



New theropod dinosaur from the Upper Cretaceous of Patagonia sheds light on the paravian radiation in Gondwana

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Abstract

The fossil record of basal paravians in Gondwana is still poorly known, being limited to the Cretaceous unenlagiids from South America and the problematic *Rahonavis* from Madagascar. Here we report on a new paravian from the Cenomanian-Turonian (Late Cretaceous) of Río Negro province, NW Patagonia, Argentina. The new taxon exhibits a derived bird-like morphology of the forelimbs (e.g., robust ulna with prominent, anteriorly oriented, and proximally saddle-shaped radial cotyle and wide medial flange on metacarpal I) and a plesiomorphic foot with a raptorial pedal digit II. Phylogenetic analysis recovers the new taxon in a monophyletic clade with *Rahonavis*, being the sister group of the remaining Avialae and more derived than other non-avian dinosaurs. Both exhibit derived forelimb traits in opposition with their plesiomorphic hind limbs. The position of the new taxon and *Rahonavis* as stem avialans indicates that Gondwanan basal paravians are represented by two different clades, at least. The new taxon probably constitutes a previously unknown grade in the avian-line theropods in which some flight-related adaptations of the forelimbs are present in cursorial taxa. The present discovery sheds light on the acquisition of flight-related traits in non-avian dinosaurs and on the still poorly known paravian radiation in Gondwana.

Keywords Theropoda · Paraves · South America · Upper Cretaceous

Introduction

The vast majority of known basal paravian theropods come from Jurassic and Cretaceous beds in the Northern Hemisphere (Makovicky and Norell 2004; Norell and

Makovicky 2004; Turner et al. 2012). In sharp contrast, the fossil record of basal paravian dinosaurs from the southern continents is restricted to a relatively small number of taxa. The best represented of these are the Late Cretaceous Patagonian unenlagiids (Novas and Puerta 1997, Makovicky et al. 2005, Novas and Pol 2005, Novas et al. 2008, Porfiri et al. 2011) and the problematic *Rahonavis* from Madagascar (Forster et al. 1998), although a few specimens are also known from the Cretaceous beds of Sudan (Rauhut and Werner 1995). Although the phylogenetic relationships of these southern taxa are still under dispute (Turner et al. 2012; Brusatte et al. 2014; Makovicky et al. 2005; Agnolín and Novas 2013; Agnolín et al. 2019), they are important in understanding the phylogeny and evolution of basal paravians due to their anatomical similarities with basal birds.

Here we report on a new paravian from Cenomanian-Turonian beds of Patagonia which differs morphologically from unenlagiids and other non-avialan paravians. The new taxon shows notably gracile hind limb elements, contrasting with its derived and robust forelimb. This finding demonstrates that the morphological disparity and taxonomic diversity of Cretaceous avian-like dinosaurs from the Southern Hemisphere was wider than previously thought.

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Materials and methods

Locality and horizon

The specimen comes from beds of the Huincul Formation (middle Cenomanian-early Turonian; Garrido 2010), cropping out at 39°23'52.37" S, 68°37'4.30" W, southeast of the Ezequiel Ramos-Mexía lake, NW Río Negro province, Argentina (the fossil locality is historically known as “Violante farm”). These beds have yielded remains of different theropod clades, including Carcharodontosauridae (i.e., *Mapusaurus rosae* and *Taurovenator violantei*) (Coria and Currie 2006; Motta et al. 2016), Abelisauridae (i.e., *Ilokelesia aguadagrandensis*, *Skorpiovenator bustingorryi*, *Huinculsaurus montesi*, and *Tralkasaurus cuyi*) (Coria and Salgado 1998, Canale et al. 2009, Baiano et al. 2020, Cerroni et al. 2020), and Megaraptora (i.e., *Gualicho shinyae* and *Aoniraptor libertatem*) (Apesteguía et al. 2016, Motta et al. 2016).

Results

Systematic paleontology

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1888

THEROPODA Marsh, 1881

MANIRAPTORA Gauthier, 1986

PARAVES Sereno, 1997

Overoraptor chimento gen. et sp. nov.

