

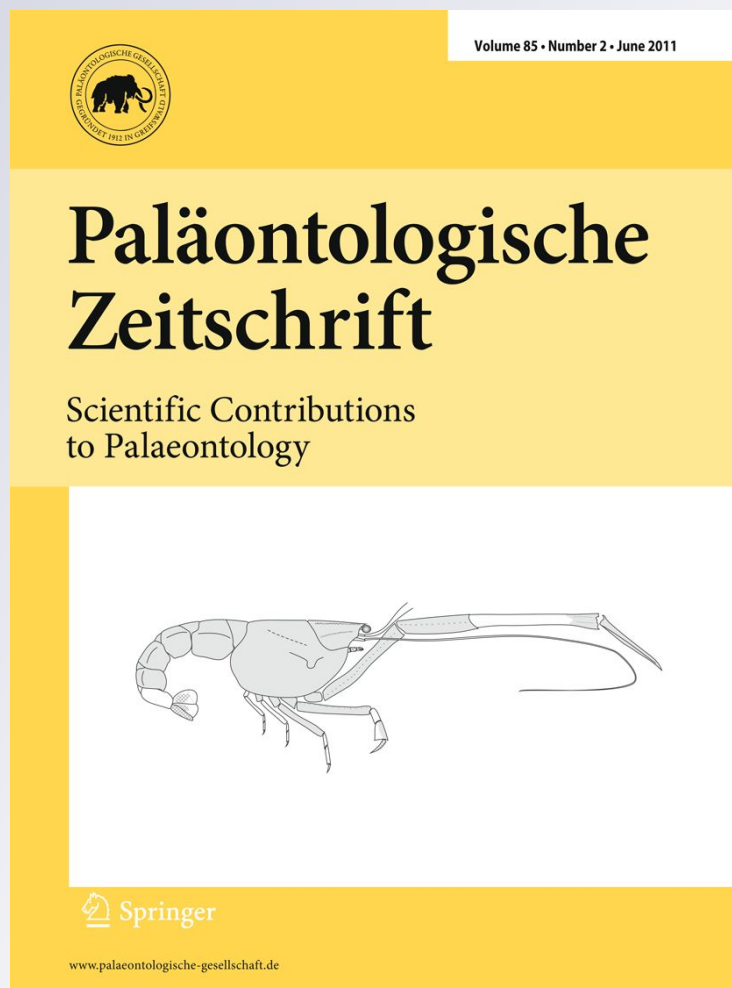
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Paläontologische Zeitschrift
Scientific Contributions to
Palaeontology

ISSN 0031-0220

Paläontol Z
DOI 10.1007/
s12542-011-0112-2



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A carpometacarpus from the upper cretaceous of patagonia sheds light on the Ornithurine bird radiation

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Received: 19 November 2010 / Accepted: 19 May 2011
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Abstract We report the discovery of an isolated avian carpometacarpus from the Upper Cretaceous Allen Formation (Campanian-Maastrichtian), Salitral Moreno, Río Negro Province, Argentina. This specimen is referred to cf. *Neornithes* because it presents a distinct but shallow infratrochlear fossa, a shortened ventral rim of the carpal trochlea that does not contact the base of the extensor process, and an extensor process conspicuously surpassing cranially the articular facet for digit I. The isolated nature of the specimen precludes its inclusion within the main neornithine lineages. Although it may represent part of the crown clade *Neornithes*, the limited data available do not confidently support placement within any particular lineage. The carpometacarpus constitutes one of the few records of Mesozoic Neornithine-like birds for South America.

