

First record of a Late Jurassic rhamphorhynchine pterosaur from Gondwana

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We describe partial remains of a non-pterodactyloid pterosaur from Upper Jurassic levels of the Atacama Desert in northern Chile. The material includes a left humerus, a possible dorsal vertebra, and the shaft of a wing phalanx, all preserved in three dimensions and likely belonging to a single individual. The humerus has a hatchet-shaped deltopectoral crest, proximally positioned, and its shaft is markedly anteriorly curved, which are characteristic features of the clade Rhamphorhynchidae. In addition, the presence of a groove that runs along the caudal surface of the phalanx, being flanked by two asymmetric crests, is a distinctive feature of the clade Rhamphorhynchinae, which includes such genera as *Rhamphorhynchus* and *Nesodactylus*. Previous to this research, known records of Rhamphorhynchinae were restricted to Laurasia; thus, the specimen studied here represents the first evidence of this group found to date in Gondwana. Associated ammonoids allow us to assign the material to a middle Oxfordian age, which makes this specimen the oldest known pterosaur found in Chile, and the first of Oxfordian age in Gondwana. This discovery suggests that the clade Rhamphorhynchidae had a global distribution during the Late Jurassic.

Key words: Pterosauria, Rhamphorhynchidae, Rhamphorhynchinae, Oxfordian, Chile, Laurasia, Gondwana.

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Introduction

Pterosaurs (Diapsida, Archosauria) have been found all over the world (Barrett et al. 2008; Upchurch et al. 2015). Despite of this, their fossil record is very biased both temporally and spatially (Dean et al. 2016). This spatial bias is particularly evident in pterosaurs that lived during the Jurassic period. Most Jurassic pterosaurs have been found in the northern

hemisphere, mainly in China, Germany, France, and England (Upchurch et al. 2015), most of these being from the lithographic limestone of the Solnhofen Formation, in Germany, where numerous pterosaur remains have been recovered (Goldfuss 1831; Wellnhofer 1970, 1975a–c). During this time lapse, these territories were part of Laurasia, a supercontinent that included North America and Eurasia (Rage 2016). In contrast, Jurassic pterosaur records from Gondwana are

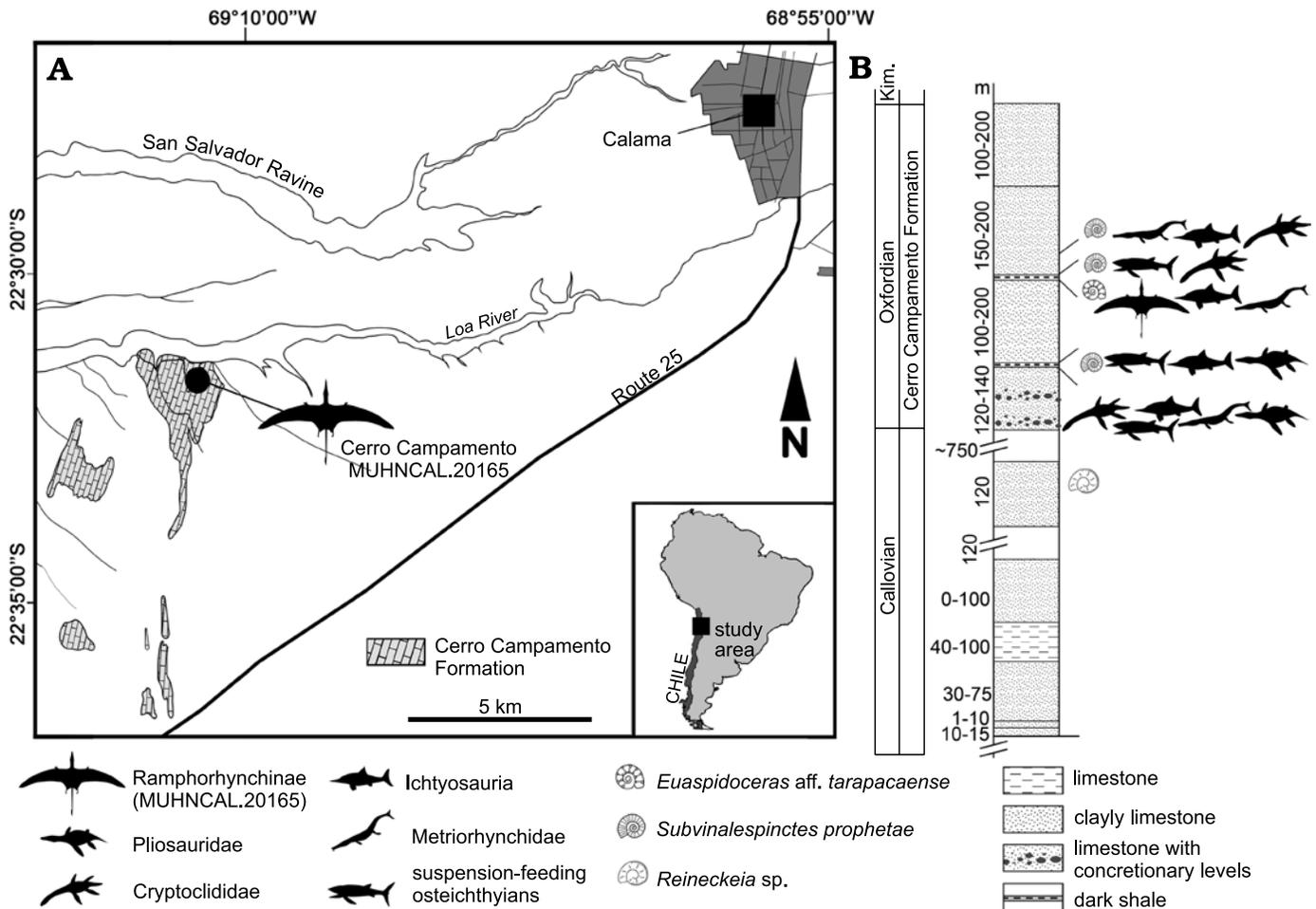


Fig. 1. A. Geographic location of the study area indicating the location of Cerro Campamento, the site where the discovery was made. B. General scheme of the stratigraphic section which includes the Cerro Campamento Formation, indicating horizons with vertebrate remains and the pterosaur materials here studied. Kim., Kimmeridgian. Modified from Biese (1961).

extremely sparse (Gasparini et al. 2004; Codorníu and Gasparini 2013; Codorníu et al. 2016). Most of the Gondwanan Jurassic pterosaurs have been recovered in Argentina, being stratigraphically restricted to Toarcian–Bathonian (Rauhut et al. 2001; Unwin et al. 2004; Codorníu et al. 2010, 2016) and Tithonian (Casamiquela 1975; Codorníu and Gasparini 2013; Codorníu et al. 2016) units of Patagonia, although other records are also known from the lower Jurassic of Antarctica (Hammer and Hickerson 1994), and from the Tithonian of Tanzania (Unwin and Heinrich 1999; Costa and Kellner 2009; Costa et al. 2015). In Chile, the pterosaur record is scarce and fragmentary, with most finds restricted to Lower Cretaceous units (Casamiquela and Chong Díaz 1978; Bell and Suárez 1989; Bell and Padian 1995; Martill et al. 2000, 2006; Soto-Acuña et al. 2015; Alarcón-Muñoz et al. 2018, 2020). There are only two mentions of Jurassic pterosaurs from Chile, both from the Oxfordian Cerro Campamento Formation (Calama, northern Chile). A brief mention of an incomplete skull (MUHNCAL.20148) was referred to an indeterminate non-pterodactyloid pterosaur (Yury-Yañez et al. 2013); however, subsequent studies and CT-scan of this material show that it belongs to the dentary of a pachycormi-

form fish (RAO, personal observation). The second find is represented by a partial skeleton of a pterosaur initially referred to Pterosauria indet. by Alarcón et al. (2015). Herein, we present the re-study of the latter specimen after additional preparation. Despite its fragmentary condition, the material preserves diagnostic traits which allow us to refer it to the Rhamphorhynchidae, and even more specifically, within the clade Rhamphorhynchinae, which includes Jurassic pterosaurs from Europe, Asia, and North America (Unwin and Martill 2017). This find represents the first evidence of Rhamphorhynchinae from Gondwana. Along with this, it represents the first pterosaur of Oxfordian age known from Gondwana.

