A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids

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Fossils of a predatory dinosaur provide novel information about the evolution of unenlagiines, a poorly known group of dromaeosaurid theropods from Gondwana. The new dinosaur is the largest dromaeosaurid yet discovered in the Southern Hemisphere and depicts bizarre cranial and postcranial features. Its long and low snout bears numerous, small-sized conical teeth, a condition resembling spinosaurid theropods. Its short forearms depart from the characteristically long-armed condition of all dromaeosaurids and their close avian relatives. The new discovery amplifies the range of morphological disparity among unenlagiines, demonstrating that by the end of the Cretaceous this clade included large, short-armed forms alongside crow-sized, long-armed, possibly flying representatives. The new dinosaur is the youngest record of dromaeosaurids from Gondwana and represents a previously unrecognized lineage of large predators in Late Cretaceous dinosaur faunas mainly dominated by abelisaurid theropods.

Keywords: Theropoda; Dromaeosauridae; Unenlagiinae; Cretaceous; South America; forelimb

Abbreviations: IGM, Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; MCF PVPH, Museo Municipal Carmen Funes, Plaza Huincul, Neuquén, Argentina; MCZ, Museum of Comparative Zoology, Cambridge, Massachussets, USA; MML, Museo Municipal de Lamarque, Río Negro, Argentina

1. INTRODUCTION

Dromaeosaurids are close avian relatives mainly known from the Northern Hemisphere. These are gracile and slender theropod dinosaurs, most of them measuring between 50 cm and 3 m in length (Ostrom 1969; Xu *et al.* 2000; Senter *et al.* 2004; Turner *et al.* 2007). A few examples from the Northern Hemisphere, however, reached up to 5 m long (e.g. *Achillobator* from Asia and *Utahraptor* from North America; Kirkland *et al.* 1993; Perle *et al.* 1999). In recent years, a few dromaeosaurid taxa have been discovered in Gondwana (Novas & Puerta 1997; Forster *et al.* 1998; Calvo *et al.* 2004; Makovicky *et al.* 2005; Novas & Pol 2005), but their evolutionary history remains poorly understood. Here we report a startling new example from Campanian–Maastrichtian beds of Patagonia, which acquired a large body size convergently with the large Laurasian taxa and departed from the characteristic morphology of dromaeosaurids.

2. DESCRIPTION AND COMPARATIVE ANATOMY

(a) *Systematic palaeontology*

Theropoda (Marsh 1884)
Coelurosauria (Huene 1920)
Deinonychosauria (Colbert & Russell 1969)
Dromaeosauridae (Matthew & Brown 1922)
Unenlagiinae (Bonaparte 1999)
Austroraptor cabazai, new taxon.

(b) *Holotype*

Specimen number MML-195 consists of right frontal and postorbital, lacrimals, maxillae and dentaries with teeth, right surangular and prearticular, cervicals 3, 5, 6, 7 and 8, dorsals 2 and 4, isolated ribs and gastralia, right humerus, manual ungual of digit III, left pubic shaft, left femur, and right tibia, astragalus, calcaneum, metatarsal III and pedal phalanges I-2, II-2, III-4 and IV-2 (figure 1).

(c) *Etymology*

Austroraptor, from *austral* in reference to southern South America, and *raptor*, thief; and *cabazai*, in honour to the late Héctor Cabaza, founder of the Museo Municipal de Lamarque.