Keywords *Neornithes* · Late Cretaceous · Argentina

Kurzfassung Der Neufund eines Vogel-Carpometacarpus aus der oberkretazischen Allen-Formation (Campan-

Maastricht) von Salitral Moreno, Provinz Río Negro, Argentinien, wird beschrieben. Das Exemplar wird zu den cf. *Neornithes* gestellt, da es eine klar definierte Fossa infratrochleare, einen kurzen ventralen Rand der Trochlea carpale, der nicht mit dem Extensor-Fortsatz im Kontakt steht, sowie einen Extensor-Fortsatz, der die Gelenkfacette des 1. Fingers deutlich in cranialer Richtung überragt, aufweist. Aufgrund des isolierten Vorkommens des Restes lässt er sich nicht in eine der Hauptentwicklungslinien dieser Gruppe einordnen. Obwohl er somit ein Taxon auf der Stammlinie der *Neornithes* repräsentieren könnte, lassen die sehr beschränkten Daten keine klare Einordnung zu. Dieser Carpometacarpus repräsentiert einen der wenigen Nachweise von *Neornithes* aus der Kreide Südamerikas.

Schlüsselwörter *Neornithes* · Oberkretazischen · Argentinien

Introduction

The Cretaceous record of South American fossil birds is mainly restricted to extinct groups, including the highly diversified Enantiornithes (Chiappe 1996; Walker 1981), the basal flightless Ornithurae *Patagopteryx* (Chiappe 1996), and the basal Carinatae *Limenavis patagonica* (Clarke and Chiappe 2001). In contrast, the Cretaceous record of modern birds (i.e., Neornithes) in South America is scarce and is only represented by the loon *Neogaeornis wetzeli* from the Maastrichtian of Chile (Olson 1992) and a possible Galliformes documented in Turonian-Coniacian outcrops from Southern Argentina (Agnolin et al. 2006). Recently, the presence of a possible charadriiform tibiotarsus was reported from the Campanian-Maastrichtian of Patagonia (Chiappe 1996; Hope 2002).

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In this paper we describe a well-preserved carpometacarpus collected in Campanian-Maastrichtian beds of Río Negro Province, NW Patagonia, which exhibits derived traits supporting its referral to Neornithes. The carpometacarpus described here constitutes one of the few South American Mesozoic records of this avian clade.

We follow Chiappe (2001) and Clarke and Chiappe (2001) for osteological nomenclature and systematic paleontology. Following those authors, the name Ornithurae includes the most recent common ancestor of the Hesperornithiformes and modern birds, plus all of its descendants. Carinatae is applied for the most recent common ancestor of *Ichthyornis* and Neornithes, plus all of its descendants. Neornithes constitutes the crown group of living birds.

Institutional abbreviation: MML, Museo Municipal de Lamarque, Río Negro province, Argentina.

Systematic paleontology

ORNITHURAE Haeckel, (1866)

cf. NEORNITHES Gadow, (1893)

Gen. et sp. indet.

Referred material: MML 206, left carpometacarpus lacking most of metacarpal III (Fig. 2).

Locality, horizon, and age: Allen Formation (Campanian-Maastrichtian; Heredia and Salgado 1999), cropping out in Salitral Moreno, at Bajo de Santa Rosa fossiliferous locality, Río Negro province, northern Patagonia, Argentina (Fig. 1). This locality also yielded the basal Carinatae *Limenavis patagonica* (Clarke and Chiappe 2001) and a