Holotype MPCA-Pv 805, incomplete and disarticulated specimen including four caudal vertebrae, two hemal arches, right scapula, right ulna, elements of right hand (metacarpal I, phalanx I-1, and unguals of digits I and II), fragment of right ilium, incomplete left pubis, right and left metatarsals II and III, and elements of left foot (phalanges I-1 and II-2 and unguals of digits I and II) (Fig. 1).

Paratype MPCA-Pv 818, fragmentary specimen, 20% smaller than the holotype (see Supplementary Material 1), represented by right manual phalanges I-1 and III-2, fragment of left ilium, nearly complete right pubis, right metatarsal II, left pedal phalanx II-1, and right pedal phalanx III-1. This individual is very similar to the holotype specimen in most anatomical traits (see “Description and comparisons”) and in the notably gracile proportions of the metatarsals and the pedal and manual phalanges.

The holotype and paratype specimens of *O. chimento* were found in a quarry measuring 1.5 m in diameter and 0.30 m in depth. They were found in association with disarticulated crocodylian and turtle bones. Some of these elements were

previously reported as belonging to Unenlagiidae (Motta et al. 2016).

Etymology *Overo* from “overo” the Spanish word meaning piebald, in reference to the coloration of the *O. chimento* bones, which consists of a pattern of light and dark spots, and *raptor* from the Latin for thief. The species name *chimento* honors its discoverer, the paleontologist Dr. Roberto Nicolás Chimento.

Diagnosis The new taxon differs from other paravians in the following combination of characters (autapomorphies are marked by an asterisk): posterior caudal centra with a complex system of lateral longitudinal ridges and concavities (also present in *Buitreraptor* and *Rahonavis*); scapula with a medially deflected distal end*; acromial process reduced and ridge-like*; robust ulna; radial cotyle of ulna saddle-shaped and prominent; metacarpal I with extensive medioventral crest*; metatarsal II with longitudinal lateroventral crest on distal half, ending distally in a posterior tubercle* (present on both specimens); metatarsal III distal end non-ginglymoidal (also present in *Pamparaptor*); metatarsal III distal end dorsoventrally deeper than transversely wide*; and strongly dorsally displaced collateral pits on pedal phalanx II-2.

Description and comparisons

Overoraptor was a gracile theropod, approximately 1.3 m in total length (Fig. 1). The scapula is proximally stout, contrasting with the slender and narrow proportions of the scapular blade (Fig. 1, b). For descriptive purposes, we assume the scapula to be aligned with the main axis of the blade horizontally. The glenoid fossa is cup-shaped; it is offset from the main body of the scapula (with a slight constriction between the articular surface and the body of the scapula) and bounded by a prominent lip all around its perimeter. The margin of the lip is notably shallow anteriorly than elsewhere. A cup-shaped glenoid fossa is also observed in *Archaeopteryx* and *Jeholornis* (Wellnhofer 2009; Rauhut et al. 2018; Lefèvre et al. 2014), but is absent in unenlagiids (Novas et al. 2018; Gianechini et al. 2018). The glenoid fossa projects laterally when the external surface of the scapular blade is dorsally oriented (Fig. 1, b). The acromial process is represented by a minute longitudinal ridge that projects dorsally (Fig. 1, b). This condition is different from other basal paravians in which the acromion is well developed and forms a sub-triangular process that projects medially (*Sinornithosaurus*, and *Jeholornis*; Xu et al. 1999, Zhou and Zhang 2003) or dorsomedially (*Unenlagia*, *Buitreraptor*, *Rahonavis*, *Archaeopteryx*, and *Anchiornis*; Novas and Puerta 1997, Makovicky et al. 2005, Gianechini et al. 2018, Forster et al. 1998, Wellnhofer 2009, Pei et al. 2017).