Geological setting

The studied material was collected in Cerro Campamento, in the locality of Cerritos Bayos, ca. 30 km west from Calama, in the Antofagasta Region, Atacama Desert, northern Chile (Fig. 1). The fossil-bearing geological unit is the Cerro Campamento Formation (Duhart et al. 2018). The ma-

terial was embedded in a concretion of yellowish-to-grey calcareous sandstone, which includes abundant ammonoid remains referable to *Subvinialesphinctes profetae* Gygi and Hillebrandt, 1991, and less frequent remains referable to *Euaspidoceras* sp. (Meléndez and Myczyński 1987; Parent 2006). Following Biese (1957, 1961), the fossiliferous concretion-bearing level is set a few meters below distinctive blackish shales that comprise the roof of the section. Biese (1957, 1961) considered these levels as belonging to upper Callovian, based on the presence of “*Cosmoceras*”. Contrary to this, the abundant remains of *Subvinialesphinctes profetae* associated to *Euaspidoceras* sp. and the lack of ammonoids referable to the *Kosmoceras* (not “*Cosmoceras*”) suggest a middle Oxfordian age for the concretion-bearing levels and for the material studied here.

Material and methods

The studied specimen was found by one of the authors (ORM) during fieldwork in 2009. All the bony elements are included in a single concretion. Their occurrence in the same block, the lack of anatomically redundant elements, and the concordance in the relative proportions, suggest that all the bones belong to a single individual. The material was exposed by cracking of the concretion in to three main blocks. Each block was mechanically prepared by JAM and SSA during 2016 and 2017, initially with Dremel Engraver Tool, and during 2018, with PaleoTools ME-9100 airscribe. The bones were consolidated with cyanoacrylate.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BSP, Bayerische Staats-

sammlung für Paläontologie und Historische Geologie, Munich, Germany; D, Dalian Natural History Museum, Dalian, China; MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MJML, Museum of Jurassic Marine Life, Kimmeridge, UK; MUHNCAL, Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Antofagasta Region, Northern Chile; NHMUK, Natural History Museum, London, UK; OUM, Oxford University Museum, Oxford, UK; PRC, Palaeontological Research and Education Centre, Mahasarakham University, Maha Sarakham, Thailand; PSB, Petrefaktensammlung Banz, Upper Franconia, Bavaria, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Systematic palaeontology

Diapsida Osborn, 1903

Archosauria Cope, 1869

Pterosauria Kaup, 1834

Breviquartossa Unwin, 2003

Rhamphorhynchidae Seeley, 1870

Rhamphorhynchinae Nopcsa, 1928

Rhamphorhynchinae gen. et sp. indet.

Figs. 2–6.

Material.—MUHNCAL.20165, a complete left humerus; two fragments of a diaphysis of a wing phalanx and a possible dorsal vertebra belonging to a single, medium sized pterosaur individual from Cerritos Bayos, west Calama, Antofagasta Region, Chile; Cerro Campamento Formation,

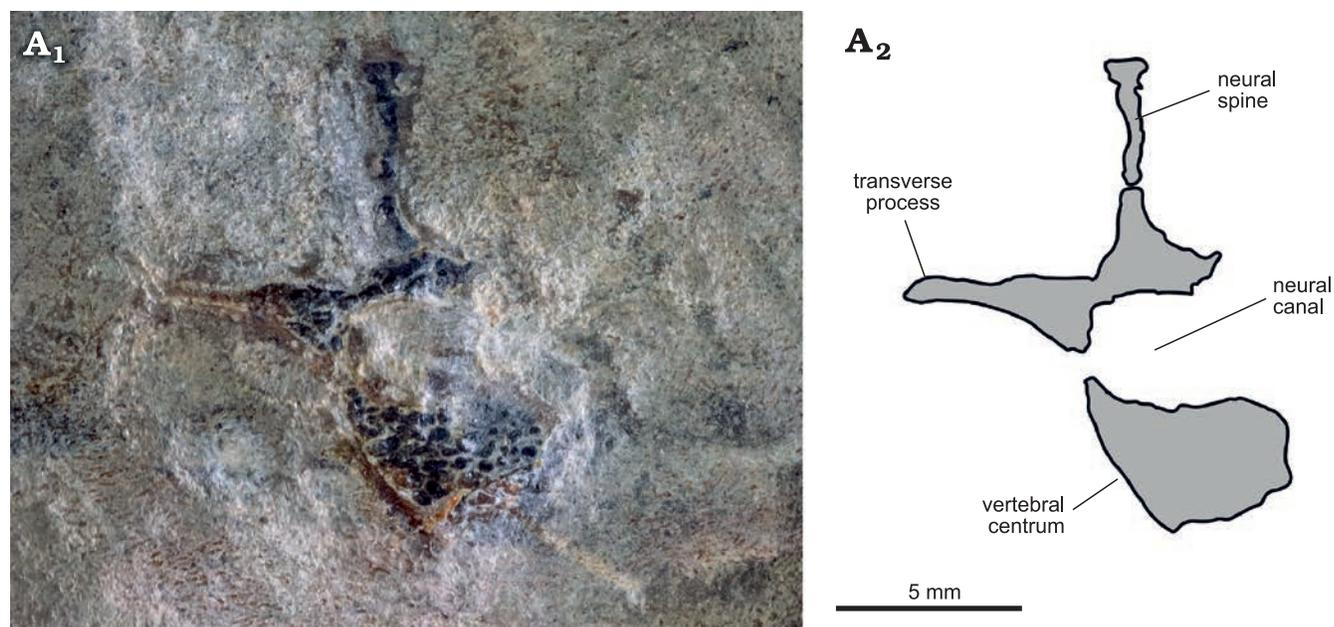


Fig. 2. Rhamphorhynchinae gen. et sp. indet. (MUHNCAL.20165) from Cerritos Bayos, west Calama, Chile; Cerro Campamento Formation, middle Oxfordian. Vertebrae of indeterminate position (A₁) and schematic representation (A₂).