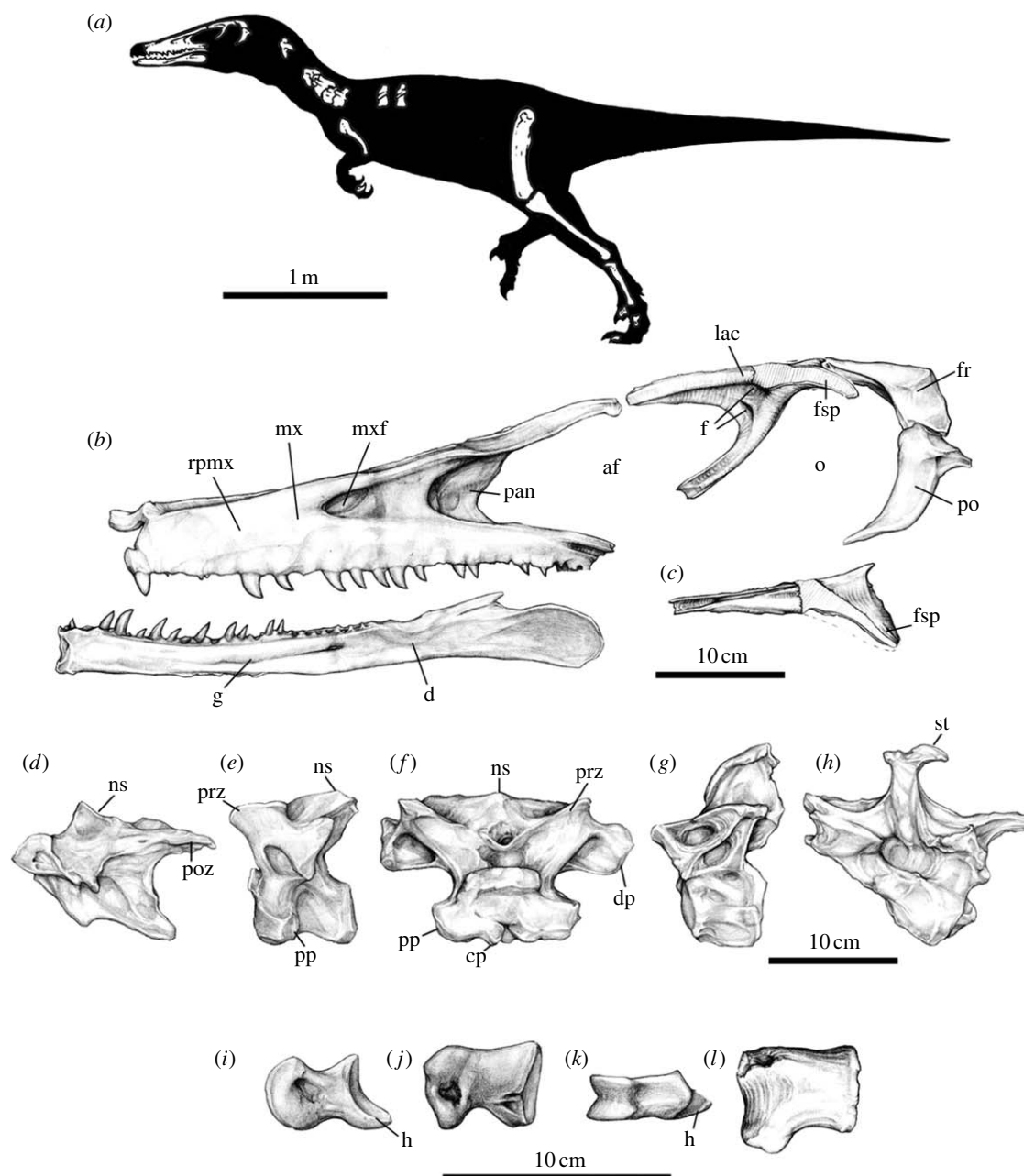*Author for correspondence (fernovas@yahoo.com.ar).

Figure 1. *Austroraptor cabazai* MML 195, holotype. (*a*) Skeletal reconstruction and body shape, indicating discovered bones. Body length was estimated following equations described by Turner *et al.* (2007). (*b*) Skull reconstruction in left lateral view. (*c*) Left lacrimal in dorsal aspect. (*d*) Cervical 3? in left lateral view. (*e,f*) Cervical 8? in (*e*) left lateral and (*f*) cranial views. (*g,h*) Dorsal 4? in (*g*) left lateral and (*h*) cranial views. (*i,k*) Pedal phalanx II-2 in (*i*) left lateral and (*k*) dorsal views. (*j,l*) Pedal phalanx IV-2 in (*j*) left lateral and (*l*) dorsal views. af, antorbital fenestra; cp, carotid process; d, dentary; dp, diapophysis; f, foramina; fr, frontal; fsp, fan-shaped process of lacrimal; g, groove; h, caudoventral heel; lac, lacrimal; mx, maxilla; mxf, maxillary fenestra; ns, neural spine; o, orbit; pan, postantral wall; po, postorbital; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; rpmx, rostral process of maxilla; st, spine table.

(d) Locality and horizon

Allen Formation (Campanian–Maastrichtian; Martinelli & Foriasepi 2004), Bajo de Santa Rosa (40°03′ 28″ S, 66°48′ 03″ W), approximately 90 km southwest of Lamarque town, Río Negro Province, Argentina. Theropod dinosaurs collected from the Allen Formation include the abelisaurid *Quilmesaurus curriei* (see Juárez Valieri *et al.* 2007), a yet unnamed alvarezsaurid (Agnolín *et al.* 2006), and indeterminate tetanurans (Coria & Salgado 2005).

