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ARTICLE



Description of new dyrosaurid specimens from the Late Cretaceous–Early Paleogene of New Jersey, United States, and comments on *Hyposaurus* systematics

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ABSTRACT

Dyrosauridae was a successful clade of marine crocodyliforms that survived the Cretaceous–Paleogene biotic crises. The most important taxon from North America is *Hyposaurus rogersii*, a species first described in the mid-19th century based on fragmentary fossils. Several new specimens are described here, comprising material that once belonged to the Yale Peabody Museum (New Haven, USA) but obtained later by L.I. Price and housed in the paleontological collections of the former Divisão de Geologia e Mineralogia (Rio de Janeiro, Brazil). The remains include postcranial bones and fragments of a lower jaw. The present work urges for the necessity of a revision about the validity of *Hyposaurus rogersii* based on the absence of diagnostic features observed in the holotype. The new specimens show new postcranial features that support the importance of the postcranial bones for dyrosaurid systematics.

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boundary

Introduction

The Dyrosauridae is a neosuchian clade of crocodyliforms, which includes species ranging from Mesozoic to Cenozoic, therefore one of the crocodyliform clades that did not go extinct at the K–Pg mass extinction (Parris 1986; Denton et al. 1997; Hill et al. 2008). Species of dyrosauridae are known from all regions of the world with occurrences in Africa, Asia, South and North America (e.g., Khosla et al. 2009; Shiller II et al. 2016; Sena et al. 2017; Young et al. 2017) and possibly Europe (Buffetaut and Lauerjat 1978). Those species are highly adapted to aquatic locomotion (Schwarz-Wings et al. 2009) and are found in both marine and freshwater environmental deposits (Troxell 1925; Hastings et al. 2010, 2011, 2014). The Hyposaurinae may have had a more variable feeding behavior than piscivory only (Schwarz-Wings 2014).

In a phylogenetic context, Hyposaurinae was erected to be closely related with Phosphatosaurinae (Buffetaut 1980). The type-species is *Hyposaurus rogersii* Owen, 1849, which was described based on two isolated vertebrae with only the centra preserved. The poor preservation of the fossils made its validity be questioned (Norell and Storrs 1989). New fossil findings around the world (e.g., Brazil, Morocco) prompt new species to be erected for the genus *Hyposaurus* (Cope 1886; Arambourg 1952). *Hyposaurus rogersii* was considered the senior synonym of all other *Hyposaurus* described from North America (i.e. *H. fraterculus*, *H. ferox* and *H. natator*; see Parris 1986). The Malian and Nigerian *Hyposaurus* species are all considered insufficiently incomplete or lacking autapomorphic features for recognizing them as unique species, thus Jouve (2007) referred to all those specimens as *Hyposaurus* sp. New materials from Africa were recently also recognized as *Hyposaurus* sp. (Salih et al. 2015;

Callahan et al., 2015). Jouve (2007) urged for a complete revision of the genus and an amendment of the diagnoses previously proposed by Buffetaut (1980) and Denton et al. (1997), which are mainly based on mandibular characters.

Despite belonging to the same genus, the phylogenetic relationship between North American and Brazilian *Hyposaurus* species has never been properly studied (e.g., Shiller II et al. 2016). The main reason is that both species are usually represented by incomplete specimens that have many postcranial material, but which are generally considered undiagnostic for Dyrosauridae. Therefore, a revision testing the validity of those species, together with a more careful study of their postcranial elements, is mandatory to the understanding of their evolution and the biogeographical relationship between the Northern and Southern landmasses during Cretaceous times.

The present contribution aims to describe eight new North American dyrosaurid specimens from New Jersey. The material was tentatively identified as *Hyposaurus rogersii* in the collection log. Besides the description, a formal identification of these materials will be provided with some anatomical comments regarding the dyrosaurid species, detailing more reliable features. Comments about the validity of *Hyposaurus rogersii* are provided.

Institutional Abbreviations: ALAM-PV, University of Alabama, Paleovertebrate Collection, USA; AUMP, Auburn (Alabama) University Museum of Paleontology, USA; BMNH, Natural History Museum of London, England; CAV, Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Brazil; CNRST, Centre National pour la Recherche Scientifique et Technique, Morocco; DG-CTG-UFPE, Departamento de

Geologia, Centro de Tecnologia e Geociências, Universidade Federal de Pernambuco, Brazil; **DGM**, Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Brazil; **IGM**, Museo Geológico, Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Colombia; **MB R SUD**, Museum für Naturkunde Berlin, Sudan field collection, Germany; **MCT**, Museu de Ciências da Terra, Serviço Geológico do Brasil, Brazil; **MNHN**, Muséum national d'Histoire naturelle, France; **MRAC**, Musée royal de l'Afrique centrale, Belgium; **NJSM**, New Jersey State Museum; **OCP DEK-GE**, Office chérifien des Phosphates, Direction exploitation de Khouribga, Service Geologie-Exploitation, Morocco; **PAS**, Museo de Paleontología de Múzquiz, Mexico; **UF**, Florida Museum of Natural History, University of Florida, USA; **YPM**, Yale Peabody Museum, USA.

Anatomical Abbreviations: **4th**, fourth trochanter; **de**, dentary alveoli; **df**, distal fossae of femur; **diap**, diapophysis; **dt**, dentary tooth; **fm**, femoral ridge; **hy**, hypapophysis; **Mg**, Meckelian groove; **para**, parapophysis; **pf**, proximal fossae of femur; **pre**, prezygapophysis; **pos**, postzygapophysis; **rc**, radial condyle; **syn**, synapophysis; **tp**, transverse process; and, **uc**, ulnar condyle.

Geological background

The first fossils of *Hyposaurus rogersii* were collected by the late professor Henry Darwin Rogers in the mid-19th century (Owen 1849). These remains came from a series of geological units of the coastal area of New Jersey collectively known as the Greensands (Troxell 1925). The Greensands extend as a belt of land between Monmouth County and Salem County (Figure 1) and experienced extensive mining activities due to its glauconite-bearing soils (Tedrow 2002). Therefore, most of the first specimens of *Hyposaurus* were collected by the pit workers of the mining industry of greensand marl (Denton et al. 1997). Marsh (1871) reported some of these findings from the 'middle marl bed at Birmingham, New Jersey', which were collected by workers of the Pemberton Marl Company pit. Originally, Owen (1849) provided no information about the type locality of *H. rogersii*, but Rapp (1944) recognized Rogers' type specimen as also coming from Birmingham, Burlington County. Additional *Hyposaurus* specimens were later recovered in Monmouth (Cream Ridge Marl Company pit, Hornerstown) and Gloucester (West Jersey Marl Company pit, Barnsboro) counties (Troxell 1925; Norell and Storrs 1989; Callahan 2015). Many of these localities were poorly described and reported over time, leading to confusion regarding the exact horizon that yielded these fossils.

The New Jersey Coastal Plain shows an important record of the K-Pg mass extinction event in a series of marine sections (Gallagher 1993; Miller et al. 2010; Obasi et al. 2011; Gallagher et al. 2012; Wiest et al. 2016). Many fossils from this time interval come from the 'Main Fossiliferous Layer' (MFL), which can be considered the most important from the paleontological perspective (Gallagher 1984, 1993; Olson and Parris 1987). The MFL was previously considered a deposit with reworked Cretaceous fossils placed at the lower levels of the Hornerstown Formation (Gallagher 1993, 2005), which age was established as Danian based on micropaleontological data (Koch and Olsson 1974, 1977; Petters 1976).



Figure 1. County Map of New Jersey showing the distribution of the Rancocas Group (geological unit in gray). Legend: blue square (dark gray square in B&W version) Creab Ridge Marl Co., Hornerstown, New Jersey; and, red prism (light gray prism in B&W version) is Birmingham New Jersey. Scale = 60 km. Modified from Gallagher (1993).

However, the base of the MFL has been regarded now as the limit for the chronostratigraphic K-Pg boundary (Wiest et al. 2016). Specimens of *H. rogersii* can be found in both the lower and upper sections of the Hornerstown Formation (Gallagher 1984), which sets the fossil record of the species completely within the Paleogene (Callahan et al. 2015).

The studied material was collected in New Jersey, USA. Six specimens featured in this study were collected in Birmingham, New Jersey (USA) by O.C. Marsh in 1868 (Middle Marl Bed, 'greensand', Navesink Formation, Upper Cretaceous; Figure 1), which include: DGM 797-R, DGM 798-R, DGM 799-R, DGM 800-R, DGM 801-R and DGM 803-R. The remaining specimens, DGM 804-R and DGM 805-R, were collected by J.G. Meirs in 1869 from Creab Ridge Marl Co., Hornerstown, New Jersey (Navesink or Hornerstown Formation; Figure 1).

Material and methods

The present work describes eight new specimens originally identified as *Hyposaurus rogersii* (Figure 2; Table 1). These specimens were obtained by the Brazilian paleontologist L.I. Price during his trip to USA, as a John Simon Guggenheim Fellow from 1951–1952 at the Yale Peabody Museum (New Haven, USA). Later this material was housed in the vertebrate paleontology collection of the Museu de Ciências da Terra, formerly the Paleontological Section of the Departamento Nacional da Produção Mineral (Brazilian Geological Survey), Rio de Janeiro, Brazil. The specimens were originally cataloged under the old acronym of the institution (i.e. DGM; see Souza et al. 2016 for clarification). The bone elements referred as DGM 805-R are here considered as belonging to the same specimen based on the information provided in the label.

Comparisons with other dyrosaurids were conducted in order to properly describe and identify the studied taxa (Table 2). The species *Hyposaurus fraterculus*, *H. ferox* and *H. natator* proposed by Troxell (1925) are considered as junior synonyms of *H. rogersii* (see Parris 1986). The following material is not included in the comparisons due to an absence of comparable bones: *Atlantosuchus coupatezi* Buffetaut & Wouters, 1979 (see Jouve et al. 2008 for other newly described specimens); *Chenanisuchus lateroculi* Jouve et al., 2005a; *Rhabdognathus aslerensis* Jouve, 2007; *R. keiniensis* Jouve, 2007 and *R. rarus* Swinton, 1930. The species *R. rarus* is also treated here as *nomen dubium* as suggested by Jouve (2007). The species *R. acutirostris* Bergounioux, 1955 and *Sokotosuchus ianwilsoni* Halstead, 1975 are not included due to insufficient data about them. The new specimen NJSM 23368 attributed to *H. rogersii* by Callahan et al. (2015) was not included in the comparisons of the present work because the material was not first-

handed studied by none of the authors and was not yet formally described and published, being only presented in abstracts and figured in poster sections. Thus, we will wait for the complete publication with the description and justification of why this specimen can be referred to *H. rogersii*.

