

AN AVIAN CORACOID FROM THE UPPER CRETACEOUS OF PATAGONIA, ARGENTINA

[Un coracoides de ave del Cretácico Superior de Patagonia, Argentina]

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RESUMEN: En el presente artículo, se describe el nuevo género y especie de ave Neornithes *Lamarqueavis australis*. El espécimen consiste en un coracoides aislado procedente de la Formación Allen (Campaniano-Maastrichtiano: Cretácico Superior) de la localidad de Bajo Trapalcó, provincia de Río Negro, Argentina. El espécimen constituye el primer registro sudamericano para el clado Cimolopterygidae, un grupo de aves previamente reconocido en estratos mesozoicos y paleógenos de Norteamérica, Europa y Asia. El nuevo género *Lamarqueavis* incluye también especies previamente descritas como “*Cimolopteryx*” *minima* y “*C.*” *petra*, provenientes del Cretácico Superior de Norteamérica. El nuevo espécimen es coincidente con la hipótesis tradicional que sugiere que las aves Ornithurae derivadas fueron los taxones dominantes de los ambientes costeros y marinos mundiales a fines del Cretácico, mientras que en los ambientes estrictamente continentales abundaron taxones basales. Finalmente, sobre la base del pobre registro fósil de Neornithes en el Mesozoico, hipótesis previas acerca del Centro de Origen de las aves modernas en Norteamérica y Antártida son discutidas y analizadas en detalle.

Palabras clave: Cretácico, Argentina, Patagonia, coracoides, Neornithes, Cimolopterygidae.

ABSTRACT: In the present paper, the new genus and species of neornithine bird, *Lamarqueavis australis* is described. The specimen consists on an isolated coracoid collected in Campanian-Maastrichtian beds of the Allen Formation, at the Bajo Trapalcó fossiliferous locality, Río Negro Province, Argentina. The specimen constitutes the first record from South America of the neornithine clade Cimolopterygidae, a group of modern-like birds that previously were known from Cretaceous and Paleogene strata of North America, Europe, and Asia. The new genus *Lamarqueavis* also includes previously described taxa, such as "*Cimolopteryx*" *minima* and "*C.*" *petra*, from the Late Cretaceous of North America. The new specimen fits well with the traditional hypothesis that suggests that derived ornithurine birds were the dominant taxa of shoreline and marine habitats during the Cretaceous, whereas in inland environments basal taxa were more abundant. Finally, on the basis of the meagre fossil neornithine record of the Cretaceous, previous hypotheses concerning the place of cradle of modern birds in Antarctica or North America are discussed.

Key words: Cretaceous, Argentina, Patagonia, coracoid, Neornithes, Cimolopterygidae.

INTRODUCTION

The South American record of fossil birds is strongly patchy and biased. In fact, in pre-Campanian outcrops only a handful of specimens belonging to basal birds, such as Enantiornithes and primitive ornithuromorphs were recovered from distant localities of Brazil and Argentina (CHIAPPE & CALVO, 1993; ALVARENGA & BONAPARTE, 1992; ALVARENGA & NAVA, 2005; AGNOLIN *et al.*, 2006). The post-Campanian bird record is more complete, being represented by specimens belonging to Enantiornithes (WALKER, 1981; DYKE *et al.*, 2007), stem ornithurines (CLARKE & CHIAPPE, 2001; AGNOLIN & MARTINELLI, 2009), and Neornithes or neornithine-like birds (OLSON, 1992; CHIAPPE, 1996; HOPE, 2002; AGNOLIN & MARTINELLI, 2009). Due to the scanty and meager Mesozoic fossil record of birds in South America, the continent is nearly excluded from biogeographical and avifaunal dynamic analyses. In this way, the presence of remains referable to derived birds in Late Cretaceous beds of South America is of seminal importance.

Molecular clocks (COOPER & PENNY, 1997) and biogeography (CRACRAFT, 2001) nest the origin of most modern bird clades (i. e. Neornithes) deep in the Cretaceous (approximately 100 MYR ago), earlier than the first adequate record for the group (70 MYR ago). Before the end of the Cretaceous, Neornithes become abundant, and were the only group (or nearly so) that survived in the Tertiary with little changes (HOPE, 2002; see MAYR, 2005). In fact, at sites well below the beginning of the Palaeocene, Neornithes and neornithine-like birds appear to be the more diverse elements of aquatic avifaunas. In most North American localities more than 80% of recovered bird bones is represented by Neornithes, whereas basal clades (i. e. Enantiornithes and basal Ornithurae) are represented by less than 20%

(HOPE, 2002). On the other hand, in many inland assemblages, Enantiornithes appear to have been far more diverse and abundant than the Ornithurae, and this pattern was considered as the generality of Cretaceous terrestrial ecosystems (MARTIN, 1980; FEDUCCIA, 2003). However, the hypothesis of niche bipartition is difficult to assess because of the poor fossil record of birds along the Cretaceous. In fact, most Late Cretaceous ornithurine fossils consist on isolated and often fragmentary skeletal elements that were usually dismissed in recent analyses (see CHIAPPE & DYKE, 2002). However, these sparse specimens are the only evidence we have concerning the evolution and diversity of Late Cretaceous birds. In spite of the incomplete nature of those specimens, the presence of several neornithine clades, such as galliform, anseriform and ratite birds in Mesozoic ecosystems appears to be strongly supported (CLARKE *et al.*, 2005). Moreover, several fragmentary isolated bones also suggest the presence of psittaciform, charadriiform, procellariform, and pelecarniform birds, among others (HOPE, 2002; but see MAYR, 2009).