(e) Diagnosis

A large dromaeosaurid with the following combination of characters that distinguish it from other members of this group (autapomorphies marked with an asterisk): lacrimal highly pneumatized, with descending process strongly curved rostraly*, and caudal process flaring out horizontally above orbit* (differing from Laurasian dromaeosaurids, but unknown for other unenlagiines); postorbital lacking dorsomedial process for articulation with the frontal*, and with squamosal process extremely reduced (differing from Laurasian dromaeosaurids, but unknown for other unenlagiines); maxillary and dentary teeth small, conical-shaped, devoid of serrations and flutted (as in *Buitreraptor*); humerus short, representing slightly less than 50 per cent of femur length (a smaller ratio than in other dromaeosaurids and paravians); pedal phalanx II-2

Table 1. Comparison of cranial and postcranial elements of selected dromaeosaurid taxa.

	Austroraptor cabazai MML-195	*Unenlagia comahuensis* MCF PVPH 78	*Buitreraptor gonzalezorum* (Makovicky *et al.* 2005)	*Velociraptor mongoliensis* (Barsbold & Osmólska 1999; Norell & Makovicky 1997, 1999)	*Deinonychus antirrhopus* MCZ 4371	*Achillobator giganticus* (Perle *et al.* 1999)	*Utahraptor ostrommaysi* (Kirkland *et al.* 1993)
maxilia							
length (cm)	39[a]	—	10[b]	10.9[c]	—	39	—
height[d] (cm)	8.5	—	1.8	3.5[c]	—	11.6	—
height/length ratio (%)	21%	—	18%	34%[c]	—	29%	—
tooth count	24	—	—	11[c]	—	11	—
humerus							
length (cm)	26.2	26.5[b]	13.5	—	25.4	—	—
least mid-shaft diameter (cm)	2.2	1.7	0.6	—	—	—	—
femur							
length (cm)	56	36.8	14.5	23.8[e]	34.4	50.5	—
least mid-shaft diameter (cm)	7.1	2.2	0.7	1.67[e]	—	6.7	—
tibia							
length (cm)	56.5	41.8[a]	>14.9	25.5[e,f]	36	49	50.5
distal transverse width (cm)	14	6.3[a]	—	3.8[e]	—	11.3	14.5
pedal phalanx 2.II							
length (cm)	5.7	—	1.8	2.4[g]	—	7.6	—
distal transverse width (cm)	1.7	—	—	0.6[g]	—	—	—
pedal phalanx 2.IV							
length (cm)	4.8	—	—	2.1[g]	—	—	—
distal transverse width (cm)	4.7	—	—	0.8[g]	—	—	—
estimated body length (cm)[h]	494.3	323.6	135	208[e]	302	445	—
estimated body mass (kg)[i]	368	95	6	23.4[e]	77	264	—

[a] Broken.
[b] Estimated.
[c] *V. mongoliensis* IGM 100/25.
[d] Height at level of rostral margin of preorbital fenestra.
[e] *V. mongoliensis* IGM 100/986.
[f] Tibiotarsus.
[g] *V. mongoliensis* IGM 100/985.
[h] Calculated on the basis of body length regression for paravians by Turner *et al.* (2007).
[i] Calculated with the equation of Christiansen & Fariña (2004) in Turner *et al.* (2007).

transversely narrow, contrasting with the extremely robust phalanx IV-2 (differing from other dromaeosaurids, including unenlagines, but resembling the condition of advanced troodontids).

(f) Description and comparisons

The holotype specimen of *A. cabazai* (figure 1a) was approximately 5 m long. The skull (figure 1b) is characteristically extremely long and low, being roughly 80 cm long as reconstructed. The depth of the maxilla (taken at level of the rostral margin of the antorbital fenestra) represents 21 per cent of the length of the bone. The antorbital fenestra is also low and elongate, but restricted to the caudal portion of maxilla. A single, large, elliptical maxillary fenestra is present. The postantral wall of the antorbital fenestra is rostrocaudally extensive. The ventral margin of maxilla is straight and bears 24 teeth. The maxilla of *Austroraptor* closely resembles

