dyrosaurid and crocodylian diversities as it did for mammalian faunas, explaining the lower Ypresian diversity? These drops in diversity are contrary to what we would expect from taxa assumed to be tropical. Even if the low diversity sets limits on the reliability of any statistical analysis, none of the tested proxies were found to correlate with dyrosaurid diversity evolution (Table 4; Appendix 9).

In well documented localities with continuous Late Cretaceous-Early Eocene fossil records such as in the Oulad Abdoun Basin in Morocco, the number of Paleocene dyrosaurid species is particularly high during the Paleocene (6 species), but the diversity is only 2 species during the Ypresian (Appendix 4; Bardet *et al.* 2014, 2017). The Ypresian dyrosaurids are particularly well preserved and known by numerous complete skeletons (Jouve *et al.* 2006). It is interesting to note that Paleocene diversity is particularly high, with a different fauna in each stage, with two species from the Danian, five during the Selandian-Thanetian, and only two during the Ypresian, while both Paleocene and Ypresian have a comparable temporal length (respectively 10 and 8.2 my). So, this African Paleocene high diversity and Ypresian decline is coherent with local observations in well sampled sites, and could thus, be a good image of the diversity, and not strongly impacted by collecting and preservation biases, at least in Africa. The Paleocene could be an epoch of high post crisis diversification,