The aim of the present paper is to report isolated bones belonging to the clade of Neornithes or “modern birds” collected in northwestern Patagonia, Argentina. Although the material here described is scarce, its neornithine affiliation brings to this incomplete evidence a special relevance. The specimens come from the Bajo Trapalcó fossiliferous locality, at Río Negro province, northeastern Patagonia, Argentina (figure 1). The fossils here described were collected in outcrops belonging to the Campanian-Maastrichtian (Late Cretaceous) Allen Formation (LEANZA *et al.*, 2004). In this sedimentary unit, a large array of fossil vertebrates were collected, including, perciform

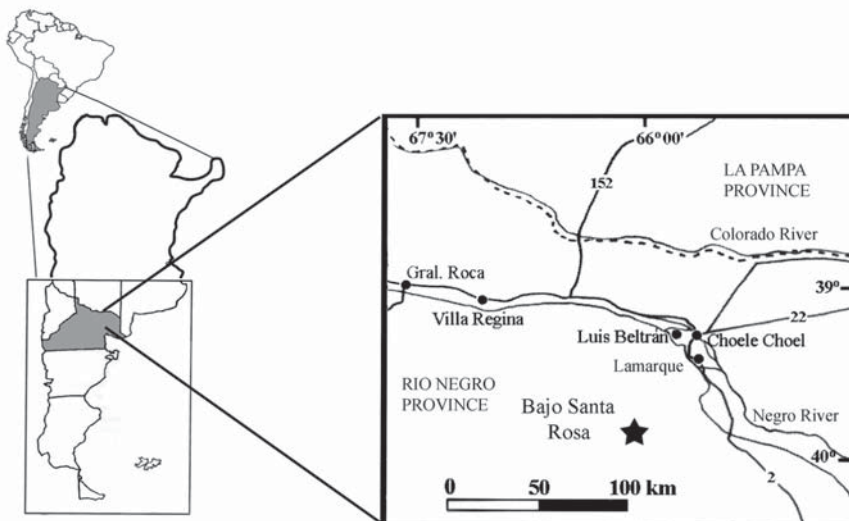


Figure 1. Geographic location of the fossil locality.
The star indicates the exact location where *Lamarqueavis australis* was collected.

and dipnoan fishes, sphenodontian lizards, chelid turtles, hadrosaurid, abelisaurid and titanosaurian dinosaurs, as well as, two ornithurine birds, and dryolestoid and multituberculate mammals (CLARKE & CHIAPPE, 2001; MARTINELLI & FORASIEPI, 2004; ROUGIER *et al.*, 2009).

MATERIALS AND METHODS

Virtually all specimens of Mesozoic carinates consist of single postcranial bones, and it has been a common practise to assign these specimens to modern clades. Although CLARKE & CHIAPPE (2001) argued that the small number of characters preserved in fragmentary material or single bones may fail to represent the signal of the entire skeleton, these fragments are the only evidence of several modern-like birds in the Cretaceous, and its detailed description and analysis is of primal importance. Moreover, the coracoid, due to its complex morphology, was considered as a useful element used in previous systematic studies (LONGRICH, 2008). Due to the fragmentary nature of the material here reported, a cladistic reconstruction is excessive, and since the classical approach of identifying specimens on overall similarities is unsatisfactory, the analysis taken here is a classic Hennigian approach based on derived shared features.

I follow the systematic taxonomic nomenclature proposed by SERENO (1998) with posterior modifications (LONGRICH, 2008). Following those authors, in the present paper the term Aves is used to include the clade that encompasses *Archaeopteryx*, *Passer*; its common ancestor, and all of its descendants. The clade Pygostylia is defined as the group including all birds with pygostyle, this is, the grouping that includes *Sapeornis*, Confuciusornithidae, *Passer*, and all of its descendants. Ornithothoraces is the clade formed by Enantiornithes and Ornithuromorpha+Ornithurae (CHIAPPE & CALVO, 1993). Ornithurae includes all birds with reduced pygostyle, and thus, includes *Archaeorhynchus*, *Hongshanornis*, and more derived taxa (ZHOU & ZHANG, 2006). Carinatae is used for the clade including the most recent ancestor of Ichthyornis and modern birds plus all of its descendants. Neornithes refers to the crown-clade birds.

In the present paper the osteological nomenclature employed by HOPE (2002) is followed.

Abbreviations. MML, Museo Municipal de Lamarque, Río Negro province, Argentina.

SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758

Ornithurae Haeckel, 1816

Neornithes Gadow, 1893

Cimolopterygidae Brodkorb, 1963

Lamarqueavis nov. gen.

