First record of chimaeroid fish *Ischyodus* from the Upper Jurassic of southwestern Gondwana

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This study presents two specimens of Chimaeriformes from Upper Jurassic strata of central Chile. The material was recovered from Tithonian levels of the Baños del Flaco Formation and includes two different individuals, one preserving two articulated mandibular plates, and the second, a fragment of an isolated palatine plate. Morphologic traits allow us to refer the material to *Ischyodus townsendi* and *Ischyodus* sp., respectively. These are the oldest Chimaeriformes known to date in the Southern Hemisphere and the first Late Jurassic record from Gondwana. The presence of *I. townsendi* in the Tithonian of central Chile evidences this taxon as part of the proposed faunal interchange between the northern Tethys and the southeastern Pacific during the Late Jurassic.

Key words: Chondrichthyes, Holocephali, Callorhinchidae, cartilaginous fishes, paleobiogeography, Mesozoic, Jurassic, Tithonian.

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Introduction

Chimaeriformes (Chondrichthyes, Holocephali) is a clade of cartilaginous fishes that appeared in the fossil record during the Paleozoic, reaching a high diversity during the Mesozoic and onwards (López-Arbarello et al. 2008). During the Jurassic, the group is well-recorded in the Northern Hemisphere and represented by several genera and species (López-Arbarello 2004; López-Arbarello et al. 2008). The oldest austral fossil Chimaeriformes are known from the Lower Cretaceous of Australia (represented by the *Ischyodus* Egerton, 1843 and *Pyctoptychion* Lees, 1986), becoming abundant during the Upper Cretaceous with records in New Zealand, South America, and Antarctica (e.g., Otero et al. 2013a, b). Then, during the Cenozoic, Chimaeriformes have been recorded globally (Stahl 1999). However, prior to the Cretaceous, there are no records of this clade along the Southern Hemisphere. This contribution presents the oldest Chimaeriformes known to date in the Southern Hemisphere and the first Upper Jurassic record from Gondwana. The material consists of two specimens which preserve enough diagnostic features for a taxonomic identification, being identified as *Ischyodus townsendi* (Buckland, 1835), while the second specimen is referred to as *Ischyodus* sp. The coeval occurrence of *I. townsendi* during the Tithonian in the northern Tethys, and now in southwestern Gondwana, is discussed here.

Institutional abbreviations.—MHNC, Museo de Historia Natural de Concepción, Chile; MJSN, Jurassica Museum (formerly Musée Jurassien des Sciences Naturelles), Porrentruy, Switzerland; NHMUK, Natural History Museum, London, UK.

Geological setting

The studied material was recovered in the facilities of Mina Del Fierro (Del Fierro Mine), owned by Minera Río Teno S.A., located in the Cajón del Fierro locality, High Andes, west of Curicó city, Región del Maule, Chile (Fig. 1). Rocks cropping out in this area belong to the Baños del Flaco Formation (Klohn 1960). This sedimentary unit overlies the Río Damas Formation through a concordant contact. The Baños del Flaco Formation is overlain through a discordant contact by a volcanoclastic sequence known as the Brownish-Red Clastic Unit (BRCU; Charrier et al. 1996; Salazar 2012), and through a concordant contact with the Colimapu Formation. The Baños de Flaco Formation was recently divided in two formal units, the Lower and the Upper Member (Salazar 2012). The unit comprises limestone, sandy limestone, and calcareous sandstone mostly grey-colored, with occasional glauconitic sandstone, limestone, and conglomerate. Salazar (2012) estimated thickness of 369 m in the studied locality.

The age of the Baños del Flaco has been debated over the years. In this sense, the abundant and diverse fauna of marine invertebrates (including ammonoids, belemnoids, bivalves, gastropods, scaphopods, echinoderms, bryozoans, porifera, foraminifera, algae, cyanobacteriae, and ichnofossils) present in the Baños del Flaco Formation was useful for increasing the precision of its age. Firstly, Klohn (1960) assigned a lower Valanginian–Hauterivian age, based on marine molluscs (mostly ammonoids) present in different outcrops of the unit. After, Covacevich et al. (1976) referred it to the lower Tithonian–Hauterivian? based on the invertebrate assemblage. Later, in more comprehensive studies, Salazar (2012) and Salazar and Stinnesbeck (2015) constrained the age of the unit to the lower middle Tithonian–lowermost Berriasian interval, based on the biostratigraphy of ammonoids.