The osteological nomenclature follows paleontological works such as Mook (1921), Romer (1956), Hoffstetter and Gasc (1969), Frey (1988), Pol (2005) Schwarz et al. (2006) and Pol et al. (2012). The modifications in the nomenclature of the vertebral structures suggested by Souza (2018) are followed.

The positioning of isolated vertebrae is based on data derived from *Dyrosaurus maghribensis* (Jouve et al. 2006) and Schwarz et al. (2006). The axial series of extant species studied by RGS are considered here as well.

Results

Positioning of isolated vertebrae on the axial skeleton of dyrosauridae

The positioning and justification for identification of isolated vertebrae are presented here based on first-hand study of extant specimens together with available information on the dyrosaurid axial skeleton.

The cervical vertebrae are diagnosed by the following features, which are missing in the 8th and 9th (i.e. first dorsals) vertebrae: diapophyseal process projected lateroventrally; parapophysis and diapophysis are anteroposteriorly elongated; and, small hypapophysis located anteriorly, without reaching anterior margin. These characteristics are observable in dyrosaurids and extant crocodylian specimens.

The eighth and ninth cervical vertebrae and the first and second dorsals are the only vertebrae that have the parapophysis located immediately below the neurocentral



Figure 2. Collection box deposited in Museu de Ciências da Terra containing all the studied specimens: DGM 797-R, DGM 798-R, DGM 799-R, DGM 800-R, DGM 801-R; DGM 803-R, DGM 804-R and DGM 805-R. Scale: 5cm.

Table 1. List of the studied specimens, with their locality and previous catalog number. All studied specimens are registered in the DGM collections as *Hyposaurus rogersii*. Numbers under Locality refer to sites described in the Geological Background section, being: 1) Birmingham, New Jersey; and 2) Creab Ridge Marl Co., Hornerstown, New Jersey. Abbreviation: **CN**, catalogue number.

DGM CN	YPM CN	Locality	Specimen
DGM 797-R	YPM 211	1	Last cervical vertebra
DGM 798-R	YPM 218	1	One middle to posterior dorsal vertebra
DGM 799-R	YPM 222	1	Third cervical vertebra
DGM 800-R	YPM 229	1	One anterior caudal vertebra
DGM 801-R	YPM 596	1	One middle to posterior dorsal vertebra and one middle to posterior caudal vertebra
DGM 803-R	YPM 240	1	One proximal portion of a left femur
DGM 804-R	YPM 476	2	Second dorsal vertebra
DGM 805-R	YPM 898	2	Two mandibular sections, one corresponding to the anterior symphyseal portion and the second to a left fragment of the posterior dentary; two posterior cervical vertebrae; one fragmentary proximal portion of a long bone (tibia?); one fragmentary distal portion of a right humerus; two posterior caudal vertebrae; one posterior dorsal vertebra; and, other fragmentary bones

synchondrosis. Additionally, for dyrosaurids the positioning of the hypapophysis helps to differentiate the eighth and ninth cervical vertebrae. The hypapophysis reaches the anterior margin of the centrum in both, but in the eighth it is less developed ventrally and reaches the mid portion of the centrum, while in the ninth it is more developed ventrally and surpasses the mid portion of the centrum. Another relevant feature to differentiate between these vertebrae is that the prezygapophyseal process and the parapophyses are displaced anteriorly in the eighth in comparison to the ninth. The first and second dorsals differ from the cervicals by having the hypapophysis more centralized at the centrum, without touching the anterior margin of the centrum.

The third dorsal is the only vertebra that has the parapophyseal and diapophyseal processes united, with the former located below the later process. This is clear due to the presence of the ventral contribution of the centrum to the parapophyseal process located at the neurocentral synchondrosis. The dorsal vertebrae posterior to the third have transverse processes (*sensu* Souza 2018) that are well-developed. The fourth and fifth also have well-developed hypapophyses. All others are difficult to identify without preservation of the parapophysis, diapophysis, and the neural spine. The caudal vertebrae have quadrangular centra with marks for the articulation with the chevron on the ventral surface. However, they can only be properly positioned with the preservation of the caudal ribs (*sensu* Souza 2018) and the neural spines.

The isolated vertebrae described here had their position in the axial skeleton inferred based on the features proposed in this section. Therefore, no further justification for the vertebral positioning is provided beside these.

Species validity of *hyposaurus rogersii*

Hyposaurus rogersii is the type species of its genus and was described by Owen (1849) based on two vertebral centra (figures 7, 8, 9, and 10 from Plate XI in Owen 1849; Figure 3). The main feature identified by Owen (1849) to recognize this species was the ventrally extended and anteroposteriorly wide hypapophyses. However, the description of several other postcranial remains of Dyrosauridae (e.g., Cope 1886; Troxell 1925; Jouve et al. 2006; Schwarz et al. 2006; Barbosa et al. 2008) showed that the ventrally extended hypapophysis is a widespread feature and cannot be considered an diagnostic feature. Parris (1986) recognized *H. rogersii* as a valid species (*contra* Norell and Storrs 1989) and considered all other *Hyposaurus* species described from North America as junior synonyms. Denton et al. (1997) described more complete specimens of *H. rogersii* and provided a new emended diagnosis. However, he did not provide any diagnostic features that were also present in the holotype of *H. rogersii*. Therefore, despite being the only valid species in North America (*sensu* Parris 1986), such status of *H. rogersii* is based only on the presence of a non-exclusive well-developed hypapophysis and the other features based on referred materials (e.g., Denton et al. 1997).

The material studied by Owen consists of a last cervical (Figure 3(a–b)) and a third dorsal vertebra (Figure 3(c–d)). In the cervical vertebra, the well-developed hypapophysis extends along the anteroposterior length of the centrum ending close to the posterior margin of the centrum without reaching it, while in other comparable specimens the hypapophysis continues only to the medial portion of the centrum, as observed in *Dyrosaurus maghribensis* and *Congosaurus bequaerti*, or it is limited to the median region of the centrum, as in *Rhabdognathus* sp. (USGS SAP 37 CR-I; Langston 1995). However, in the specimen OCP DEK-GE 252 of *D. maghribensis* the aforementioned characteristics are observed on the ninth cervical vertebra (Jouve et al. 2006). Therefore, the most distinct feature present in the holotype cannot be considered as an diagnostic trait.

The species *Hyposaurus rogersii* should be considered as a *nomen dubium*, as the absence of autapomorphies. The holotype anatomy is in agreement with the observed in several other specimens from the region, which enabled the recognition of new specimens to the species and a synonymization process (e.g., Troxell 1925; Denton et al. 1997). Future works are necessary to evaluate if *H. rogersii* should be considered a *nomen dubium* or if the already now specimens can be used to keep the species validity. Until a detailed revision of *H. rogersii* is expected, the present work consider for a matter of identification and comparison the referred specimen YPM 380 as an auxiliary for the understanding of the *H. rogersii* anatomy.

Systematics

CROCODYLOMORPHA Walker, 1970

CROCODYLIFORMES Hay, 1930

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

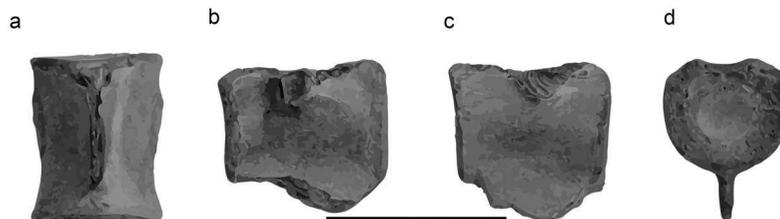
DYROSAURIDAE de Stefano, 1903 (*sensu* Buffetaut 1976)

Hyposaurus Owen, 1849

Type species: *Hyposaurus rogersii*.

Table 2. Dyrosaurid species and specimens used for comparisons. *, type material; **Bold**, specimen personally studied.

Species	Specimen	References
<i>Acherontisuchus guajiraensis</i>	UF / IGM 34; UF / IGM 35; UF / IGM 37; UF / IGM 38; UF / IGM 39	Hastings et al. 2011
<i>Anthracosuchus balrogus</i>	UF/IGM 67; UF/IGM 68	Hastings et al. 2014
<i>Arambourgisuchus khouribgaensis</i>	OCP DEK-GE 18; OCP DEK-GE 269; OCP DEK-GE 1200	Jouve et al. 2005b
<i>Cerrejonisuchus improcerus</i>	UF/IGM 30; UF/IGM 31	Hastings et al. 2010
<i>Congosaurus compressus</i>	MNHM TGE 4034	Buffetaut 1980
<i>Congosaurus bequaerti</i>	MRAC 1741-1743; MRAC 1745; MRAC 1796; MRAC 1797; MRAC 1802-1803; MRAC 1806; MRAC 1809-1811; MRAC 1823; MRAC 1828; MRAC 1839; MRAC 1852; MRAC 1854; MRAC 1895; MRAC 1870-1871; MRAC 1887; MRAC 1894	Dollo 1914; Swinton 1950; Jouve and Schwarz 2004
<i>Dyrosaurus maghribensis</i>	OCP DEK-GE 255; OCP DEK-GE 36, OCP DEK-GE 43, OCP DEK-GE 78, OCP DEK-GE 88, OCP DEK-GE 252, OCP DEK-GE 253, OCP DEK-GE 254, OCP DEK-GE 255, OCP DEK-GE 256, OCP DEK-GE 257, OCP DEK-GE 258, OCP DEK-GE 259, OCP DEK-GE 263, OCP DEK-GE 362, OCP DEK-GE 323, IRSNB R146	Jouve et al. 2006
<i>Dyrosaurus phosphaticus</i>	Uncatalogued; MNHN 1901-11; MNHN APH 27	Thomas 1893; Arambourg 1952; Jouve 2005
<i>Guarinisuchus munizi</i>	DG-CTG-UFPE 5723; CAV 0056-V; UFRPE 5142; CAV 0010-V; UFRPE 2814; CAV 0012-V; CAV 0011-V	Barbosa et al. 2008; Sena et al., 2017
<i>Hyposaurus derbianus</i>	BMNH R 8672	Cope 1886
<i>Hyposaurus paucidens</i>	Uncatalogued	Arambourg 1952
<i>Hyposaurus rogersii</i>	Uncatalogued; ALAM-PV 990.019; AUMP 1240; NJSM 10416; NJSM 10861; NJSM 12293; SC 83-78-10; YPM 380; YPM 753; YPM 985	Owen 1849; Troxell 1925; Denton et al. 1997
<i>Oceanosuchus boecensis</i>	MNH 9036	Hua et al. 2007
<i>Phosphatosaurus gavialoides</i>	MNH 1966-17; CNRST SUNY 275	Bergounioux 1955; Buffetaut 1979; Hill et al. 2008
<i>Sabinosuchus coahuilensis</i>	PAS 945-PAS 947; PAS 945-PAS 949; PAS 950 and PAS 951	Schiller II et al. 2016
<i>Tilemsisuchus lavocati</i>	MNH TGE 500	Buffetaut 1980