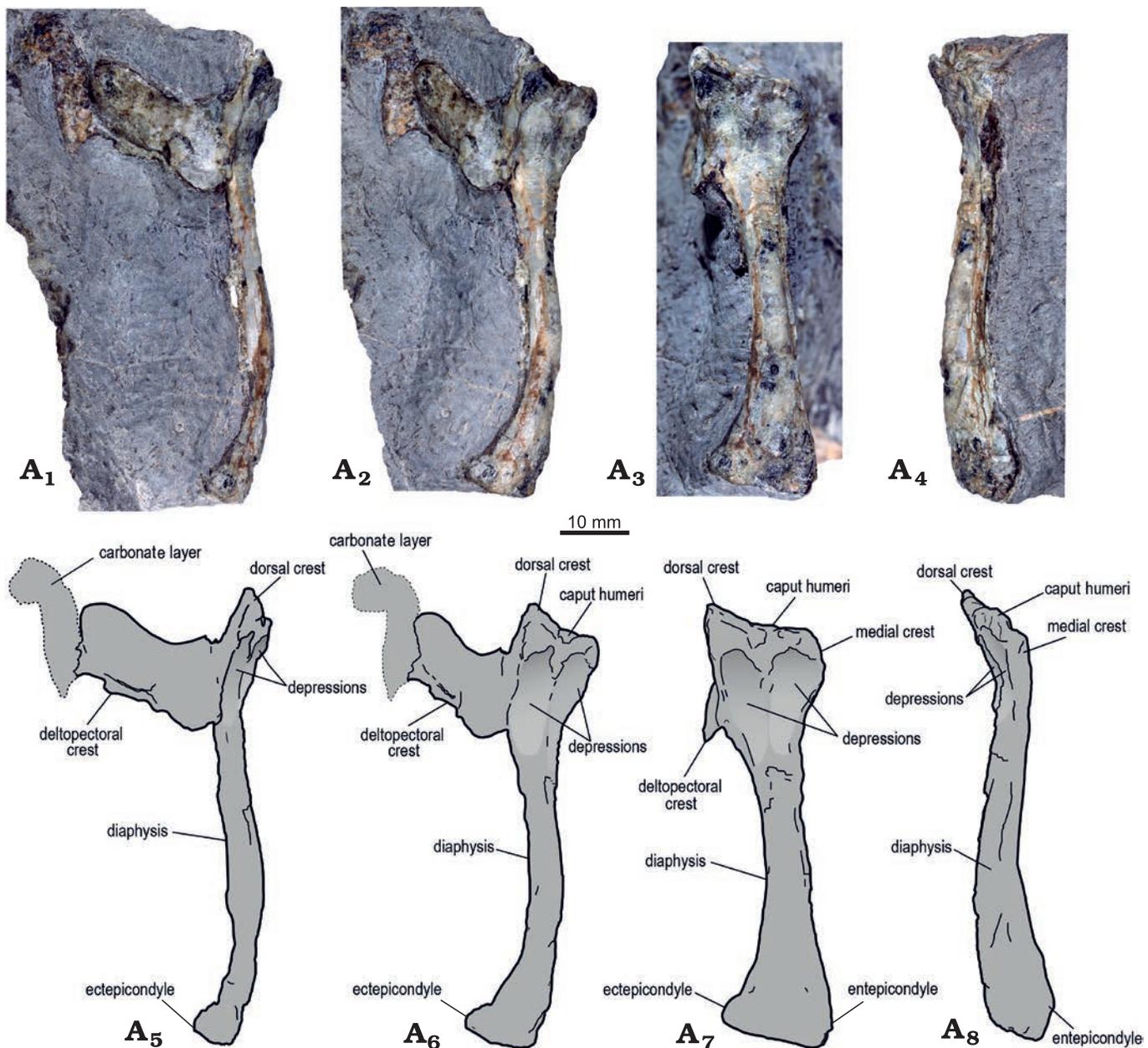


Fig. 3. Rhamphorhynchinae gen. et sp. indet. (MUHNCAL.20165) from Cerritos Bayos, west Calama, Chile; Cerro Campamento Formation, middle Oxfordian. Left humerus in dorsal (A₁, A₅), posterodorsal (A₂, A₆), posterior (A₃, A₇), and ventral (A₄, A₈) views, photographs (A₁–A₄) and explanatory drawings (A₅–A₈).

Zone of *Subvinialesphinctes prophetae* and *Euaspidoceras* sp., middle Oxfordian.

Descriptions.—*Vertebra*: Among the remains there is a single incomplete vertebra (Fig. 2). This is visible in articular view and it is very eroded; it is difficult to establish whether it is exposed in anterior, posterior, or in an approximately oblique view. The neural spine is tall (preserved height is 6.3 mm), as described for Rhamphorhynchinae (Witton 2013: 129) especially in the cervical vertebrae, although relatively tall and rectangular neural spines are also seen in the anterior dorsal vertebrae of *Rhamphorhynchus* (see Bonde and Christiansen 2003: fig. 5). The neural spine is laterally compressed and slightly higher than the preserved vertebral

centrum. However, we cannot assure that this ratio is natural since the vertebral centrum is not complete. Only one incomplete transverse process is preserved (preserved length of ~4.5 mm). This arises from the top of the neural arch and has a dorsolateral orientation. Proximally, the height of the transverse process represents almost half of the centrum height, narrowing distally. Due to its incompleteness, its extension cannot be established. The neural canal is broad, being wider than high and representing ca. three fifths of the preserved centrum width. The poor preservation of the material makes it difficult to assess the exact shape and proportions of the neural canal, although it appears to have a dorsoventrally compressed oval shape. The centrum is