For the Cajón del Fierro locality, Klohn (1960) described outcrops of Baños del Flaco Formation as fossiliferous marine sediments with N8E/30W strike and dip strike, being represented by a thick succession of limestone and marl with intercalated cross-bedded calcareous sandstone, and



Fig. 1. A. Map indicating location of the studied area in central Chile. B. Enlarged map of Mina Del Fierro area where the material was collected.

conglomerate levels, both concordantly overlying to breccias and conglomerates with andesitic clasts from the Río Damas Formation. Particularly, in the studied locality, Maldonado (2016) described the basal part of the Lower Member of Baños del Flaco Formation, conformed by conglomerate, conglomeratic limestone, sandy limestone, calcareous sandstone, intercalated tuff, calcirudite, and calcareous shale. For this section, the fossil content is abundant (Quinzio and Varela 2015), being present in most levels of the section and comprising bioturbation and marine invertebrates (ammonoids, belemnoids, gastropods, inoceramids, nautiloids, and trigoniids) all of which indicate a Tithonian age. The nature of this assemblage, in addition to the stratigraphic section described by Quinzio and Varela (2015), allows to assess the stratigraphic position of the two vertebrate specimens studied here. These are detailed in Fig. 2. Both specimens were recovered from upper levels of the Lower Member of the Baños del Flaco Formation, thus, having a Tithonian age.

Material and methods

The material is included in a single sandstone block with two articulated mandibular plates; no other skeletal portions were found nearby. This specimen was discovered in 2019 by personnel of Mina Del Fierro as part of a monitoring policy for mitigation of the mining operation, following the Chilean heritage law. Therefore, as the fossil-bearing geologic unit (Baños del Flaco Formation) is known to host frequent marine invertebrates, the area was the subject of a periodic paleontological survey, as requested by the local Chilean heritage authority (Consejo de Monumentos Nacionales) which was carried out under a paleontological excavation permit of the Chilean authority for one of the authors (CFB; Ord. CMN N° 2275/17).



Fig. 2. Stratigraphic section of the levels were the studied material was recovered. Modified from Quinzio and Varela (2015).

The site of the finding was firstly inspected by two of the authors (SFC and PSH) during the paleontological survey of the mining activities, recognizing the stratigraphic provenance of the material. The block was originally removed from its natural occurrence by mine blasting, together with several large blocks of calcareous rocks.

Among the rescued material, a single sandstone block was recovered, originally showing a partial broken dental plate and part of a second, likely complete and articulated plate. The articulated plates were later prepared by one of the authors (RAO) during December 2019 and January 2020 in facilities of the Red Paleontológica U-Chile, Laboratorio de Ontogenia y Filogenia, Departamento de Biología, Universidad de Chile (Santiago, Chile). The extraction of the sediment was carried out with a 9100 air scribe, while the fragile specimen was consolidated with Paraloid B-76 using different concentrations, and cyanoacrylate for bonding. The second isolated plate was not prepared, and it is shown in its natural occurrence, which is enough for its anatomical interpretation. After, both specimens were included in the formal repository of the Museo de Historia Natural de Concepción, together with the rest of the fossil invertebrate collection from the studied locality.

The studied material was compared with Late Jurassic species within the *Ischyodus*, based on literature review. The anatomical terminology used here follows Popov and Machalski (2014), adding an anatomical topology (plm, prominence of the labial margin) discussed in the diagnosis of the *Ischyodus* by Stahl (1999).

Systematic palaeontology

Chimaeroidei Patterson, 1965

Callorhinchidae Garman, 1901

Callorhinchinae Stahl, 1999

Genus Ischyodus Egerton, 1843

Type species: Chimaera townsendi Buckland, 1835; Tithonian of England.

Ischyodus townsendi (Buckland, 1835)

Fig. 3A.

Material.—MHNC.35.444, two articulated mandibular plates from Mina Del Fierro, Andes Cordillera, Región del Maule, Chile; Baños del Flaco Formation, Tithonian (Upper Jurassic).