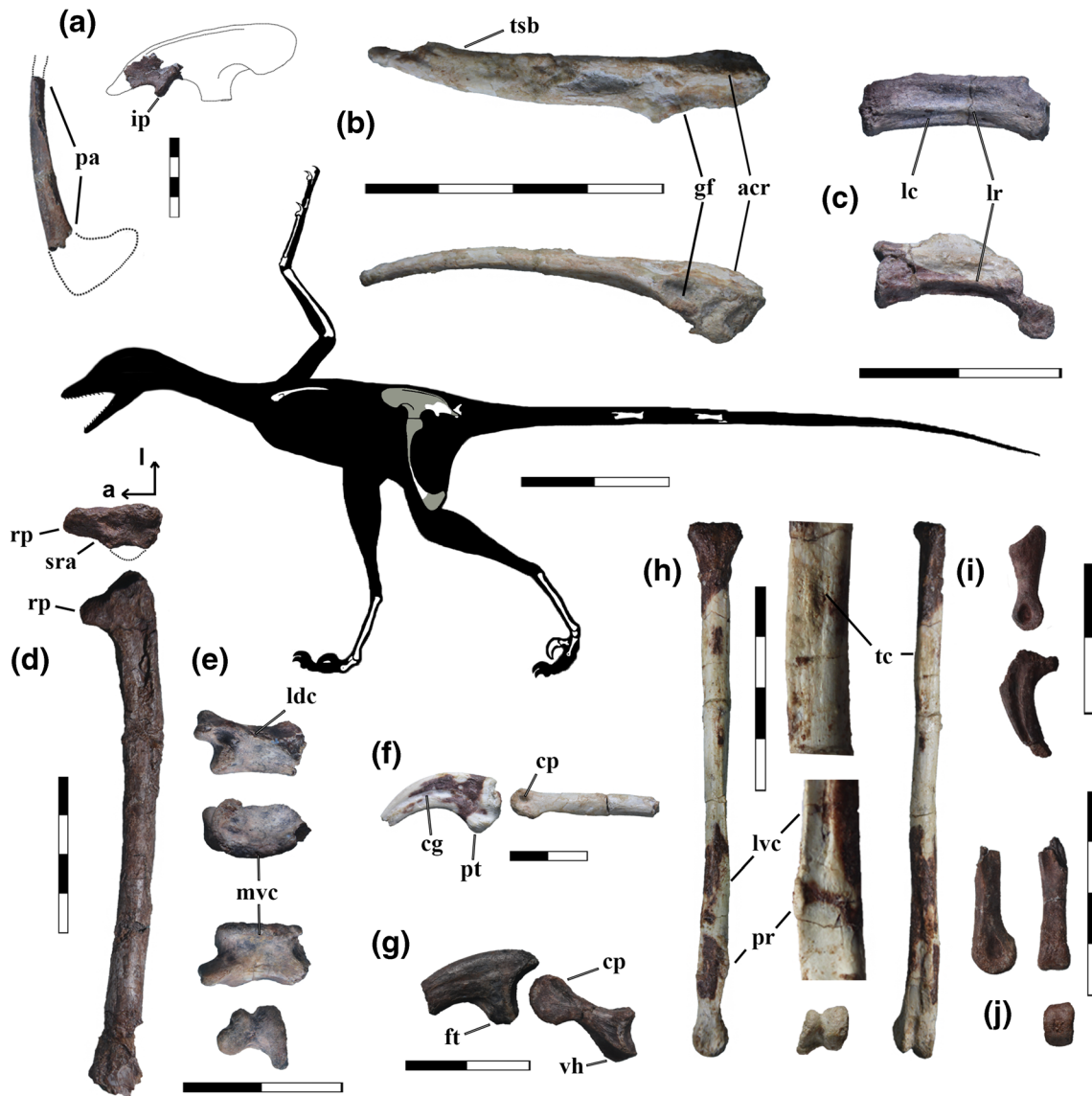


Fig. 1 Silhouette of *Overoraptor chimento* gen. et sp. nov. (MPCA-Pv 805) showing selected skeletal elements. (a) Pelvic girdle elements including fragments of ilium in lateral (top) view and left pubis in medial (left) view, (b) right scapula in dorsal (top) and lateral (bottom) views, (c) mid-caudal vertebra in left lateral view, (d) right ulna in lateral (bottom) and proximal (top) views, (e) right metacarpal I in dorsal (top), medial, ventral, and distal (bottom) views, (f) right manual phalanx I-1 and manual ungual of digit I in medial view, (g) left pedal phalanx II-2 and left pedal ungual of digit II in medial view, (h) left metatarsal II in lateral (left), dorsal (right), and distal (bottom) views, (i) left pedal phalanx I-1