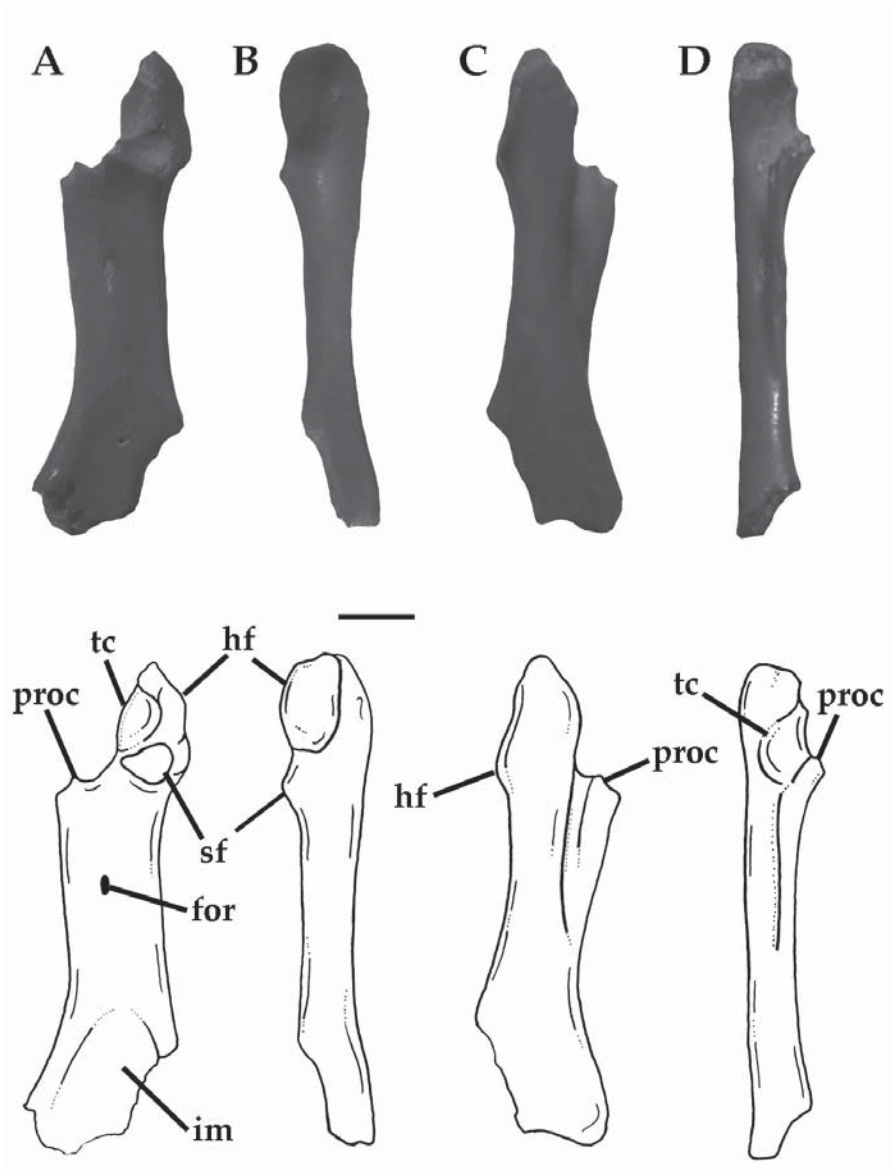


Figure 2. *Lamarqueavis australis* (MML 207; holotype), right coracoid in: A, dorsal; B, lateral; C, ventral; and D, medial views. Abbreviations: for, foramen for *n. supracoracoidei*; hf, humeral facet; im, impression for the *m. sternocoracoidei*; proc, procoracoidal process; sf, scapular facet; tc, triosseal canal. Scale bar 1 mm.

Diagnosis. Small sized bird distinguishable from other cimolopterygids by the following combination of features: 1) an extended and large procoracoid process; 2) humeral articular surface sub-rectangular in contour; 3) scapular cotyla transversely elongate with respect to the long axis of the coracoid.

Type species. *Lamarqueavis australis* nov. sp.

Included species. *L. australis* nov. sp. (figure 2), “*Cimolopteryx*” *minima* Brodkorb, 1963 (figure 4 B); “*C.*” *petra* HOPE, 2002 (figure 4 A).

Etymology. Lamarque, locality near the outcrops where the holotype specimen was found; avis, from the Latin, meaning bird.

Temporal and geographic distribution. Campanian-Maastrichtian (Late Cretaceous) of South and North America.

Lamarqueavis australis nov. sp.

Holotype. MML 207, right coracoid with damaged sternal and omal extremities, and lacking acrocoracoidal process (figure 2).

Locality and horizon. Cerro Tortugas fossiliferous locality (GPS: 39_ 470 02.1 S; 66_ 420 17.9 W) at Bajo Trapalcó, Río Negro province, northeastern Patagonia, Argentina. Collected in the Allen Formation (Campanian-Maastrichtian; Late Cretaceous; Leanza *et al.*, 2004).

Diagnosis. *L. australis* differs from other cimolopterygids in having the following autapomorphies: 1) large and longitudinally convex procoracoid process; 2) foramen for n. supracoracoidei distally located; 3) humeral facet of coracoid strongly tilted medially.

Etymology. *Australis*, from the Latin, coming from South.

Measurements. Total length (preserved): 12.1 mm; maximum length of scapular cotyla: 1.7 mm; maximum width of scapular cotyla: 1.5 mm; maximum width of humeral articular surface: 1.8 mm; maximum length of humeral articular surface: 3.2 mm; maximum width of procoracoidal process (preserved): 2.1 mm; minimum width of coracoidal neck: 2.3 mm; maximum width of sternal end (preserved): 4.2 mm.

Description. The coracoid comes from a very small bird, the size of a house sparrow (*Passer domesticus*). The specimen is elongate and shows a flattened coracoidal neck, which is oval in cross section.

The humeral articular surface is roughly subrectangular in contour. It shows its proximal and distal margins slightly convex, whereas its medial and lateral edges are nearly straight. The humeral articular surface is medially tilted and extends posteriorly to the mid-level of the scapular cotyla. The scapular cotyla is transversely elongate with respect to the anteroposterior axis of the coracoid. This cotyla is cup-shaped and relatively deep. A dorsal fossa is absent. The triosseal canal is relatively deep and lacks any sign of muscular ridges or pneumaticity.

Although incompletely preserved the procoracoidal process is very wide, prominent and laminar. It shows its medial margin longitudinally convex. The foramen for the n. supratoracoides is ovoid in contour and is very distally located with respect to the scapular cotyla.

A faintly defined ventrolateral intermuscular line is present, as is diagnostic of ornithurine birds (LONGRICH, 2008). In dorsal view, the impression for the m. sternocoracoidei is very deep and well defined, subtriangular in contour and taller than wide.