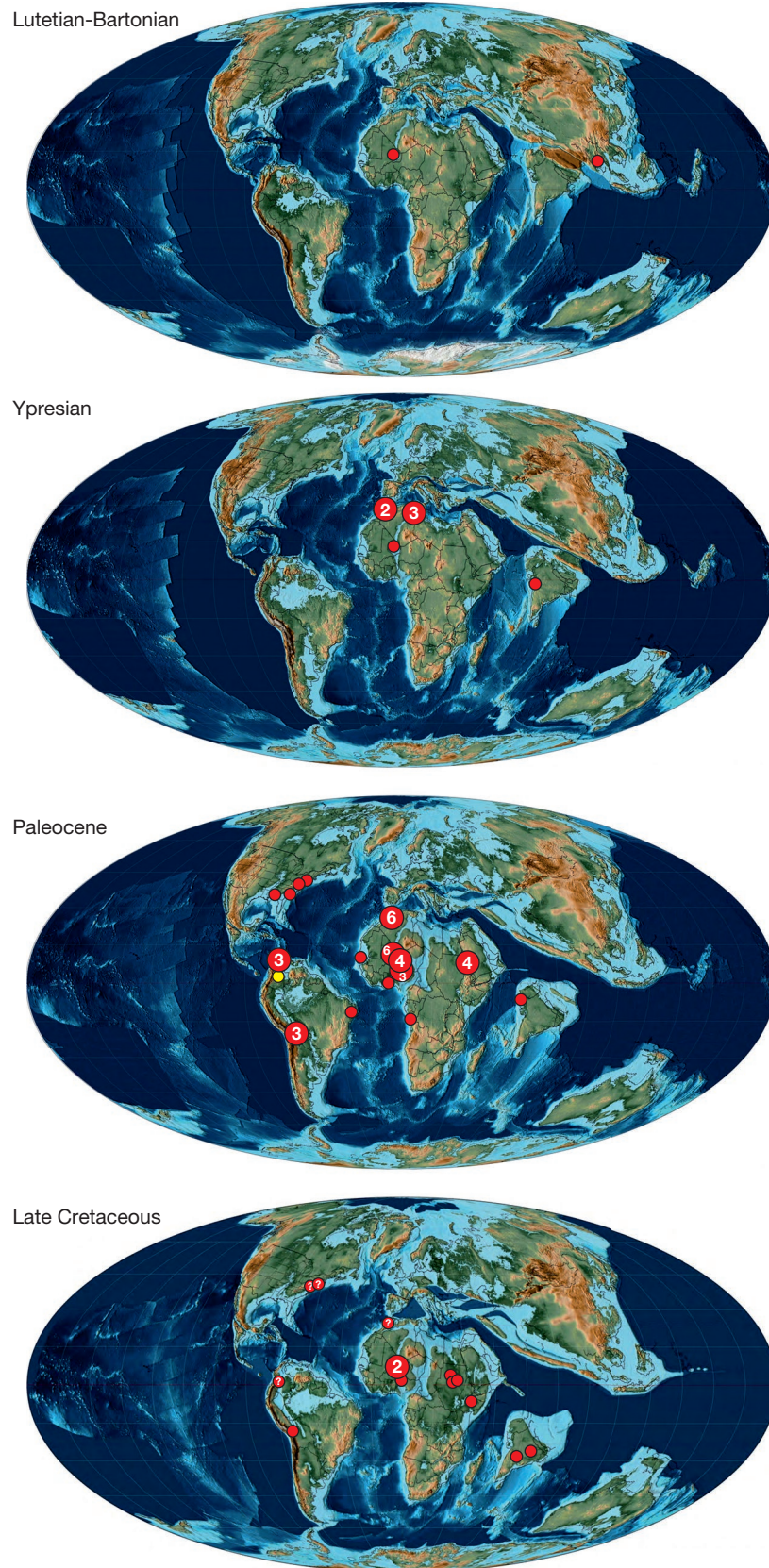


FIG. 7. — Geographical distribution of dyrosaurids from Late Cretaceous to middle Eocene. The Late Cretaceous map is represented by the Maastrichtian, the Paleocene by the Selandian, and the Lutetian-Bartonian by the Bartonian. Paleogeographic maps from Scotese (2014), modified from Markwick & Valdes (2004), Gayet *et al.* 1993, Boucot *et al.* 2013 and Jouve (2021). Circled numbers correspond to the number of species present in the locality. Yellow circle is the location of the specimen described herein

TABLE 3. — Pearson's correlations between crocodylian and dyrosaurid diversities. Crocodylian diversity is represented by global uncorrected, global sub-sampled, and North American raw diversities, and dyrosaurid diversity is represented by taxic and phylogenetically corrected global and African diversity count (from De Celis *et al.* 2020; Appendix 4). Spearman's correlations are provided in Appendix 9.

	Taxic global dyrosaurid diversity, number of species		Global dyrosaurid diversity corrected with phylogeny	
	Pearson	p	Pearson	p
Raw global crocodylian diversity	0.83144	0.040226	0.83964	0.036512
Sub-sampled global crocodylian diversity	0.98613	0.00028728	0.95967	0.0024075
Raw North American crocodylian diversity	0.80683	0.052368	0.74016	0.092504

	African taxic diversity, number of species		African diversity corrected with phylogeny	
	Pearson	p	Pearson	p
Raw global crocodylian diversity	0.80497	0.053347	0.80614	0.052728
Sub-sampled global crocodylian diversity	0.96891	0.0014346	0.96697	0.0016181
Raw North American crocodylian diversity	0.88913	0.017756	0.83155	0.040174

TABLE 4. — Pearson's correlation between δO^{18} , δO^{18} proxy for sea surface temperatures and sea level (Appendices 5–8), with dyrosaurid diversity datasets, represented by taxic and phylogenetically corrected diversity counts (Appendix 4). Spearman's correlations are provided in Appendix 9.

	Taxic diversity, number of species		Diversity corrected with phylogeny	
	Pearson	p	Pearson	p
Mean δO^{18} (Cramer <i>et al.</i> 2009)	–0.38075	0.31204	–0.23556	0.54176
Mean δO^{18} SST (Phan SST2)	–0.12552	0.74764	–0.030997	0.9369
Sea level (Miller <i>et al.</i> 2005)	0.28106	0.46379	0.097215	0.80351

related to intense colonisation of new environments, liberated by the extinction of large marine Mesozoic reptiles (Jouve 2021), but likely with a quick rate of turnover. Differences in dyrosaurid environmental preferences, fresh water during the Cretaceous versus marine during the Paleogene (Jouve 2021), are congruent with this hypothesis. The Ypresian could have been a more stable period for dyrosaurid diversity, with a low rate of diversification, and not a real decline. In the Oulad Abdoun Basin the same three species are present during all the Ypresian (two dyrosaurids and a crocodylian species). In this basin, the same phenomenon is observed with the che-lonians, with at least nine Paleocene and only three Ypresian species (Bardet *et al.* 2014, 2017). This postcrisis restoration, then stabilisation, is followed by a strong climatic cooling reaching its acme during the Priabonian. The dyrosaurids did not survive to this period. The role that each successive and sometimes overlapping event played on dyrosaurid diversity during this relatively short interval of geologic time (latest Cretaceous-middle Eocene) cannot be clearly distinguished at present. Similar evolution is observed for crocodylians in the Northern Hemisphere, in particular in North America: a strong Maastrichtian-Paleocene rise, Selandian high turnover (high speciation and extinction rates), positive Thanetian diversification with high speciation and low extinction rates, and an Ypresian-Lutetian drop (Solórzano *et al.* 2019; De Celis *et al.* 2020). The Ypresian crocodylian diversity compared to the Paleocene shows a much lower speciation rate, a low extinction rate, and a null rate of diversification. The diversity is stable (Solórzano *et al.* 2019). This pattern could correspond to what is observed in dyrosaurids, explaining the possible correlation observed between the evolution of both taxa (Table 3).