Description.—Both plates are visible in basal view (Fig. 3A). The mandibular plates remain articulated in nearly anatomical position. The right mandibular plate is the most damaged by diagenesis or transport, with the basal surface lost and a few tritors broken, being exposed in different sections. This preservation allows us to observe the tritor distribution. Its posterior occlusal surface is preserved as a thin bone layer attached to the matrix, which is why this was not removed. The preserved surface indicates a sudden mechanical break-up, judging by the fresh bone exposed. This is consistent with damage derived from rock blasting, discarding erosive agents. On the broken surface (basal view) it can be recognized a larger tritor pad placed medially, and therefore, being identified as the median tri-



Fig. 3. Chimaeroid fishes from Mina Del Fierro, Andes Cordillera, Región del Maule, Chile; Baños del Flaco Formation, Tithonian (Upper Jurassic). A. *Ischyodus townsendi* (Buckland, 1835) (MHNC.35.444); two articulated mandibular plates in basal view. B. *Ischyodus* sp. (MHNC.35.445); ventral view of the bony contour of a right palatine attached to the matrix, preserving the occlusal surface of the tritors. Abbreviations: ait, anterior inner tritor; aot, anterior outer tritor; bk, beak; lm, left mandibular; mt, median tritor; out, outer tritor; pit, posterior inner tritor; plm, prominence of the labial margin; pot, posterior outer tritor; r, ridges; rm, right mandibular; syt, symphyseal tritor. Photographs (A₁, B₁), schematic illustrations (A₂, B₂).

tor which covers two-thirds of the plate width. A cylindrical tritor, identified as the posterior outer tritor (pot), flanks labially to the median tritor (mt). Over the labial margin of each plate there is a prominence. The broken right mandibular plate shows the anterior outer tritor (aot) near to this prominence. The left mandibular shows two marked ridges (r) over the basal surface, which reflect the internal position of the symphyseal tritor (syt) of laminated pleromin and the median tritor, respectively. On its basal margin, the symphyseal tritor is broken, leaving a cavity. The median tritor is visible, it is also partially broken, but prominent. Flanking the latter, there is a posterior exposure of the posterior outer tritor. The beak (bk) is preserved in both plates, being prominent and slightly recurved laterally. Its anteriormost tip is worn. Measurements of both specimens are provided on Table 1.

Remarks.—MHNC.35.444 can be referred to the genus *Ischyodus* based on the possession of mandibular plates with a large central median tritor flanked by a short anterior outer tritor, an elongate posterior outer tritor, and the existence of a symphyseal tritor of laminated pleromin at the mesial tip of the tooth plate (Stahl 1999; Popov and Machalski 2014). The occurrence of two small tritors exposed at the prominence on the wavy labial margin of the mandibular plate has been considered as another diagnostic feature of the genus (Stahl 1999: 131); however,

Table 1. Measurements (in mm) of the two studied specimens. Mesiodistal length definition follows Popov and Machalski (2014).

Taxon	Specimen number	Plate	Mesiodistal length
Ischyodus townsendi	MHNC.35.444	left mandibular	995
Ischyodus sp.	MHNC.35.444	right mandibular	102
	MHNC.35.445	right palatine	721

this feature is not present in the holotype of *Ischyodus townsendi*, which only has a single tritor (anterior outer) in this position. Nevertheless, the absence of a second tritor is related to the wearing suffered in larger/old mandibular plates, being instead a consequence of the ontogeny rather than being a diagnostic value (Ward and Grande 1991; Popov and Machalski 2014).

Stratigraphic and geographic.—Baños del Flaco Formation, Tithonian (Upper Jurassic). Mina Del Fierro, Andes Cordillera, Región del Maule, Chile.

Ischyodus sp.

Fig. 3B.

Material.—MHNC.35.445, an isolated, fragmentary right palatine plate from Mina Del Fierro, Andes Cordillera, Región del Maule, Chile; Baños del Flaco Formation, Tithonian (Upper Jurassic).

Description.—MHNC.35.445 is an isolated and poorly preserved palatine plate attached to the matrix. The basal surface is lost, allowing us to see the internal part of the tritors. The labial and symphyseal contour are preserved as a cast in the sandstone matrix, allowing us to observe the triangular shape of the plate. The posterior inner tritor is suboval and it is the larger tritor in the plate. The labial margin shows three aligned tritors, identified as fragments of the median tritor, the outer tritor, and the anterior inner tritor.

Remarks.—MHNC.35.445 possesses a large, oval posterior inner tritor, a median tritor likely smaller, an outer tritor axially elongated, and an anterior inner tritor slightly rounded. These features are present in different species of the *Ischyodus* (Stahl 1999: fig. 138A, C; Popov and Machalski 2014: fig. 4D1). The incompleteness of this mandibular plate precludes a more specific identification.