**Figure 3.** Illustrations from Figure 7, 8, 9, and 10 from Plate XI in Owen, 1849. (a) and (b) represent a last cervical and (c) and (d) is a third dorsal. (a) ventral view; (b) and (c) right lateral view; and, (d) anterior view. Scale: 10cm.

Hyposaurus rogersii Owen, 1849 (Figures 3–6)

Referred specimens

DGM 797-R; the last cervical vertebra (Figure 4); and DGM 805-R; two mandibular fragments, one corresponding to the anterior symphyseal region, and the second to a fragment of the posterior portion of the left dentary; two posterior cervical vertebrae; one fragmentary proximal portion of a long bone (tibia?); one fragmentary distal portion of a right humerus; two posterior caudal vertebrae; one posterior dorsal vertebra; and other non-identified fragmentary bones (Figure 4–6).

Description

The specimen DGM 805-R comprises bones of the lower jaw (Figure 4(a–c)). The most complete mandibular element is the anterior portion of a dentary bone, preserving the symphyseal region. The measurements of this element are in Table 3. There are eight alveoli preserved in each side of the mandible (Figure 4(a–b)). Their margins are at the same level in occlusal (Figure 4(a–b)) and lateral (Figure 4(c)) views. The third and fourth alveoli are close to each other and are similar in size (Figure 4(a–b)). The

seventh and eighth are also similar in size (Figure 4(a–b)) but the interalveolar space between them is large, about the same size of the eighth alveolus (Figure 4(a–b)). The ninth alveolus was not preserved itself, however it is possible to observe the interalveolar space between the eighth and ninth alveoli in the left side (Figure 4(a–c)). The space between these alveoli is even larger, greater than the size of the eighth alveolus (Figure 4(a–c)).

There is a preserved tooth in the seventh alveolus on the left side of the jaw, which is broken at its apex. On the other hand, there is a well-preserved tooth in the eighth alveolus on the right side (Figure 4a(d–e)), and a well-preserved tooth in the eighth alveoli on the left side. These teeth have curved crowns and show well-marked straight mesial and distal carinae (Figure 4(d–e)). The teeth show some parallel longitudinal ridges on the lingual and labial surfaces of the enamel, which are well-marked near the base and disappear near the apex (Figure 4(d–e)).

The external surface of the dentary is weakly ornamented with small and subcircular pits, mainly on its anterior portion (Figure 4(c)). The mandible is broken ventrally, at the interalveolar space between the fifth and sixth alveoli (Figure 4(c)). Therefore, this region shows a more accentuated ventral projection than the rest of the mandible in lateral view

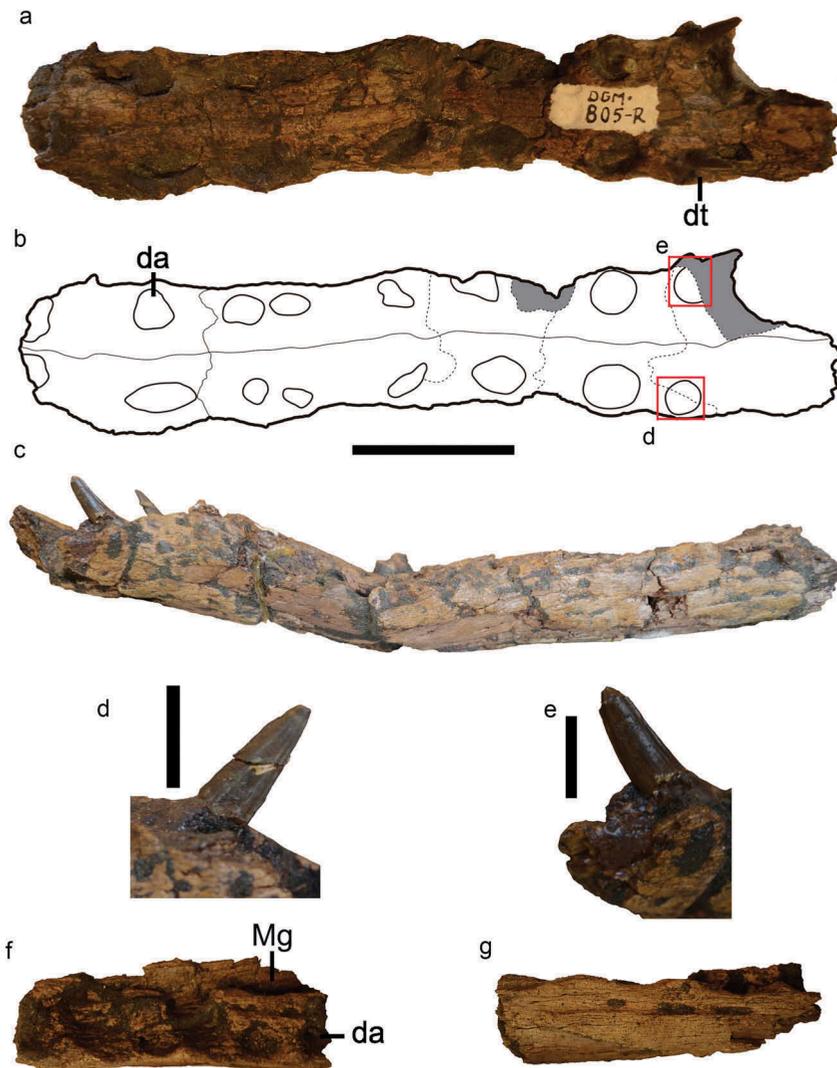


Figure 4. DGM 805-R, mandibular elements. (a) anterior symphyseal portion of mandible in occlusal view; (b) Line drawing of figure (a), the boxes represents the alveoli from which the figured teeth came from; (c) mandible in right lateral view; (d) left dentary tooth; (e) right dentary tooth; (f) second mandibular element in dorsal view; (f) abd (g) second mandibular element in dorsal and lateral view, respectively. For abbreviations, see text. Scale: (a), (b), (c), (f) and (g) 5cm; (d) and (e) 1cm.

(Figure 4(c)). The splenial and its symphysis were not preserved. The dentary symphysis extends for more than eight alveoli. In lateral view, both dorsal (i.e. occlusal) and ventral margins are straight. The anterior-most region of the dentary is rounded, with the first pair of alveoli procumbent. The height of the mandible in lateral view is smaller than its width, in dorsal view (see Jouve 2007).

The other jaw element corresponds to the left posterior ramus of the mandible (Figure 4(f–g)). This posterior portion is considered here as part of the first mandibular element, as both pieces were referred to the same specimen. There are six alveoli preserved. The first alveolus preserves only its posterior portion and the last alveolus preserves only its anterior portion. The three alveoli, posterior to the first one, are lacking their lingual margins. The penultimate alveolus is completely preserved. Considering the presence of the splenial bone, the diminutive interalveolar space, and the small size of the preserved alveoli (which decrease in size posteriorly), this element is here interpreted as the left

postsymphyseal portion of the mandible. In lateral view, there are two anteroposterior elongated foramina close to the alveolar margin. The internal wall of the Meckelian groove is preserved and can be observed in medial view.

DGM 805-R also comprises two cervical vertebrae. The first one corresponds to the eighth element of the cervical series (Figure 5(a–d)). It shows both neural arch peduncles. The right one is fully preserved, including the diapophyseal process and the prezygapophysis. The centrum is amphicoelous and almost cylindrical. In lateral view, the posterior region of the centrum has several missing parts. The amphicoelous centrum is thinner at its ventral region as it is lateromedially compressed at its medial portion (Figure 5(a)). The ventral margin of the centrum is convex (Figure 5(b)). The anterior and posterior articular fossae of the centrum are shallow and subcircular in shape (Figure 5(c–d)). The anterior facet of the centrum has a straight dorsal margin, it is subcircular in shape, and shows a dorsoventral compression (Figure 5(d)). The dorsal margin of the posterior facet is straight, but the compression is lateromedial, with the lateral