that of *Buitreraptor*, but both sharply contrast with most Laurasian dromaeosaurids (e.g. *Deinonychus*, *Velociraptor*, *Saurornitholestes*, *Bambiraptor*, *Dromaeosaurus*, *Atrociraptor*, *Achillobator*; Currie & Varrichio 2004; see table 1) because in the latter ones the maxilla is deeper in side view (i.e. maxillary depth at the level of rostral margin of antorbital fenestra is 30% or more than the length of the bone), two fenestrae (i.e. maxillary and promaxillary fenestrae) are nested into a well-marked antorbital fossa and the postantral wall is not caudally projected. Besides, the ventral margin of the maxilla in northern dromaeosaurids is ventrally convex, and the number of teeth is lower (9–15 tooth positions; Norell & Makovicky 2004). The frontal of *Austroraptor* is triangular shaped in dorsal aspect, tapering rostrally as in troodontids (Currie 1987a,b). The supratemporal depression invades the caudal portion of the bone, being rostrally bounded by a straight, oblique ridge different from the sigmoid one of

dromaeosaurids (Barsbold & Osmólska 1999; Xu & Wu 2001). Moreover, the frontal of *Austroraptor* lacks the conical caudolateral process characterizing some Laurasian deinonychosaurs (Currie 1987a). The lacrimal is low in side view, in agreement with the shallow maxilla. The descending process is rostrally curved, resembling the troodontid *Saurornithoides* (see Barsbold 1974), but differing from the T-shaped condition characterizing Laurasian dromaeosaurids (Barsbold & Osmólska 1999; Xu & Wu 2001). The lacrimal of *Austroraptor* also differs from other known dromaeosaurids in having an extensive excavation on the caudodorsal corner of the antorbital fossa, which contains two large foramina. Moreover, the caudal extremity of the lacrimal is horizontally expanded into a fan-shaped process that largely contributes to the craniodorsal roofing of orbit (figure 1c), a bizarre condition yet unrecorded in other theropod dinosaurs.

The dentary of *Austroraptor* is gracile, elongate and almost straight in occlusal view. Nutrient foramina on the external surface of dentary lie within a deep groove, a feature shared with *Buitreraptor* and troodontids (Currie 1987b; Makovicky *et al.* 2005). Twenty-five tooth positions are present. Both maxillary and dentary teeth are small, conical shaped, caudolingually hooked, and devoid of mesial and distal carinae and denticles, features that are also present in *Buitreraptor*. However, the enamel tooth surface in *Austroraptor* is fluted, a condition resembling that of spinosaurid theropods (Sues *et al.* 2002).

The ventral surface of cranial cervical vertebrae (figure 1d) is smooth and gently grooved, being limited laterally by longitudinal ridges. Carotid processes are present on the cranioventral margin of Cv3. Cervical centra are trapezoidal in lateral view, with both cranial and ventral surfaces meeting at an obtuse angle in lateral view, excepting for Cv7 in which the cranial and ventral surfaces of the vertebra are coplanar and ventrally faced. Posterior cervicals (figure 1e,f) are craniocaudally short and devoid of both neural spine and epipophyses, in contrast with other deinonychosaurians in which such processes are usually present. Anterior dorsals (figure 1g,h) bear an enlarged spine table.

The humerus is short and robust, representing approximately 46 per cent of femoral length, thus contrasting with the elongate and delicate humeri of other dromaeosaurids (e.g. *Unenlagia*, *Buitreraptor*, *Sinornithosaurus*; Xu 2002; Makovicky *et al.* 2005; Novas & Pol 2005). The deltopectoral crest projects cranially and is laterally flat, instead of being craniolaterally oriented and laterally excavated as in *Unenlagia* and *Buitreraptor*. Manual ungual of digit III is small but strongly curved, describing an arch that is much more pronounced than that in other dromaeosaurids (e.g. *Deinonychus*; Ostrom 1969).

The femur is robust, bearing a strongly marked obturator ridge along the proximal part of the caudal surface of the bone. The femoral length is estimated as 56 cm when complete. It is therefore subequal to the length of the tibia (56.5 cm long). Metatarsal III is roughly 33 cm long, representing 58 per cent of tibial length. Phalanx II-2 exhibits a constricted 'neck' between both proximal and distal articular surfaces, and a caudoventrally projected 'heel', as characteristically occurs among paravians. However, phalanx IV-2 (figure 1j,l) is unusually robust, duplicating the transverse width of

phalanx II-2 (figure 1i,k), indicative of a marked asymmetry in foot construction. This is in sharp contrast with other dromaeosaurids (e.g. *Deinonychus*, *Velociraptor*, *Neuquenraptor*; Ostrom 1969; Norell & Makovicky 1999; Novas & Pol 2005), in which pedal phalanx II-2 is slightly narrower with respect to phalanx IV-2.