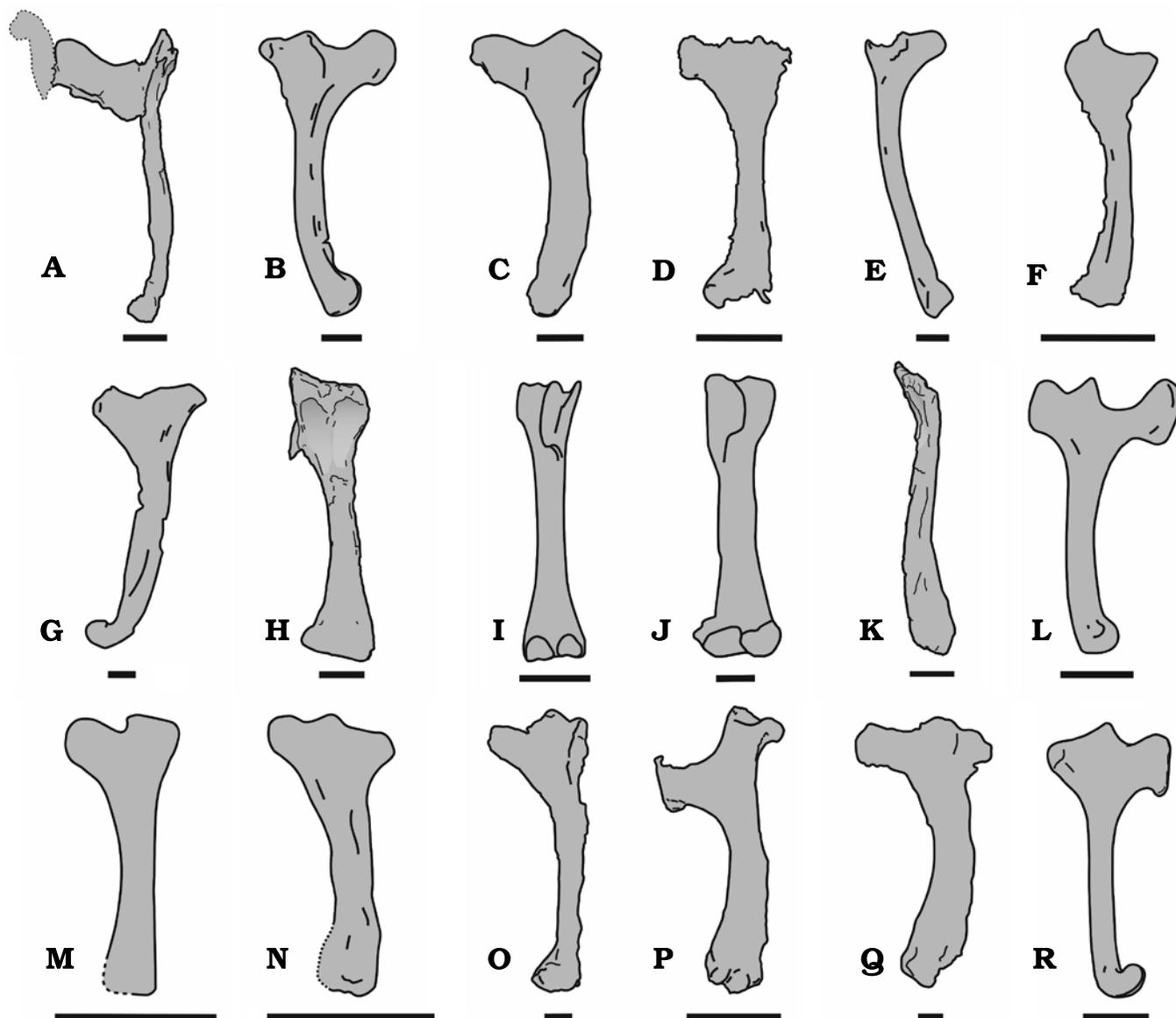


Fig. 4. Comparison between the humeri of Rhamphorhynchinae gen. et sp. indet. (MUHNCAL.20165) and other rhamphorhynchids in dorsal (A–C, E–G), ventral (D, K–R), posterior (H), and anterior (I, J) views. **A.** Rhamphorhynchinae gen. et sp. indet., left humerus (MUHNCAL.20165). **B.** *Dorygnathus banthensis* Theodori, 1830, right humerus (PSB 759a, from Padian and Wild 1992). **C.** *Dorygnathus banthensis* Theodori, 1830, left humerus (MB 1905.15, from Unwin and Martill 2017). **D.** Rhamphorhynchidae indet. right humerus (NHMUK PV R 40126b, from O’Sullivan and Martill 2018). **E.** Rhamphorhynchidae indet., right humerus (NHMUK PV R 40126c, from O’Sullivan and Martill 2018). **F.** Rhamphorhynchidae indet., left humerus (NHMUK PV R 28160a, from O’Sullivan and Martill 2018). **G.** Rhamphorhynchidae indet., left humerus (OUM J.23043, from O’Sullivan and Martill 2018). **H.** Rhamphorhynchinae gen. et sp. indet., left humerus (MUHNCAL.20165). **I.** *Rhamphorhynchus muensteri* Goldfuss, 1831, left humerus from Wellnhofer 1975a: 23, fig. 11e). **J.** *Dorygnathus banthensis* Theodori, 1830, right humerus (SMNS 50164, from Witton 2015). **K.** Rhamphorhynchinae gen. et sp. indet., left humerus (MUHNCAL.20165). **L.** *Rhamphorhynchus muensteri* Goldfuss, 1831, left humerus from Wellnhofer 1975a: 23, fig. 11d). **M.** *Qinglongopterus guoi* Lü, Unwin, Zhou, Gao, and Shen, 2012, left humerus (D3080/1, from Lü et al. 2012). **N.** *Bellubrunnus rothgaengeri* Hone, Tischlinger, Frey, and Röper, 2012, left humerus (BSP–1993–XVIII–2, from Hone et al. 2012). **O.** *Sericipterus wucaiwanaensis* Andres, Clark, and Xing, 2010, right humerus (IVPP V14725, from Andres et al. 2010). **P.** *Rhamphorhynchus etchesi* O’Sullivan and Martill, 2015, right humerus (MJML K-1597, from O’Sullivan and Martill 2015). **Q.** Rhamphorhynchinae gen. et sp. indet., right humerus (PRC 64, from Buffetaut et al. 2015). **R.** *Nesodactylus hesperius* Colbert, 1969, left humerus (AMNH 2000, redraw from Colbert 1969). Scale bars: A–C, E–M, O–R, 10 mm; D, N, 5 mm.

poorly preserved, too. The preserved height is ~8.2 mm. Apparently, its articular contour has a semicircular shape, whereas its dorsal margin was concave, given by the ventral contour of the neural canal. The general morphology of the vertebra resembles that of a dorsal vertebra, but due its incompleteness cannot be conclusively ascertained.

Humerus: An almost complete left humerus is preserved. It is three-dimensionally preserved and is exposed in posterior view (Fig. 3). The humerus is 71 mm long, and the mediolateral width of the diaphysis at its midpoint is 7.7 mm, with a length/width ratio of 9.2. The humerus is assigned to a pterosaur based on the posterior inclination of the caput hu-

meri, the presence of a well-expanded anterior deltopectoral crest, and relatively thin cortical bone (Wellnhofer 1978, 1991; Buffetaut et al. 2015). The deltopectoral crest is located at the proximal end of the humerus. The deltopectoral crest is almost complete, dorsoventrally narrow, and well extended anteriorly. It is elongated and projects approximately perpendicular from the humeral shaft. As in several non-pterodactyloid pterosaurs and in some basal pterodactyloids, the proximal and distal margins of the deltopectoral crest lie almost on the same level as the medial crest (Wellnhofer 1978: fig. 1b–d; Unwin and Martill 2017). Furthermore, the deltopectoral crest is proximodistally constricted at its base and expanded anteriorly, in a hatchet-shaped form. At its anterior end, the deltopectoral crest is partially fractured. This portion joins with a carbonate layer present in the rock, making it difficult to determine the exact morphology of the anterior edge of the deltopectoral crest. However, it is observed that the proximodistal edge curves distally, which gives the deltopectoral crest an ax-like shape.

The hatchet or tongue-shaped form of the deltopectoral crest and its proximal location are features considered diagnostic of Rhamphorhynchidae by Kellner (2003) and Unwin (2003). This morphology is present in several rhamphorhynchids (Fig. 4), such as species of *Rhamphorhynchus* (Wellnhofer 1975a, 1978; O'Sullivan and Martill 2015), *Dorygnathus* (Padian 2008b), *Nesodactylus* (Colbert 1969), *Qinglongopterus* (Lü et al. 2012), and *Bellubrunnus* (Hone et al. 2012). The shape of the deltopectoral crest MUHNCAL.20165 especially resembles that present in the genera *Rhamphorhynchus* and *Nesodactylus*, in which the hatchet-shaped deltopectoral crest is especially evident (Colbert 1969: fig. 8; Wellnhofer 1975a: fig. 11; Fig. 4E, R). However, the deltopectoral crest of MUHNCAL.20165 is more elongated anteroposteriorly than in *Nesodactylus hesperius* (Fig. 4). The morphology of the deltopectoral crest of MUHNCAL.20165 is quite different of species of *Campylognathoides*, in which the deltopectoral crest is short, approximately triangular in shape and its proximal end is proximally curved (see O'Sullivan et al. 2013: fig. 5h, i). The proximal portion of the humerus is dorsoventrally expanded and has two well-marked depressions, limited proximally by the posterior edge of the humeral head, and separated by a medial crest. The caput humeri is partially eroded, and it is flexed posteriorly, as apparently in all pterosaurs (Wellnhofer 1978; Unwin 2003). The proximal portion of the caput humeri has a saddle-shaped articular surface, as is common in pterosaur humeri (Rauhut et al. 2017). Thus, the articular end is concave mediolaterally, and convex anteroposteriorly. The humeral head is slightly displaced posteriorly with respect to the diaphysis axis, a feature apparently present in all pterosaurs (Wellnhofer 1978; Unwin 2003; Unwin and Martill 2017). Its articular surface is partially eroded, although there are two bulges separated by a short groove. The dorsal crest of the humeral head is triangular and well projected proximodorsally, as in species of *Rhamphorhynchus* (Wellnhofer 1975a) and *Nesodactylus* (Colbert 1969). The depressions located below the humeral head extend distally

until the beginning of the diaphysis. The lateral depression is wider and more excavated than the medial.