and pedal ungual of digit I in medial view, (j) left metatarsal III in dorsal (right), lateral (left) and distal (bottom) views. Abbreviations: **a** anterior, **acr** acromion, **cg** collateral groove, **cp** collateral pit, **ft** flexor tubercle, **gf** glenoid fossa, **ip** ischium pedicle of ilium, **l** lateral, **lc** lateral crest, **lr** lateral ridge, **lvc** lateroventral crest, **ldc** laterodorsal crest, **mvc** medioventral crest, **rp** radial process of ulna, **sra** surface for radial articulation, **tc** bump representing the *m. tibialis cranialis* insertion, **tsb** tapered scapular blade, **pa** pubic apron, **pr** protuberance, **pt** proximal tubercle, **vh** ventral heel. Scale bar equals 50 cm in the silhouette; 4 cm in a, b, d, h, and j; and 2 cm in c, e, f, g, and i

In *Overoraptor*, the distal tip of the scapular blade is broken; however, it is remarkable that the lateral and internal margins tend to converge distally. Furthermore, the blade is not only curved to match the shape of the thorax outline, as is usual among dinosaurs, but also has a medially deflected distal end (as seen in dorsal view; Fig. 1, b) as in *Rahonavis* (Forster et al. 1998). This contrasts with *Unenlagia* and *Buitreraptor* in which the scapular blade is strap-like (Novas and Puerta 1997; Gianechini et al. 2018).

The ulna is large and stout (Fig. 1, d). The ulna/metatarsal length ratio is 1.08, within the typical range for non-avian paravians (1–1.5) but contrasting with the values exceeding 1.5 that are usual for avialans (see Table 2 in Supplementary Material 1). The posterior margin of the ulna is longitudinally convex so that the ulna is bowed as in most basal paravians (e.g., *Deinonychnus*, *Buitreraptor*, *Archaeopteryx*, and *Alcmonavis*) (Ostrom 1969; Novas et al. 2018; Gianechini et al. 2018; Wellnhofer 2009; Rauhut et al. 2018; Rauhut

et al. 2019) but in contrast to the straight ulna observed in *Anchiornis* (Pei et al. 2017). The olecranon process is small. In proximal view, the ulna is asymmetrically sub-triangular in outline (Fig. 1, *d*), with a wide and concave notch for the reception of the radius (Fig. 1, *d-sra*). The radial process (Fig. 1, *d-rp*) for articulation with the latter bone is prominent and anteriorly oriented, similar to the condition present in *Rahonavis* and living birds (Baumel 1993). In basal paravians (e.g., *Deinonychus*, *Buitreraptor*, and *Bambiraptor*) (Ostrom 1969; Makovicky et al. 2005; Gianechini et al. 2018; Burnham 2004), by contrast, the corresponding process is anterolaterally oriented. As in modern birds and some basal paravians (such as *Bambiraptor* and *Alcmonavis*; Burnham 2004, Rauhut et al. 2019), the radial process of *Overoraptor* has a saddle-shaped radial cotyle proximally, a condition that presumably allowed a mobile articulation with the radius (Carpenter 2002), whereas it is flat in basal paravians (e.g., *Deinonychus* and *Buitreraptor*) (Ostrom 1969; Novas et al. 2018; Gianechini et al. 2018).

