



Systematic palaeontology (Vertebrate palaeontology)

## New enantiornithine bird (Aves, Ornithothoraces) from the Late Cretaceous of NW Argentina

*Un oiseau enantiornithine (Aves, Ornithothoraces) du Crétacé supérieur du Nord-Ouest de l'Argentine*

Fernando Emilio Novas<sup>a,\*</sup>, Federico Lisandro Agnolín<sup>a,b</sup>, Carlos Agustín Scanferla<sup>a</sup>

<sup>a</sup> Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470 (C1405BDB), Buenos Aires, Argentina

<sup>b</sup> Fundación de Historia Natural "Félix de Azara", Departamento de Ciencias Naturales y Antropología, CEBBAD - Universidad Maimónides, Valentín Virasoro 732 (C1405BDB), Buenos Aires, Argentina

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### ABSTRACT

A new enantiornithine bird, *Intiornis inexpectatus* gen. et sp. nov., is described here. It is based on a partial hind limb found in beds of the Upper Cretaceous Las Curtiembres Formation (Campanian), North-West Argentina. The new taxon is referred to the family Avisauridae on the basis of its cranially convex third metatarsal. Several features suggest close relationships between *Intiornis* and the avisaurid *Soroavisaurus*, from the Lecho Formation (Maastrichtian; North-West Argentina). *Intiornis* was the size of a sparrow, thus representing the smallest Enantiornithes known from South America. The new species shows adaptations for a perching mode of life. Moreover, the hypothesis suggesting that the flying pterosaur reptiles decrease in taxonomic diversity due to competitive interaction with birds is discussed. The new species shows adaptations for a perching mode of life. Moreover, the hypothesis suggesting that the flying pterosaur reptiles decrease in taxonomic diversity due to competitive interaction with birds is discussed.

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### RÉSUMÉ

Un nouvel oiseau enantiornithine, *Intiornis inexpectatus* gen. et sp. nov., est décrit ici. Cette description est fondée sur une partie de membre postérieur, trouvé dans les couches du Crétacé supérieur de la Formation Curtiembres (Campanien) du Nord-Ouest de l'Argentine. Le nouveau taxon est rapporté à la famille des Avisauridae, sur la base de son troisième métatarsien en gouttière convexe. Plusieurs caractères suggèrent une relation étroite entre *Intiornis* et l'avisauridé *Soroavisaurus* de la formation Lecho (Maastrichtien, Nord-Ouest de l'Argentine). *Intiornis* avait la taille d'un moineau, et ainsi, est le plus petit des représentants des Enantiornithes, connu en Amérique du Sud. La nouvelle espèce montre des adaptations à un mode de vie perché. On discute, en outre, l'hypothèse selon laquelle la diversité taxonomique des reptiles ptérosaures volants diminue en raison d'une interaction compétitive avec les oiseaux. La nouvelle espèce montre des adaptations à un mode de vie perché. On discute, en outre, l'hypothèse selon laquelle la diversité taxonomique des reptiles ptérosaures volants diminue en raison d'une interaction compétitive avec les oiseaux.

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\* Corresponding author.

E-mail addresses: fernovas@yahoo.com.ar, Argentina.fernovas@yahoo.com.ar (F.E. Novas), fedeagnolin@yahoo.com.ar (F.L. Agnolín), agustin.scanferla@yahoo.com.ar (C.A. Scanferla).

## 1. Introduction

Enantiornithes was a diverse group of birds that inhabited inland and littoral environments during the Cretaceous, becoming extinct at the Cretaceous-Tertiary boundary (Chiappe and Walker, 2002; Feduccia, 1995). Geographically, enantiornithine birds were distributed worldwide, with the exception of Antarctica (Chiappe, 1996; Close et al., 2009). Probably due to their considerable geographical range, the Enantiornithes developed a wide array of morphologies and ecological types: there were wading and diving forms (i.e., *Lectavis* and *Yungavolucris* (Chiappe, 1993)), as well as flying taxa with perching abilities (e.g. *Sinornis*, *Vescornis* (Sereno and Rao, 2002; Zhang et al., 2004)). Basal enantiornithines included toothed birds (e.g., *Jibeinia*, *Longipteryx* (Hou, 2000; Zhang et al., 2001)), whereas in others their teeth were restricted to the rostral portion of the maxilla, or were toothless (e.g. *Longirostravis*, *Gobipteryx* (Hou et al., 2004; Kurochkin, 2000)).