Since the humerus is exposed in posterior view, it is not possible to corroborate the presence of pneumatopores piercing the anterior surface of the proximal end of this bone. The absence of pneumatopores has been described in basal pterosaurs (Claessens et al. 2009), such as *Rhamphorhynchus muensteri* Goldfuss, 1831 (Bonde and Christiansen 2003). Likely, the absence of pneumatic pores in the humerus is a common character among non-pterodactyloids: in Pterodactyloidea, the humeri usually have pneumatopores (Bonde and Christiansen 2003; Claessens et al. 2009; Elgin and Hone 2013; Unwin and Martill 2017). The medial crest (also called ulnar crest) is almost squared with its more medially expanded edge slightly rounded and its distal edge forming an obtuse angle with the diaphysis. This structure corresponds to the area in which the subcoracoscapularis muscle was fixed (Colbert 1969). The medial crest is shorter than in species of *Rhamphorhynchus* (Wellnhofer 1975a, 1978), *Dorygnathus* (Padian 2008a), and *Nesodactylus* (Colbert 1969). The medial crest of MUHNCAL.20165 differs from that of species of *Nesodactylus* in that it is more extended proximo-distally and its posterior end does not form such an acute angle (Fig. 4). The medial crest of MUHNCAL.20165 also differs from that of *Nesodactylus hesperius* Colbert, 1969; in the latter species the medial extension of the crest is much larger than in MUHNCAL.20165 (see Colbert 1969: fig. 8).

The diaphysis of MUHNCAL.20165 is robust and straight in posterior view but is more gracile than that in the humeri of rhamphorhynchids such as *Rhamphorhynchus muensteri* (Wellnhofer 1975a, 1978; Fig. 4D, E) and *Rhamphorhynchus etchesi* O'Sullivan and Martill, 2015 (O'Sullivan and Martill 2015; Fig. 4P). In dorsal and ventral views, the diaphysis of MUHNCAL.20165 is anteriorly curved, as in non-pterodactyloid pterosaurs, although the degree of curvature and extent are variable (Unwin and Martill 2017). The curvature of the shaft of the humerus of MUHNCAL.20165 is well marked (Figs. 3, 4), as in rhamphorhynchids such as species of *Rhamphorhynchus* (Wellnhofer 1975a, 1978), *Dorygnathus* (Wellnhofer 1978; Padian 2008b), and *Nesodactylus* (Colbert 1969), and as in some unidentified rhamphorhynchid species from the Taynton Limestone Formation, Stonefield, Oxfordshire, UK (O'Sullivan and Martill 2018). The three-dimensional preservation of the humerus of MUHNCAL.20165 suggests that no relevant taphonomic distortion occurred, which indicates that the anteriorly curved shaft constitutes a distinctive feature of this taxon. In Pterodactyloidea, the shaft of the humerus tends to be straighter (Unwin and Martill 2017). The distal end is quite eroded, which makes it difficult to observe many of its features. Because the humerus is preserved in posterior view, it is not possible to observe the capitulum or the trochlea.

The distal epiphysis is lateromedially expanded, similar to the humerus of *Rhamphorhynchus muensteri* (Wellnhofer 1975a, 1978; Fig. 4D), of *Dorygnathus banthensis* Theodori, 1830 (PSB 759a, see Theodori 1852; Padian and Wild 1992;

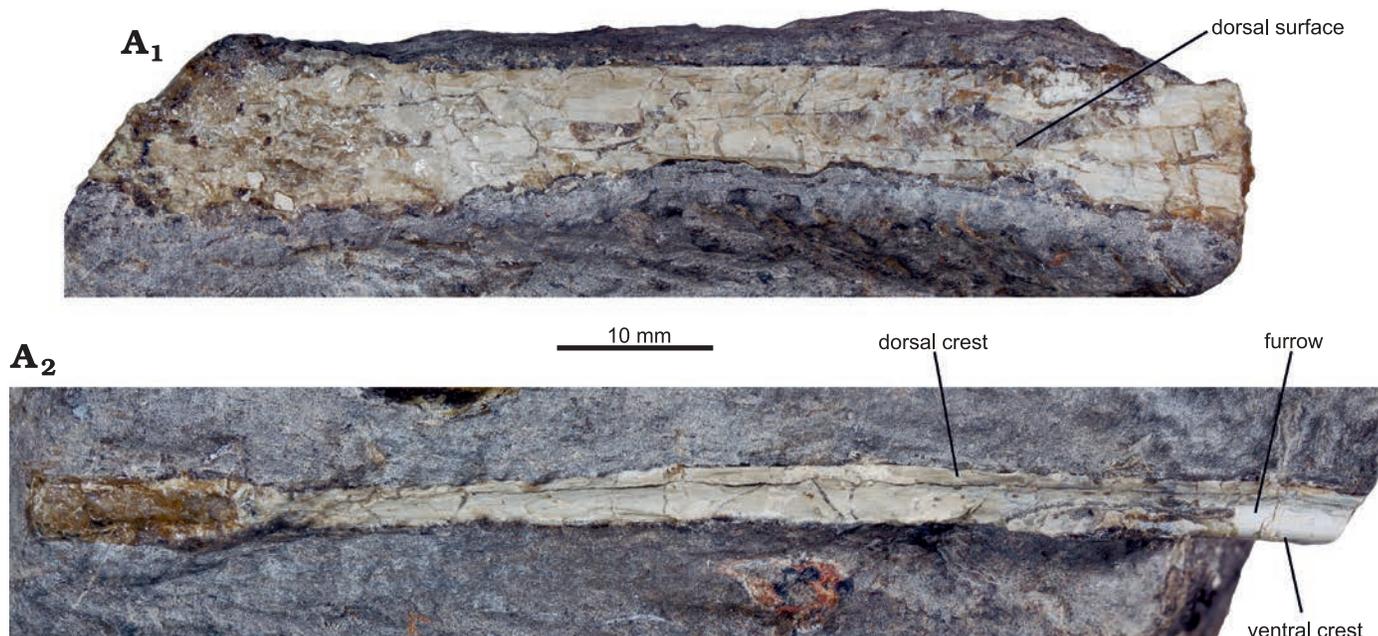


Fig. 5. Rhamphorhynchinae gen. et sp. indet. (MUHNCAL.20165) from Cerritos Bayos, west Calama, Chile; Cerro Campamento Formation, middle Oxfordian. Fragments of a wing phalanx in dorsal (A₁) and posterior (A₂) views.

Fig. 4H), and a distal fragment of a humerus of an unidentified rhamphorhynchid species from Oxford Clay Formation, England (NHMUK PV R 1995 illustrated in O’ Sullivan 2018: fig. 4). The ectepicondyle is located more proximally than the entepicondyle. The ectepicondyle is dorsally protruding and triangular in shape, whereas the entepicondyle does not protrude ventrally. The ventral half of the distal epiphysis of MUHNCAL.20165 is more distally extended than the dorsal half, whereas in the species of *Rhamphorhynchus* both portions of the distal epiphysis are approximately at the same level (Wellnhofer 1975a, 1978; Fig. 4D).

Wing phalanx: The diaphysis of a wing phalanx is preserved in two fragments (Fig. 4). The close association of the phalanx with the left humerus suggests that both elements could correspond to the same wing, however, the incomplete preservation of the phalanx fragments makes it difficult to ascertain. The pterosaurs generally have four phalanges in the wing finger which vary in length, morphology of the epiphyses and thickness (Wellnhofer 1991; Unwin 2006).

