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Phylogenetic relationships of the Cretaceous Gondwanan theropods *Megaraptor* and *Australovenator*: the evidence afforded by their manual anatomy

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Abstract

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General comparisons of the manual elements of megaraptorid theropods are conducted with the aim to enlarge the morphological dataset of phylogenetically useful features within Tetanurae. Distinctive features of *Megaraptor* are concentrated along the medial side of the manus, with metacarpal I and its corresponding digit being considerably elongated. Manual ungual of digit I is characteristically enlarged in megaraptorids, but it is also transversely compressed resulting in a sharp ventral edge. We recognize two derived characters shared by megaraptorans and coelurosaurs (i.e., proximal end of metacarpal I without a deep and wide groove continuous with the semilunar carpal, and metacarpals I and II long and slender), and one derived trait similar to derived tyrannosauroids (i.e., metacarpal III length <0.75 length of metacarpal II). However, after comparing carpal, metacarpal and phalangeal morphologies, it becomes evident that megaraptorids retained most of the manual features present in *Allosaurus*. Moreover, *Megaraptor* and *Australovenator* are devoid of several manual features that the basal tyrannosauroid *Guanlong* shares with more derived coelurosaurs (e.g., *Deinonychus*), thus countering our own previous hypothesis that Megaraptora is well nested within Tyrannosauroidea.

Keywords

Dinosauria, Theropoda, Megaraptoridae, Cretaceous, Argentina, Australia, morphology.

Introduction

Megaraptoridae is a Cretaceous theropod family including several taxa recorded from different regions of Gondwana (Novas et al., 2013). The best known megaraptorids are *Megaraptor namunhuaiquii* (Novas, 1998; Calvo et al., 2004; Porfiri et al., 2014), *Orkoraptor bukei* (Novas et al., 2008), and *Aerosteon riocoloradensis* (Sereno et al., 2008), coming from different formations of Turonian through Santonian age of Argentina; and *Australovenator wintonensis* (Hocknull et al., 2009; White et al., 2012, 2013), from Cenomanian rocks of Australia.

The megaraptorids and their sister taxon *Fukuiraptor kitadaniensis* (Azuma and Currie, 2000), from Barremian beds of Japan, constitutes the clade Megaraptora, originally coined by Benson et al. (2010a). After a comprehensive phylogenetic analysis, these authors considered megaraptorans as allosauroids closely related with carcharodontosaurid theropods, an interpretation subsequently followed by later authors (Carrano et al., 2012; Zanno and Makovicky, 2013). However, recent studies conducted by some of us (e.g., Novas et al., 2013; Porfiri et al., 2014) have suggested that megaraptorans are not representative of archaic allosauroid tetanurans, but instead argued that megaraptorans are coelurosaurs, and representatives of a basal tyrannosauroid radiation in particular (Novas et al., 2013). Recent discovery of cranial remains of a juvenile specimen of *Megaraptor namunhuaiquii* (Porfiri et al., 2014) offered novel anatomical information that supported this phylogenetic interpretation.

The fossil record of megaraptorids in Gondwana has increased over the last few years. Additional evidence of the presence of megaraptorids in regions of South America other than Argentina comes from Brazil, from which isolated caudal vertebrae have been described (Mendez et al., 2013). Cretaceous formations of Australia have yielded several isolated elements referred to Megaraptoridae, including *Rapator ornitholestoides* (Huene, 1932; Agnolín et al., 2010; White et al., 2012), an isolated ulna closely similar to that of *Megaraptor* and *Australovenator* (Smith et al., 2008), more than one hundred isolated teeth (Benson et al., 2012), and probably an isolated astragalus (Molnar et al., 1981; Fitzgerald et al., 2012), and paired pubes originally described as tyrannosauroid (Benson et al., 2010b; Novas et al., 2013).

Available information demonstrates that megaraptorans were a diverse and relatively abundant clade of large predatory dinosaurs in the southern landmasses (Novas, 1998, 2008; Calvo et al., 2004; Benson et al., 2010a; Novas et al., 2013), sharing with abelisauroids and carcharodontosaurids the role of top predators.

We offer here a comparative survey of the manual bones of *Megaraptor* and *Australovenator* with the aim to recognize anatomical features characterizing these theropods. Also, we briefly discuss the distribution of some manual features among theropods that may inform the phylogenetic relationships of megaraptorid among Tetanurae.

Institutional abbreviations

AODF, Australian Age of Dinosaurs Fossil, Winton, Australia; BMNH, British Museum of Natural History, London, England; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; UUVP, University of Utah Vertebrate Paleontology, Utah, USA; YPM, Yale Peabody Museum, New Haven, USA.

Materials and Methods

Material examined. A comparative study of the holotype and referred specimens of *Megaraptor namunhuaiquii* (MUCPv 595, MUCPv 1353, and MUCPv 341), *Australovenator wintonensis* (AODF 604), and cast of *Rapator ornitholestoides* (cast of BMNH R3718) was conducted. The following specimens were also studied: *Guanlong wucaii* (IVPP V14531), *Allosaurus fragilis* (cast of UUVP 6000), *Deinonychus antirrhopus* (cast of YPM 5205), *Xuanhanosaurus qilixiaensis* (cast of IVPP V6729), *Coelurus fragilis* (cast of YPM 2010), and *Ornitholestes hermanni* (cast of AMNH 619).