The fossil record of South American enantiornithes is mainly represented by discoveries made in Upper Cretaceous rocks from Argentina (Chiappe, 1993; Chiappe and Walker, 2002; Walker et al., 2007). The Argentine record is made up by six genera and species, including *Neuquenornis volans*, from the Santonian-Campanian Bajo de la Carpa Formation of NW Patagonia (Chiappe and Calvo, 1994), and *Enantiornis leali*, *Soroavisaurus australis*, *Lectavis brevicola*, *Yungavolucris brevipedalis*, and *Martinavis vincei* from the Maastrichtian Lecho Formation of NW Argentina (Chiappe, 1993; Walker, 1981; Walker et al., 2007).

In the present article, we describe a new genus and species of enantiornithine bird, *Intiornis inexpectatus*, which adds significant information about diversity of this archaic bird group in South America.

## 2. Geological setting

The specimen was recovered from levels of the Las Curtiembres Formation (Campanian, Upper Cretaceous), which also yielded large number of individuals of the small pipid frog *Saltenia ibanezi* (Báez, 1981; Narváez and Sabino, 2008). Recent field trips conducted by the senior author resulted in the discovery of basal teleostean fishes, probable podocnemidid pleurodiran turtles, and remains of mesoeucrocodylian crocodiles, and theropod and sauropod dinosaurs (Scanferla pers. obs.) (Fig. 1).

## 3. Systematic palaeontology

Aves Linnaeus, 1758

Ornithothoraces Chiappe and Calvo, 1994

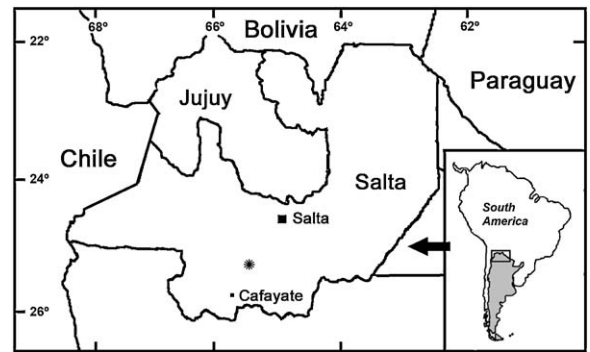
Enantiornithes Walker, 1981

Euenantiornithes Chiappe, 2002

Avisauridae Brett-Surman & Paul, 1985

*Intiornis inexpectatus* gen. et sp. nov.

**Holotype:** MAS-P/2 1 (Paleontological Collection of the Museo de Antropología, Salta City, Salta province, Argentina), slab and counter-slab preserving a right foot, articulated with the distal end of the corresponding tibiotarsus



**Fig. 1.** Map indicating the fossiliferous locality in northwestern Argentina (Salta Province). The asterisk indicates the place where *Intiornis inexpectatus* was collected.