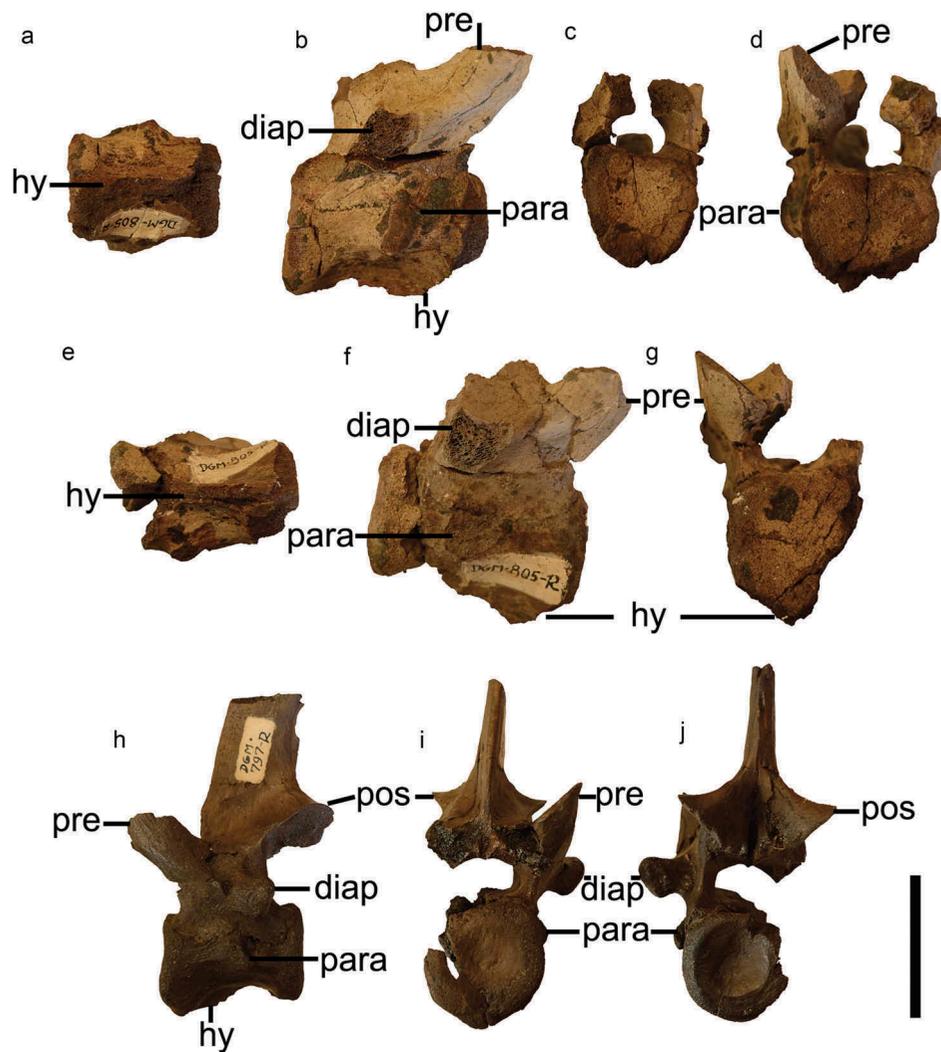


Figure 5. DGM 797-R (a), (b), (c) and (d) and DGM 805-R (e), (f), (g), (h), (i) and (j) cervical vertebrae. (a), (b), (c) and (d) represent a ninth cervical vertebra, while (e), (f) and (g) represent the eighth cervical vertebra and (h), (i) and (j) represents the ninth cervical vertebrae. (a) ventral view; (b) right lateral view; (c) posterior view; (d) anterior view; (e) ventral view; (f) right lateral view; (g) posterior view; (h) left lateral view; (i) anterior view; and (j) posterior view. For abbreviations, see text. Scale: 5cm.

margins converging medioventrally (Figure 5(c)). Despite being broken, the hypapophysis reaches the anterior margin of the centrum, but its posterior length cannot be inferred (Figure 5(a–d)). The neurocentral synchondrosis remains open and has a concavo-convex shape, with the concavity being dorsal (Figure 5(b)). This synchondrosis runs at the medial height of the centrum. The parapophysis is located at the medial portion of the centrum (Figure 5(b)). It is sub-circular and slightly dorsoventrally elongated, with its dorsal margins surpassing the neurocentral synchondrosis. The diapophysis is located dorsal and posterior to the parapophysis (Figure 5(b)). It is circular and its ventral margin is aligned with the dorsal surface of the centrum. Both parapophyseal and diapophyseal processes are short and laterally projected (Figure 5(d)). The prezygapophysis is anterodorsally inclined and exceeds the centrum anteriorly (Figure 5(b)). In anterior view, the prezygapophysis is more inclined dorsally, forming an acute angle with the medial axis of the vertebra (Figure 5(d)). There is a ridge connecting the lateral facet of the prezygapophysis with the anterior margin of the diapophyseal process (Figure 5(b)).

The second vertebra corresponds to the last cervical element (Figure 5(e–g)). It is missing the neural spine, both postzygapophyses, the hypapophysis, and the left peduncle of the neural arch, and only the right prezygapophysis is preserved. The anterior and posterior margins of the centrum are straight, in lateral view. The ventral surface of the centrum is concave in lateral view (Figure 5(f)). The anterior articulation has its external margins forming an inverted pentagon, whereas the posterior one has square-shaped external margins, with rounded corners (Figure 5(g)). The anterior and posterior articular fossae of the centrum are shallow and circular in shape. The hypapophysis reaches the anterior margin of the centrum but its posterior length cannot be inferred (Figure 5(e–f)). The neurocentral synchondrosis is concavo-convex, with its ventral portion located above the parapophyseal process (Figure 5(f)). Therefore, the neurocentral synchondrosis is ventral to the anterior and posterior dorsal margins of the centrum. The parapophyseal process is located near the ventral margin of the centrum and is slightly posterior to the medial portion but does not reach the posterior margin.

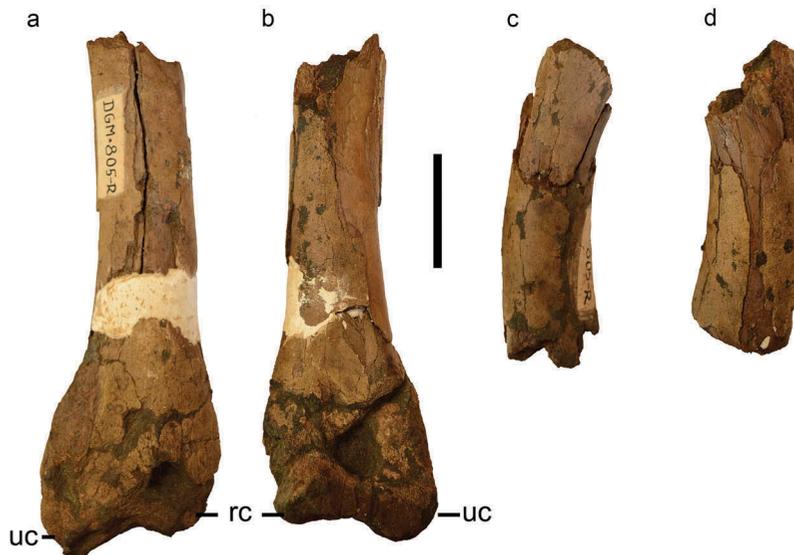


Figure 6. DGM 805-R long bone elements. (a) and (b) is a humerus in anterior and posterior view, respectively. (c) and (d) is a dubious long bone in anterior (?) and posterior (?) views, respectively. For abbreviations, see text. Scale: 5cm.

The process is slightly laterally projected and subcircular in shape as is the parapophysis. The diapophyseal process is located over the neurocentral synchondrosis and is slightly posterior to the parapophysis (Figure 5(f)). It projects slightly more laterally than the parapophyseal process and is subcircular in shape. The diapophyseal process has an anterior ridge that projects anterodorsally and reaches the lateral margin of the prezygapophyseal process. The prezygapophyseal process is inclined anterodorsally and extends anterior to the anterior margin of the centrum (Figure 5(f)). The prezygapophysis has an acute angle with the medial axis (Figure 5(f)).

DGM 797-R is the last vertebra of the cervical series. This vertebra is damaged on its right side, with a broken neural arch peduncle, and preserves only the postzygapophysis (Figure 5(h-i)). The right side of the centrum is also damaged and exposes the internal compact bone tissue at its medial portion. The anterior and posterior articular regions are relatively well-preserved (Figure 5(i-j)). The right parapophysis, diapophysis and hypapophysis, along with the dorsal half of the neural spine are missing (Figure 5(h-i)). The centrum is amphicoelian and gets thinner at its ventral region by being lateromedially compressed at its medial region. In lateral view, the ventral margin of the centrum, excluding the hypapophysis, is dorsally convex (Figure 5(h)). The anterior region of the centrum is taller than the posterior one (Figure 5(h)). The anterior and posterior articular fossae are circular in shape, the latter being shallower than the former (Figure 5(i-j)). Despite the hypapophysis not being preserved, it seems that it would range along the entire ventral surface of the centrum (Figure 5(h)). The neurocentral synchondrosis is open and visible in lateral view (Figure 5(h)). The anterior and posterior portions are more dorsal than the medial region, giving the synchondrosis a concavo-convex aspect in lateral view (Figure 5(h)). The neural arch peduncle is vertical in posterior view. The parapophysis is located at the medial region of the centrum, immediately ventral to the

Table 3. Mandibular height and width measured at each alveolar pair preserved in the most complete mandibular element of DGM 805-R. All measurements are in centimeters.

Alveolus	Height	Width
1	2.89	3.42
2	2.89	4.74
3	2.89	4.47
4	2.89	4.47
5	2.10	4.47
6	2.89	4.21
7	2.37	4.74
8	2.37	5.26

neurocentral synchondrosis (Figure 5(h)). The parapophyseal process is small and laterally displaced. The parapophysis has an elliptical outline with the anterior portion being more dorsal than the posterior one (Figure 5(h)). The diapophysis is above the neurocentral synchondrosis and slightly posterior to the parapophysis (Figure 5(h)). The diapophyseal process is lateroposteriorly displaced, being larger than the parapophyseal process (Figure 5(h)). The diapophysis is larger than the parapophysis, being elliptical, but more vertically aligned than the parapophysis (Figure 5(h)). The prezygapophyses and postzygapophyses exceed the anterior and posterior margins of the centrum, respectively (Figure 5(h)). The anterior margin of the prezygapophysis is dorsally positioned. The articular surfaces of both zygapophyses are displaced in relation to the neural spine by approximately 45° (Figure 5(i-j)). In dorsal view, the postzygapophyses point posteriorly. The dorsal margins of the prezygapophyses and postzygapophyses are anteroposteriorly aligned. There is a horizontal ridge that connects the posterior margin of the prezygapophysis with the anterior margin of the postzygapophysis (Figure 5(h)). The lateral surface of the prezygapophysis forms a posteroventral ridge connecting with the anterior margin of the diapophyseal process (Figure 5(h)). There is a concavo-convex ridge connecting the anterior margin of the postzygapophysis with the dorsal margin of the diapophyseal process

(Figure 5(h)). The anterior region, for the elastic ligament, is shallow and has half the height of the prezygapophyses, whereas the posterior region for the elastic ligament is deeper and has the same height as the postzygapophyses (Figure 5(i–j)). The neural spine is incomplete, but was likely three times taller than the centrum (Figure 5(h–j)). Its anteroposterior length extends from the posterior margin of the prezygapophyses to almost the posterior margin of the postzygapophyses. The neural spine is lateromedially compressed and is slightly curved posteriorly in lateral view (Figure 5(h)).