The wing phalanx of MUHNCAL.20165 is robust, as in *Rhamphorhynchus muensteri* (see Wellnhofer 1975a: fig. 15). The total length of the wing phalanx (corresponding to the sum of both fragments) is 161.7 mm (85.6 and 76.1 mm, respectively). The preserved length of the wing phalanx of MUHNCAL.20165 is greater than the length of the first wing phalanx of *Sericipterus wucaiwanaensis* Andres, Clark, and Xing, 2010, corresponding to 127.4 mm (Andres et al. 2010). The preserved length of the wing phalanx of MUHNCAL.20165 is less than that of wing phalanges I–III of *Rhamphorhynchus etchesi*, corresponding to 171, 175, and 163 mm, respectively (O’ Sullivan and Martill 2015). However, it is possible that the complete wing phalanx of MUHNCAL.20165 was similar or even longer than that of

at least one of the first three wing phalanges of *R. etchesi*. In addition, the preserved length of the wing phalanx of MUHNCAL.20165 is less than that of one of the longest wing phalanx described in *Rhamphorhynchus muensteri*, which measures about 180 mm (see Bennett 1995: fig. 1). However, as in the case of *R. etchesi*, it is not possible to determine with certainty whether the length of the complete phalanx of MUHNCAL.20165 was indeed less than the length of the longest wing phalanges of *R. muensteri*. The maximum anteroposterior width of the phalanx is 9.1 mm, and the maximum dorsoventral height is 8.3 mm. The ratio between the anteroposterior width of the mid-point of the diaphysis of the humerus and that of the wing phalanx is 0.85. This value is slightly less than in *Jianchangopterus zhaoianus* Lü and Bo, 2011 (which is the widest wing phalanx of this pterosaur) corresponding to 0.96 (Lü and Bo 2011). The preserved length of the phalanx in relation to the preserved length of the humerus does not support correspondence to one of the two most distal phalanges (III and IV) since these tend to be much more gracile and shorter (especially the terminal phalanx) in relation to the humerus than the two more proximal ones, as is described in *Qinglongopterus guoi* Lü, Unwin, Zhou, Gao, and Shen, 2012 (Lü et al. 2012). In one specimen of *R. muensteri*, Hone et al. (2015) mention that the wing phalanges I and II are slightly longer than the phalanges III and IV, but the latter two are more gracile. Thus, the preserved shaft probably corresponds to the first or second wing phalanx. Unfortunately, none of these fragments preserve proximal or distal ends, making it difficult to assess the complete morphology and the whole phalanx length, and therefore, precluding accurate comparisons with other pterosaurs.

In the wing phalanx of MUHNCAL.20165, there is a longitudinal furrow which is flanked by two asymmetric

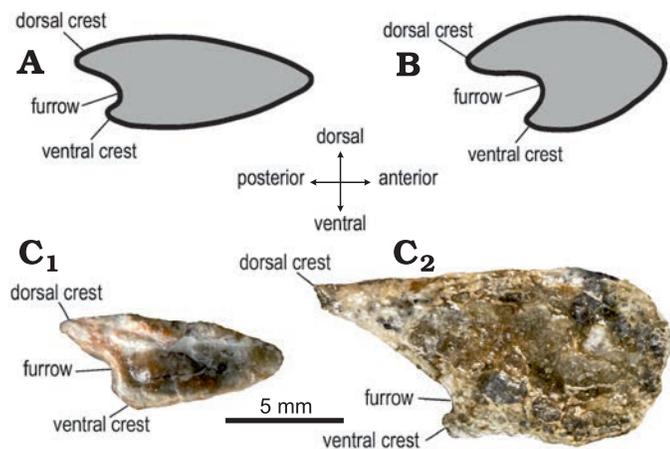


Fig. 6. Comparison of sections of the wing phalanx of rhamphorhynchinae pterosaurs. **A.** *Nesodactylus hesperius* Colbert, 1969 (modified from Colbert 1969). **B.** *Rhamphorhynchus muensteri* Goldfuss, 1831 (modified from Colbert 1969). **C.** Rhamphorhynchinae gen. and sp. indet. MUHCAL.20165, Cerritos Bayos, west Calama, Chile; Cerro Campamento Formation, middle Oxfordian. C₁ and C₂, cross sections of two portions of the wing phalanx. A and B, not to scale.

crests, of which the dorsal one is more prominent than the ventral one (Fig. 5). The presence of this furrow is considered a diagnostic feature of Rhamphorhynchinae (Unwin 2003). This trait was described in the rhamphorhynchines *Nesodactylus hesperius* of the Oxfordian of Cuba (Colbert 1969: fig. 10, modified from Gross 1937), *R. muensteri* from the Tithonian of Germany (Colbert 1969: fig. 10, modified from Gross 1937; see Wellnhofer 1978: fig. 13) and *R. etchesi* from the Tithonian of England (O'Sullivan and Martill 2015: figs. 4, 9). In *R. muensteri* and *R. etchesi*, the fourth wing phalanges present the furrow on its caudal surface, which covers practically all of its extension. In addition, this furrow can be clearly seen in the first wing phalanx of an indeterminate Rhamphorhynchinae from the Oxford Clay Formation (NHMUK PV R 4759, O'Sullivan 2018: fig. 5).

The cross-section is similar to that of *R. muensteri* and *N. hesperius*, as illustrated in Colbert (1969: fig. 10) and this work (Fig. 5). Its area is variable along the diaphysis, and we interpreted the larger area as the most proximal portion of the phalanx. As in the first wing phalanx of *N. hesperius* (Colbert 1969: fig. 10) and *R. muensteri* (Gross 1937), the anterior surface of the wing phalanx of MUHCAL.20165 is partially sharp in what we interpret as the distal portion of the phalanx, becoming more rounded in what we interpret as the proximal portion, as in the first wing phalanx section of *R. muensteri* illustrated in Gross (1937).

The only pterosaur outside of Rhamphorhynchinae in which the presence of a longitudinal furrow in a wing phalanx has been described is in the dimorphodontid *Caelestiventus hanseni* Britt, Dalla Vecchia, Chure, Engelmann, Whiting, and Scheetz, 2018, of the Upper Triassic from North America (Britt et al. 2018). This furrow was described in the terminal phalanx of this pterosaur (the only preserved postcranial element of this species). However, it is not known whether

the proximal phalanges of *C. hanseni* had a longitudinal furrow. Furthermore, the age at which this species (and the Dimorphodontidae family) lived together along with other anatomical differences between the humeri of dimorphodontids and rhamphorhynchids do not support the inclusion of MUHCAL.20165 in Dimorphodontidae (see discussion on this issue).

Discussion

Morphological features.—The studied material shows characters typical of pterosaurs, such as a well-developed wing-like deltopectoral crest, the posterior flexion of the humeral head with respect to the axis of the diaphysis, and extremely thin walls of the appendicular bones (Wellnhofer 1978, 1991; Kellner 2003; Unwin 2003, 2006; Buffetaut et al. 2015; Unwin and Martill 2017). Although the available bones are scarce, they have some features present in pterosaurs of the clade Rhamphorhynchidae. According to the definition of Unwin (2003), Rhamphorhynchidae includes *Sordes pilosus*, *Rhamphorhynchus muensteri*, their most recent common ancestor, and all its descendants, and is composed of the subclades Rhamphorhynchinae and Scaphognathinae. However, the phylogenetic relationships of the clade Rhamphorhynchidae are currently controversial, so the inclusion of several species in Rhamphorhynchidae is debated (Andres et al. 2014; Vidovic and Martill 2018; Baron 2020). The deltopectoral crest of the humerus of MUHCAL.20165 suggest affinities of this specimen with Rhamphorhynchidae. In the humerus, Unwin (2003) describes the deltopectoral crest of the rhamphorhynchid pterosaurs as “tongue shaped”, while Kellner (2003) describes it as “hatchet-shaped”, since this structure is anteriorly expanded and narrowed to the base, although it should be noted that the shape of the deltopectoral crest changed along ontogeny (see Wellnhofer 1975a: fig. 11). Furthermore, both Kellner (2003) and Unwin (2003) add that the deltopectoral crest in Rhamphorhynchidae is located proximally, unlike Nyctosauridae, which present a deltopectoral crest with a similar morphology, but it is displaced distally. According to Unwin (2003), this morphology is especially evident in *R. muensteri*, although it is also observed in *Dorygnathus banthensis* and *Nesodactylus hesperius*. Although the deltopectoral crest in MUHCAL.20165 is incomplete, its general shape and proximal location clearly agree with that described in Rhamphorhynchidae. Added to this is the marked anterior curvature of the diaphysis, which is a common feature in humeri of rhamphorhynchids (Wellnhofer 1975a, 1978; Unwin 2003; Kellner 2003; Hone et al. 2012; Lü et al. 2012; Unwin and Martill 2017).