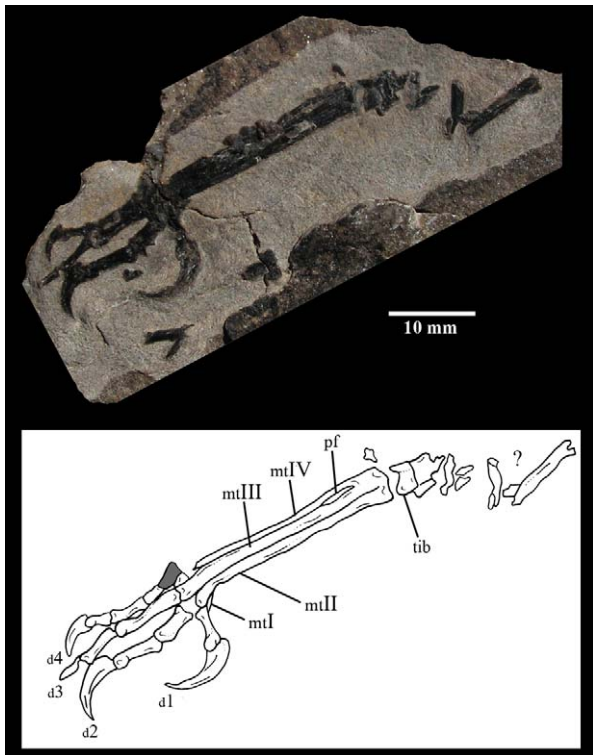
**Fig. 1.** Carte indiquant la localité fossilifère en Argentine nord-occidentale (Province de Salta). L'astérisque indique l'endroit où *Intiornis inexpectatus* a été récolté.

**Diagnosis.** Avisaurid enantiornithine with the following diagnostic features: 1) tall and cup-like intercotylar prominence, even more developed than in *Lectavis*; 2) phalanx IV-4 anteroposteriorly short, being subequal in length to phalanx IV-2; 3) phalanx I-1 proportionally short and stout

**Etymology.** *Inti*, sun in Quechua language; and *ornis*, bird in Greek. *inexpectatus*, in reference of the casual and weird technical situation of the finding of the holotype specimen

## 4. Description

*Intiornis* is a sparrow-sized enantiornithine bird (metatarsal length, 21 mm.) with an elongate tarsometatarsus. As typically occurs in enantiornithine birds, the distal end of the tibiotarsus shows a large and anteriorly flat medial condyle, a narrow and deep intercondylar sulcus, and distal condyles proximally cut off. Correspondingly, the proximal end of the tarsometatarsus shows an enlarged medial cotyle and a well-developed and cup-like intercotylar tubercle, even more developed than in the peculiar enantiornithine *Lectavis* (Chiappe, 1993). However, in *Intiornis* this prominence is even more developed proximally, being reminiscent to the condition present of the Ornithothoraces (Morrison et al., 2005). The tarsometatarsal lateral cotyle is smaller than the medial one, but it is well excavated proximally. As occurs in most other Enantiornithes, the tarsometatarsus of *Intiornis* is fused only proximally (Martin, 1995). In cranial view, the proximal end of the tarsometatarsus is well excavated, as documented in other Enantiornithes (e.g. *Lectavis*, *Soroavisaurus*, *Avisaurus* (Chiappe, 1993; Varricchio and Chiappe, 1995)). All metatarsals are nearly straight, with metatarsal II being tightly appressed to metatarsal III in cranial view, as also applies for *Soroavisaurus* and *Avisaurus*. The shaft of metatarsal III shows its cranial edge convex in cross-section, a feature interpreted as diagnostic of Avisauridae (Chiappe, 1993). The shaft of metatarsal II is wider than that of III, and both are broader than IV, as characteristically occurs in Enantiornithes (Chiappe and Walker, 2002). An elongate and narrow proximal fenestra exists between



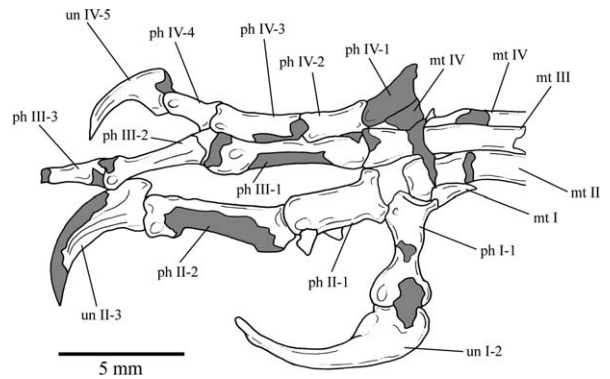
**Fig. 2.** *Intiornis inexpectatus* (MAS-P/2 1; holotype), A–B, right partial hindlimb. Abbreviations: I–IV, metatarsals or digits I–IV; pf, proximal fenestra; tib, distal end of tibiotarsus. Scale bar 1 cm.