Compared to South America and Africa, the dyrosaurid history seems to be different in North America and India, where the diversity is low. They are known from fragmentary remains on the Indian continent from Maastrichtian to Bartonian (Buffetaut 1978b; Khosla *et al.* 2009), and from Maastrichtian to Thanetian, maybe Priabonian, in North America (Ehret & Hastings 2013) (Appendix 4). These land masses may have different reasons for their similarly low dyrosaurid diversities. While the Maastrichtian-Eocene crocodyliform fauna of India is poorly known, several species are known from abundant material in North America, where at least four longirostrine crocodylians and one dyrosaurid have been recovered, spanning the Cenomanian to Eocene (Brochu 2004, 2006; Jouve 2021). In North America, two to three contemporaneous marine gavialoid species are found in each stage from Campanian to Thanetian, when they are scarce and probably restricted to fresh-water environments in Africa. Due to the occurrence of multiple crocodylian species during this time, the relative lack of dyrosaurid species in North America likely indicates that this is not a sampling bias and that actual dyrosaurid diversity was indeed low. The lower dyrosaurid diversity might be due to the presence of several crocodylian species and/or a combination of a cooler climate and the presence of the paleo Gulf Stream (Jouve 2021). To the contrary, the reliability of the weak Indian diversity is doubtful. The complete absence of dyrosaurids in Eurasia could be due to cooler climatic conditions and the presence of colder oceanic currents, less favourable to them than to crocodylians (Jouve 2021).

There is a strong correlation between North American crocodylian diversity and African dyrosaurid diversity. It seems to