The posterior dorsal vertebra of DGM 805-R has only the amphicoelous centrum preserved. It is cylindrical and slightly compressed dorsoventrally. There is no hypapophysis and its ventral margin is concave. The anterior and posterior surfaces are subcircular and they present a shallow articular concavity.

There are two posterior caudal vertebrae of DGM 805-R, which have only the centra preserved. In both vertebrae, there are articulation facets for the chevrons. The centra are amphicoelous and compressed lateromedially in dorsal view. The anterior and posterior articular surfaces have squared external margins with rounded corners.

The right humerus of DGM 805-R corresponds to the proximal portion, with part of the shaft and the proximal epiphysis preserved (Figure 6(a–b)). The fractures in the fossil were filled using plaster. The distal end has a perforation visible in both anterior and posterior views (probably caused by pre-diagenetic events). The shaft has a sub-circular cross-section. The condyles are slightly displaced from their original position. The ulnar condyle is projected more distally than the radial condyle (Figure 6(a–b)). There is an antero-posterior constriction separating the condyles. In posterior view, there are no marked ridges. The proximal portion of the epiphysis of a long bone was also associated with DGM 805-R (Figure 6(c–d)). This bone has a concave surface on one side, which probably corresponds to the anterior surface, whereas the other one is convex. It is sub-circular in cross-section. The curvature preserved in this shaft resembles those observed in tibiae.

Some unidentifiable bones are also associated with DGM 805-R (see Figure 2). However, due to their fragmentary nature and absence of diagnostic information, no further descriptions and discussions will be provided.

Comparisons

The mandible of DGM 805-R has procumbent first alveoli (Figure 4(a–b)), as observed in *Cerrejonisuchus improcerus* (UF/IGM 30), *Dyrosaurus phosphaticus* (MNHN APH 27), *Guarinisuchus munizi* (CAV 0056-V), *Hyposaurus paucidens* and *Hyposaurus* sp. (specimens MNHN TGE 4320 and MNHN 1964-27 GE3, corresponding to morphotype 1 *sensu* Jouve 2007). Different morphologies are present in *Arambourgisuchus khouribgaensis* (OCP DEK–GE 18, OCP DEK–GE 1200, OCP DEK–GE 269), *H. rogersii* (YPM 380), *Sabinosuchus coahuilensis* (PAS 945–PAS 947 and PAS 945–PAS 949), *Tilemsisuchus lavocati*, *Rhabdognathus* sp. (MNHN TGE 3394, TGE 3395 and TGE 3331) and *Hyposaurus* sp. (MNHN TGE 4374 and MNHN 1964-27 GE3, corresponding to morphotype 2 *sensu* Jouve 2007), which show the first pair of alveoli dorsally directed.

The alveolar margins are at the same level of the occlusal surface of the mandible in DGM 805-R as well as in *Acherontisuchus guajiraensis* (UF/IGM 34, UF/IGM 35 and UF/IGM 36); *Guarinisuchus munizi* (CAV 0056-V and DG-CTG-UFPE 5723), *Hyposaurus derbianus*, *Oceanosuchus boecensis*, *Sabinosuchus coahuilensis* and *Hyposaurus* sp. (MNHN TGE 4374 MNHN 1964-27 GE3, corresponding to morphotype 2 *sensu* Jouve 2007). The alveolar margins are above the occlusal surface in *Cerrejonisuchus improcerus* (UF/IGM 30), *Congosaurus bequaerti*, *Dyrosaurus phosphaticus* (MNHN APH 27), *H. paucidens*, *H. rogersii* (YPM 380 and YPM 753), *Tilemsisuchus lavocati*, *Hyposaurus* sp. (MB R SUD 001a *sensu* Sallih et al. 2015), *Rhabdognathus* sp. (MNHN TGE 3394, TGE 3395 and TGE 3331), *Hyposaurus* sp. (MNHN TGE 4320 MNHN 1964-27 GE3, corresponding to morphotype 1 *sensu* Jouve 2007), and *Phosphatosaurus gavialoides* (CNRST SUNY 275).

In occlusal view, the lateral margins of the alveoli are straight in DGM 805-R (Figure 5(a–b)) and in *Arambourgisuchus khouribgaensis* (OCP DEK–GE 18, OCP DEK–GE 1200 and OCP DEK–GE 269), *Congosaurus compressus* (MNHN TGE 4034), *Congosaurus bequaerti*, *Dyrosaurus phosphaticus* (MNHN APH 27), *Guarinisuchus munizi* (CAV 0056-V and DG-CTG-UFPE 5723), *Oceanosuchus boecensis*, *Sabinosuchus coahuilensis*, *Tilemsisuchus lavocati*, *Hyposaurus* sp. (MB R SUD 001a *sensu* Sallih et al. 2015) and *Hyposaurus* sp. (MNHN TGE 4374 and MNHN 1964-27 GE3, corresponding to morphotype 2 *sensu* Jouve 2007). *Acherontisuchus guajiraensis* have irregular margins due to lateral projections of the alveoli in UF/IGM 34, while in UF/IGM 36 they get thinner anteriorly. *H. derbianus* and *H. paucidens* have concave lateral margins with lateral projections of the alveoli, and *Rhabdognathus* sp. (MNHN TGE 3394 and TGE 3395, TGE 3331) also has concave lateral margins. *Hyposaurus* sp. (MNHN TGE 4320 and MNHN 1964-27 GE3, corresponding to morphotype 1 *sensu* Jouve 2007) and *Phosphatosaurus gavialoides* (CNRST SUNY 275) has an anterior end that is laterally expanded at the level of the second dentary alveoli.

In lateral view, the occlusal surface is straight in DGM 805-R (Figure 4(c)), *Arambourgisuchus khouribgaensis* (OCP DEK–GE 18, OCP DEK–GE 1200 and OCP DEK–GE 269), *Congosaurus compressus* (MNHN TGE 4034), *C. bequaerti*, *Dyrosaurus phosphaticus* (MNHN APH 27), *Guarinisuchus munizi* (CAV 0056-V and DG-CTG-UFPE 5723), *Tilemsisuchus lavocati*, *Hyposaurus* sp. (MB R SUD 001a *sensu* Sallih et al. 2015), *Rhabdognathus* sp. (MNHN TGE 3394, TGE 3395 and TGE 3331), and *Hyposaurus* sp. (MNHN TGE 4374 and MNHN 1964-27 GE3, corresponding to morphotype 2 *sensu* Jouve 2007). The species *Acherontisuchus guajiraensis* (UF/IGM 36) and *Sabinosuchus coahuilensis* have mandibles that become thinner anteriorly at the occlusal surface of the anterior portion. *H. derbianus* has a concave occlusal surface, while the ventral region is convex. The species *H. paucidens* and *Hyposaurus* sp. (MNHN TGE 4320 and MNHN 1964-27 GE3, corresponding to morphotype 1 *sensu* Jouve 2007) have occlusal surfaces in which the anterior portion of the mandible (i.e. up to the fourth alveolus) is situated ventral to the rest of the dentary.

The dentary symphysis extends until the eighth alveolus in *Cerrejonisuchus improcerus* (UF/IGM 30), *Guarinisuchus munizi* (CAV 0056-V and DG-CTG-UFPE 5723) and *Hyposaurus paucidens*. They differ from DGM 805-R, *Acherontisuchus guajiraensis* (UF/IGM 34 and UF/IGM 35), *H. derbianus*, *H. rogersii* (YPM 380), *Oceanosuchus boecensis*, *Phosphatosaurus gavialoides*, *Sabinosuchus coahuilensis*, *Tilemsisuchus lavocati*, *Hyposaurus* sp. (MB R SUD 001a *sensu* Sallih et al. 2015), *Phosphatosaurus gavialoides* (CNRST SUNY 275), and *Rhabdognathus* sp. (MNHN TGE 3394, TGE 3395 and TGE 3331), which have dentary symphyses that extend posterior to the eighth alveolus.

The ratio between width and height for each alveolar pair is usually used as a morphometric tool used for distinguishing species and genera (e.g., Jouve 2007). This ratio determines only the degree of dorsoventral compression of the mandible, which does not necessarily imply a phylogenetic or diagnostic feature. DGM 805-R and the species *Arambourgisuchus khouribgaensis* (OCP DEK-GE 18, OCP DEK-GE 1200 and OCP DEK-GE 269), *Dyrosaurus phosphaticus* (MNHN APH 27), *Guarinisuchus munizi* (CAV 0056-V and DG-CTG-UFPE 5723), *Hyposaurus paucidens*, *Hyposaurus* sp. (MB R SUD 001a *sensu* Sallih et al. 2015), *Hyposaurus* sp. (MNHN TGE 4320 and MNHN 1964-27 GE3, corresponding to morphotype 1 *sensu* Jouve 2007) and *Hyposaurus* sp. (MNHN TGE 4374 and MNHN 1964-27 GE3, corresponding to morphotype 2 *sensu* Jouve 2007) have mandibles that are wider than they are high. This condition is opposed to what is observed in *Acherontisuchus guajiraensis* (UF/IGM 36), *Cerrejonisuchus improcerus* (UF/IGM 30), *Congosaurus compressus* (MNHM TGE 4034), *C. bequaerti*, *H. derbianus*, *Sabinosuchus coahuilensis*, *Tilemsisuchus lavocati*, and *Rhabdognathus* sp. (MNHN TGE 3394, TGE 3395 and TGE 3331), which have similar ratios for width to height.