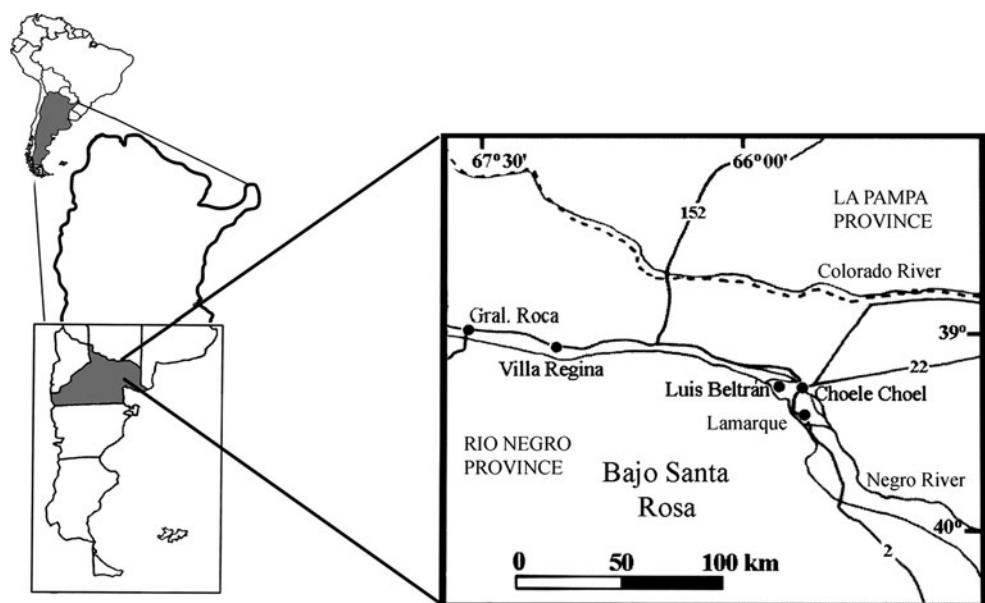
dubious charadriiform tibiotarsus (Hope 2002), as well as a large variety of non-avian vertebrates, including the abelisaurid *Quilmesaurus curriei*, the titanosaurian *Bonatitan reigi*, the dromaeosaurid *Austroraptor cabazai*, as well as hadrosaurid dinosaurs, leptodactylid and pipid frogs, chelid turtles, sphenodontid squamates, madtsoid snakes, and a wide variety of fresh-water fishes (Coria 2001; Martinelli and Forasiepi 2004; Novas et al. 2008).

Measurements: Maximum proximodistal length of entire carpometacarpus: 21 mm; maximum anteroposterior width of the proximal end: 4.3 mm; maximum distal width: 3.5 mm; length of extensor process: 2 mm

Description

The proximal end of the carpometacarpus bears a distinct pulley-like carpal trochlea, as typically occurs in birds more derived than *Archaeopteryx* (Chiappe 2001). Metacarpals are fused on both proximal and distal extremities, contrasting with the condition present in more primitive birds (e.g., *Confusiusornis* and *Enantiornithes*; Hou 1995) in which the distal extremities remain unfused (Fig. 2). The trochlear rims are subcircular in contour, and the ventral rim is not continuous with the extensor process, constituting a diagnostic trait of Neornithes (Longrich 2006). The infratrochlear fossa is placed near the dorsal margin of the carpal trochlea, as also occurs in most carinate birds (e.g., *Ichthyornis*, *Limenavis*; Clarke and Chiappe 2001; Fig. 3). This fossa is large, shallow, and ovoidal in contour. The pisiform process is prominent and proximo-medially oriented as occurs in modern birds (Clarke and Chiappe

Fig. 1 Map showing location of Bajo de Santa Rosa fossiliferous locality, indicated by a star. (Planned for page width)