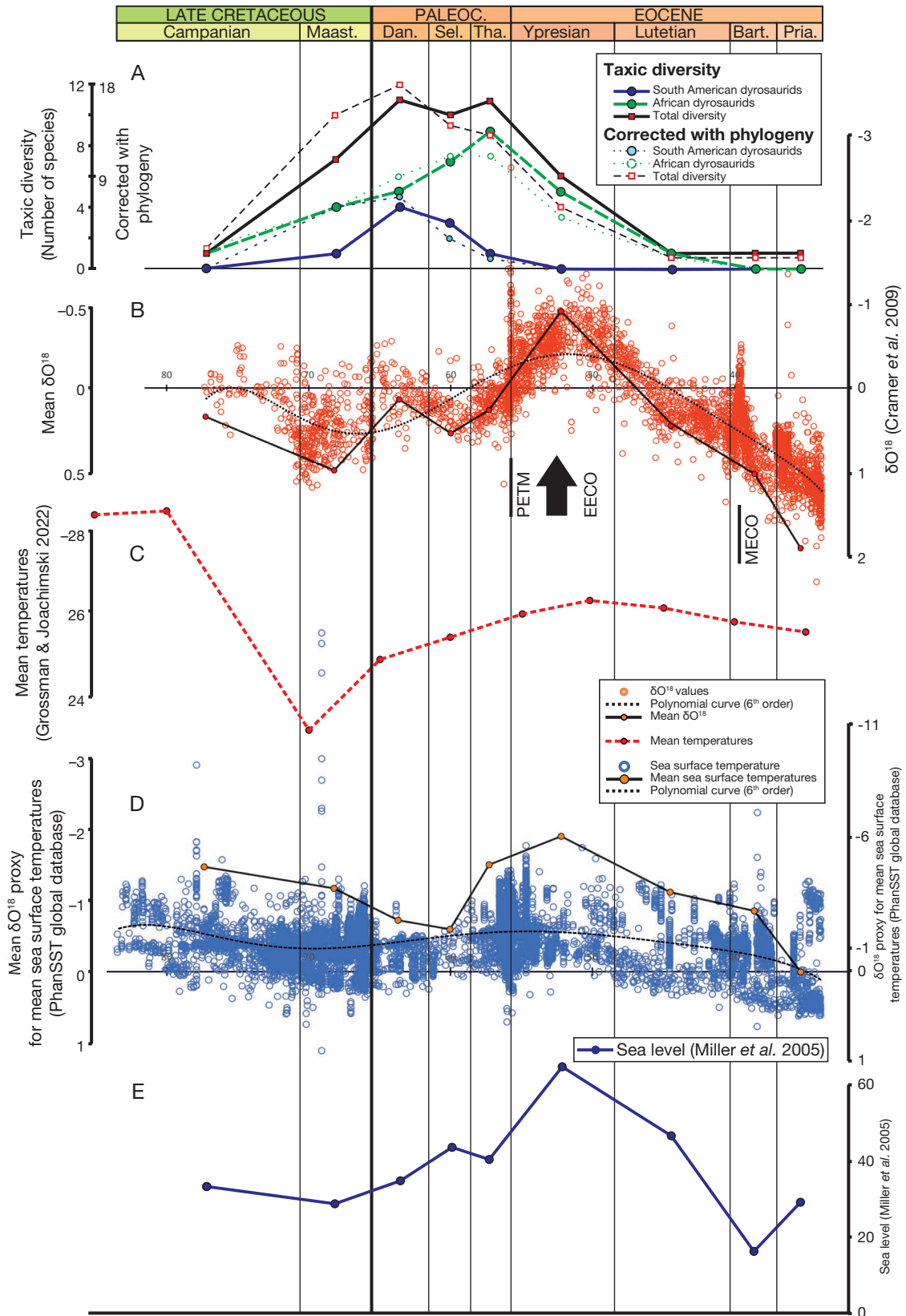


FIG. 8. — Comparison of taxic and phylogenetically corrected diversity with various extrinsic factors, such as proxies for temperatures, sea surface temperatures, and sea level: **A**, taxic and phylogenetically corrected diversity (dashed lines) (for data, see Appendix 3); **B**, δO^{18} data and mean and polynomial curves used as proxy for temperatures (Cramer *et al.* 2009; for data, see Appendix 4); **C**, mean temperatures (Grossman & Joachimski 2022; for data, see Appendix 5); **D**, δO^{18} data and mean and polynomial curves as proxies for sea surface temperatures (PhanSST global database, Judd *et al.* 2022; for data, see Appendix 6); **E**, sea level (Miller *et al.* 2005; for data, see Appendix 7).

be stronger than that obtained between global crocodylian diversity and African dyrosaurid diversity, as the Spearman's and Pearson's correlations for all datasets are significant, corrected or uncorrected (Table 3; Appendix 9). This suggests that both groups in both continents have a similar evolution to their diversity, and are probably impacted by the same factors. On the contrary, the evolution of crocodylians in Europe through the K-Pg crisis strongly differs from what is observed in North America, with a strong drop in diversity (Puértolas-Pascual *et al.* 2015; De Celis *et al.* 2020). So, regional particularities must also be considered when evaluating crocodyliform diversity.

The new dyrosaurid from Colombia suggests that Late Paleocene-middle Eocene South American dyrosaurid diversity is particularly poorly known, and this prevents meaningful comparison between its evolution and that of North America and Africa.

CONCLUSIONS

Dyrosaurids are widely distributed, but they are better known in Africa. The present specimen originates from the Thanetian and is thus the youngest known South American dyrosaurid. It suggests the presence of dyrosaurids later than previously supposed, to at least the end of the Paleocene. This new record provides a different image of the evolution of South American dyrosaurids, with a history that may be more like that of Africa.

Evaluating dyrosaurid diversity is particularly difficult, because its low diversity precludes the use of reliable statistical methods for comparison to changes in biotic and abiotic factors as well as their evolution being tied to multiple global events: the K-Pg extinction, colonisation of new ecological spaces, the Paleocene-Eocene Thermal Maximum, and the Early Eocene Climatic Optimum. All these events confuse the interpretation and identification of which and when each factor is at play. The same is true for the evolution of the crocodylians in the northern hemisphere. The reasons why the dyrosaurids declined and became extinct during the Eocene are obscure. Competition with crocodylians and climatic changes are the most frequently mentioned reasons, but the Paleocene high diversification and turnover mask the clear identification of the stage of their real decline. As suggested here, our knowledge of the African fauna suggests that the Ypresian was probably a stage of stabilisation in dyrosaurid diversity, and not a period of a real decline, congruent with what is observed for crocodylians in the northern hemisphere. The Lutetian could be the real beginning of their decline in diversity, corresponding to a strong drop in temperature and strong climatic cooling, which is more congruent with the climatic sensitivity usually hypothesised for crocodyliforms, and in particular dyrosaurids. A similar Lutetian decline is observed in crocodylian diversity. Contrary to the distribution of crocodylians across the warm temperate climatic belt, dyrosaurids were less diversified and restricted to tropical climates, which are likely to be more impacted by cooling, thereby reducing their chances for survival and potentially causing extinction.

A clear faunal segregation exists between crocodylians from the northern hemisphere and dyrosaurids in the southern hemisphere, yet we found strong similarities between their evolution. The African and South American dyrosaurid diversity from the Late Cretaceous to middle Paleocene has a quite similar evolution to those of crocodylians, particularly in North America. To the contrary, late Paleocene and Eocene diversity is particularly low in South America compared to what is observed for African dyrosaurids and northern hemisphere crocodylians. No South American dyrosaurids were known from this period of time previous to the present discovery, and this strongly suggests that the Late Paleocene-Early Eocene South American dyrosaurid diversity is probably poorly known and underexplored. So, we recommend focusing prospecting work in South America on the poorly known Thanetian to Late Eocene. New material could provide information on the evolution of South American dyrosaurids and help evaluate whether their history on this continent is close to that observed in Africa (and also North American crocodylians) or represents a regional particularity (like the European post K-Pg crisis). This could provide new tools to study the impact of climatic variations on crocodyliform evolution and the influence of regional factors.

Acknowledgements

The authors are grateful to Dr Alex Hastings, an anonymous reviewer, and editor E. Côté for their constructive comments.