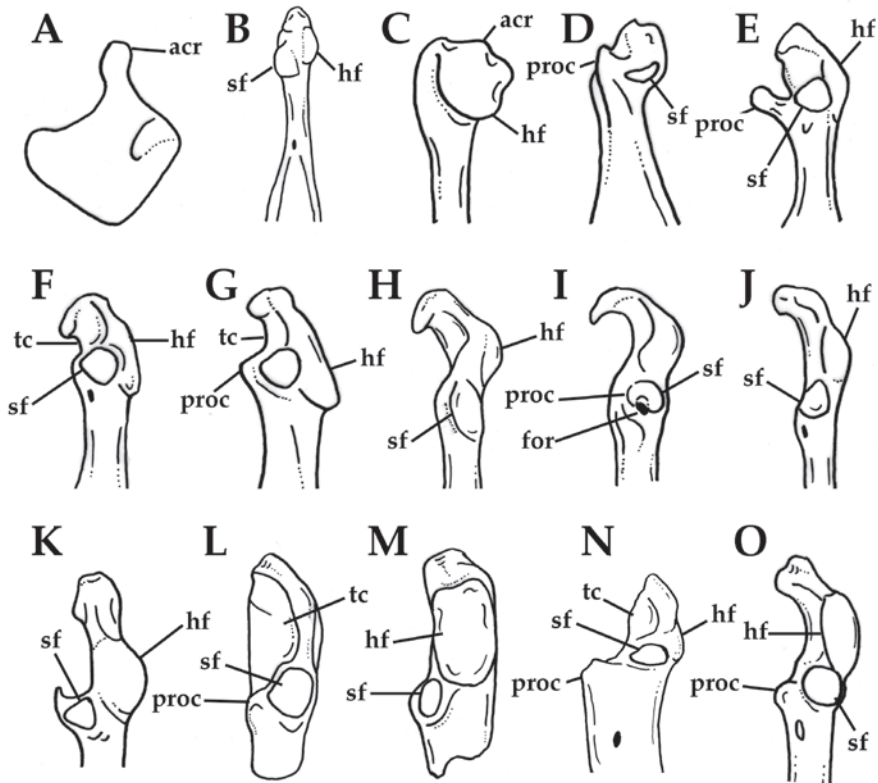


Figure 3. Comparative figure of left coracoids of selected birds in dorsal views. A, *Sapeornis chaoyangensis*; B, *Enantiornis leali*; C, *Patagopteryx deferrariisi*; D, *Baptornis advenus*; E, *Yixianornis grabaui*; F, *Ichthyornis* validus; G, *Ichthyornis dispar*; H, *Meleagris gallopavo* (*Galliformes, Meleagridae*); I, *Eudromia elegans* (*Tinamiformes, Tinamidae*); J, *Apatornis celer*; K, *Aix sponsa* (*Anseriformes, Anatidae*); L-M, *Ceramornis major*; N, *Lamarqueavis australis*; O, *Cimolopteryx rara*. (A, modified from ZHOU & ZHANG, 2003; B, modified from CHIAPPE & WALKER, 2002; C, modified from CHIAPPE, 2002; D, modified from MARTIN & TATE, 1976; F-G, modified from CLARKE, 2004; J, O, modified from HOPE, 2002; L-M, modified from BRODKORB, 1963). Abbreviations: acr, acrocoracoidal process; for, scapular foramen; hf, humeral facet; proc, procoracoidal process; sf, scapular facet; tc, triosseal canal. Not to scale.

COMPARISONS AND PHYLOGENETIC POSITION OF *LAMARQUEAVIS*

With regards to its phylogenetic position, *Lamarqueavis australis* may be included within Ornithurae because it shows the presence of a procoracoidal process, a concave cotyla scapularis, and lacks a dorsal fossa (LONGRICH, 2008; figure 3). In addition, the presence of a deep and concave sulcus for the triosseal canal may be an additional derived trait for Ornithurae (figure 3). In non-ornithothoracine birds (e. g. *Archaeopteryx*, *Sapeornis*, *Jeholornis*, *Zhongornis*, Confuciusornithidae; ZHOU & ZHANG, 2003a, b; MAYR *et al.*, 2007; GAO *et al.*, 2008; CHIAPPE *et al.*, 1999) the triosseal canal of the coracoid is not concave, being surely absent. In Enantiornithes the omal extremity of the coracoid is columnar and lacks any sign of a triosseal concavity; moreover the triosseal canal in these birds was surrounded in a larger extent by the scapula rather than the coracoid (WALKER, 1981; CHIAPPE & WALKER, 2003). In one of the basalmost ornithurine birds, *Patagopteryx*, the coracoid is so modified that the morphology of the triosseal canal is uncertain (see CHIAPPE, 2002). However, in remaining Ornithurae (e. g. *Yixianornis*, *Gansus*, *Yanornis*, *Apsaravis*, *Jianchangornis*; CLARKE *et al.*, 2006; ZHOU & ZHANG, 2001; YOU *et al.*, 2006; CLARKE & NORELL, 2002; ZHOU *et al.*, 2009) the triosseal sulcus is represented by a distinctive and deep concavity located on the omal extremity of the coracoid. This concavity is delimited medially by a ridge that connects the scapular cotyla with the acrocoracoidal process, and anteriorly by the brachial tuberosity. Regrettably, in the basal ornithurines *Archaeorhynchus* and *Hongsbanornis* (ZHOU & ZHANG, 2005, 2006) the coracoid is poorly preserved and the morphology of the triosseal sulcus cannot be properly observed.

Another trait that may be diagnostic of Ornithurae is the laterally protrudent humeral articular surface (figure 3). In fact, in *Archaeopteryx*, *Sapeornis* and Confuciusornithidae the humeral facet is a concave surface located posterolaterally, being dorsoventrally oriented and lacking lateral protrusion. In contrast, *Jeholornis* appears to exhibit a dorsolaterally oriented and protrudent humeral articular facet (ZHOU & ZHANG, 2003b) which superficially resembles the condition of derived Ornithurae. Regrettably, in known specimens of *Jeholornis* the coracoids and its morphology could not be observed in detail due to its poor preservation. In Enantiornithes, in contrast to the condition seen in non-ornithothoracine birds, the humeral articular surface has migrated dorsally, but still lacks a lateral protrusion (CHIAPPE & WALKER, 2003). In Ornithurae the humeral articular surface is an oval-shaped, flat, and dorsally facing surface, a condition reminiscent to that of Enantiornithes. However, in Ornithurae the humeral articular surface is laterally oriented, and forms the strongly convex lateral margin of the omal end of the coracoid seen in ornithurine birds. This condition is present in all known Ornithurae, including the basal genera *Archaeorhynchus*, *Hongsbanornis*, *Jianchangornis*, *Yanornis*, *Yixianornis*, and *Patagopteryx*, as well as derived taxa (e. g. *Ichthyornis*, *Ambiortus*, and *Neornithes*) (ZHOU & ZHANG, 2001; HOPE, 2002; CLARKE & NORELL, 2002; CLARKE, 2004; CLARKE *et al.*, 2006; YOU *et al.*, 2006; ZHOU *et al.*, 2009).

Within Ornithurae, the morphology of *Lamarqueavis* is clearly reminiscent to that of the crown-bird clade Neornithes. In fact this genus could be included within Neornithes on the basis of the following apomorphic feature: humeral articular surface not extended sternally beyond the omal margin of the scapular cotyla (see figure 3). This condition was originally defined by HOPE (2002) as a derived trait unique to Neornithes. In fact, in most non-ornithurine (e. g. *Enantiornithes*, *Confuciusornis*, *Archaeopteryx*; CHIAPPE *et al.*, 1999; CHIAPPE & WALKER, 2003; MAYR *et al.*, 2007) and basal ornithurine birds (e. g. *Ichthyornis*, *Yanornis*, *Apsaravis*; CLARKE & NORELL, 2002; CLARKE, 2004; CLARKE *et al.*, 2006) the humeral articular surface reaches the level of the sternal end of the scapular cotyla (contra LONGRICH, 2008). In known Hesperornithiformes (e. g. *Hesperornis*, *Baptornis*; MARTIN & TATE, 1976) the coracoid is highly modified, but the plesiomorphic condition is present, being the humeral articular surface sternally displaced with respect to the scapular cotyla.