Comparative Anatomy

Megaraptor and *Australovenator* are currently the only megaraptorans in which the forelimb bones are fairly well documented (Calvo et al., 2004; Hocknull et al., 2009; White et al., 2012). Specimen MUCPv 341 of *Megaraptor namunhuaiquii* preserves articulated forearm bones (i.e., ulna and radius) and manus, but no humerus (fig. 3). However, the recent discovery of a juvenile specimen of *M. namunhuaiquii* (Porfiri et al., 2014) documents for the first time the humeral morphology in this genus. Although the humerus does not preserve complete proximal and distal ends, it offers reliable information to calculate humeral proportions in this Patagonian taxon. The type specimen of *Australovenator* preserves most of the forelimb except metacarpal III and some manual phalanges.

Humerus. The humerus of *Megaraptor* (Porfiri et al., 2014) and *Australovenator* (White et al., 2012) resembles basal tetanurans (e.g., *Allosaurus, Acrocanthosaurus, Piatnitzkysaurus*; Madsen, 1976; Currie and Carpenter, 2000; Bonaparte, 1986) and basal coelurosaurs (e.g., *Coelurus, Ornitholestes, Guanlong;* Osborn, 1903; Carpenter, 2005; Xu et al., 2006; fig. 1) in being sigmoid-shaped in anterior and lateral views, with a prominent deltopectoral crest. These characters are absent in non-coelurosaurian theropods like *Xuanhanosaurus* (Dong, 1984), *Ceratosaurus* (Madsen and Welles, 2000), *Torvosaurus* (Galton and Jensen, 1979), *Baryonyx* (Charig and Milner, 1997), and some coelurosaurs including ornithomimids (Kobayashi and Lü, 2003; Nichols and Russel, 1985), and tyrannosaurids (Brochu, 2002) (fig. 1). The internal tuberosity also resembles basal tetanurans in being conical-shaped (e.g., Bonaparte et al., 1990). However, the humerus of both *Megaraptor* and *Australovenator* exhibits a deep longitudinal furrow that runs on the medial surface of the shaft, distally to the internal tuberosity, a feature also present in *Fukuiraptor* and some coelurosaurs (*Deinonychus*, tyrannosaurids; Ostrom, 1969; Brochu, 2002). This character is absent in other coelurosaurs like *Chilantaisaurus*, *Ornitholestes, Coelurus,* oviraptorosaurs (Benson and Xu, 2008; Osborn, 1903; Carpenter, 2005; Lu, 2002), and non-coelurosaurian tetanurans (e.g. *Allosaurus, Acrocanthosaurus, Piatnizkysaurus;* Madsen, 1976; Currie and Carpenter, 2000; Bonaparte 1986) (fig. 1). Furthermore the entire distal end bends anteriorly, showing a sigmoid shape in lateral view. Notably, the distal humeral condyles of *Australovenator* (White et al., 2012) are well-defined and much more rounded anteriorly than those of *Allosaurus, Acrocanthosaurus* or *Xuanhanosaurus* (Madsen 1976; Currie and Carpenter, 2000; Dong 1984) (fig. 2), and are separated by deep extensor and flexor grooves not present in non-celurosaurian tetanurans. In this regards, the distal end of the humerus of *Australovenator* (White et al., 2012) resembles coelurosaurs like *Coelurus, Ornitholestes* (Carpenter, 2005), *Guanlong* (IVPP IVPP V14531), *Deinonychus* (Novas, 1996) (fig. 2) and Aves, and may suggest a more complex folding system than in basal theropods, a hypothesis that needs to be tested properly. Apart from the similarity with some coelurosaurs described for the distal end, the robust construction of the humerus in *Megaraptor* and *Australovenator* is closer to *Allosaurus* (width:length ratio approximately 40; Madsen, 1976; Hocknull et al., 2009; Porfiri et al., 2014) than the elongate and more gracile humeral proportions of *Guanlong* and *Deinonychus* (width:length ratio approximately 30; pers. obs.).

Ulna. As already noted by previous authors (e.g., Novas, 1998; Calvo et al., 2004; Smith et al., 2008; Agnolin et al., 2010; Benson et al., 2010a; Hocknull et al., 2009; White et al., 2012; Novas et al., 2013), the megaraptorid ulna exhibits a transversally compressed blade-like olecranon process, and a robust and dorsoventrally extended lateral tuberosity. These two features are absent in the remaining theropods, including the basal megaraptoran *Fukuiraptor*, thus they have been interpreted as unambiguous synapomorphies of Megaraptoridae (Novas et al., 2013). The megaraptorid ulna narrows distally, a condition similar to that of *Allosaurus* (e.g., Madsen, 1976) or basal coelurosaurs (e.g. *Guanlong, Ornitholestes, Coelurus;* Ornithomimids; Nichols and Russel, 1985; Xu et al., 2006; Osborn, 1903; Carpenter, 2005). But absent in megalosauroids (Dong, 1984; Charig and Milner, 1997) and derived coelurosaurs (e.g. *Deinonychus*; Ostrom, 1969).