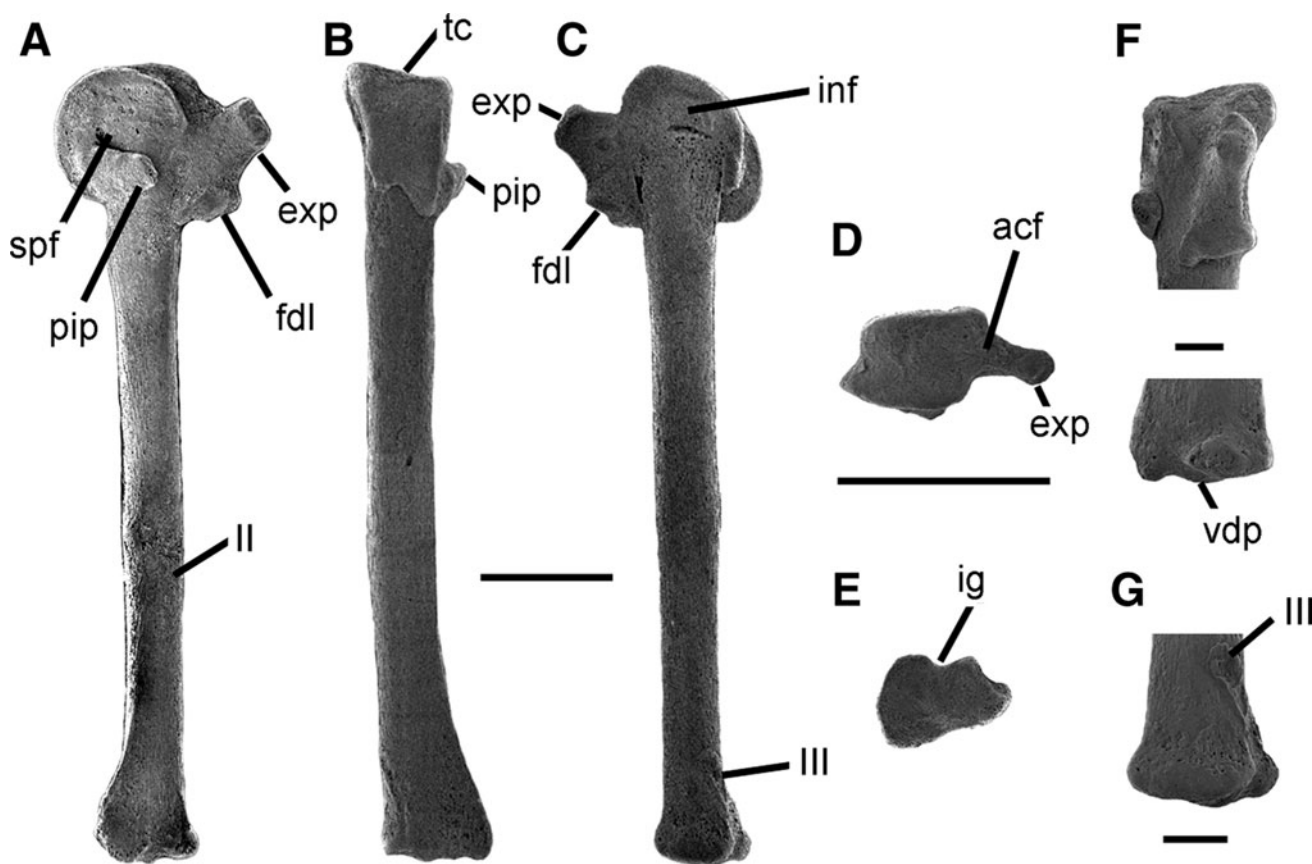


Fig. 2 MML 206 left carpometacarpus without the third metacarpal in **a** ventral, **b** medial, **c** dorsal, **d** proximal, and **e** distal views; **f** proximal and distal extremes in lateral view; **g** distal end in lateral view. *acf* anterior carpal fossa, *exp* extensor process, *fdl* articular facet

for first phalanx, *ig* interosseous groove, *inf* infratrochlear fossa, *pip* pisiform process, *spf* supratrochlear fossa, *tc* trochlea carpalis, *vdp* ventro-distal process, *II* second metacarpal, *III* fragment of the third metacarpal. Scale bar **a–e**, 5 mm; **f–g**, 1 mm. (Planned for page width)

2001). This condition contrasts with that of non-neornithine birds, in which this process is bump-like (e.g., *Apsaravis*, *Ichthyornis*, *Yixianornis*; Longrich 2006). As is usual in Neornithes, the extensor process is well developed and proximally oriented, being subquadrangular in contour (see Hope 2002). In contrast to most diving birds, this process is not distally located (Longrich 2006). Metacarpal I bears a small but deep concavity for the articulation of phalanx 1. Metacarpal II is straight, and its distal end is slightly expanded. It shows a deep interosseous groove and a well-defined tendinal sulcus. In distal view, metacarpal II is dorsoventrally low with a medially projected ventral process. Metacarpal III is lost, with the exception of a distal fragment attached to the shaft of metacarpal II. This piece of bone is, however, informative, showing that metacarpal III does not reach the level of the distal ginglymoid of metacarpal II. This condition is present in charadriiform and procellariiform taxa among neornithine birds (Clarke and Chiappe 2001).