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*Submitted on 6 September 2023;
accepted on 3 March 2024;
published on 7 November 2024.*

APPENDICES

APPENDIX 1. — Digital 3D point cloud reconstruction of the vertebra UN-DG-Rp-1001 that was created using photogrammetry. The 3D image was created using 171 colour photos at 3648 × 2736 resolution acquired from a Canon PowerShot ELPH 190 IS digital camera. They were processed using VisualSFM (Wu 2011) and were edited using MeshLab (Cignoni *et al.* 2008). <https://doi.org/10.7934/P5579>

APPENDIX 2. — Specimens, locality information, measurements of centrum lengths (D4 and D5) and total lengths (TL) taken from Iijima & Kubo (2020). Centrum lengths and total lengths were used to estimate total body length of UN-DG-Rp-1001.

Taxon	Specimen #	Locality	D4 (mm)	D5 (mm)	TL (m)
<i>Alligator mississippiensis</i>	UF 37231	USA, Florida, Palm Beach Co., Loxahatchee Refuge	18.2	18.4	1.61
<i>Alligator mississippiensis</i>	UF 42548	USA, Florida, Clay Co., St. John River	42.1	42.1	3.734
<i>Caiman crocodilus</i>	UF 45438	USA, Florida, Dade Co., Homestead	12.5	12.3	1.26
<i>Caiman crocodilus</i>	UF 45439	USA, Florida, Dade Co., Homestead	18.2	17.9	1.235
<i>Caiman yacare</i>	UF 120651	Paraguay, Alto Paraguay	10.4	10.9	0.913
<i>Caiman yacare</i>	UF 120653	Paraguay, Alto Paraguay	26.1	26.5	1.986
<i>Caiman yacare</i>	UF 120726	Paraguay, Pres. Hayes Dept.	19.0	19.5	1.46
<i>Caiman yacare</i>	UF 121204	Paraguay, Pres. Hayes Dept.	31.8	31.1	2.412
<i>Caiman yacare</i>	UF 121226	Paraguay, Alto Paraguay	8.6	8.9	0.791
<i>Caiman yacare</i>	UF 121232	Paraguay, Alto Paraguay	32.0	32.6	2.393
<i>Caiman yacare</i>	UF 121238	Paraguay, Alto Paraguay	23.9	24.5	1.813
<i>Caiman yacare</i>	UF 121245	Paraguay, Alto Paraguay	22.8	22.1	1.709
<i>Caiman yacare</i>	UF 121251	Paraguay, Alto Paraguay	11.8	12.3	1.01
<i>Caiman yacare</i>	UF 121268	Paraguay, Pres. Hayes Dept.	35.3	32.1	2.459
<i>Caiman yacare</i>	UF 120684	Paraguay, Alto Paraguay	31.9	31.6	2.36
<i>Melanosuchus niger</i>	UF 66428	—	19.0	19.3	1.65
<i>Melanosuchus niger</i>	UF 72914	—	33.1	33.2	2.59
<i>Melanosuchus niger</i>	USNM 257786	Peru, Madre De Dios, Manu National Park	22.2	23.6	1.86
<i>Paleosuchus palpebrosus</i>	UF 75020	Guyana, no other data	8.7	8.8	0.705
<i>Paleosuchus palpebrosus</i>	UF 87980	Guyana, no other data	9.2	9.7	0.681
<i>Paleosuchus trigonatus</i>	USNM 213705	—	16.9	17.2	1.15
<i>Crocodylus acutus</i>	UF 56580	USA, Florida, Dade Co., Turkey Pt.	46.4	45.8	3.77
<i>Crocodylus acutus</i>	UF 63930	USA, Florida, Monroe Co., Lake Surprise	31.1	31.1	2.66
<i>Crocodylus acutus</i> (Natasha)	USNM 247943	Panama, Barro Colorado Island, Barbour Point	38.9	39.7	3.1
<i>Crocodylus porosus</i>	NTM R16036	Australia, Northern Territory, Mary River	62.2	63.6	5.13
<i>Gavialis gangeticus</i>	UF 70592	—	15.7	15.9	1.36
<i>Gavialis gangeticus</i>	UF 118998	India, Lucknow, Kukrail Crocodile Center	45.7	47.0	3.25
<i>Tomistoma schlegelii</i>	UF 84888	—	36.5	36.6	3.0036
<i>Tomistoma schlegelii</i>	UF 107493	—	36.2	36.7	3.23
<i>Tomistoma schlegelii</i>	USNM 52972	Indonesia, Borneo, Samarinda	32.4	32.9	3.1

APPENDIX 3. — Centrum lengths of the *Dyrosaurus maghribensis* specimens OCP DEK-GE 254, OCP DEK-GE 255, and the reconstruction proposed by Jouve *et al.* (2006). Abbreviations: **DSL**, dorsal skull length; **Pv**, Position of the vertebra; **Lc**, length of the centrum; **C**, cervical; **D**, dorsal; **S**, sacral; **Ca**, caudal; **CL**, caudal length. The proportion of the tail compared to the body length is based on *Macrospodylus bollensis* Re1193/1(Tübingen) in which the length of the cervical + dorsal vertebrae is 59% of the tail length (Caudal length is thus 169.5% the length C1-D15). Length from C1 to last sacral (C1-S2) = 177.83; Length from C1 to D15 (C1-D15) = 164.85; Caudal length estimated (= 169.5 % × C1-D15) (**CL**) = 279.4; Total body length (DSL + C1-S2 + CL) = 540.