Within Neornithes, the affiliation of *Lamarqueavis* to any particular extant or extinct avian clade is uncertain. Although this genus shows an amount of features that may be considered as a whole diagnostic of charadriiform neornithines (i. e. coracoidal neck massive at the level of the humeral articular surface, shaft of coracoid tilted medially in relation to the sternal end, distally posited foramen for *n. supracoracoidei*; HOPE, 2002), this combination of characters probably reflects a plesiomorphic morphology, and thus the referral of *Lamarqueavis* to Charadriiformes is unwarranted (HOPE, 2002; see also LONGRICH, 2008).

The overall morphology of the coracoid of *Lamarqueavis* is highly reminiscent to that of the genera *Cimolopteryx* Marsh, 1889 and *Ceramornis* Brodkorb, 1963, which constitute the Family Cimolopterygidae. In fact, *Lamarqueavis* and the above mentioned genera may be grouped within Cimolopterygidae on the basis of the following combination of derived traits: 1) humeral articular surface strongly oriented ventrally; 2) procoracoidal process well extended sternally and developed as a thin lamina; and 3) large and ventrally located foramen for the *n. supracoracoidei*. Within Ornithurae

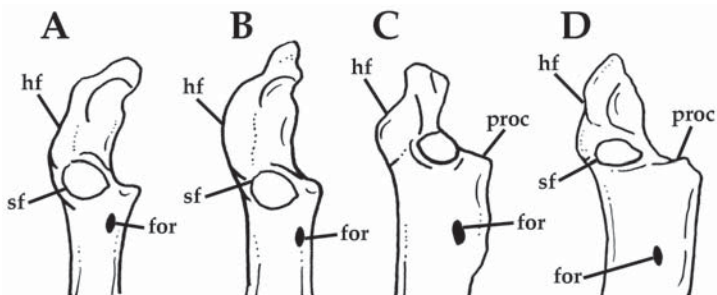


Figure 4. Comparative figure of left coracoids of *Lamarqueavis* in dorsal views. A, *Lamarqueavis* *petra*; B, *L. minima*; C, *L. sp.*; D, *L. australis*. (A-B, modified from HOPE, 2002; C, modified from LONGRICH, 2008). Abbreviations: for, foramen for *n. supracoracoidei*; hf, humeral facet; proc, procoracoidal process; sf, scapular facet. Not to scale.

most taxa (e. g. *Yanornis*, *Archaeorhynchus*, *Iaceornis*, *Apsaravis*, *Ichthyornis*; CLARKE & NORELL, 2002; CLARKE, 2004; CLARKE *et al.*, 2006) show a laterally oriented humeral articular surface. However, in *Cimolopteryx* species the humeral articular surface shows its main transverse axis dorsoventrally oriented (figures 3-4). This condition is also shown by *Lamarqueavis* (i. e. *L. australis*, "*C.*" *minima*, and "*C.*" *petra*; BRODKORB, 1963), as well as by *Ceramornis major*, in which this condition is less developed, and its humeral articular surface is still exposed in dorsal view (BRODKORB, 1963; HOPE, 2002; figure 3 M-N). Another trait useful to diagnose Cimolopterygidae may be the presence of a well developed and laminar procoracoidal process (figure 3). Although the presence of such structure is currently considered as diagnostic of Ornithurae (LONGRICH, 2008), the development of this process is variable within this clade, being absent in several taxa (AGNOLIN *et al.*, 2006). In *Cimolopteryx rara* Marsh, 1892 the procoracoid is well developed and laterally extended, and approaches the medial edge of the acrocoracoidal process. This condition is also seen in *Lamarqueavis* and *Ceramornis* in which the procoracoidal process is even more extensive, and differs from that of *Cimolopteryx* in being more extended sternally. Regrettably the procoracoid is not preserved in the holotype and referred specimens of *Cimolopteryx maxima*, and thus the condition in this species is unknown (BRODKORB, 1963). This process is also very well developed and extensive in very basal ornithurine birds, such as *Gansus*, *Yanornis*, and *Yixianornis* (YOU *et al.*, 2006; CLARKE *et al.*, 2006), although its sternal expansion is not as developed as in cimolopterygids. On the other hand, in most derived non-neornithine ornithurine birds the procoracoid process is reduced (e. g. *Apsaravis*; CLARKE & NORELL, 2002) or is only developed as a subtriangular knob lacking any sternal projection (e. g. *Ambiortus*, *Ichthyornis*, *Iaceornis*, *Archaeorhynchus*, *Baptornis*; CLARKE, 2004; KUROCHKIN, 1999; ZHOU & ZHANG, 2005). In Neornithes, procoracoid morphology is highly variable, although a procoracoidal process appears to be invariably absent in basal clades (i. e. Ratitae, Tinamiformes, Lithornithidae, Galliformes; HOPE, 2002; AGNOLIN *et al.*, 2006). Finally, in the Cretaceous galliform-like genus *Palintropus* the procoracoid is also absent (HOPE, 2002; LONGRICH, 2008).

Another cimolopterygid diagnostic trait is the location of the foramen for the *n. supracoracoidei*. In *Cimolopteryx rara* this foramen is located well beyond the scapular cotyla and is separated from this foramen by at least half of the length of the main axis of this cotyla (BRODKORB, 1963; figure 3). In *Lamarqueavis* the same condition is present, with the exception of *L. australis*, in which this foramen is autapomorphically located well beyond the scapular cotyla, being separated from it by one and a half times the length of the main axis of the cotyla. In *Ceramornis* a similar condition to that of *C. rara* is also present (BRODKORB, 1963). Regrettably, in the holotype of *C. maxima* the portion of the foramen for the *n. supracoracoidei* is not preserved, consequently, the condition of the foramen is not known in this species (BRODKORB, 1963).

On the other hand, in basal ornithurines, such as *Yixianornis* and *Ichthyornis*, the *n. supracoracoidei* foramen is near in contact with the cotyla

scapularis (CLARKE *et al.*, 2006; CLARKE, 2004). The *n. supracoracoidei* foramen in hesperornithiform birds is located proximally, within the base of the procoracoid process (MARTIN & TATE, 1976). In *Apsaravis* this foramen is distally located, but it is placed within a large and deep dorsal fossa (CLARKE & NORELL, 2002), a condition very different to that seen in cimolopterygids, being reminiscent to the plesiomorphic configuration shared by all Enantiornithes (CHIAPPE & WALKER, 2003).