Discussion

Late Jurassic records of Ischyodus and comparison with the studied specimen.—Twenty-two nominal species within Ischyodus have been described from the Jurassic of Europe, with eight species known in the Tithonian (Table 2). However, more recent reviews (Stahl 1999; Duffin 2004; Lauer et al. 2019) have reduced this initial great diversity. Tithonian species from Germany initially included Ischyodus schuebleri Quendstedt, 1858, Ischyodus suevicus Philippi, 1897, Ischvodus quendstedti Wagner, 1857, Ischvodus rostratus Meyer, 1859, and Ischvodus acutus Meyer, 1859. From these, Ischvodus rostratus and I. suevicus were synonymized to I. schuebleri by Riess (1887) and by Heimberg (1949), respectively. The most informative Tithonian species from Germany is represented by I. quendstedti, which is based in a complete holotype and several referred specimens, including well preserved mandibular plates (Leuzinger et al. 2017).

Duffin (in Stahl 1999) considered *I. rostratus*, *I. suevicus*, and *I. schuebleri* to be synonyms of *I. quendstedti*. Besides the latter, the remaining species *I. acutus* was based in a unique known vomerine (Meyer 1859), making any direct comparison to the Chilean specimen impossible. Finally, *Ischyodus avitus* (Meyer, 1862) from the Tithonian of Solnhofen, Germany, is known by several fairly complete specimens, but their dentition was not sufficiently exposed for a good description (Stahl 1999). This species was later referred to *Ischyodus avitus* (Riess, 1887). More recently, Duffin (2004) and Lauer et al. (2019) transferred the species to the genus *Elasmodectes* Newton, 1878. Therefore, the currently valid known *Ischyodus* species from the Tithonian of Germany can be reduced to only two species, *Ischyodus quendstedti* and *I. acutus*, the latter known by a single vomerine, rising reasonable doubts about its eventual synonymy with *I. quendstedti*.

Additional Tithonian records of *Ischyodus* are known from France and England, represented by *Ischyodus dutertrei* Egerton, 1843, and *Ischyodus townsendi* (Buckland, 1835), respectively. Agassiz (1837, tome III) mentioned *I. dutertrei* "as very similar to *I. townsendi*, but being one third smaller. The exterior [= labial margin] of the lower mandible [= mandibular plate] is not strongly grooved as in *Ischyodus townsendi*; [...] the most evident difference lays in the obtuse angle formed by the tooth crown [= beak] with the upper board of the mandible [= posterior part of the labial margin]. In other words, the tritorial surfaces are used in a more obliquous position in its mandibles [= mandiblar plates]".

The description of Agassiz (1837, tome III) indicated that the occlusal curvature of the plate was more pronounced in *I. townsendi* than in *I. dutertrei*. This feature, plus the larger size of the former, could be better explained by the different ontogenetic stages of each specimen. Otherwise, the topology of the tritors is very similar in both species (see Sauvage 1896: pl. 21: 1, 2).

Comparison of MHNC.35.444 with the *I. townsendi* (holotype, BMNH P474; currently under acronym and numeration NHMUK 010039966 PV), *I. quendstedti* (referred, MJSN SCR010-1000), and *I. dutertrei* (holotype, specimen number 3402, Musée Boulogne-sur-le-mer, France) revealed a very similar topology of the tritorials in all cases (Fig. 4). Different plate outlines are explainable due to their respective ontogenetic stages. Ward and Grande (1991: fig. 4) brilliantly