**Fig. 2.** *Intiornis inexpectatus* (MAS-P/2 1; holotype), A–B Partie de membre postérieure droite. Abréviations : I–IV, métatarsiens ou doigts I–IV; pf, fenestra proximale; tib, extrémité distale du tibiotarse. Barre d'échelle : 1 cm.

metatarsals IV and III, constituting a feature that *Intiornis* uniquely shares with *Soroavisaurus* (Chiappe, 1993). The distal trochlea of metatarsal II is incompletely preserved, but appears to be broader than that of metatarsals III and IV, another diagnostic trait of Enantiornithes (Sereno, 2000). The distal trochlea of metatarsal III is poorly excavated and shows poorly defined trochlear rims, in contrast with the well developed trochlea exhibited by derived Ornithothoraces (Morrison et al., 2005). The distal trochlea of metatarsal IV is highly damaged, but the preserved portion indicates that it was thinner than metatarsals II and III (Figs. 2–3).

Pedal digits are gracile and elongate, and pedal unguals are acute and recurved. *Intiornis* shows a typical anisodactyl foot, its pedal digit III being the longest, followed in decreasing length by digits IV, II, and I, an arrangement also reported for *Sinornis* (Sereno et al., 2002). Similar to other birds, the phalangeal formula is 2–3–4–5–X.

Digit IV bears four short and stout pre-ungual phalanges. Pedal phalanx IV-4 is short and stout, being subequal in length to phalanx IV-2. In contrast, in remaining Enantiornithes, including *Sinornis* and *Concornis* phalanx IV-4 is slender and elongate, being much longer than phalanx IV-2 (Sereno et al., 2002). Pedal unguual IV is acute, elongate, and strongly curved, as in most Enantiornithes. An enlarged proximodorsal lip is present. The proximal artic-



**Fig. 3.** *Intiornis inexpectatus* (MAS-P/2 1; holotype), line drawing of right partial pes. In deep grey are indicated broken portions of bone. Abbreviations: I–IV, metatarsals or digits I–IV; 1–5, phalangeal number; mt, metatarsal; ph, phalanx; un, unguual. Scale bar 5 mm.

**Fig. 3.** *Intiornis inexpectatus* (MAS-P/2 1; holotype), dessin au trait d'une partie de pied droit. En gris foncé, fragments d'os cassé. Abréviations : I–IV métatarsiens ou doigts I–IV ; 1–5 phalanges ; mt, métatarsiens ; un, griffes (?) Barre d'échelle : 5 mm.

ular surface is strongly concave, and the flexor tubercle is large and bulbous.

Digit III shows very elongate non-ungual phalanges, with phalanx III-1 being the longest, in contrast to *Sinornis* in which the longest phalanx is III-2, being the same proportions as present in *Sinornis* (Sereno et al., 2002). Phalanx III-1 shows a constricted phalangeal neck, and elongate distal flexor pits. Phalanx III-2 shows a laterodistally expanded flange.

Digit II is poorly preserved. The phalanx II-1 is short and stout, and shows on its proximal end subquadrangular lateral and medial expansions, a feature also seen in *Sinornis* (Sereno et al., 2002). Phalanx II-2 is longer than II-1, and shows elliptical shaped flexor pits. Pedal unguual of digit II is elongate and shows a poorly developed flexor tubercle, but a well developed proximodorsal lip.