Other informative features of MUHCAL.20165 is the presence of a caudal longitudinal furrow of the wing phalanx. A caudal furrow like that present in the phalanx of MUHCAL.20165 has been recorded exclusively in two pterosaur lineages, the Rhamphorhynchinae (Wellnhofer 1975a, b, 1978; Unwin 2003; O'Sullivan and Martill 2015;

Table 1. Summary of findings of skeletal remains from Gondwana initially attributed to Rhamphorhynchidae, and their subsequent identifications.

Specimen numeration	Original identification	Current taxon	Anatomic elements	Litostratigraphic unit	Age	Country	References
MB.R.2845	<i>Rhamphorhynchus tendagurensis</i> Reck, 1931	Pterosauria indet.	incomplete radius and ulna	Tendaguru Formation	Kimmeridgian–Tithonian	Tanzania	Reck 1931; Unwin and Heinrich 1999
N° K 49/884 (GSI type N°. 17868, I.S.I.R.49)	<i>Rhamphorhynchus</i> sp.	Pterosauria indet.	postcranial remains	Kota Formation	Middle–Late Jurassic	India	Rao and Shah 1963; Jain 1974; Padian 2008a
I.S.I.R.48	<i>Campylognathoides indicus</i> Jain, 1974	Osteichthyes indet.	left and right premaxillae	Kota Formation	Middle–Late Jurassic	India	Jain 1974; Barrett et al. 2008; Padian 2008a
MPEF PV 3607, 3609, 3613, 3615	Rhamphorhynchidae indet.	<i>Allkaruen koi</i> Codorníu Carabajal, Pol, Unwin, and Rauhut, 2016	mandible, braincase, and cervical vertebrae	Cañadón Asfalto Formation	Toarcian–Bathonian	Argentina	Rauhut et al. 2001; Unwin et al. 2004; Codorníu et al. 2010

Table 2. Record of skeletal remains of valid Jurassic pterosaurs from Gondwana.

Taxon	Age	Chronostratigraphic unit	Locality	References
Pterosauria indet.	Hettangian–Sinemurian	Upper Elliot Formation	Farm Spioenkop, Senekal District, Free State, South Africa	Blackbeard and Yates 2007
Pterosauria indet.	Hettangian–Pliensbachian	Hanson Formation	Mount Kirkpatrick, Central Transantarctic Mountains, Antarctica	Hammer and Hickerson 1994
<i>Allkaruen koi</i> Codorníu Carabajal, Pol, Unwin, and Rauhut, 2016	Toarcian–Bathonian	Cañadón Asfalto Formation	Cerro Cóndor, Chubut Province, Argentina	Codorníu et al. 2016
Pterosauria indet.	Middle Jurassic	Kota Formation	Paikasigudem village, India	Prasad and Parmar 2020
Pterosauria indet.	Middle Jurassic	Kota Formation	Chanda District, Deccan, India	Padian 2008a
“Rhamphorhynchoidea” indet.	Bathonian	Isalo III Formation	Faritany Majunga, Madagascar	Dal Sasso and Pasini 2003
Rhamphorhynchidae indet.	Bathonian	Anoual Formation	Guelb el Ahmar, Morocco	Haddoumi et al. 2016
Pterosauria indet.	Bathonian	Anoual Formation	Guelb el Ahmar, Morocco	Haddoumi et al. 2016
<i>Tendaguripterus recki</i> Unwin and Heinrich, 1999	Kimmeridgian–Tithonian	Tendaguru Formation	Saurian Beds, Mtwara, Tanzania	Unwin and Heinrich 1999
Dsungaripteroidea indet.	Kimmeridgian–Tithonian	Tendaguru Formation	Saurian Beds, Mtwara, Tanzania	Costa and Kellner 2009
Archaeopterodactyloidea indet.	Kimmeridgian–Tithonian	Tendaguru Formation	Saurian Beds, Mtwara, Tanzania	Costa and Kellner 2009
<i>Wenupteryx uzi</i> Codorníu and Gasparini, 2013	middle–late Tithonian	Vaca Muerta Formation	Los Catutos, Neuquén Province, Argentina	Codorníu and Gasparini 2013
Pterodactyloidea indet.	middle–late Tithonian	Vaca Muerta Formation	Los Catutos, Neuquén Province, Argentina	Codorníu and Gasparini 2013
<i>Herbstosaurus pigmaeus</i> Casamiquela, 1975	late Tithonian	Vaca Muerta Formation	Picún Leufú stream, Neuquén Province, Argentina	Casamiquela 1975
Ctenochasmatae (?Gnathosaurinae) indet.	Late Jurassic–Early Cretaceous	Ksar Metlili Formation	Ksar Metlili, Morocco	Lasseron et al. 2019
?Rhamphorhynchidae indet.	Late Jurassic–Early Cretaceous	Ksar Metlili Formation	Ksar Metlili, Morocco	Lasseron et al. 2019

O’Sullivan 2018) and Dimorphodontidae (Britt et al. 2018). Unwin (2003) considered the presence of a furrow that runs along the caudal surface of the wing phalanges as a diagnostic feature of Rhamphorhynchinae. This feature has been described in the rhamphorhynchines as *R. muensteri*, *R. etchesi* (Wellnhofer 1978; O’Sullivan and Martill 2015) and *N. hesperius* (Colbert 1969). Additionally, some isolated wing phalanges with a caudal longitudinal furrow have been referred to Rhamphorhynchinae based on this trait (O’Sullivan 2018). Regarding Dimorphodontidae,

this feature has been recognized in a single species, *Caelestiventus hanseni*, from the Upper Triassic of North America, which bears a similar caudal longitudinal furrow (Britt et al. 2018). However, the presence of a furrow in the proximal phalanges of this species is unknown. Further, the clade Dimorphodontidae so far is restricted to the Late Triassic and Early Jurassic, while Rhamphorhynchinae is restricted to the Late Jurassic (Witton 2013). In addition, other dimorphodontids such as *Dimorphodon macronyx* Buckland, 1829, completely lack furrows on the caudal sur-