The third and fourth alveoli are close to each other and are similar in size in DGM 805-R (Figure 4(a–b)), *Guarinisuchus munizi* (CAV 0056-V and DG-CTG-UFPE 5723), *Hyposaurus* sp. (MNHN TGE 4374 and MNHN 1964-27 GE3, corresponding to morphotype 2 *sensu* Jouve 2007), *H. rogersii* (YPM 380), *H. derbianus*, and *Rhabdognathus* sp. (MNHN TGE 3394, TGE 3395 and TGE 3331). This condition is opposed by the fourth alveolus being larger than the third as observed in *Cerrejonisuchus improcerus* (UF/IGM 30), *H. paucidens*, *H. rogersii* (NJSM 108601), *Hyposaurus* sp. (MNHN TGE 4320 and MNHN 1964-27 GE3, corresponding to morphotype 1 *sensu* Jouve 2007), and *Phosphatosaurus gavialoides* (CNRST SUNY 275).

In all studied specimens the seventh alveolus is smaller than the eighth alveoli. However, they are very similar in size in DGM 805-R (Figure 4(a–b)) and this could be consequence of a pathology where the ‘true’ seventh alveoli are closed and the two observed alveoli correspond to the eighth and ninth. This condition was recognized for other specimens such as NJSM 10891 (pers. commun. S. Jouve).

Regarding the dentition, DGM 805-R, *Arambourgisuchus khouribgaensis* (OCP DEK-GE 18, OCP DEK-GE 1200 and OCP DEK-GE 269) and *Hyposaurus derbianus* have teeth with curved crowns, well-marked carinae, and parallel longitudinal ridges. The species *Acherontisuchus guajiraensis* (UF/IGM 34) differs from them in having a less curved tooth crown.

The axial skeleton also shows important differences between dyrosaurid species. The eighth cervical vertebra of DGM 805-R presents the parapophysis anterior to the diapophysis, as in *Dyrosaurus maghribensis*, but differs from *Congosaurus bequaerti*, which has the parapophysis and diapophysis dorsoventrally aligned. The anterodorsally inclined parapophyseal process is similar in anterior extension to what is observed in *D. maghribensis* and differs from *C. bequaerti*, which has a less projected process that does not surpass the anterior margin of the centrum. The parapophyseal process in *D. maghribensis* is more horizontal.

DGM 797-R, DGM 805-R (i.e. last cervical vertebra), and *Hyposaurus rogersii* present a prezygapophyseal process inclined anterodorsally that surpasses the anterior margin of the centrum, therefore differing from the short prezygapophyseal process observed in *Congosaurus bequaerti* and *Dyrosaurus maghribensis*. The anterior margin of the centrum is taller than the posterior one in DGM 797-R and *H. rogersii*, which differs from *C. bequaerti* and *D. maghribensis*, which have the anterior and posterior margins similar in size. In DGM 797-R, the last cervical vertebra of DGM 805-R, *H. rogersii*, and *D. maghribensis* (specimen OCP DEK-GE 252) the hypapophysis runs from the anterior to the posterior margins of the centrum, but without reaching the posterior margin. On the other hand, in *C. bequaerti* and *D. maghribensis* the posterior margin of the hypapophysis reaches the medial portion of the centrum. The remaining observed vertebrae (i.e., the dorsal and caudal ones) do not differ in morphology from other vertebrae referred to Dyrosauridae.

The humerus, due its fragmentary state, can have only its distal portion compared with other species. However, in *Hyposaurus derbianus* the distal portion is also badly preserved, precluding its comparison with the new material. The lateral condyle is distally projected in relation to the medial one in DGM 805-R and in *H. rogersii* (YPM 985), which differs from the laterodistally projected lateral condyle of *Congosaurus bequaerti*.

Remarks

As Jouve (2007) previously commented about the importance and the need of a phylogenetic revision of *Hyposaurus* and its allies, we also suggest the inclusion of the characters discussed here in a future analyses. It is important to note that the differences between *Hyposaurus* morphotypes 1 and 2 proposed by Jouve (2007) could be the result of sexual dimorphism rather than phylogenetic variations. The presence of mandibular lateral expansions that are matched with premaxillary lateral expansions in longirostrine species is known as *Greifapparat* (Kálin 1933), and it has been proposed as a sexual dimorphic feature observed in species like *Gryposuchus croizati* and *Chalawan thailandicus* (Riff and Aguilera 2008; Martin et al. 2013).

DGM 797-R and DGM 805-R (last cervical vertebra) shares the difference in size of the anterior and posterior margins of the centrum and the long and anterodorsally inclined prezygapophyseal process.

The distal projection of the lateral condyle in the humerus seems to be a feature exclusively shared among *Hyposaurus* species. However, further dyrosaurids humeri material is needed to evaluate morphological variation of the distal epiphysis of this bone.

Hyposaurus cf. *Hyposaurus rogersii***Referred specimen**

DGM 799-R; third cervical vertebra (Figure 7).

Description

DGM 799-R is an anterior cervical vertebra, probably the third. The centrum is well-preserved, but the neural arch was almost completely lost, except for the right neural arch peduncle. The centrum is amphicoelous and almost cylindrical, with small foramina on the lateral surface between the parapophysis and diapophysis (Figure 7(b)). The anterior and posterior surfaces of the centrum are inclined posteriorly and anteriorly, respectively (Figure 7(b)). In this way, the dorsal surface of the centrum is shorter than the ventral one. The ventral surface of the centrum is concave (Figure 7(b)). The posterior articulation has its external margins forming an inverted heptagon (Figure 7(c)). The anterior centrum articulation has its external margins forming an inverted pentagon, with the dorsal and lateral margins straight (Figure 7(d)). The anterior and posterior articular fossae are circular in shape. The hypapophysis is a small protuberance located at the anterior portion of the ventral surface of the centrum, located between the left and right parapophyses (Figure 7(a)). There is a tenuous crest extending to the posterior margin of the ventral surface, posterior to the hypapophysis (Figure 7(a)). The neurocentral synchondrosis is straight anteriorly and posteriorly to the diapophyseal process and aligned with the dorsal margin of the centrum (Figure 7(b)). This synchondrosis follows the shape of the diapophyseal process at the medial portion of the vertebra, forming a convexity ventral to the process. The parapophyseal process is located near the ventral margin of the vertebra, as observed in lateral view (Figure b–d). Its position is slightly anterior to, but does not reach, the anterior margin of the centrum. The process itself is anteroposteriorly large but has the same height as the parapophysis. This latter bone process has an elliptical shape and is dorsoventrally compressed. The diapophyseal process is located over the neurocentral synchondrosis and is slightly posterior to the parapophysis (Figure 7(b–d)). It is formed dorsally by the lateral projection of the neural arch peduncle, while its ventral portion is composed by a lateral projection of the centrum. This dual composition of the diapophyseal process is evidenced by the neural arch synchondrosis crossing it (Figure 7(b)). The diapophyseal process projects slightly more laterally than the parapophyseal process. From the parapophyseal process there is a posterior ridge reaching the posterior margin of the centrum (Figure 7(b)). The diapophyseal process has a dorsal ridge that projects slightly anteriorly and reaches the posterior margin of the prezygapophysis (Figure 7(b)).

Comparisons

The prezygapophyseal process of DGM 799-R is anterodorsally inclined, exceeding anteriorly the anterior margin of the centrum. Also, it is positioned far from the neurocentral synchondrosis. Such features are shared with *Hyposaurus rogersii* (YPM 985) and *Guarinisuchus munizi* (DG-CTG-UFPE 5723), but differs from *Congosaurus bequaerti* (MRAC 1840), which shows a prezygapophyseal process that is more horizontal and closer to the neurocentral synchondrosis. The diapophyses are horizontal and have similar sizes as the parapophyses, as in *H. rogersii* (YPM 985), but differ from *C. bequaerti* (MRAC 1840), *G. munizi* (DG-CTG-UFPE 5723) and *Oceanosuchus boecensis* (MHNH 9036), which have diapophyses shorter than the parapophyses. In *C. bequaerti* (MRAC 1840) those structures are inclined in a dorsoventral fashion. DGM 799-R, *H. rogersii* (YPM 985) and *G. munizi* (DG-CTG-UFPE 5723) differ from *C. bequaerti* (MRAC 1840) and *O. boecensis* (MHNH 9036) in having a reduced hypapophysis on the third cervical vertebrae. The diapophyses are located below the dorsal level of the centrum with the neurocentral synchondrosis passing underneath this structure in DGM 799-R, *C. bequaerti* (MRAC 1840), *H. rogersii* (YPM 985) and *G. munizi* (DG-CTG-UFPE 5723), differing from *O. boecensis* (MHNH 9036), which has a diapophysis that is located above the dorsal level of the centrum. The designation of DGM 799-R as *Hyposaurus rogersii* (YPM 985) is plausible but must be seen with caution, because this species is the only *Hyposaurus* specimen to have direct comparable material.

Remarks

Based on comparisons with other species, the following features could be considered potentially diagnostic for *Hyposaurus rogersii*, or at least exclusively shared among *Hyposaurus* species: 1) the prezygapophyseal processes of the third cervical vertebra are anterodorsally inclined and positioned far from the neurocentral synchondrosis; 2) the diapophyses are horizontal and are similar in size to the parapophyses.

Hyposaurus sp.

[non] *Hyposaurus* sp. sensu Jouve 2007 (morphotype 1 specimens: MNHN TGE 4320 and MNHN 1964-27 GE3; morphotype 2 specimens: MNHN TGE 4374 and MNHN 1964-27 GE3).

[non] *Hyposaurus* sp. sensu Sallih et al. 2015 (specimen: MB R SUD 001a).

Referred specimen

DGM 803-R; one proximal portion of a left femur (Figure 8).

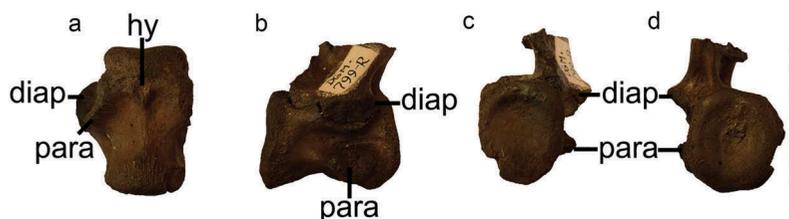


Figure 7. DGM 799-R, a third cervical vertebra. (a) ventral view; (b) left lateral view; (c) posterior view; and, (d) anterior view. For abbreviations, see text. Scale: 5cm.