Metacarpal I is block-like and morphologically complex (Fig. 1, *e*), being proportionally shorter and wider than metacarpal I of *Deinonychus*, *Buitreraptor*, *Anchiornis*, and *Archaeopteryx* (Ostrom 1969; Novas et al. 2018; Gianechini et al. 2018; Pei et al. 2017; Wellnhofer 2009). The proximodistally short metacarpal I of *Overoraptor* resembles that of *Alcmonavis* (Rauhut et al. 2019). In *Overoraptor*, the lateral surface for articulation with metacarpal II is bounded by a sharp margin, which forms a convex prominence close to the distal end of the bone. The distal ginglymoid surface is strongly asymmetrical due to the strong distal projection of the lateral condyle (Fig. 1, *e*). *Overoraptor* exhibits a peculiar set of features on metacarpal I. The medial margin of the bone extends uninterruptedly from the proximomedial corner to the medial distal condyle, forming a dorsoventrally narrow ridge (Fig. 1, *e*). This medial flange resembles a similar structure in *Confuciusornis* and more derived birds (Paul 2002) whereas in *Deinonychus* and *Buitreraptor*, metacarpal I bears a ventromedial flange that is restricted to the proximal third of the bone. The lateral condyle shows a deep concavity for reception of metacarpal II (as in *Deinonychus*; Ostrom 1969) (Fig. 1, *e*).

The manual phalanges of *Overoraptor* are notably slender (Fig. 1, *f*) as in *Buitreraptor* and *Archaeopteryx* (Novas et al. 2018; Wellnhofer 2009; Rauhut et al. 2018), showing a well-developed distal ginglymoidal articular surfaces. The manual unguals are sharp, strongly mediolaterally compressed, and curved (Fig. 1, *f*). The proximal tubercle is expanded and separated from the articular surface by a wide groove. The dorsal lip is small, such as in *Alcmonavis*, but contrasting with most basal paravians (Rauhut et al. 2019).

The incomplete ilium is represented by the acetabular region and postacetabular blade (Fig. 1, *a*). There is no sign of a brevis fossa or medial brevis shelf, a derived condition among Paraves (Novas 2004). The shaft of the pubis has a slight

posterior curvature (Fig. 1, *a*), similar to unenlagiids, *Rahonavis*, and *Anchiornis*. In anterior view, the lateral margin of the pubis appears to be weakly sigmoid. The pubic apron is restricted to the distal half of the bone.

The foot is sub-arctometatarsalian, with the central metatarsal proximally pinched between metatarsals II and IV (Fig. 1, *i*). As in *Velociraptor* (Norell and Makovicky 1997), the metatarsal II shows a slight bump in the proximal portion of the cranial surface, presumably for the insertion of *m. tibialis cranialis* (Fig. 1, *h*). Metatarsal II is also distinctive in that the distal portion of the posterior surface bears a sharp flange along the lateral margin, ending distally in a protuberance. This is different from the condition in other paravians (e.g., *Sinornithosaurus*, *Buitreraptor*, and *Rahonavis*) (Xu et al. 1999; Novas et al. 2018; Forster et al. 1998), in which the main longitudinal crest on metatarsal II runs along the medial margin, and the lateral edge is devoid of a distal crest and protuberance. Metatarsal III in *Overoraptor* is anteroposteriorly compressed proximally, but distally becomes T-shaped in cross-section (Fig. 1, *i*), as also occurs in troodontids, unenlagiids, and *Rahonavis* (Xu 2002; Brissón Egli et al. 2017; Forster et al. 1998). Distally, metatarsal III ends in an articular surface that is non-ginglymoid, as in *Pamparaptor* and the Öösh deinonychosaur (Porfiri et al. 2011; Prieto-Márquez et al. 2012), but this surface is transversely narrow and anteroposteriorly deep.

The foot exhibits the characteristic raptorial digit II (Gauthier 1986). Phalanx II-1 is short and robust, with a well-developed proximodorsal process. The proximoventral heel of phalanx II-2 is restricted to the medial half of the bone (Fig. 1, *g*), as occurs in *Rahonavis* and unenlagiids (Makovicky et al. 2005). The distal collateral pits of phalanx II-2 are dorsally displaced and in close proximity to one another, as occurs in *Buitreraptor* (Novas et al. 2018). The ungual phalanx of digit II is similar to those of other paravians in being enlarged, transversely compressed, and ventrally sharp and in having asymmetrical collateral groove and a prominent flexor tubercle (Ostrom 1969). In pedal digit I, the proximal phalanx has a ginglymoid distal end, and the ungual phalanx is slightly ventrally curved (Fig. 1, *h*).