The above mentioned combination of features is only present in the genera *Cimolopteryx*, *Lamarqueavis*, and *Ceramornis*, as well as several specimens coming from the Upper Cretaceous (Campanian) of Canada described by LONGRICH [2008 as *Ornithurae* indet. (A) to (F); see also TOKARYK & JAMES, 1989] and two isolated coracoids from the Palaeocene of Kazakhstan illustrated by NESSOV (1992) and considered as *Cimolopteryx*-like forms by HOPE (2002). All these coracoids may be considered together as belonging to the family Cimolopterygidae.

Within cimolopterygids HOPE (2002) recognized a “species group” including several *Cimolopteryx* species (i. e. *C. petra*, and *C. minima*), and isolated coracoids cited by previous authors as *Cimolopteryx* spp. This “species group” is here named as *Lamarqueavis* and is diagnosed by a unique combination of traits (see *Lamarqueavis* generic diagnosis). These include a large and posteriorly extended procoracoid process which is straight or slightly convex along its medial margin (see figure 4). As indicated above, in *Cimolopteryx sensu stricto*, and *Ceramornis* the procoracoid is relatively smaller, and is concave along its entire medial margin. The *Lamarqueavis* condition is clearly present in *L. australis* in which the procoracoid shows a slightly convex medial rear. Another diagnostic feature shared by all *Lamarqueavis* species (i. e. “*C. petra*”, “*C. minima*”, and *L. australis*) is the presence of a subrectangular humeral articular surface with dorsal and ventral margins nearly straight, whereas omal and sternal edges

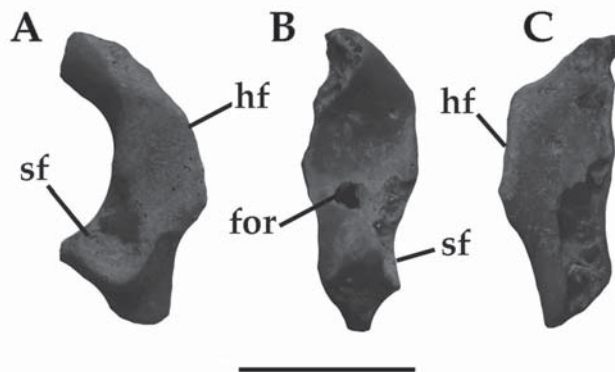


Figure 5. *Cf. Cimolopterygidae* indet. (MML 208), proximal end of left coracoid in: A, dorsal; B, medial; and C, ventral views. Abbreviations: for, foramen; hf, humeral facet; sf, scapular cotyla. Scale bar 5 mm.

are slightly convex. In most ornithurines (e. g. *Yixianornis*, *Yanornis*, *Ichthyornis*; CLARKE, 2004; CLARKE *et al.*, 2006), including Neornithes (and also *Cimolopteryx sensu stricto* and *Ceramornis*) the humeral articular surface is ovoidal in contour and shows all margins strongly convex. In addition, in contrast to remaining cimolopterygids (i. e. *Cimolopteryx*, *Ceramornis*), *Lamarqueavis* shows the scapular facet of the coracoid slightly elongate transverse to the main axis of the coracoid, whereas in remaining genera this cotyla is entirely round. The above mentioned combination of traits is present in *Lamarqueavis australis*, "*Cimolopteryx*" *minima*, "*C.*" *petra*, and "Ornithurae B" of LONGRICH (2008), suggesting that they all may be included within the genus *Lamarqueavis*.

In addition to the above mentioned derived features, *Lamarqueavis* may be distinguished from other basal and derived Ornithurae based on a large combination of traits. *Lamarqueavis* is distinguished from *Hongsbanornis* in having a thinner coracoidal neck, a nearly straight lateral margin of the distal end of the coracoid, and the thinner procoracoid, which is not knob-like (ZHOU & ZHANG, 2005). *Lamarqueavis* differs from *Gansus* and *Archaeorhynchus* in having a more gracile coracoid and in the coracoidal diaphysis strongly tilted medially (ZHOU & ZHANG, 2005; YOU *et al.*, 2006). In addition, in *Gansus* the procoracoid is strongly concave on its medial margin and is more robust than in the new genus (YOU *et al.*, 2006). *Lamarqueavis* may be distinguished from *Yixianornis* in the different shape and morphology of the humeral articular surface and scapular cotyla, and in the absence of a distally enlarged procoracoid process (CLARKE *et al.*, 2006). From *Ambiortus* clearly differs, among other minor details, in showing a distal expansion of the procoracoid (KUROCHKIN, 1999).

Lamarqueavis further differs from *Apsaravis* in having a deeper and cup-shaped scapular cotyla, different shape of the humeral articular surface, and in the absence of a dorsal fossa (CLARKE & NORELL, 2002). *Lamarqueavis* species may be distinguished from *Iaceornis* in the more robust proportions of the coracoid, a more deeply excavated triosseal canal, and in the poorly defined dorsal intermuscular line (CLARKE, 2004).

The new genus is distinguished from *Ichthyornis* in the wider coracoidal neck, transversely elongate cotyla scapularis, less defined intermuscular line, and shallower impression for the m. sternocoracoidei (CLARKE, 2004). From "*Ichthyornis*" *validus* Marsh, 1880 *Lamarqueavis* differs in the different shape of the humeral articular surface, in the smaller and deeper scapular cotyla, and the foramen for the n. *supracoracoidei* visible in dorsal view (CLARKE, 2004).

From the Cretaceous neornithine *Palintropus* Brodkorb, 1970 *Lamarqueavis* is clearly distinguishable on the basis of a smaller scapula cotyla, presence of a well developed procoracoidal process, and the absence of a medial muscle scar within the triosseal canal (LONGRICH, 2008).