3. PHYLOGENETIC ANALYSIS

Discovery of *Austroraptor* has important consequences in the understanding of the evolution of southern dromaeosaurids, and sheds new light about the modifications in body size and forelimb proportions within Dromaeosauridae (Turner *et al.* 2007).

Phylogenetic analysis here performed (figure 2a; see electronic supplementary material) depicts the new Patagonian taxon as deeply internested within Deinonychosauria and Dromaeosauridae. As in all deinonychosaurs, *Austroraptor* shows a modified pedal digit II allowing hyperextension, and a well-developed anterodorsal process of lacrimal (also present in *Archaeopteryx*). The inclusion of *Austroraptor* within Dromaeosauridae is supported by the extension of the supratemporal fossa over most of the frontal process of the postorbital, teeth with unconstricted crown–root junction, epipophyses of cranial cervical vertebrae placed distally on postzygapophyses, and anterior cervical centra level with posterior margin of neural arch. Moreover, when *Austroraptor* is added to the data matrix, the result differs from that of previous analyses as it recovers a monophyletic Unenlagiinae (Makovicky *et al.* 2005; Novas & Pol 2005; Turner *et al.* 2007), a clade of Gondwanan dromaeosaurids also including the Patagonian *Unenlagia comahuensis*, *Unenlagia paynemilli*, *Neuquenraptor argentinus*, *Buitreraptor gonzalezorum* and the Malagasy *Rahonavis ostromii* (Novas & Puerta 1997; Forster *et al.* 1998; Calvo *et al.* 2004; Makovicky *et al.* 2005; Novas & Pol 2005). Postcranial synapomorphies of Unenlagiinae, which are present in *Austroraptor* include: dorsal vertebrae with transverse processes shortened, top of dorsal neural spines transversely expanded into a spine table and metatarsal III proximally pinched. *Austroraptor* and *Buitreraptor* are the only unenlagiines preserving skull material, allowing the recognition of several synapomorphic features (e.g. skull exceeding femoral length at least by 25%, rostral process of maxilla low, maxillary fenestra enlarged and not dorsally displaced, postantral wall backwardly expanded, maxillary and dentary teeth small and unserrated, dentary nutrient foramina set within a deep groove) that may characterize Gondwanan unenlagiines as a whole.