The only preserved anterior caudal vertebra resembles those of *Unenlagia* and *Velociraptor* (Norell and Makovicky 1997) in being dorsoventrally compressed and in having notably expanded transverse processes. The posterior caudals are notably elongated and show a complex system of ridges and concavities on the lateral surface of the centrum (Fig. 1, *c*), as in unenlagiids, *Rahonavis*, and *Archaeopteryx* (Motta et al. 2018).

Discussion

In order to evaluate the phylogenetic position of *Overoraptor* among paravians, we performed a phylogenetic analysis

employing recent datasets which are focused on Coelurosauria (Agnolin and Novas 2013; Brusatte et al. 2014; Gianechini et al. 2017; Hu et al. 2018) (see Supplementary Material 1 for more details). We coded *Overoraptor* into original data matrices by Brusatte et al. (Brusatte et al. 2014), Gianechini et al. (2017), and Hu et al. (2018). Also, we modified the Agnolin and Novas (2013) data matrix in light of newly published data (Brissón Egli et al. 2017; Novas et al. 2018; Gianechini et al. 2018). The analyses performed with these data sets variously recover *Overoraptor* as part of a polytomy at the base of Maniraptora (Brusatte et al. 2014), Pennaraptora (Hu et al. 2018) or within Paraves (Gianechini et al. 2017). However, when the analysis was performed using a modified version of Agnolin and Novas (Agnolin and Novas 2013) (see Supplementary Material 1), *Overoraptor* was found to be nested with *Rahonavis* in a monophyletic clade positioned as the sister group of Avialae, clearly separated from unenlagiids (Fig. 2a, *Overoraptor*+*Rahonavis* branch support values: 1/12/(6); Bremer support, absolute bootstrap, and GC bootstrap, respectively; see Supplementary Material 1 for the extended tree). In this analysis, Troodontidae, Dromaeosauridae, Microraptora, Unenlagiidae, and *Overoraptor*+*Rahonavis* are recovered as closer to Avialae. *Overoraptor* and *Rahonavis* share with Avialae several synapomorphies (see Supplementary Material 1), including ulna with asymmetrical proximal end and prominent and saddle-shaped radial process. The position of *Overoraptor* within this branch of the paravian tree may reflect the unique mixture of plesiomorphic and derived characters seen in this taxon as discussed below.

Overoraptor shares with unenlagiids *Rahonavis* and *Sinornithosaurus* a medially restricted ventral heel on phalanx II-2, elongated and narrow manual phalanges with dorsally displaced collateral ligament pits, and a tongue-like expansion on metatarsal III that overlaps metatarsal II (Makovicky et al. 2005; Brissón Egli et al. 2017; Novas et al. 2018). In spite of such similarities, *Overoraptor* lacks most unenlagiid synapomorphies whose presence or absence can be assessed in the available material, such as a well-developed posteromedial crest on metatarsal II. *Overoraptor* is also clearly distinguishable from the similar-sized *Buitreraptor* in lacking pronounced lips surrounding the glenoid fossa and having a block-like rather than elongated metacarpal I (Fig. 2b, c).

Overoraptor shares with *Rahonavis* a unique combination of traits, including a well-developed and complex system of ridges and concavities on the lateral surfaces of the mid- and posterior-caudal centra and scapular blade with a medially deflected distal end. Nevertheless, *Overoraptor* is distinguished from *Rahonavis* by several traits, including strong transverse compression of the proximal end of metatarsal III, absence of a distal ginglymoid articular surface on metatarsal III, and ulna only slightly longer than the metatarsus.

Furthermore, *Overoraptor* shows a combination of characters in the forelimb and shoulder girdle that are unknown in other Gondwanan paravians but that are shared with basal avialans, as outlined below. The scapular blade is strongly distally tapering, a character present in basal avialans such as *Anchiornis* and *Jeholornis*, but absent in *Rahonavis* and unenlagiids such as *Unenlagia* and *Buitreraptor* (Forster et al. 1998; Novas et al. 2018; Gianechini et al. 2018; Ostrom 1976; Bakker et al. 1992). The glenoid cavity of *Overoraptor* resembles those of basal avialans such as *Archaeopteryx* and *Jeholornis* in that most of the glenoid fossa is formed by a cup-shaped surface on the scapula whereas the glenoid fossa is not delimited by lips in *Unenlagia* or *Buitreraptor* (Rauhut et al. 2018; Novas et al. 2018) (Fig. 2c).