OCP DEK-GE 255		Reconstruction of <i>Dyrosaurus maghribensis</i>	
DSL (cm)	89	DSL (cm)	82.77
Pv	Lc (cm)	Pv	Lc (cm)
D15	–	C1-2	11.3
S1	7	C3	7.5
S2	7	C4	7
Ca1	6	C5	7
Ca2	6	C6	7
Ca3	6.5	C7	7.5
Ca4	6.5	C8	7.5
Ca5	6.3	C9	7.7
Ca6	6	D1	8
Ca7	6	D2	8
Ca8	5.5	D3	7.5
Ca9	6	D4	7.5
Ca10	6	D5	7
Ca11		D6	6.5
Ca12	6	D7	6.1
Ca13	6.3	D8	6
Ca14	6	D9	6.3
Ca15	6	D10	6
Ca16	6	D11	6.2
Ca17	6	D12	6.5
Ca18	5.5	D13	7
Ca19	5.5	D14	7
		D15	6.75
		S1	6.49
		S2	6.49
		Ca1	5.56
		Ca2	5.56
		Ca3	6.02
		Ca4	6.02
		Ca5	5.84
		Ca6	5.56
		Ca7	5.56
		Ca8	5.1
		Ca9	5.56
		Ca10	5.56
		Ca11	5.56
		Ca12	5.56
		Ca13	5.84
		Ca14	5.56
		Ca15	5.56
		Ca16	5.56
		Ca17	5.56
		Ca18	5.1
		Ca19	5.1

APPENDIX 4. — Geographic and stratigraphic distribution of dyrosaurids.

Stage	Substage	Continent	Species	Locality And Formation	References
Upper Cretaceous	Campanian-Maastrichtian	Africa	<i>Brachiosuchus kababishensis</i>	Kababish Formation, Jebel Abyad Plateau, north central Sudan	Salih <i>et al.</i> 2021
		Africa	Dyrosauridae indet.	Lubur sandstone (Turkana grits), Kenya	Sertich <i>et al.</i> 2006; Tiercelin <i>et al.</i> 2012; Owusu Agyemang <i>et al.</i> 2019
				Wadi Milk Formation, Sudan	Buffetaut <i>et al.</i> 1990
			Hyposaurinae indet.	Shendi Formation, Robert's bonebed, Sudan	Salih <i>et al.</i> 2015
	Maastrichtian	North America	Dyrosauridae indet. ?	Monmouth County, New Jersey, New Egypt Formation?	Troxell 1925
				Severn or Brightseat Formation, Hechinger Site, Prince George's County, Maryland, USA	Morgan <i>et al.</i> 2018
		South America	Dyrosauridae indet. ?	Huarachani, Bolivia	Argollo <i>et al.</i> 1987; Gayet <i>et al.</i> 1991, 1993
			Dyrosauridae indet. ?	Locality V-4940, Tolima, Colombia	Langston 1965
		India	Dyrosauridae indet.	Vikarabad area, Andhra Pradesh, southern India	Rana 1987; Prasad & Singh 1991
			Dyrosauridae indet.	Kisalpur intertrappean section, Kharmer River, Kisalpur Village, Dindori District, Madhya Pradesh, Central India	Khosla <i>et al.</i> 2009
		Africa	<i>Sokotosuchus ianwilsoni</i>	Gypsiferous shale member, Dukamaje Formation, southern flank of hills, Gilbedi, Sokoto State, Iullemeden Basin, Nigeria	Halstead 1975; Halstead & Middleton 1976
			Dyrosauridae indet. (' <i>Chenaniusuchus</i> ' sp.)	Ménaka Formation, Iullemeden Basin, Mali 8, Unit 10, Mali	Hill <i>et al.</i> 2008
			Hyposaurinae indet. (' <i>Rhabdogathus keiniensis</i> ')	Ménaka Formation, Iullemeden Basin, Mali 8, Unit 10, Mali	
			Dyrosauridae indet. ?	Oulad Abdoun Basin, Morocco	Jouve 2004
Paleocene	Danian-Selandian-Thauetian	Africa	<i>Rhabdogathus</i> sp.	Umm Himar Formation, Jabal Umm Himar, Near Turabah, Mecca Region, Saudi Arabia	Langston 1995
			<i>Phosphatosaurus</i> sp. Hyposaurinae indet. sp. <i>Congosaurus compressus</i>		
	Danian	North America	<i>Hyposaurus natator</i>	Inversand Company Marl Pit, Pemberton Marl Co., Cream Ridge Marl Co. Pits, Sewell, Mantua Township, Gloucester County, mid.marl Bed, Greensand Formation, Hornerstown Formation, Hornerstown, Barnsboro, Birmingham, New Jersey, USA	Denton <i>et al.</i> 2014
				Black Mingo Group, Williamsburg Fm, 2.74 km north of St. Stephen, Berkeley County, South Carolina, USA	Erickson 1998
			Dyrosauridae indet. ?	Severn or Brightseat Formation, Hechinger Site, Prince George's County, Maryland, USA; Midway Group, Clayton Formation, M. Till Farm, north of Braggs, Wilcox County, Alabama, USA	Denton <i>et al.</i> 1997; Morgan <i>et al.</i> 2018
		Africa	<i>Atlantosuchus coupatezi</i>	Oulad Abdoun Basin, Morocco	Buffetaut 1979a; Jouve <i>et al.</i> 2008
			<i>Hyposaurus paucidens</i> aff. <i>Phosphatosaurus gavialoides</i>		Arambourg 1952; Arambourg 1952; Bardet <i>et al.</i> 2017
			Dyrosauridae indet.	Ndayane Formation, Sénégal (middle-late Danian)	Tessier 1952; Martin <i>et al.</i> 2019