Discussion

MML 206 exhibits the following derived traits uniting it with the Carinatae: (1) metacarpals distally fused; (2) extensor process well developed; (3) metacarpal I with a cup-shaped distal articular facet for phalanx 1-I; (4) metacarpal II distally expanded; (5) infratrochlear fossa present (Clarke and Chiappe 2001) (Fig. 3). Additionally, the Patagonian carpometacarpus presents the following apomorphic features of Neornithes: (6) extensor process surpassing the articular facet of digit I for more than half the width of this facet, thus producing a well developed knob; (7) ventral rim of the proximal trochlea not in contact with the extensor process; (8) infratrochlear fossa shallow (Clarke and Chiappe 2001; Clarke and Norell 2002; Longrich 2006) (Fig. 3). Although the above-mentioned characters support the identity of MML 206 to the stem lineage leading to Neornithes, because of its incomplete nature it cannot be positively supported within one of

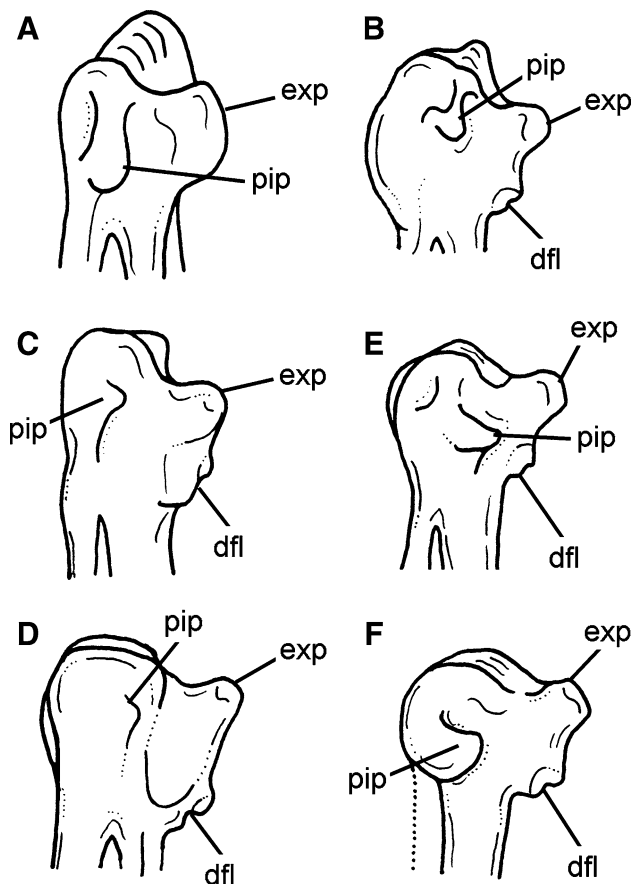


Fig. 3 Proximal carpometacarpus of select fossil and living birds. **a** *Enantiornis leali* (Aves, Enantiornithes), **b** *Yixianornis grabaui* (Aves, Ornithurae), **c** *Ichthyornis dispar* (Aves, Ornithurae), **d** *Limenavis patagonica* (Aves, Ornithurae), **e** *Stercorarius skua* (Aves, Neornithes, Charadriiformes), **f** MML 206. Specimens depicted in ventral view and at different magnifications; not to scale. *exp* extensor process, *dfi* articular facet for first phalanx, *pip* pisiform process. Not to scale. (**a** modified from Chiappe and Walker 2002; **b** modified from Clarke et al. 2006; **c** modified from Clarke 2004; **d** modified from Clarke and Chiappe 2001). (Planned for page width)

its two main component lineages (Palaeognathae, Neognathae). As such, MML 206 may represent part of the crown clade Neornithes, but the limited data available do not confidently support placement within any particular lineage of the extant neornithine radiation, and it is thus considered as cf. Neornithes indet.