Species	Age	Geographic occurrences	References
Ischyodus aalensis	Bajocian	Württemberg, Germany	Quendstedt 1858; Riess 1887
Ischyodus personati	Bajocian	Württemberg, Germany	Quendstedt 1858
Ischyodus colei	Bathonian	England	Agassiz 1837, tome III
Ischyodus curvidens	Bathonian	England	Egerton 1843
Ischyodus ferrugineus	Bathonian	Württemberg, Germany	Riess 1887
Ischyodus emarginatus	Bathonian	England	Egerton 1843
Ischyodus obruchevi	"Middle Jurassic"	Russia	Averianov 1992
Ischyodus egertoni	Callovian–Kimmeridgian	south England	Buckland 1835
Ischyodus dufrenoyi	Kimmeridgian	Boulogne, France	Egerton 1843
Ischyodus baeumonti	Kimmeridgian	Boulogne, France	Egerton 1843
Ischyodus beaugrandi	Kimmeridgian	Boulogne, France	Sauvage 1867
Ischyodus bouchardi	Kimmeridgian	Boulogne, France	Sauvage 1867
Ischyodus suprajurensis	Kimmeridgian	Boulogne, France	Sauvage 1867
Ischyodus sauvaugei	Kimmeridgian	Boulogne, France	Hamy 1866
Ischyodus schuebleri	Tithonian	Württemberg, Germany	Quendstedt 1858
Ischyodus suevicus	Tithonian	Württemberg, Germany	Philippi 1897
Ischyodus quendstedti	Tithonian	Bavaria, Germany	Wagner 1857; Riess 1887
Ischyodus rostratus	Tithonian	Hannover, Germany	Meyer 1859
Ischyodus acutus	Tithonian	Hannover, Germany	Meyer 1859
Ischyodus dutertrei	Tithonian	Boulogne, France	Egerton 1843
Ischyodus avitus	Tithonian	Solnhofen, Germany	Meyer 1862
Ischyodus townsendi	Tithonian	south England	Buckland 1835



Fig. 4. Comparison of mandibular plates of Tithonian species within *Ischyodus* Egerton, 1843. All in occlusal view. A. *Ischyodus quendstedti*, MJSN SCR010-1000), Tithonian of Switzerland; right mandibular, mirrored for comparison (modified from Leuzinger et al. 2017). B. *Ischyodus townsendi* (MHNC.35.444), Tithonian of central Chile; outline of the left mandibular (only visible in basal view) is overlapped in dashed lines for a better understanding of the complete plate outline. C. *Ischyodus dutertrei* (holotype, specimen number 3402, Musée Boulogne-sur-le-mer, France), Kimmeridgian–Tithonian of France (modified from Sauvage 1896). D. *Ischyodus townsendi* (holotype, BMNH P474; currently NHMUK 010039966 PV), Tithonian of England (modified from Natural History Museum, London, Data Portal, data.nhm.ac.uk, https://doi.org/10.5519/0002965). Abbreviations: act, accessory tritor; aot, anterior outer tritor; mt, median tritor; pot, posterior outer tritor; syt, symphyseal tritor.

illustrated how wearing by occlusion and growth define the outline of the mandibular plates of the *Ischyodus*. The strictly ontogenetic changes reported by these authors are reflected in the enlargement of each tritor pad and the separation between tritors coupled to the plate growth. Wearing can explain the reduction or even the loss of the small tritors located close to the labial margin and the reduction of the beak sharpness.

With all these considerations, MHNC.35.444 shares with I. townsendi, I. dutertrei, and I. quendstedti the presence of a large median tritor, flanked labially by the posterior outer tritor. It differs from I. dutertrei, which lacks the anterior outer tritor (although, this could be a consequence of the wearing). Based on the referred specimen (MJSN SCR010-1000; Leuzinger et al. 2017), the anterior outer tritor of *I. quendstedti* is placed anterolateraly to its median tritor. In I. townsendi (holotype) and in the Chilean specimen, the anterior outer tritor is placed laterally to their respective median tritor. This condition cannot be assessed in *I. dutertrei* (holotype) because the anterior outer tritor is not present. Also, the posterior outer tritor of I. quendstedti (referred specimen) is well-exposed in occlusal view. Older individuals of the genus show this tritor embedded within the plate, which is the case of the Ischvodus spp. mandibular plates compared on Fig. 4. On the lingual margin, the Chilean specimen, I. dutertrei (holotype) and I. townsendi (holotype) have partial exposition of the posterior outer tritor, seen in cross-section, and closely placed lateral to the median tritor.

Under these considerations, *I. dutertrei* and *I. townsendi* could likely belong to the same species, as first pointed

out by Agassiz (1833–1843) himself. However, a review of the valid species of the genus elsewhere is out of the scope of this study. Nevertheless, the completeness of the *I. townsendi* holotype compared with other Tithonian species, allows us to establish more detailed comparisons. The presence in *I. townsendi* of an anterior outer tritor laterally placed relative to the median tritor (contrary to the anterior outer tritor placed anterior to the median tritor in *I. quendstedti*) in effect occurs in the Chilean specimen. Following Grande and Ward (1991), the ontogenetic stage can cause lateral separation of the tritors, but a rostral migration seems more unlikely. Based on these traits, we refer MHNC.35.444 to the species *I. townsendi*.