The derived ornithurine *Limenavis patagonica* CLARKE and CHIAPPE, 2001, comes from the same locality and stratigraphical horizon where *Lamarqueavis*

australis was found. Regrettably, the only known specimens of *Limenavis* did not preserve its coracoidal bone. However, although direct comparisons with *Lamarqueavis* are not possible, the *Limenavis* holotype represents a bird much larger than *Lamarqueavis*. Moreover, *Limenavis* is considered by CLARKE & CHIAPPE (2001) as a basal Carinatae bird, whereas the specimens here described belong to a more derived bird nested within the lesser inclusive clade Neornithes.

cf. Cimolopterygidae Brodkorb, 1963

Genus and species indeterminate

Referred material. MML 208, proximal end of left coracoid lacking omal extremity (figure 5).

Measurements. Total length (preserved): 9 mm; maximum length of scapular cotyla: 2.4 mm; maximum width of scapular cotyla: 2.5 mm; maximum width of humeral articular surface: 3 mm; maximum length of humeral articular surface: 4.6 mm; maximum width of procoracoidal process: 1.2 mm.

Description. The coracoid comes from a small-sized bird, the size of an ovenbird (*Furnarius rufus*). It shows a thin coracoidal neck, which is oval in cross section.

The humeral articular surface is subrectangular in contour; it shows its proximal margin straight, and its distal margin slightly convex, whereas its medial and lateral edges are nearly straight. The humeral articular surface is medially tilted and posteriorly reaches the mid-level of the scapular cotyla. The scapular cotyla is subcircular in contour, showing its transverse axis slightly larger than the anteroposterior one. The scapular cotyla is cup-shaped and relatively deep. The triosseal canal is relatively deep and lacks any sign of muscular ridges; on the other hand, it shows a large pneumatic foramen. The procoracoid is short and spike-like. A dorsal fossa is absent.

COMPARISONS OF MML 208

MML 208 may be included within Ornithurae because it shows the presence of a well developed procoracoidal process, a concave scapular cotyla, a deep and concave sulcus for the triosseal canal, and a laterally protrudent humeral articular surface (LONGRICH, 2008; present paper). MML 208 resembles Neornithes in the humeral articular surface not extended sternally beyond the omal margin of the scapular cotyla (HOPE, 2002). In spite of its incompleteness, MML 208 resembles *Lamarqueavis* in the subrectangular-shaped humeral articular surface, which is strongly oriented ventrally (see above). However, MML 208 differs from *Lamarqueavis* in having a smaller procoracoidal process, and in the presence of a large pneumatic foramen within the triosseal canal; a feature unknown in

remaining cimolopterygids. Moreover, MML 208 shows a larger size, and a shorter humeral articular surface with a straight anterior margin.

Because of its fragmentary nature, and contradictory combination of traits, MML 208 could not be located more precisely within Neornithes, and is here considered as cf. Cimolopterygidae indet.

DISCUSSION

THE FOSSIL RECORD OF LATE CRETACEOUS FOSSIL BIRDS

Cimolopterygidae may be considered as the most numerically abundant and specifically diverse group of stem Neornithes known from the Mesozoic (HOPE, 2002). In fact, at least eight species are currently assigned to this group, ranging in sizes from a gull to a sparrow (HOPE, 2002; this paper). In spite of its abundance, up to now the geographic range of cimolopterygids was restricted to the continents of North America and Eurasia (see HOPE, 2002). In the present paper Cimolopterygidae is added to the Mesozoic avifauna of the South American continent. In this regard I disagree with the proposal of FOUNTAINE *et al.* (2005) which indicate that “the relative quality (comparing diversity and completeness) of the fossil record of birds in the Mesozoic is just as good as that of many other terrestrial vertebrates” (see also FARA & BENTON, 2000). In contrast with this proposal, Campanian-Maastrichtian fossil birds from Patagonia include only a handful of bird specimens, including recently published Ornithurae, that probably represent less than seven different taxa (i. e. four indetermined Ornithurae, cf. Hesperornithes, *Limenavis patagonica*, and *Alamitornis minutus*; CLARKE & CHIAPPE, 2001; HOPE, 2002; AGNOLIN & MARTINELLI, 2009). This record is in clear contrast with that of other vertebrate groups, among them: fishes, turtles, snakes, anurans, and dinosaurs, several of which are represented by hundreds of collected specimens (ALBINO, 1987; BÁEZ, 1987; BONAPARTE *et al.*, 1984, 1987; CIONE, 1987; MARTINELLI & FORASIEPI, 2004). Moreover, there are abundant tooth representing at least 20 different mammalian taxa (BONAPARTE, 1990, 2002; ROUGIER *et al.*, 2009). The meagre fossil avifaunal record, together with the fact that each new discovery of a fossil bird in South America consistently adds new and previously unknown component to these bird faunas, indicate that the Cretaceous record of Aves in South America is extremely incomplete. In this way, previous claims (FARA & BENTON, 2000; FOUNTAINE *et al.*, 2005) proposing that the Mesozoic fossil bird record is accurate are not applicable for South America, at least.

THE CRETACEOUS-PALEOGENE EXTINCTION EVENT

Some authors, based mainly on molecular data have suggested that birds were not severally affected by the K/T extinction event, and that most clades of Neornithes were well in progress along most of the Late Cretaceous (see detailed discussion in FEDUCCIA, 2003; SLACK *et al.*, 2006). The material here

reported, does not lend support to the idea that birds suffered a mass extinction at the end of the Cretaceous (contra FEDUCCIA, 1995, 1996, 2003; LONGRICH, 2006), and is in concordance with some data yielded by molecular biologists (see detailed discussion in FEDUCCIA, 2003; SLACK *et al.*, 2006), which dismiss bird extinction at the Cretaceous/Palaeocene boundary. In this way, cimolopterygids were probably not affected by such extinction event, and survived the K/T boundary, being well represented in Mesozoic avifaunas of several continents, as well as in Palaeocene strata from Asia (HOPE, 2002; this paper).