Appendix 4. — Continuation.

Paleocene (cont.)	Danian (cont.)	South America	<i>Hyposaurus derbianus</i>	Maria Farinha Formation, Pernambuco Basin, Brazil	Cope 1885
			<i>Dorbignysuchus niatui</i>	Santa Lucia Formation, Bolivia	Jouve <i>et al.</i> 2021
			<i>Rodeosuchus machukirui</i>		
			<i>Luciasuchus lusingqai</i>		
		Indian continent	Dyrosauridae indet.	Lakhra Formation, Barhi Nala, Lohige Nala, Pakistan Khadro Formation Ranikot Group, Sindh, Southern Pakistan	Lydekker 1879; Storrs 1986; S.J. pers. Obs.
	Selandian	South America	<i>Cerrejonisuchus improcerus</i>	Cerrejón coal mine, Guajira Department, northeastern Colombia	Hastings <i>et al.</i> 2010
			<i>Anthracosuchus balrogus</i>		Hastings <i>et al.</i> 2015
			<i>Archerontisuchus guajiraensis</i>		Hastings <i>et al.</i> 2011
		Africa	<i>Congosaurus bequaerti</i>	Bed 8, Landana cliff, Cabinda, Angola	Jouve & Schwarz 2004; Solé <i>et al.</i> 2018
	Selandian- Thanetian	Africa	<i>Hyposaurus</i> sp.	Gypsiferous shale member, Dange Formation, Wurno, Sokoto State, Nigeria	Swinton 1930, Halstead & Middleton 1976
			<i>Rhabdognathus</i> sp. <i>Congosaurus compressus</i>		Buffetaut 1980
			<i>Hyposaurus</i> sp. 1	Clay-sands, Taoudeni Basin, Mali	Buffetaut 1980; Jouve 2007.
			<i>Hyposaurus</i> sp. 2 <i>Congosaurus compressus</i>	Clay-sands, Taoudeni Basin, Mali Clay-sands, In Farghas, Tilemsi Valey, Taoudeni Basin, Mali	
			<i>Rhabdognathus keiniensis</i>	Clay-sands, Cheit Keini and In Farghas, Tilemsi Valley, Taoudeni Basin, Mali	
			<i>Rhabdognathus aslerensis</i>	Mali 8, Taoudeni Basin, Mali	Brochu <i>et al.</i> 2002; Jouve 2007.
			<i>Phosphatosaurus</i> sp.	Cheit Keini, Mali	Buffetaut 1979b
			<i>Hyposaurus</i> sp. 1 <i>Hyposaurus</i> sp. 2 <i>Congosaurus compressus</i>	Dange Formation, Iullemeden Basin, Niger	Jouve 2007
			<i>Phosphatosaurus</i> sp.		Buffetaut 1979b
			Thanetian	North America	Dyrosauridae indet.
	cf. <i>Hyposaurus</i> sp.	Piscataway member, Aquia Formation, Liverpool Point, Charles County, Maryland, USA (early Thanetian)			Denton <i>et al.</i> 2014.
Africa	<i>Rhabdognathus</i> sp.	Oulad Abdoun Basin, Morocco		Jouve 2004; Bardet <i>et al.</i> 2017	
	aff. <i>Phosphatosaurus gavialoides</i>			Jouve 2004; Bardet <i>et al.</i> 2017	
	cf. “ <i>Hyposaurus</i> ” <i>paucidens</i>			Arambourg 1952; Jouve 2004	
	<i>Chenanisuchus lateroculi</i>			Jouve <i>et al.</i> 2005a.	
	<i>Arambourgisuchus khouribgaensis</i>			Jouve <i>et al.</i> 2005b.	
	Dyrosauridae indet.	WACEM and SCAN-TOGO quarries, Tabligbo, Togo		Stromer 1910; Amoudji <i>et al.</i> 2021	
South America	Dyrosauridae indet.	Piñalerita Creek, Cuervos Formation, Colombia (late Thanetian-early Ypresian)		Present paper	

Appendix 4. — Continuation.