Digit I is reverted, as in most modern birds and other Enantiornithes (Chiappe and Calvo, 1994). Phalanx I-1 is short and stout, in contrast with the narrow and elongate morphology present in most Enantiornithes, including *Sinornis*, *Soroavisaurus*, *Gobipteryx*, and *Vescornis* (Kurochkin, 1995; Zhou and Zhang, 2006). Phalanx I-1 shows a well-developed proximodorsal lip, and a wide and ovoid distal flexor pit. Pedal unguual of digit I is large and strongly curved, being larger than unguuals of digits II and IV, at least, constituting a diagnostic trait of Enantiornithes (Kurochkin, 2000). Pedal unguual of digit I is poorly preserved. It shows a dorsoventrally extended proximal articular surface, features considered as diagnostic of Enantiornithes by some authors (Kurochkin, 2000). In addition, this phalanx exhibits a large and craniocaudally extended flexor tubercle.

## 5. Discussion

We identify *Intiornis* as a member of Enantiornithes on the basis of the following traits: tibiotarsus with a bulbous and inflated medial condyle (much larger than the lateral one) with its cranial surface nearly flat, a condition that is

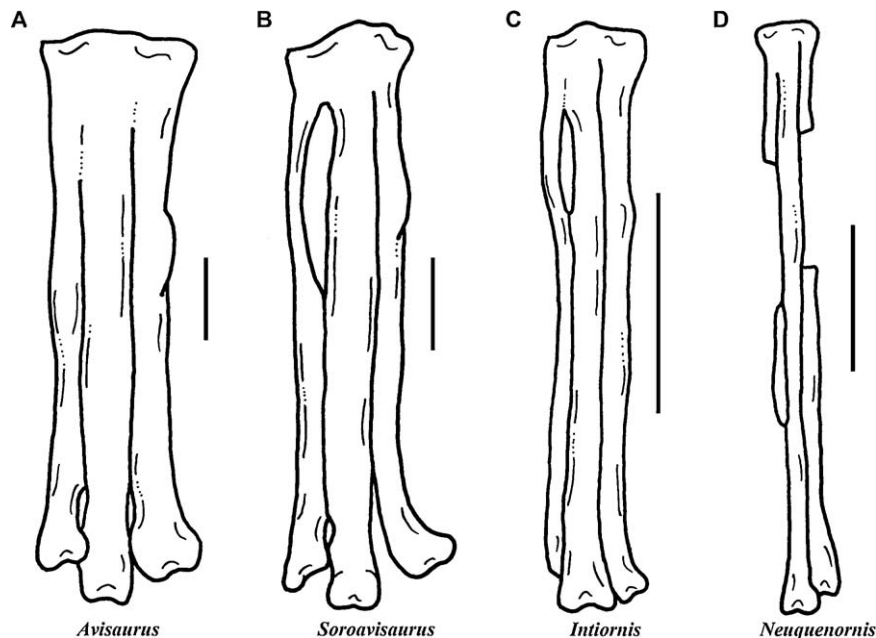
mirrored by an enlarged medial cotyle of the tarsometatarsus; distal articular surface of metatarsal II expanded, being larger than that of the metatarsal III, and ungual of digit I very large, with enlarged proximal surface for articulation with the first phalanx (Kurochkin, 1995; Martin, 1995; Sereno, 2000; Walker, 1981). In addition, *Intiornis* lacks several traits diagnostic of the more derived Ornithomorphs, including metatarsal III not displaced plantarly with respect to metatarsals II and IV, absence of a proximal vascular foramen, and trochlea of metatarsal III poorly developed (Kurochkin, 2000). Within Enantiornithes *Intiornis* is referred to Euenantiornithes because it has a very narrow and deep intercondylar sulcus on distal tibiotarsus that clearly delimits distal condyles, and distal end of metatarsal IV narrower than metatarsals II and III (Chiappe and Walker, 2002).