The proximal end of the ulna of *Overoraptor* exhibits a strongly asymmetric subtriangular outline with a wide concave surface for articulation with the radius and a saddle-shaped surface on the radial cotyle. This morphology resembles that of *Alcmonavis* (Rauhut et al. 2019) and suggests a mobile articulation with the radius (Carpenter 2002). A similar morphology is also observed in living birds and plays an important role in facilitating condition for their automatic wing folding (Vazquez 1994; Carpenter 2002). This condition is different from that exhibited by most basal paravians, including *Buitreraptor*, in which the radial process is laterally oriented and lacks a saddle-shaped articular surface for the radius (Novas et al. 2018; Gianechini et al. 2018). However, *Overoraptor* has plesiomorphic ulnar proportions (the ulna being barely longer than the metatarsals) similar to those of other basal paravians, but different from those of *Rahonavis* and more derived avialans in which the ulna is considerably longer than the metatarsals (Forster et al. 1998).

Metacarpal I of *Overoraptor* has a wide medial flange, resembling the condition in pygostylian birds (i.e., *Confuciusornis* IVPP V 11374- and pp. 46 and 49 in Chiappe and Meng 2016), but contrasting with the absence of such a flange in basal paravians (e.g., *Deinonychus*, *Archaeopteryx*, and *Buitreraptor*) (Ostrom 1969, Wellnhofer 2009, Novas et al. 2018) (Fig. 1, b). This flange represents the site of insertion of the main manus extensor muscles (*m. extensor longus alulae* and *m. extensor carpi radialis*, Baumel 1993). In contrast to *Confuciusornis*, the metacarpal I of *Overoraptor* shows a proximal articular surface that represents contact with the wrist, a plesiomorphic paravian trait (Xu et al. 2008, 2011).

In summary, the forelimb of *Overoraptor* shows a combination of derived features that is absent in other non-avian paravians, including unenlagiids, dromaeosaurids, microraptorans, and troodontids. The position of *Overoraptor*, together with *Rahonavis* in a clade that is sister to Avialae, reflects the unique combination of a plesiomorphic hind limb and a derived forelimb, probably representing a