4. DISCUSSION

It was hypothesized (Turner *et al.* 2007) that dromaeosaurids underwent at least three independent events of gigantism, the ostrich-size *Unenlagia* being an example of such evolutionary trend among southern dromaeosaurids. Discovery of *Austroraptor* supports this hypothesis, but demonstrates that some late unenlagiines attained sizes exceeding 1.5 times that of *Unenlagia*. In this phylogenetic context, it is interpreted that *Austroraptor* convergently acquired with the Laurasian *Achillobator* and *Utahraptor* (Kirkland *et al.* 1993; Perle *et al.* 1999) the largest sizes among Dromaeosauridae (table 1).
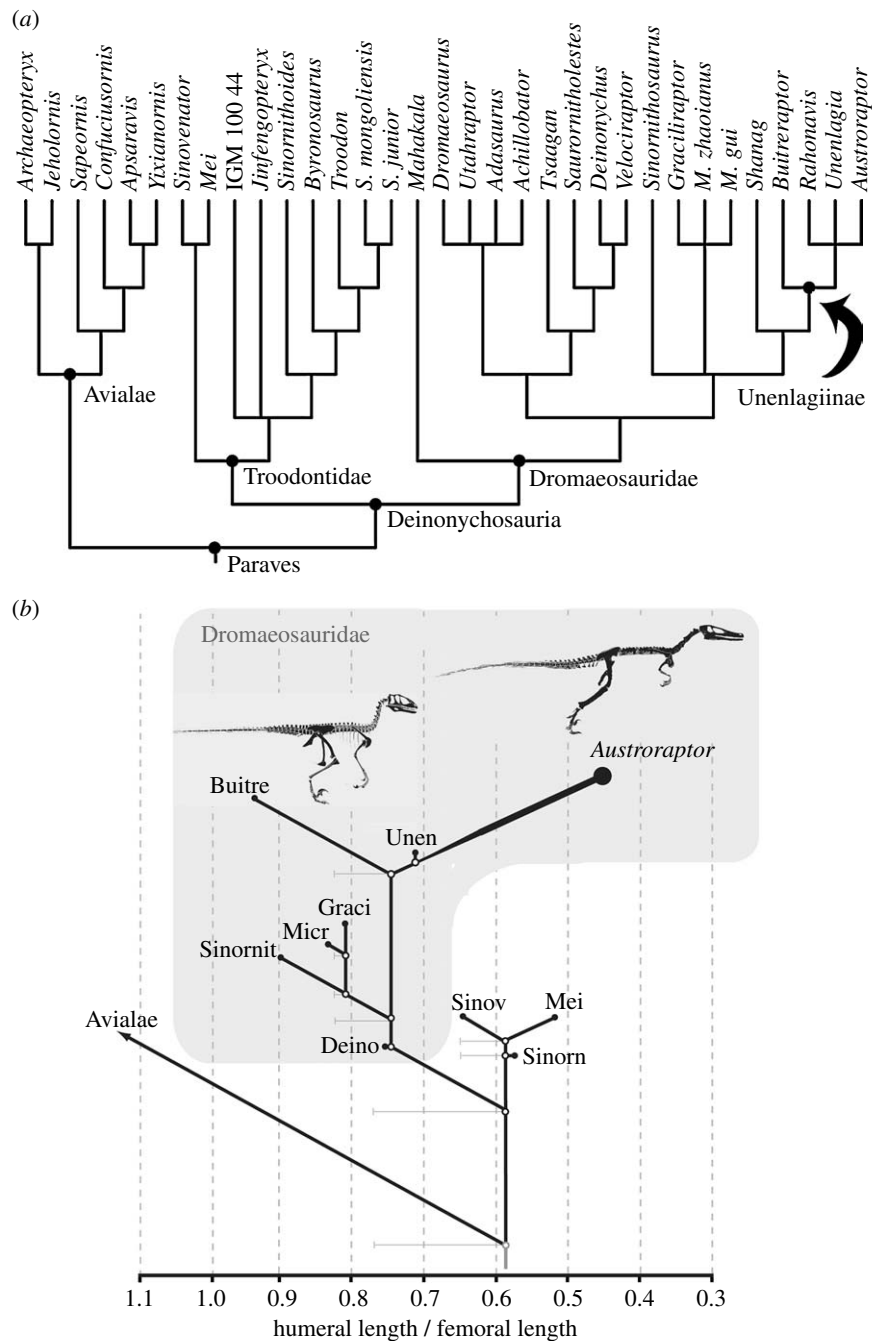
Figure 2. Phylogenetic relationships of *Austroraptor cabazai*. (*a*) Summarized strict consensus depicting the phylogenetic relationships of *Austroraptor* within Paraves. *Austroraptor* is deeply nested within Dromaeosauridae and Unenlagiinae. The affinities of *A. cabazai* were tested using recently published datasets within the broad context of Coelurosauria (Turner *et al.* 2007) and analysed with equally weighted parsimony in TNT27 (Goloboff *et al.* 2008). Further phylogenetic data and a complete strict consensus tree are offered in the electronic supplementary material. (*b*) Phylogenetic tree of paravian coelurosaurs displaying the evolution of forelimb/hindlimb proportions, as measured by the humeral length/femoral length ratio (*H/F*) optimized as a continuous character using linear parsimony in TNT27. Root of the tree located at the bottom of the figure (marked in grey) and derived branches to the top. The location of nodes and taxa along the horizontal axis represents the *H/F* ratio (filled circles, measured taxa; open circles, inferred ancestral values; error bars, ranges of possible ancestral values or intraspecific variation for terminal taxa). Grey box encloses dromaeosaurid maniraptorans, exemplified by two silhouettes: a generalized dromaeosaurid with elongated forelimbs, based on *Deinonychus* (Ostrom 1969), and *Austroraptor* with reduced forelimbs. See the electronic supplementary material for further explanation. Buitre, *Buitreraptor*; Deino, *Deinonychus*; Graci, *Graciliraptor*; Micr, *Microraptor*; Sinorn, *Sinornithoides*; Sinornit, *Sinornithosaurus*; Sinov, *Sinovenator*; Unen, *Unenlagia*.