The shaft of metatarsal III, with its cranial margin convex in cross-section, supports the inclusion of *Intiornis* within the euenantiornithine clade Avisauridae (Chiappe, 1993). Three genera are currently recognized as composing this clade: *Avisaurus*, from the Campanian and Maastrichtian of North America (Varricchio and Chiappe, 1995), *Soroavisaurus* from the Maastrichtian of NW Argentina (Chiappe, 1993), and *Neuquenornis*, from Santonian deposits of NW Patagonia (Chiappe and Calvo, 1994). More recently, Dyke and Ösi (2010) described the peculiar avisaurid genus *Bauxitornis* from the Late Cretaceous of Hungary. Recent works by Cau and Arduini (2008) indicate that the genera *Concornis* (Osi, 2008), *Halimornis* (Chiappe et al., 2002), and *Enantiophoenyx* (Cau and Arduini, 2008) may also belong to this clade. Regrettably, in *Halimornis* the tarsometatarsus is unknown, thus direct comparisons with *Intiornis* are

not possible; however, the size difference between both taxa may serve as a distinguishing feature (Chiappe et al., 2002). With regards to *Concornis*, *Intiornis* clearly differs from this genus, among other anatomical details, in having shorter phalanx IV-1, more elongated phalanx IV-3, and in the less distally located metatarsal II which is distant to the distal end of metatarsal III, and in some other minor details (Sanz and Buscalioni, 1992; Sanz et al., 1995). On the other hand, *Intiornis* may be distinguished from the poorly known genus *Enantiophoenyx* in having metatarsal III thinner at mid-shaft, the metatarsal IV relatively broader, and the phalanx I-1 stouter (Cau and Arduini, 2008). *Intiornis* is clearly distinguishable from *Bauxitornis* in lacking the proximodistally abbreviate metatarsal II and the elongate metatarsal IV present in the latter genus (Dyke and Ösi, 2010). Moreover, *Intiornis* lacks the laterally bowed proximal end of metatarsals II and III exhibited by *Bauxitornis* (Dyke and Ösi, 2010).

Among conventional avisaurids, the sparrow-sized *Intiornis* is distinguished from the pigeon-sized *Neuquenornis* in that the first one has a stouter tarsometatarsus, stouter phalanx I-1, and long and narrow fenestra between proximal halves of metatarsals III and IV (Fig. 4B, D). *Intiornis* differs from *Neuquenornis* and resembles *Soroavisaurus* and *Avisaurus* (Chiappe, 1993) in having a medially directed metatarsal II (Varricchio and Chiappe, 1995) and broad distal trochleae of metatarsals II and III, suggesting that these three taxa may conform a group within Avisauridae, exclusive of *Neuquenornis*.

*Intiornis* differs from *Avisaurus* in lacking a crescent-shaped trochlea of metatarsal IV (Varricchio and Chiappe, 1995), and in having a more elongated tarsometatarsus,



**Fig. 4.** Comparative figure of right tarsometatarsus of selected Avisauridae. A, *Avisaurus*; B, *Soroavisaurus*; C, *Intiornis*; D, *Neuquenornis*. (A, B, D, modified by Chiappe and Calvo, 1994). Scale bar 10 mm.

**Fig. 4.** Comparaison entre tarsométatarses d'Avisauridés sélectionnés A, *Avisaurus* ; B, *Soroavisaurus* ; C, *Intiornis* ; D, *Neuquenornis*. (A, B, D, modifiés par Chiappe et Calvo, 1994). Barre d'échelle : 10 mm.



and a well defined intercotylar knob on its proximal end (Fig. 4).

On the other hand, among avisaurids, *Intiornis* more nearly resembles *Soroavisaurus* in having an elongate tarsometatarsus and a long and narrow fenestra between proximal metatarsals IV and III (Chiappe, 1993). However, *Intiornis* is clearly distinguishable from *Soroavisaurus* in having shortened pedal phalanx I-1, and unguis of digit 2 more elongate and acute, among other minor details (see generic diagnosis of *Intiornis*) (Fig. 4).