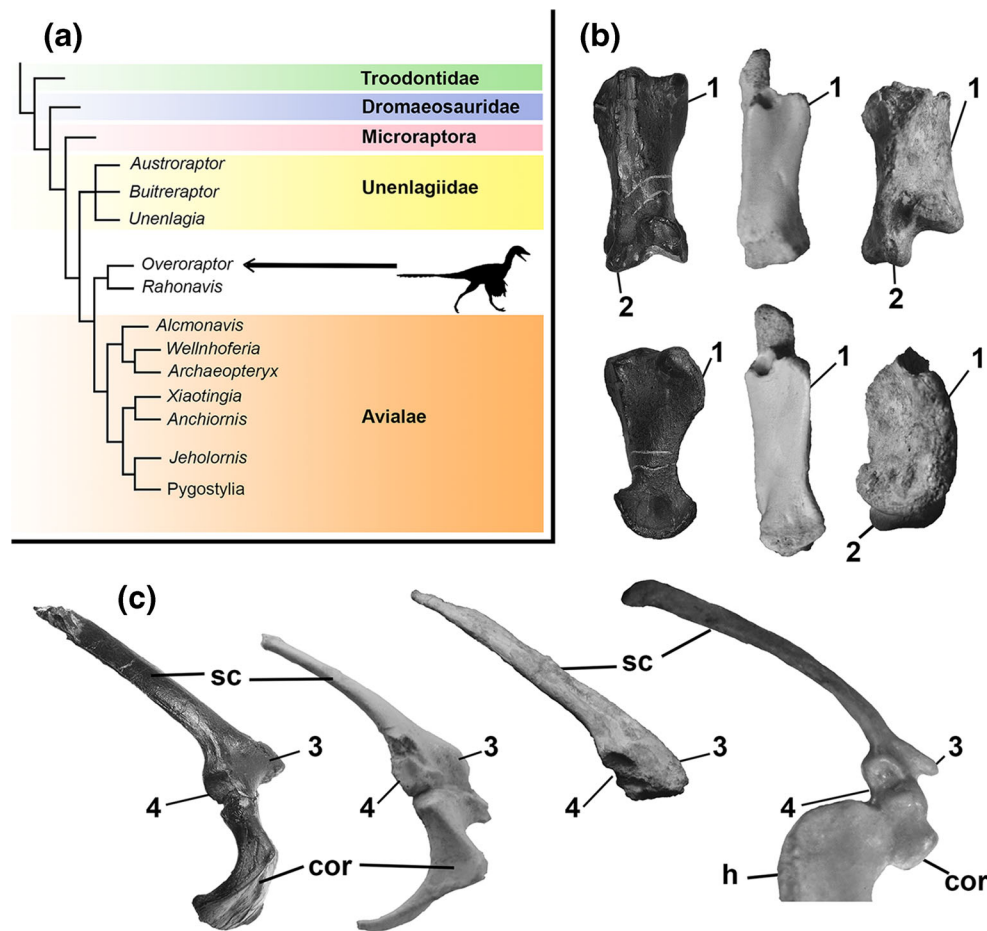


Fig. 2 Phylogenetic relationships and comparisons of *Overoraptor chimentoii* with other paravians. **a** Strict consensus depicting the phylogenetic relationships of *Overoraptor* within Paraves. *Overoraptor* forms a monophyletic clade with *Rahonavis* (see Supplementary Material 1), being not closely related to Unenlagiidae. The affinities of *Overoraptor* were tested using a modified version of the Agnolin and Novas (2013) dataset and were analyzed using a combination of the tree search algorithms Wagner trees, tree bisection reconnection (TBR) branch swapping, sectorial searches, and Ratchet and Tree Fusing in

TNT v. 1.5. Phylogenetic data and complete strict consensus tree are offered in Supplementary Material 1. **b** Comparative image of the right metacarpal I of *Deinonychus*, *Buitreraptor*, and *Overoraptor* in dorsal (top) and medial (bottom) views. **c** Comparative image of the right scapulacoracoid of *Bambiraptor*, *Buitreraptor*, *Overoraptor*, and *Archaeopteryx* in lateral view. Image not to scale. Abbreviations: 1 medioventral crest, 2 lateral distal condyle, 3 acromion, 4 glenoid cavity, *sc* scapula, *cor* coracoid, *h* humerus

previously unrecognized evolutionary grade on the avian stem. The hind limbs of *Overoraptor* retained a plesiomorphic raptorial digit II, unfused metatarsals, and poorly curved ungual phalanx I, features that are correlated with cursorial habits. This contrasts with derived forelimb traits that show some adaptations related to active flight. *Overoraptor* probably constitutes a previously unknown grade in the avian-line theropods in which some flight-related adaptations of the forelimbs (e.g., automatic folding mechanism) were present in still cursorial taxa. These modifications could have provided some important support during the cursorial ability but not during the flight, probably as a stabilizer during rapid or irregular movements, as occurs in extant running birds, such as *Rhea*. Regrettably, the incomplete nature of *Overoraptor* makes it difficult to test this hypothesis, and future discoveries may shed some light on this topic.

Unenlagiid theropods from Patagonia include a diversity of forms, ranging from turkey-sized taxa with elongated forelimbs (i.e., *Buitreraptor*) to large ones that reach 5 m long and have notably short forelimbs (i.e., *Austroraptor*) (Novas et al. 2008). The discovery of *Overoraptor* documents the presence of basal paravians other than unenlagiids in South America, thus increasing the known taxonomic diversity and morphological disparity of paravian theropods in the Late Cretaceous of Patagonia. This partially contradicts recently proposed paleobiogeographic analyses (e.g., Xu and Zhang 2005, Foth and Rauhut 2017) supporting an Asian origin of the bird lineage by following multiple dispersal events to other landmasses. Available evidence from Patagonia and other regions of the southern continents suggests a more complex evolutionary history of basal paravians in Gondwana.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Code availability Not applicable.

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