The forelimbs of *Austroraptor* are notably reduced with respect to hindlimb length, constituting an exceptional departure from the characteristic long-armed construction of dromaeosaurids (Gauthier 1986; Padian & Chiappe 1997; figure 2*b*). In particular, the forelimb length reduction documented in *Austroraptor* is in sharp contrast

with the considerably elongated forelimbs of the smaller unenlagiines *Buitreraptor* and *Rahonavis*, which are proportionally similar to those of flying ornithuran birds (Senter 2007). Shortening of the humerus to half of femur length was accompanied in *Austroraptor* by a reversal to the (plesiomorphic) cranial orientation of the deltopectoral

crest, different from the avian-like, craniolateral orientation of this crest present in *Unenlagia* (see Novas & Puerta 1997) and *Buitreraptor* (see Makovicky *et al.* 2005).

The new discovery amplifies the range of variation among unenlagiines, demonstrating that they were morphologically and ecologically more diverse than previously thought. Available information speaks in favour that they conformed an autochthonous lineage of southern dromaeosaurids with important morphological distinctions from their northern relatives. By the end of the Cretaceous period, unenlagiine diversification included giant, short-armed forms (i.e. *Austroraptor*) alongside with crow-sized, winged representatives (i.e. *Rahonavis*; Forster *et al.* 1998; Chiappe 2007).

The new Patagonian taxon, together with the previously recorded evidence, indicates that by Maastrichtian times southern South America was populated by large coelurosaurians belonging to different lineages, including the basal coelurosaurian *Orkoraptor* (see Novas *et al.* 2008), the derived maniraptoran *Unquillosaurus* (see Novas & Agnolin 2004) and the unenlagiine *Austroraptor*. This record is in agreement with previous ideas suggesting that large-sized coelurosaurians became common after the loss of dominance of carcharodontosaurid tetanurans (Leanza *et al.* 2004). In this regard, towards the latest Cretaceous, large dromaeosaurids shared the role of large predators (approx. 5 m long) with abelisaurid ceratosaurians (e.g. *Quilmesaurus*), a faunal assemblage not recorded before.

REFERENCES

Agnolin, F. L., Novas, F. E., & Powell, J. E. 2006 New alvarezsaurid theropod from the Latest Cretaceous of Río Negro province, Patagonia, Argentina. *XXII Jornadas Argentinas de Paleontología de Vertebrados* (Boletín de Resúmenes), p. 1.

Barsbold, R. 1974 Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America. *Palaeontol. Pol.* **30**, 5–22.

Barsbold, R. & Osmólska, H. 1999 The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. *Acta Palaeontol. Pol.* **44**, 189–219.

Calvo, J. O., Porfiri, J. D. & Kellner, A. W. A. 2004 On a new maniraptoran dinosaur (Theropoda) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* **62**, 549–566.

Chiappe, L. M. 2007 *Glorified dinosaurs: the origin and early evolution of birds.* Hoboken, NJ: Wiley.

Christiansen, P. & Fariña, R. A. 2004 Mass prediction in theropod dinosaurs. *Hist. Biol.* **16**, 85–92. (doi:10.1080/08912960412331284313)

Coria, R. & Salgado, L. 2005 Last Patagonian non-avian theropods. In *The carnivorous dinosaurs* (ed. K. Carpenter), pp. 153–160. Indiana, IN: Indiana University Press.

Currie, P. J. 1987*a* Theropods of the Judith River Formation of Dinosaur Provincial Park, Alberta, Canada. In *Fourth Symp. on Mesozoic Terrestrial Ecosystems* (eds P. J. Currie & E. H. Koster), pp. 52–60. Drumheller, Alberta: Tyrrell Museum of Paleontology.

Currie, P. J. 1987*b* Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *J. Vert. Paleontol.* **7**, 72–81.

Currie, P. J. & Varrichio, D. J. 2004 A new dromaeosaurid from the Horseshoe Canyon Formation Upper Cretaceous of Alberta, Canada. In *Feathered dragons: the origin of birds and flight* (eds P. Currie, E. Kolpellhus & E. Martin), pp. 150–166. Indiana, IN: Indiana University Press.

Forster, C. A., Sampson, S. D., Chiappe, L. M. & Krause, D. W. 1998 The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* **279**, 1915–1919. (doi:10.1126/science.279.5358.1915)

Gauthier, J. A. 1986 Saurischian monophyly and the origin of birds. In *The Origin of Birds and the Evolution of Flight,* number 8 in Memoirs of the California Academy of Sciences (ed. K. Padian), pp. 1–55. California Academy of Sciences, San Francisco.

Goloboff, P., Farris, J. & Nixon, K. 2008 TNT: tree analysis using new technology, vers. 1.1 (Willi Hennig Society Edition). Program and documentation. See www.zmuc.dk/public/phylogeny/tnt.