Zhou and Zhang (2006) hypothesized that there was a tendency towards increasing body size among the derived bird clade Ornithurae, being the size of early basal taxa smaller than more derived and latter forms. These authors indicated that, in contrast to Ornithurae, the Enantiornithes retained minute size until the Late Cretaceous, because they must retain small body size in order to obtain a flapping flight with a less perfect flight apparatus. However, although several Late Cretaceous Enantiornithes showed medium to large body sizes, some taxa still exhibited minute body proportions, as is the case of *Intiornis*, *Alexornis* and an unnamed taxon from Hungary (Brodkorb, 1976; Osi, 2008). This indicates that although several latest Enantiornithes were large-sized, there also existed an array of minute forms coexisting with them (Gong et al., 2004). Hone et al. (2005) indicate that the small size of the Latest Cretaceous modern birds (i.e. Neornithes) probably allowed this clade to survive the Cretaceous–Palaeocene boundary, since smaller organisms are the more likely survivors of extinction events at the expense of its larger counterparts. Nevertheless, *Intiornis* and *Alexornis*, both coming from Latest Cretaceous beds are very small sparrow-sized taxa, rivalizing the size of the smallest Late Cretaceous Neornithes (see Chiappe and Dyke, 2002). They suggest that size was probably not a relevant feature for the extinction of Enantiornithes nor survivorship of Neornithes at the Cretaceous–Palaeocene boundary.

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## References

Báez, A.M., 1981. Redescription and relationships of *Saltenia ibanezi*, a Late Cretaceous pipid frog from northwestern Argentina. *Ameghiniana* 3, 127–154.

Brodkorb, P., 1976. Discovery of a Cretaceous bird, apparently ancestral to the orders Coraciiformes and Piciformes (Aves: Carinatae). *Smith. Contrib. Paleobiol.* 27, 67–77.

Cau, A., Arduini, P., 2008. *Enantiophoenyx electrophyla* gen. et sp. nov. (Aves, Enantiornithes) from the Upper Cretaceous (Cenomanian) of Lebanon and its phylogenetic relationships. *Atti Sci. Nat. Mus. Civico Storia Nat. Milano* 149, 293–324.

Chiappe, L.M., 1993. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of Northwestern Argentina. *Am. Mus. Novit.* 3083, 1–27.

Chiappe, L.M., 1996. Early avian evolution in the southern hemisphere: fossil record of birds in the Mesozoic of Gondwana. *Mem. Queens. Mus.* 39, 533–556.

Chiappe, L.M., Calvo, J.O., 1994. *Neuquenornis volans*, a new Late Cretaceous bird from Patagonia Argentina. *J. Vert. Paleont.* 14, 230–246.

Chiappe, L.M., Dyke, G.J., 2002. The Mesozoic radiation of birds. *Ann. Rev. Ecol. Syst.* 33, 91–124.

Chiappe, L.M., Walker, C.A., 2002. Skeletal morphology and systematics of Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In: Chiappe, L.M., Witmer, L.M. (Eds.), *Mesozoic birds: above the heads of dinosaurs*. Berkeley University Press, Berkeley, pp. 168–218.

Chiappe, L.M., Lamb, J.P., Ericson, P.G.P., 2002. New enantiornithine bird from the marine Upper Cretaceous of Alabama. *J. Vert. Paleont.* 22, 170–174.

Close, R.A., Vickers-Rich, P., Trusler, P., Chiappe, L.M., O'Connor, J., 2009. Earliest gondwanan bird from the Cretaceous of southeastern Australia. *J. Vert. Paleont.* 29, 616–619.

Dyke, G.J., Ösi, A., 2010. A review of Late Cretaceous fossil birds from Hungary. *Geol. J.* 45 (4), 434–444.

Feduccia, A., 1995. Explosive evolution in Tertiary birds and mammals. *Science* 267, 637–638.