PALAEOECOLOGY OF LATE CRETACEOUS BIRDS

Traditionally, derived ornithurine birds (including Neornithes) were considered as the dominant taxa of shoreline and marine habitats through the Cretaceous, whereas in the continental deposits basal taxa (Enantiornithes) and “archaic” ornithurines were more abundant and diverse (MARTIN, 1983; FEDUCCIA, 1995, 2003). However, recent claims argued that this pattern may be more apparent than real. NORELL & CLARKE (2001; see also CLARKE & NORELL, 2002) indicated that this apparent pattern may be considered a preservation artefact or a bias in the collecting sampling. In the same way, CHIAPPE *et al.* (2002), MORRISON *et al.* (2005), and TYKOSKI & FIORILLO (2010) suggested that Enantiornithes played a more important role in Late Cretaceous marine environments than previously thought. The later authors based their proposal only on three disarticulated and incomplete skeletons and a couple of single isolated bones, which represent the only enantiornithine specimens found in all Cretaceous marine deposits around the world. In the same way, in very rich and abundant ornithurine-dominated avifaunas from Late Cretaceous marine deposits (e. g. Judith River, Lance Creek, Los Alamitos; HOPE, 2002; LONGRICH, 2008; AGNOLIN & MARTINELLI, 2009) enantiornithes are absent, or nearly so. Additionally, YOU *et al.* (2006), on the basis on fossil record and phylogenetic bracket, proposed that Neornithes may have originated in water environments, and that probably aquatic niches played an important role in Ornithurine evolution. Accordingly, DYKE *et al.* (2007) indicated that the presence of more modern birds in Mesozoic (and Early Palaeocene) aquatic environments is likely independent of its preservation potential, and may suggest that ornithurines were prevalent in those habitats. This hypothesis is in agreement with the Allen Formation’s avifaunal record, which yielded at least four different derived ornithurines, but no single bone belonging to enantiornithine or an “archaic” ornithurine was found up to now.

THE PLACE OF ORIGIN OF MODERN BIRDS

LONGRICH (2008) indicate that in the Late Cretaceous of North America, ornithurines were probably both more speciose and abundant than in other landmasses, as suggested by the fossil record. In this way, this author argued that available fossils indicated that Ornithurae and Neornithes may have its origin in Laurasia, because the majority of gondwanan mesozoic birds are

Enantiornithes or very basal stem-Ornithurae. However, some evidence argues against this hypothesis. On the first hand, the fossil record of Neornithes (e. g. OLSON, 1992; CHIAPPE, 1996; CASE & TAMBUSI, 1999; CHATTERJEE, 2002; HOPE, 2002; CLARKE *et al.*, 2005; AGNOLIN *et al.*, 2006; TAMBUSI & ACOSTA HOSPITALECHE, 2007; CORIA *et al.*, 2008) and very derived Ornithurae (e. g. CLARKE & CHIAPPE, 2001; AGNOLIN & MARTINELLI, 2009; this paper) in both Antarctica and South America, indicate that diverse Ornithurae-faunas were also present in Gondwana. Moreover, there is more complete and informative neornithine fossil evidence in Late Cretaceous of South America and Antarctica (see for example CHATTERJEE, 2002; CLARKE *et al.*, 2005), than in Laurasian landmasses, where the record is still extremely patchy and biased (see HOPE, 2002; CLARKE, 2004). In this regard, the evidence at hand precludes considering a Laurasian origin of modern birds.

On the other hand, CHATTERJEE (2002) indicate that the Antarctic fossil record suggests that some groups of plants and animals may have had its origin in Antarctic landmasses. This author suggested that Antarctica may be the cradle of most modern neornithine groups. This hypothesis is also contradicted by the fossil record, which evidences the presence of Neornithes or neornithine-like forms since Campanian times in North America, Europe, Asia, and South America (HOPE, 2002). In fact, the meagre evidence shows that it is likely that Neornithes have reached all great landmasses well before the end of the Cretaceous. In conclusion, because of the paucity of the fossil record, the cradle of modern birds is up to now uncertain.

BIRDS AND PTEROSAUR RADIATION AND EXTINCTION

Pterosaurian archosaurs were the dominant group of flying reptiles along most of the Cretaceous (WANG *et al.*, 2005). However, an important decrease in taxonomic diversity and size disparity was detected by some authors at the end of this period, being most Latest Cretaceous pterosaurs large to gigantic forms belonging to the clade Azhdarchidae (OSI *et al.*, 2005). SLACK *et al.* (2006) proposed that this decrease in pterosaur diversity and size was probably due to competitive interaction with birds (SLACK *et al.*, 2006; BUTLER *et al.*, 2009) suggested that perhaps critical in the expansion of bird clades was the extinction or loss of small pterosaurs (less than 2 meters wingspan) in Late Cretaceous times. Moreover, although underrepresented in the fossil record, small to medium sized pterosaurs are still present in several Late Cretaceous sediments (AVERIANOV *et al.*, 2005; MCGOWEN *et al.*, 2002; AGNOLIN & VARRICCHIO, in prep.), indicating that Late Cretaceous pterosaurs were not only large sized forms. SLACK *et al.* (2006), following UNWIN (2003), noted a decline in pterosaur taxonomic diversity at the end of the Cretaceous, which they related to an increase in avian (mainly neornithine) diversification (but see CHIAPPE & DYKE, 2002). We agree with these authors that the latest Cretaceous record of pterosaurs is mainly restricted to the Azhdarchidae, a group found almost around the world, excluding Antarctica (BUFFETAUT *et al.*, 1996, 2002; KELLNER & LANGSTON, 1996; PEREDA-SUBERBIOLA *et al.*, 2003; OSI *et*

al., 2005; HENDERSON & PETERSON, 2006). This Late Cretaceous dominance of azhdarchids was considered as indicative of relatively uniform post-Campanian pterosaur faunas (BUFFETAUT *et al.*, 1996; MCGOWEN *et al.*, 2002). However, Campanian-Maastrichtian beds of Europe yielded isolated remains referable to the Ornithocheiroidea clade and several other non-azhdarchid taxa (WELLNHOFER, 1991; AVERIANOV *et al.*, 2005; AGNOLIN & VARRICCHIO, in prep.), and Campanian-Maastrichtian beds of USA and Brazil yielded specimens of pteranodontid-like taxa and Nyctosauridae, respectively (WELLNHOFER, 1991; BUFFETAUT *et al.*, 2002). Additionally, a nearly complete rostrum from the Maastrichtian of USA was recently assigned to the Tapejaridae (KELLNER, 2004). All these specimens suggest that the diversity of Latest-Cretaceous pterosaurs was probably comparable to that of Early Cretaceous times. This contrasts with previous authors (BUFFETAUT *et al.*, 2002; SLACK *et al.*, 2006; BUTLER *et al.*, 2009) which proposed poor taxonomic pterosaurian diversity at the end of this period. All these evidence suggest that the hypothesis of competitive interaction between birds and pterosaurs is dubious, at least.

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