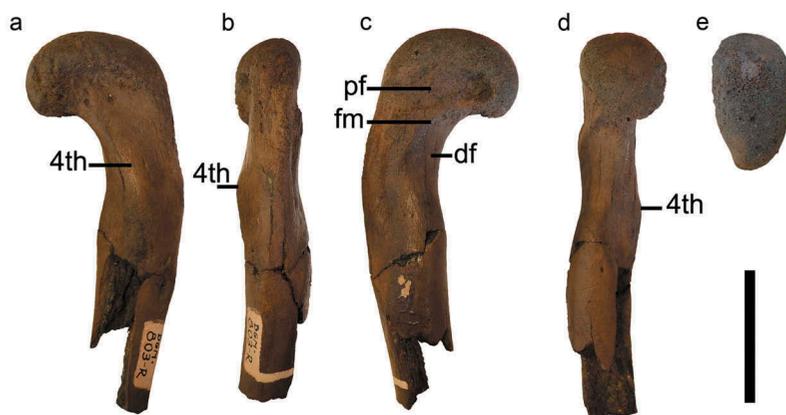


Figure 8. DGM 803-R, left femur. (a) posterior view; (b) lateral view; (c) anterior view; (d) medial view; and, (e) proximal view. For abbreviations, see text. Scale: 5cm.

Description

The specimen DGM 803-R comprises a left femur. It corresponds to the proximal epiphysis of the bone, including part of the diaphysis (Figure 8). There are some irregular fractures on its preserved distal portion. The fractures expose the medullary canal that shows expanded walls of thick external compact bone, which is thicker than the internal layer. There is spongy bone tissue between the compact bone layers. The femur is slightly sigmoidal, as observed in anterior and posterior views (Figure 8(a–c)). The femoral head is inclined medially, with the lateral margin straight and the medial margin convex (Figure 8(c)). The articular surface of the femoral head is concave, with a medial portion that is more distally directed than the lateral portion (Figure 8(e)). The ventral margin of the articular surface of the femoral head is convex in both anterior and posterior views (Figure 8(a–c)). In medial and lateral views, the femoral head is aligned with the shaft. In proximal view, it shows an irregular subcircular outline with the medial surface anteroposteriorly wider than the lateral one. The diaphysis is directed medially in anterior and posterior views. The cross-section of the shaft is subcircular, being anteroposteriorly compressed. The fourth trochanter is well-developed and elongated proximodistally in posterior view (Figure 8(a–b)). It is medially displaced and extends from the ventral end of the medial convexity to the proximal portion of the shaft. Like the fourth trochanter, there is a femoral ridge ranging from the femoral head to the proximal portion of the shaft in anterior view (Figure 8(c)). This ridge delimits two fossae: one proximal (proximal fossa; Figure 8(c)) and another one that is medially and distally located (distal fossa; Figure 8(c)). The proximal boundary of the proximal fossa is delimited by the distal portion of the femoral articulation. There are small foramina at the proximal portion of the shaft, which can be observed in medial view.

Comparison

Regarding the femoral anatomy, the specimen DGM 803-R has a femoral head with convex distal end in both anterior and posterior views, as observed in *Hyposaurus paucidens* and *H. rogersii*. Such morphology differs from that of *Acherontisuchus guajiraensis* (UF/IGM 39), which has a straight surface, and also from *Congosaurus bequaerti* and *Guarinisuchus* cf. *Guarinisuchus munizi* (CAV 0010-V), which have lateral portions of the distal ends that are straight and mediolaterally

inclined. All compared specimens have fossae near the articular surfaces of their femoral heads, in anterior view.

Remarks

A feature exclusively shared among *Hyposaurus* species is the convex end of the proximal epiphysis in both anterior and posterior views. This exclusive feature strengthens the assignment of CAV 0010-V to *Guarinisuchus* by differing it from the expected morphological pattern of *Hyposaurus*.

DYROSAURIDAE indet.

Referred specimens

second dorsal vertebra (DGM 804-R; Figure 9(a–c)); one middle to posterior dorsal vertebra (DGM 798-R; Figure 9(d–f)); one middle to posterior dorsal vertebra (DGM 801-R; Figure 9(g–i)); anterior caudal vertebra (DGM 800-R; Figure 9(j–m)); and one middle to posterior caudal vertebra (DGM 801-R; Figure 9(n–q)).

Description

The specimen DGM 804-R comprises one anterior dorsal vertebra, probably the second element in the dorsal segment of the vertebral column (Figure 9(a–c)). The dorsal portion of the neural spine is broken. Both postzygapophyses and diapophyses are lost. The amphicoelus centrum is lateromedially thinner at its ventral region because it is more compressed at its medial region. The ventral margin of the centrum, excluding the hypapophysis, is convex dorsally in lateral view (Figure 9(c)). The anterior region of the centrum is taller than the posterior one (Figure 9(c)). The anterior and posterior articular fossae of the centrum are subcircular, and dorsoventrally compressed (Figure 9(a–b)). The hypapophysis starts close to the anterior margin and ends shortly after the parapophyses, not reaching the posterior margin of the vertebra (Figure 9(c)). The neurocentral synchondrosis is almost fully-closed but still visible mainly at the posterior surface, as observed in lateral view (Figure 9(c)). The synchondrosis is linear all along the centrum, being more dorsally placed at the anterior and posterior ends (Figure 9(c)). The neural arch peduncles slope laterally. The parapophysis is located over the

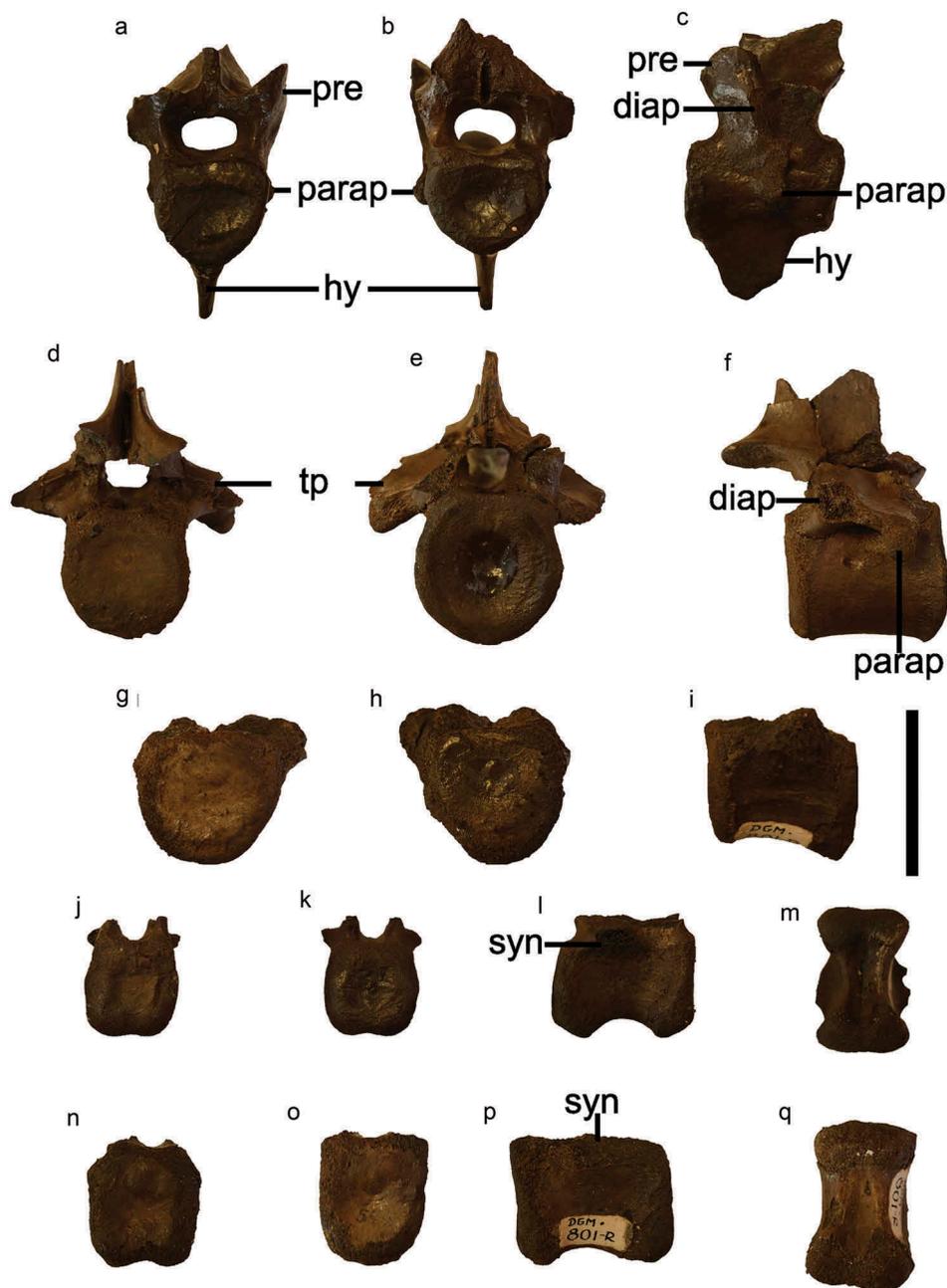


Figure 9. *Dyrosauridae* indet. specimens. (a), (b) and (c) DGM 804-R second dorsal vertebra in anterior, posterior, left lateral and ventral views; (d), (e) and (f) DGM 798-R, middle to posterior dorsal vertebra in anterior, posterior and left lateral view, respectively; (g), (h), and (i) DGM 801-R, middle to posterior dorsal vertebra in anterior, posterior, right lateral and ventral view, respectively; (j), (k), (l) and (m) DGM 801-R, middle caudal vertebra in anterior, posterior, left lateral and ventral views, respectively; and, (n), (o), (p) and (q) DGM 800-R, anterior caudal vertebra in posterior, anterior and right lateral view, respectively. For abbreviations, see text. Scale: 5cm.

neurocentral synchondrosis, aligned with the medial axis of the neural spine (Figure 9(c)). The parapophyseal process is laterally directed but extremely reduced. The parapophysis is elliptical in shape, being anteroposteriorly compressed (Figure 9(c)). The prezygapophyses do not surpass anteriorly the anterior margin of the centrum, and they are almost vertical in lateral view (Figure 9(c)). In anterior view, its articular surface is acutely displaced in relation to the neural spine, forming an angle of ca. 45° (Figure 9(a)). The lateral surface of the prezygapophysis forms a posteroventral ridge connecting with the dorsal margin of the parapophyseal process (Figure 9(c)). The anterior area for the elastic ligament is

shallow and has half the height of the prezygapophysis, while the posterior area for the elastic ligament is deeper (Figure 9(a–b)). The anteroposterior length of the neural spine extends from the medial portion of the prezygapophyses to almost the posterior margin of the centrum. The neural spine is lateromedially compressed and, in lateral view, is slightly curved posteriorly (Figure 9(c)).