Gong, E., Hou, L., Wang, L., 2004. Enantiornithine bird with diapsid skull and its dental development in the Early Cretaceous in Liaoning, China. *Acta Geol. Sinica* 78, 1–7.

Hone, D.W.E., Dyke, G.J., Haden, M., Benton, M.J., 2005. Body size evolution in Mesozoic birds. *J. Evol. Biol.* 21, 618–624.

Hou, L., 2000. Mesozoic birds of China. Taiwan Provincial Feng Huang Ku Bird Park, Nan Tou, Taiwan, 2000, 228 p.

Hou, L., Chiappe, L.M., Zhang, F., Choung, C., 2004. New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds. *Naturwissenschaften* 91, 22–25.

Kurochkin, E.N., 1995. A new enantiornithid of the Mongolian Late Cretaceous, and a general appraisal of the infraclass Enantiornithes (Aves) Russian Academy of Science, Paleontological Special Issue (1995) 1–50.

Kurochkin, E.N., 2000. Mesozoic birds of Mongolia and the former USSR. In: Benton, M.J., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (Eds.), *The age of dinosaurs in Russia and Mongolia*. Cambridge University press, Cambridge, pp. 533–559.

Martin, L.D., 1995. The Enantiornithes: terrestrial birds of the Cretaceous. *Cour. Forsch. Senck.* 181, 23–36.

Morrison, K., Dyke, G.J., Chiappe, L.M., 2005. Cretaceous fossil birds from Hornby Island (British Columbia). *Canad. J. Earth Sci.* 42, 2097–2101.

Narváez, P.L., Sabino, I.F., 2008. Palynology of the Las Curtiembres Formation (Late Cretaceous, Salta Group Basin), Las Conchas Creek area, northwestern Argentina. *Ameghiniana* 45, 473–482.

Osi, A., 2008. Enantiornithine bird remains from the Late Cretaceous of Hungary. *Oryctos* 7, 55–60.

Sanz, J.L., Buscalioni, A.D., 1992. A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Palaeontology* 35, 829–845.

Sanz, J.L., Chiappe, L.M., Buscalioni, A.D., 1995. The osteology of *Concornis lacustris* (Aves: Enantiornithes) from the Lower Cretaceous of Spain and a reexamination of its phylogenetic relationships. *Am. Mus. Novit.* 3133, 1–23.

Sereno, P.C., 2000. *Iberomesornis romerali* (Aves, Ornithothoraces) reevaluated as an Early Cretaceous enantiornithine. *N. Jahrb. Geol. Paleont.* 215, 365–395.

Sereno, P.C., Rao, C., Li, J., 2002. *Sinornis santensis* (Aves: Enantiornithes) from the Early Cretaceous of Northeastern China. In: Chiappe, L.M., Witmer, L.M. (Eds.), *Mesozoic birds: above the heads of dinosaurs*. University Press, Berkeley, pp. 184–208.

Varricchio, D.J., Chiappe, L.M., 1995. A new enantiornithine bird from the Upper Cretaceous Two Medicine Formation of Montana. *J. Vert. Paleont.* 15, 201–204.

Walker, C.A., 1981. New subclass of birds from the Cretaceous of South America. *Nature* 292, 51–53.

Walker, C.A., Buffetaut, E., Dyke, G.J., 2007. Large euenantiornithine birds from the Cretaceous of southern France, North America and Argentina. *Geol. Mag.* 144, 977–986.

Zhang, F., Ericson, P.G.P., Zhou, Z., 2004. Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China. *Can. J. Earth Sci.* 41, 1097–1107.

Zhang, F., Zhou, Z., Hou, L., Gu, G., 2001. Early diversification of birds: evidence from a new opposite bird. *Chinese Sci. Bull.* 46, 945–949.

Zhou, Z., Zhang, F., 2006. Mesozoic birds of China - A synoptic review. *Vertebrata Palasiatica* 44, 74–98.