Records of Austral Mesozoic Chimaeriformes.-The studied material represents the first Late Jurassic Chimaeriformes recorded in South America. Previous to this research, the oldest austral Callorhinchidae were represented by Aptian-Albian records from Queensland, Australia, including Ischyodus cf. thurmanni Pictet and Campiche, 1858 (Popov 2011; Popov and Machalski, 2014); Ptyktoptychion tayyo Lees, 1986, and Pyctoptychion wadeae Bartholomai, 2008. In addition, Albian-Cenomanian records from western Australia include material referred to Callorhinchus cf. borealis and Ischvodus sp. (Popov 2011; Popov and Machalski 2014). During the Late Cretaceous, the genus Ischyodus was recorded in the Campanian-Maastrichtian of New Zealand (Pictet and Campiche 1858), and in the upper Maastrichtian of Seymour Island, Antarctica (Stahl and Chatterjee 2002). It is also documented during the Paleogene of Antarctica and southern South America (Ward and Grande 1991; Kriwet and Gaździcki 2003; Otero et al. 2013a; Otero and Soto-Acuña 2015). The material from central Chile studied here represents the oldest Chimaeriformes known to date in the Southern Hemisphere and the oldest known occurrence of the group in Gondwana.

Paleobiogeography.—The presence of the Ischyodus in the Tithonian of central Chile adds to a growing body of evidence regarding the interchange of marine vertebrates between the northern Tethys and the southeastern Pacific. Gasparini et al. (2007) synthesized the Middle and Late Jurassic record of ichthyosaurs, thalattosuchians, plesiosaurians, and Testudines from the Neuquén Basin (Argentina and Chile), suggesting that the common occurrence of several genera in the northern Tethys and the southeastern Pacific are likely explained as the result of an interchange through the Caribbean Seaway (sensu Iturralde-Vinent 2003). In addition, Arratia (1994, 2015) reviewed the osteichthyan fossil record from Chile, where phylogenetic analyses endorse a narrow relationship between the osteichthyan faunas from Europe, Cuba, and northern Chile, pointing out the Caribbean Seaway as the main path for such interchange. In this sense, the material here studied represents the first paleobiogeographically valuable evidence, now including chondrichthyans to the proposed connection. Previously, there was a single known record of an indeterminate neoselachian from the Tithonian of central Chile, likely representing a palaeospinacid or a hybodontid (Suárez and Otero 2011). Its still unsolved generic status precludes a palaeobiogeographic approach.

Conclusions

We present two new specimens of the Ischvodus (Chimaeriformes) from Tithonian levels of the Baños del Flaco Formation of central Chile. Available elements include one partial specimen comprising two articulated mandibular plates of a single individual, preserving enough diagnostic traits for an alpha-taxonomic identification. The specimen is here referred to Ischyodus townsendi (Buckland, 1835), a species previously restricted to the Tithonian of England. The common presence of this taxon in the northern Tethys and now in the southeastern Pacific reinforces the Caribbean Seaway as a fully functional path of marine faunal interchange, at least during the Late Jurassic. Evidence of this interhemispheric marine faunal interchange was already noted during the Middle and Late Jurassic on several groups of marine vertebrates (i.e., thalattosuchians, ichthyosaurians, plesiosaurians and osteichthtyes), although, previous to this research, no evidence of such interchange was verified among chondrichthyans. The studied material represents the first record of I. townsendi in the Southern Hemisphere, the first find of a Chimaeriformes in the Upper Jurassic of Gondwana, and the oldest known callorhinchid from South America.

Author's contributions

PSH, survey of the collecting site, detailed stratigraphy, stratigraphic column, geologic setting, manuscript writing; SFC, survey of the collecting site, manuscript writing and review; CFB, survey of the collecting site, data processing, manuscript writing and review. AVT, data processing, manuscript writing and review; CSG, survey of the collecting site, complementary stratigraphy, data processing, manuscript writing; RAO, preparation of the material, conceptualization of the research, methods, anatomical identification and taxonomic determinations, elaboration of pictures and schemes, manuscript writing and review.

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