The specimen DGM 798-R is an amphicoelous middle to posterior dorsal vertebra (Figure 9(d–f)). The centrum is well-preserved, but the neural arch is missing both prezygapophyses, the dorsal half of the neural spine, and the lateral extremities of the transverse processes. Only the right

parapophysis is preserved on the vertebral centrum, thus both diapophyses are missing (Figure 9(d–f)). The anterior region of the centrum is as tall as the posterior one (Figure 9(f)). The anterior and posterior articular fossae of the centrum are concave and have a circular shape, but the anterior is shallower than the posterior one (Figure 9(d–e)). The centrum does not present any lateromedial compression, with a generally cylindrical shape. There is a small medial foramen below the transverse process on each lateral surface (Figure 9(f)). There are no developed hypapophyses or crests on the ventral surface of the centrum. Its outline is straight in lateral view. The neurocentral synchondrosis is open. It shows an undulated line in lateral view, with the anterior and posterior portions placed more dorsally. The synchondrosis runs immediately below the transverse process (Figure 9(f)). The transverse process is wide and has almost the same in size as the centrum, being ventrally directed at its lateral portions. The anterior portion, which corresponds to the parapophyseal process, is ventral relative to the posterior one, i.e., the diapophyseal process. Therefore, the morphology of the transverse process assumes an anteriorly-inclined configuration (Figure 9(f)). The parapophysis is rounded and placed below the neurocentral synchondrosis. The postzygapophyses surpass the posterior margin of the centrum posteriorly. The articular surface is visible in lateral view. It is displaced in relation to the neural spine by approximately 15°. The orientation of the postzygapophyses is visible in dorsal view. They are posteriorly directed. There is a well-developed and almost horizontal ridge connecting the posterior margin of the transverse process to the anterior margin of the postzygapophysis (Figure 9(f)). The posterior area for the elastic ligament is deep and almost twice as tall as the postzygapophyses (Figure 9(d–e)). The total height of the neural spine and its anteroposterior length are unknown due to missing parts. However, it is lateromedially compressed and apparently is dorsally oriented in lateral view.

DGM 801-R comprises two amphicoelous vertebrae (Figure 9(g–i, n–q)); one is a middle to posterior dorsal vertebra and the other is a middle caudal vertebra. The centrum of the dorsal vertebra is cylindrical with the dorsal surface lateromedially expanded, therefore the articulation surfaces with the neural arch peduncles are also expanded (Figure 9(g–i)). The anterior articulation has rounded external margins with a straight dorsal margin (Figure 9(g)). The external margins of the posterior articulation form an inverted pentagon with rounded corners and straight dorsal and lateral margins (Figure 9(h)). The anterior articular fossa is shallow while the posterior articular fossa is markedly concave and circular in shape. There is no ventral keel or hypapophysis. In lateral view, the ventral margin is concave (Figure 9(i)).

DGM 800-R is an anterior caudal vertebra, which presents a closed neurocentral synchondrosis between the well-preserved centrum and the neural arch peduncles (Figure 9(j–m)). The proximal portion of the caudal ribs are preserved and are fused with the vertebra (Figure 9(l)). The amphicoelous centrum has a well-marked ventral concavity in lateral view, with the anterior and posterior margins aligned (Figure 9(l)). A B-shaped rugose surface can be seen in ventral view,

delimiting the anterior and posterior margins for the articulation with the haemal arches (Figure 9(m)). The ventral surface has its medial portions mediolaterally compressed (Figure 9(m)). There is a deep sulcus delimited by two parallel crests at the ventral surface of the centrum (Figure 9(m)). Both anterior and posterior articulation surfaces of the centrum are quadrangular in external shape, with their margins almost straight (Figure 9(n–o)). The only exception is the ventral margin, which presents a ventral concavity in its medial portion (Figure 9(n–o)). The anterior and posterior cotyles are circular in shape (Figure 9(n–o)). The caudal ribs are anteroposteriorly short and dorsoventrally compressed. They are located on the posterior region of the neurocentral synchondrosis.

The caudal vertebra of DGM 801-R is cylindrical but compressed lateromedially. In lateral view, the dorsal margin is straight and the ventral margin is concave (Figure 9(n–q)). The anterior and posterior articulations are dorsoventrally straight and have their ventral limits aligned anteroposteriorly (Figure 9(n–o)). The external margins of the anterior surface are quadrangular, with a rounded ventral margin (Figure 9(o)). The external margins of the posterior surface are straight and forms a hexagonal outline, with a concave ventral surface (Figure 9(n)). The anterior articular fossa is shallow while the posterior articular fossa is more concave (Figure 9(n–o)).

Comparison

The anterior dorsal vertebra of DGM 804-R, which is probably the second element in the dorsal segment of the vertebral column, have an almost vertical prezygapophyseal process. This bony element does not surpass anteriorly the anterior margin of the centrum, as opposed to what is observed in *Congosaurus bequaerti* and *Dyrosaurus maghribensis*. Also, its hypapophysis does not reach the anterior margin of the centrum, as in *C. bequaerti* and *D. maghribensis*. However, this structure is in a slightly anterior position when compared with the previous species.

The dorsal vertebrae of DGM 798-R and DGM 801-R are similar in morphology to *Carrejonisuchus improcerus* (UF/IGM 31), *Congosaurus bequaerti*, *Dyrosaurus maghribensis*, *Hyposaurus derbianus*, *H. paucidens* and *H. rogersii*. Those species differ from *Acherontisuchus guajiraensis* (UF/IGM 37). This latter taxon has a vertebra that is more lateromedially compressed at its medial portion, in ventral view. In addition, the ventral margin of the posterior region of its centrum is in a more ventral than anterior position.

The general morphology of the caudal vertebrae of the specimens DGM 800-R and DGM 801-R are remarkably similar to those observed in *Anthracosuchus balrogus* (UF/IGM 68), *Congosaurus bequaerti*, *Dyrosaurus maghribensis*, *Guarinisuchus munizi*, *Hyposaurus derbianus*, *H. paucidens* and *H. rogersii*.

Remarks

The almost vertical prezygapophyseal process observed in DGM 804-R is, for now, a feature exclusive to this specimen. However, further studies on postcranial bones of Dyrosauridae are necessary to better understand those morphological differences. Regarding the specimens represented

by dorsal and caudal vertebrae, no differences among species were identified. However, this does not necessarily imply the absence of morphological variation among them, due to the absence of more complete dorsal and caudal vertebral series, as well as the preservation of further comparable regions of the studied material. Therefore, further studies of the morphology of each dorsal and caudal vertebra must be made. These vertebrae cannot be treated as one evolutionary unit but must be treated individually to understand significant variation in homologous structures throughout the series.

Discussion and conclusion

The original description of *Hyposaurus rogersii* made by Owen (1849) emphasized the exclusive well-developed hypapophysis that extends along the ventral surface of the centrum. Parris (1986) and Denton et al. (1997) argued that despite the fact that postcranial material is undiagnostic (as suggested by Norell and Storrs 1989, see discussion below) the characteristic hypapophysis is enough to identify new referred materials, and also that the other *Hyposaurus* species described for North America must be synonymized because they do not present any unique features differentiating them from the holotype of *H. rogersii*. The results presented here agree with the synonymization defended by Parris (1986). We propose that the ‘characteristic hypapophysis’ of the holotype of *H. rogersii* is not a diagnostic feature that can support the taxonomic validity of the species but is distinguishable enough to enable the assignment of the new specimens from the same geological formation (e.g., Troxell 1925; Denton et al. 1997) to *H. rogersii*.

Norell and Storrs (1989) argue that the postcranial bones of dyrosaurid are undiagnostic. However, the present work demonstrates that this is not the case. Some interesting features are present in the postcranial skeleton, which with more future works and new specimens could be recognized as key features to identify isolated postcranial bones. Despite some efforts in describing dyrosaurids postcranial elements (e.g., Langston 1995; Schwarz et al. 2006), descriptive works like the present one are still necessary and helps to elucidate the intraspecific variation in those species with more than one specimen described. Some of the postcranial features discussed here could be recognized as diagnostic for some species or groups of species by future work, for example: the proximal end of the femoral head is convex in both anterior and posterior views (*Hyposaurus*); the prezygapophyseal process is anterodorsally inclined and is positioned far from the neurocentral synchondrosis in the third cervical vertebra (*Hyposaurus* but potentially exclusive for *H. rogersii*); the diapophyses are horizontal and have similar size to the parapophyses (*Hyposaurus* but potentially exclusive for *H. rogersii*); the lateral condyle is distally projected in relation to the medial condyle in the humerus (*Hyposaurus* but potentially exclusive for *H. rogersii*).

Hyposaurus rogersii could be considered as *nomen dubium* due a lack of diagnostic features, however the designation of a more complete specimen (e.g. NJSJ 23368) as neotype can prevent this situation. The description of new materials and comparisons with known dyrosaurids support some of the

postcranial features as potentially useful for phylogenetic systematics. The inclusion of the characters discussed here in future phylogenetic works is suggested. The results improve the identification of isolated postcranial bones of dyrosaurids. The proper identification of such specimens along the North Atlantic Sea also provides important information for the systematics and biogeography of the group and its relationship with gondwanan species, such as *Hyposaurus derbianus* and *Guarinisuchus munizi*, during the Cretaceous–Paleogene times.

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