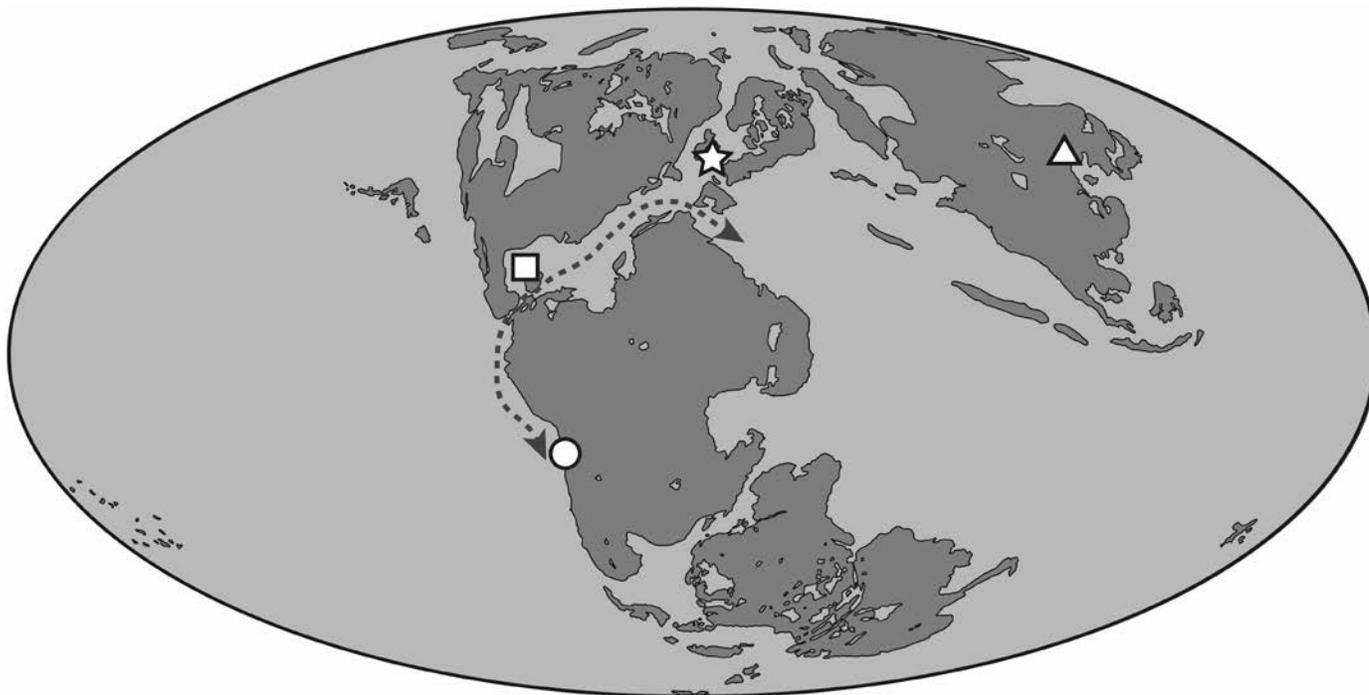


Fig. 7. Simplified map of the world during the Oxfordian. The dashed line represents the hypothetical route that would have allowed the dispersal of marine vertebrates and invertebrates between Tethys and South America during the Late Jurassic (Caribbean corridor). The finds of Oxfordian rhamphorhynchids: MUHNCAL.20165 (Rhamphorhynchinae gen. et sp. indet.), Cerro Campamento Formation, Chile (circle); *Cacibupteryx caribensis* (Gasparini et al. 2004) and *Nesodactylus hesperius* (Colbert et al. 1969), Jagua Formation, Cuba (square); Rhamphorhynchinae gen. et sp. indet. (Lydekker 1890, O'Sullivan 2018), Oxford Clay Formation, UK (star); *Qinglongopterus guoi* (Lü et al. 2012), Tiaojishan Formation, China (triangle). Modified map from Scotese (2014).

face of the wing phalanges (Padian 1983; Britt et al. 2018). Finally, the morphology of the humerus MUHNCAL.20165 associated with the phalanx, specially of the deltopectoral crest, does not agree with that of dimorphodontids, since the deltopectoral crest in these pterosaurs is not hatchet or tongue shaped (see Wellnhofer 1978: fig. 10). Considering this evidence, the morphology and position of the deltopectoral crest, the presence of a caudal furrow in the wing phalanx of MUHNCAL.20165 plus the Oxfordian age of this specimen, support its adscription to the clade Rhamphorhynchinae.

Paleobiogeography.—The clade Rhamphorhynchidae is well represented in Upper Jurassic rocks of former Laurasia. In contrast, specimens referred to this clade are much scarcer in the territories that were part of Gondwana (Barret et al. 2008). To date, specimens referred to Rhamphorhynchidae have been reported from the Middle and Upper Jurassic of India (Reck 1931; Rao and Shah 1963; Colbert 1969; Jain 1974; Unwin and Heinrich 1999; Barrett et al. 2008; Padian 2008a), Upper Jurassic of Tanzania (Reck 1931), and the Lower–Middle Jurassic of Argentinean Patagonia (Rauhut et al. 2001; Unwin et al. 2004; Codorniu et al. 2010, 2016). All these records were later reassigned to other groups of pterosaurs, and even to other groups of vertebrates (Table 1). However, recently, isolated teeth from the Bathonian Guelb el Ahmar in Morocco have been assigned to indeterminate rhamphorhynchids (Haddoumi et al. 2016). Additionally, an isolated tooth from Upper Jurassic–Lower Cretaceous of

Ksar Metlili, Morocco, was tentatively assigned to Rhamphorhynchidae (Lasseron et al. 2020).

The partial pterosaur skeleton from Cerro Campamento Formation constitutes the first and only representative of the clade Rhamphorhynchinae known to date from Gondwana. In addition, pterosaurs of Oxfordian age are globally scarce, and mostly restricted to Laurasia (Lydekker 1890; Sharov 1971; Colbert 1969; Buffetaut et al. 1985; Buffetaut and Guilbert 2001; Gasparini et al. 2004; Barret et al. 2008; Lü et al. 2012; O'Sullivan 2018). Therefore, the new austral record sheds light on a broader geographic distribution of rhamphorhynchines during that lapse. This may not be unexpected, given the volant capabilities of Pterosauria, and the intermittent land connectivity between Laurasia and Gondwana during the Middle and Late Jurassic.

The subsistence of most Rhamphorhynchidae was probably tied to marine and coastal ecosystems. The recovery of MUHNCAL.20165 from marine units is consistent with the fact that most known rhamphorhynchine specimens have been found in rocks formed from sediments deposited in shallow marine environments (Newton 1888; Wellnhofer 1975c; Gasparini et al. 2004; O'Sullivan and Martill 2015; although some rhamphorhynchines from China are preserved in continental rocks: He et al. 1983, Czerkas and Ji 2002; Andres et al. 2010; Lü et al. 2012). In addition, specimens of *Rhamphorhynchus muensteri* from Solnhofen Formation show preservation of gut contents corresponding to fish scales and a whole fish individual (Frey and

Tischlinger 2012; Witton 2018), suggesting that fish may have been one of the most important food sources for these pterosaurs.

During the Oxfordian, the coasts of Gondwana and Laurasia were continuous not only through the western and eastern margins of these supercontinents, but also at the margins of internal seaways such as the Caribbean corridor and the Trans-Erythrean corridor. The fully functional Caribbean Corridor (Smith 1983; Iturralde-Vinent 2006) represents the shortest paleogeographical distance between Chile and Laurasia throughout which similar coastal ecosystems may have existed. In this regard, the Caribbean corridor has been proposed as an explanation for faunal similarities of marine deposits among Europe (UK, Germany), Cuba and South America during the Oxfordian (Fig. 7), as accounted by diapsids (Gasparini and Iturralde-Vinent 2006; Gasparini 2009; Otero et al. 2020) and bony fishes (Arratia 1994, 2008). Coeval rhamphorhynchids from marine deposits of the Caribbean Corridor at Cuba (particularly *Nesodactylus hesperius*, Colbert 1969) are therefore of special interest for comparison to Chilean forms. Hopefully, better materials from Chile will allow a more detailed assessment of any special affinities. While discussion of such matters requires further evidence, the new material from Chile is already sufficient to document a broader distribution of Rhamphorhynchidae beyond Laurasia. They prove this clade had a global distribution and increase the knowledge about the diversity of pterosaurs that inhabited Gondwana during the Jurassic, which remains very scarce (Table 2).

Conclusions

The specimen described here represents to date the oldest record of a pterosaur found in Chile, and the first confidently referable to the clade Rhamphorhynchinae so far known in Gondwana. However, the absence of more complete and diagnostic material precludes a generic and specific referral for the moment.

In recent years, the findings of marine fossil vertebrates in the Cerro Campamento Formation have increased in number. Several of these finds, mainly of marine reptiles, have supported the proposals regarding the existence of close biogeographic connections between the southwestern margin of Gondwana and Europe at the end of the Jurassic. However, until now, it is not clear whether non-marine vertebrates that inhabited the same areas and at the same time, such as pterosaurs, followed similar patterns. In the studied locality, the abundance of concretions with three-dimensional preservation of delicate vertebrate remains (among which are fish and the pterosaur described here), offer good perspectives for the discovery of new well-preserved pterosaur specimens, which may help solve current questions related to their taxonomic identity, diversity, phylogenetic relationships, and biogeography.

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