In addition to the characters enumerated above, MML 206 differs in many features from several non-neornithine ornithurine birds. MML 206 may be clearly distinguished from the derived carinate *Limenavis patagonica* Clarke and Chiappe, 2001, coming from the same locality and horizon, in several features. MML 206 contrasts with *Limenavis* in having a rounded carpal trochlea in dorsal view (ellipsoidal in *Limenavis*; Clarke and Chiappe, 2001), in possessing a subrectangular and distally truncate extensor process (more

acute and distally rounded in *Limenavis*; Clarke and Chiappe, 2001), in the more developed and dorsally oriented pisiform process (more reduced and ventrally directed in *Limenavis*; Clarke and Chiappe, 2001), in possessing the distal end of metacarpal III distally surpassed by metacarpal II (subequal in *Limenavis*; Clarke and Chiappe, 2001), and in having a proximodistally reduced distal metacarpal symphysis (extensive in *Limenavis*; Clarke and Chiappe, 2001).

Moreover, MML 206 also differs from the advanced ornithurine birds *Ichthyornis dispar* Marsh, 1872 and *Iaceornis marshi* Clarke, 2004 (*sensu* Clarke, 2004) in many features. MML 206 differs from both genera in the same characters enumerated under the comparisons with *Limenavis* (see below). Moreover, MML 206 may be distinguished from *Ichthyornis* by several additional features. MML 206 lacks the large and cup-like notch for the lig. radiocarpometacarpale on the proximal margin of external trochlear rim; it also lacks both a lateral extensor groove along the dorsal margin of the shaft of metacarpal III and a well-developed tubercle at the postero-distal margin of metacarpal III diaphysis (Clarke 2004). Moreover, in MML 206 the extensor process is more dorsoventrally compressed than in *Ichthyornis* (Clarke, 2004). Furthermore, MML 206 is clearly different from *Iaceornis* in having a more rounded proximal end of the carpal trochlea, a more reduced facet for digit I, and dorsoventrally narrower proximal metacarpal symphysis (Clarke 2004).

Recently, Feduccia (2003) suggested that neornithine birds were absent (or nearly so) in Gondwanan landmasses during Mesozoic times. Similarly, O'Connor and Forster (2010), on the basis of a fossil bird assemblage of latest Cretaceous beds (Maastrichtian) from Madagascar, indicated that Gondwanan late Mesozoic avifaunas were dominated by Enantiornithes and other non-ornithurine birds. This was in sharp contrast to Laurasian assemblages in which mixed ornithurine-enantiornithine and ornithurine-dominated faunas have been reported (O'Connor and Forster 2010). However, the neornithine-like carpometacarpus here described, together with the fossil loon *Neogaeornis* from the Maastrichtian of Chile (Olson 1992), isolated neornithine-like remains from Patagonia (Hope 1999, 2002), the derived carinate *Limenavis patagonica* (Clarke and Chiappe, 2001), and an indeterminate galliform-like coracoid from the Turonian of Patagonia (Agnolin et al. 2006), demonstrate that very derived ornithurines were present in South America since the Turonian, at least. More recently, Agnolin and Martinelli (2009) described a diverse avifauna from the latest Cretaceous of Patagonia, and reported a large amount of ornithurine and neornithine-like remains, but no enantiornithine has been collected yet. Moreover, recent discoveries indicate that Neornithes were present and well diversified in the Late Cretaceous of

Antarctica (Chatterjee 2002; Clarke et al. 2005). As such, available evidence suggests that during the Campanian-Maastrichtian very advanced ornithurines (including Neornithes) were present not only in the Northern Hemisphere, but around the world, a hypothesis that is reinforced by the specimen here described.

Acknowledgments We thank Pablo Tubaro and Jorge Navas (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina) for allowing us to study comparative material under their care. We are deeply indebted to Daniel Cabaza (MML) for allowing us to study the present specimen. We thank M. Ezcurra and D.F. Pais for the critical reading of the manuscript, and Fabián Tricárico for the MEB images. Finally, we also thank J. Clarke and an anonymous reviewer who made very useful comments on the manuscript, and W. Volkheimer for his translation of the German abstract.

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