Eocene	Ypresian	Africa	<i>Dyrosaurus phosphaticus</i>	Djebel Teldja, Metlaoui, Tunisia; Tebessa, Algeria	Thévenin 1911; Piveteau 1935; Bergounioux 1955, 1956; Jouve 2005
			<i>Phosphatosaurus gavialoides</i>	Tunisia; Mali 20, Taoudenit Basin, Mali	Bergounioux 1955, 1956; Hill <i>et al.</i> 2008; O'Leary <i>et al.</i> 2019
			<i>Dyrosaurus maghribensis</i> Hyposaurinae indet.	Oulad Abdoun Basin, Morocco	Jouve <i>et al.</i> 2006
			<i>Rhabdognathus acutirostris</i>	Tunisia	Jouve 2004; Bardet <i>et al.</i> 2017
		Indian Continent	Dyrosauridae indet.	Tadkeshwar, India	Bergounioux 1955, 1956
	Lutetian	Africa	<i>Tilemsichus lavocati</i>	Tamagulelt, Tilemsi valley, Mali	Smith <i>et al.</i> 2016
	Bartonian	Indian Continent	Dyrosauridae indet.	Pondaung Formation, west of Mandalay, Burma	Buffetaut 1980
	Priabonian	North America	Dyrosauridae indet.	Yazoo Clay, Clark County, Alabama, USA	Buffetaut 1978b
					Ehret & Hastings 2013

APPENDIX 5. — δO^{18} data from Cramer *et al.* (2009) used for Fig. 6 and Table 3. <https://doi.org/10.7934/P5579>

APPENDIX 7. — δO^{18} proxy for sea surface temperature (PhanSST global database). <https://doi.org/10.7934/P5579>

APPENDIX 6. — Comparison of δO^{18} -derived low-latitude temperatures (Grossman & Joachimski 2022) and global mean age of the sea floor (**OcF Age**) and global mean accretion rate (**AccR**). From V  rard & Veizer (2019).

APPENDIX 8. — Sea level (Miller *et al.* 2005).

Age [Ma]	Locfit mean T (PO4+CaCO3; iceV, lat, arag, bel corr)	OcF age [Ma]	AccR [km ² /yr]
35	25.307	49.288	3.747
40	25.663	47.362	3.772
45	26.157	45.706	3.732
50	26.392	44.145	3.554
55	25.945	42.510	3.418
60	25.121	40.777	3.741
65	24.326	39.139	4.372
70	21.844	37.951	4.713
75		37.448	4.397
80		37.377	4.040
85	29.613	37.364	4.499
90	29.410	37.214	6.000

Sea level (Miller <i>et al.</i> 2005)	
Campanian	33.34827586
Maastrichtian	28.60967742
Danian	34.97955556
Selandian	43.638
Thanetian	40.37454545
Ypresian	64.65879518
Lutetian	46.79060606
Bartonian	16.56970588
Priabonian	29.1252381

APPENDIX 9. — Spearman's correlations between δO^{18} , δO^{18} proxy for sea surface temperatures, sea level (Appendices 5-8), with dyrosaurid diversity datasets, represented by taxic and phylogenetically corrected diversity counts. Spearman's correlations between crocodylian and dyrosaurid diversities. Crocodylian diversity is represented by global uncorrected, global sub-sampled, and North American raw diversities, and dyrosaurid diversity datasets represented by taxic and corrected phylogenetically global and African diversity counts (Appendix 4).

	Taxic diversity, number of species		Diversity corrected with phylogeny	
	Spearman's rs	p	Spearman's rs	p
Mean δO^{18} (Cramer <i>et al.</i> 2009)	-0.49839	0.18122	-0.44074	0.23846
Mean δO^{18} SST (Phan SST2)	-0.10492	0.78519	-0.084758	0.84104
Sea level (Miller <i>et al.</i> 2005)	0.25357	0.50873	0.10171	0.80638
Raw global crocodylian diversity (De Celis <i>et al.</i> 2020)	0.81969	0.066667	0.66674	0.16111
Sub-sampled global crocodylian diversity (De Celis <i>et al.</i> 2020)	0.94112	0.016667	0.81168	0.072222
Raw North American crocodylian diversity (De Celis <i>et al.</i> 2020)	0.88041	0.05	0.84067	0.044444
	African taxic diversity, number of species		African diversity corrected with phylogeny	
	Spearman's rs	p	Spearman's rs	p
Raw global crocodylian diversity (De Celis <i>et al.</i> 2020)	0.69573	0.13333	0.71429	0.13611
Sub-sampled global crocodylian diversity (De Celis <i>et al.</i> 2020)	0.7537	0.11111	0.77143	0.10278
Raw North American crocodylian diversity (De Celis <i>et al.</i> 2020)	0.98561	0.0055556	0.88571	0.016667