Juárez Valieri, R., Fiorelli, L. & Cruz, L. 2007 *Quilmesaurus curriei* Coria, 2001 (Dinosauria, Theropoda). Su validez taxonómica y relaciones filogenéticas. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" nueva serie* **9**, 59–66.

Kirkland, J. I., Burge, D. & Gaston, R. 1993 A large dromaeosaur (Theropoda) from the Lower Cretaceous of eastern Utah. *Hunteria* **2**, 1–16.

Leanza, H., Apesteguía, S., Novas, F. E. & de la Fuente, M. S. 2004 Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Res.* **25**, 61–87. (doi:10.1016/j.cretres.2003.10.005)

Makovicky, P. J., Apesteguía, S. & Agnolín, F. L. 2005 The earliest dromaeosaurid theropod from South America. *Nature* **437**, 1007–1011. (doi:10.1038/nature03996)

Martinelli, A. & Forasiepi, A. M. 2004 Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", nueva serie* **6**, 257–305.

Norell, M. A. & Makovicky, P. J. 1997 Important features of the dromaeosaur skeleton: information from a new specimen. *Am. Mus. novit.* **3215**, 1–28.

Norell, M. A. & Makovicky, P. J. 1999 Important features of the dromaeosaurid skeleton. II: Information from newly collected specimens of *Velociraptor mongoliensis*. *Am. Mus. novit.* **3282**, 1–45.

Norell, M. A. & Makovicky, P. J. 2004 Dromaeosauridae. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson & H. Osmólska), pp. 196–209. Berkeley, CA: University of California Press.

Novas, F. E. & Agnolin, F. L. 2004 *Unquillosaurus ceibali* Powell, a giant maniraptoran (Dinosauria, Theropoda) from the Late Cretaceous of Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", nueva serie* **6**, 61–66.

Novas, F. E. & Pol, D. 2005 New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature* **433**, 858–861. (doi:10.1038/nature03285)

Novas, F. E. & Puerta, P. F. 1997 New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* **387**, 390–392. (doi:10.1038/387390a0)

Novas, F. E., Ezcurra, M. D. & Lecuona, A. 2008 *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Res.* **29**, 468–480. (doi:10.1016/j.cretres.2008.01.001)

Ostrom, J. H. 1969 Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum Bull.* **30**, 1–165.

Padian, K. & Chiappe, L. M. 1997 Bird origins. In *Encyclopedia of dinosaurs* (eds P. J. Currie & K. Padian), pp. 71–79. San Diego, CA: Academic Press.

Perle, A., Norell, M. A. & Clark, J. M. 1999 A new maniraptoran theropod—*Achillobator giganticus* (Dromaeosauridae)—from the Upper Cretaceous of Burkhant, Mongolia. *Contributions of the Department of Geology, National University of Mongolia* **101**, 1–105.

Senter, P. 2007 A new look at Coelurosauria phylogeny. *J. Syst. Palaeontol.* **5**, 429–463.

Senter, P., Barsold, R., Britt, B. B. & Burnham, D. A. 2004 Systematics and evolution of Dromaeosauridae (Dinosauria, Theropoda). *Bull. Gunma Museum of Natural History* **8**, 1–20.

Sues, H.-D., Frey, E., Martill, D. M. & Scott, D. M. 2002 *Irritator challangeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *J. Vert. Paleontol.* **22**, 535–547. (doi:10.1671/0272-4634(2002)022[0535:ICASDT]2.0.CO;2)

Turner, A., Pol, D., Clarke, J., Erickson, G. & Norell, M. A. 2007 A basal dromaeosaurid and size evolution preceding avian flight. *Science* **317**, 1378–1381. (doi:10.1126/science.1144066)

Xu, X. 2002 Deinonychosaurian fossils from the Jehol Group of Western Lioning and the Coelurosaurian evolution. Doctoral dissertation, Chinese Academy of Sciences.

Xu, X. & Wu, X.-C. 2001 Cranial morphology of *Sinornithosaurus milleni* Xu *et al.* 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China. In *Results from the Sino-Canadian Dinosaur Project. Part 3.* (ed P. J. Currie). *Can. J. Earth Sci.* **38**, 1739–1752.

Xu, X., Zhou, Z. & Wang, X. 2000 The smallest known non-avian theropod dinosaur. *Nature* **408**, 705–708. (doi:10.1038/35047056)