Remarkable features characterizing megaraptorids correspond to the manus, in particular the formidable development of the manual unguals of digits I and II, and the

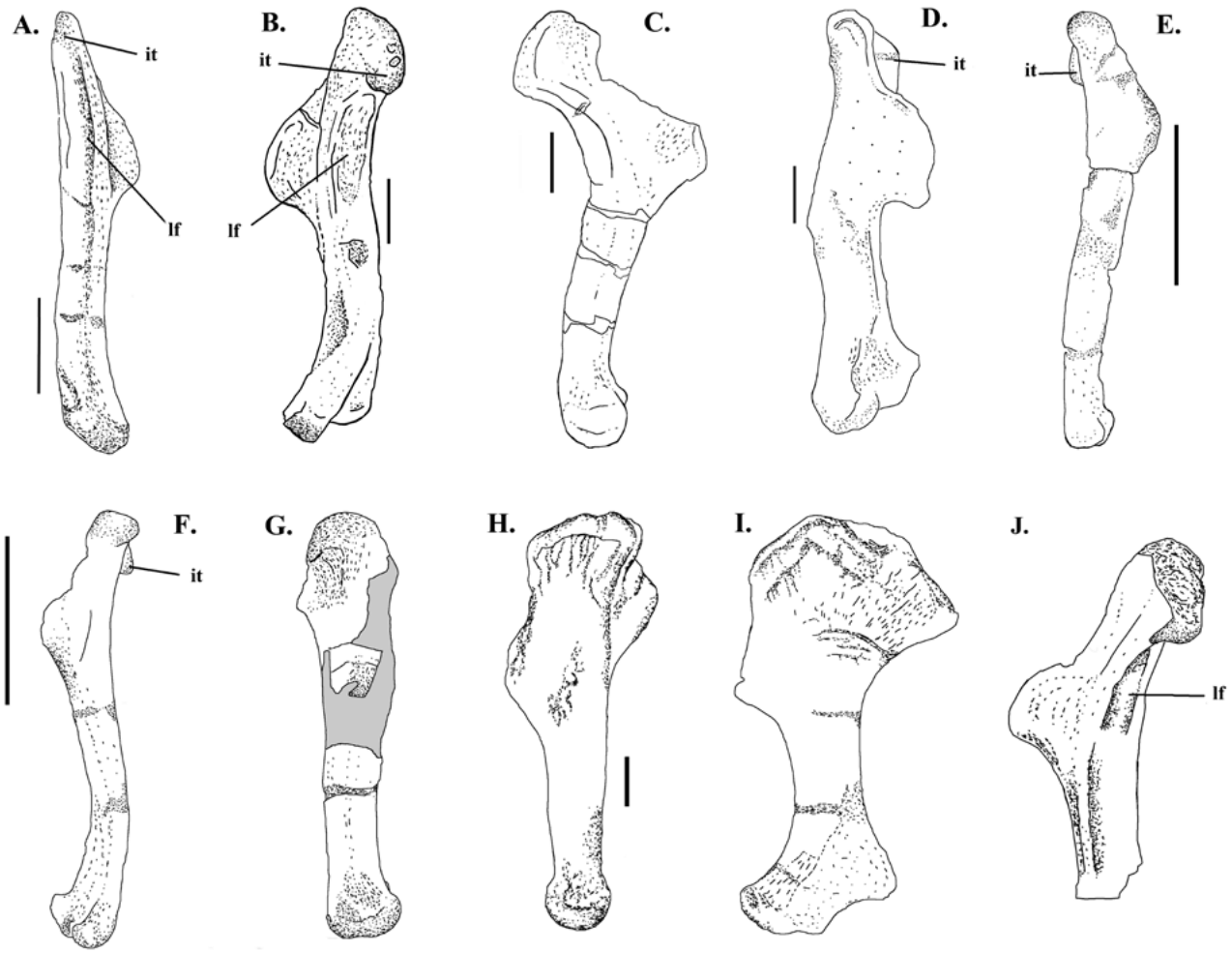

Figure 1. Humerus in lateral (C-I) and medial (A-B,J) views of: A, *Megaraptor* (MUCPv 341), B, *Australovenator*, C, *Allosaurus*, D, *Acrocanthosaurus*, E, *Coelurus,* F, *Ornitholestes*, G, *Xuanhanosaurus*, H, *Torvosaurus*, and I, *Baryonyx*. J, *Fukuiraptor.* B, modified from White et al. (2012). D, modified from Currie and Carpenter (2000). H, modified from Galton and Jensen (1979). I, modified from Charing and Milner (1997). Scale bar: 5cm. **Abbreviations**: it, internal tuberosity; lf, longitudinal furrow.

transverse compression and ventral sharpness of the ungual of digit I (Calvo et al., 2004; Novas et al., 2013).

Carpus. In *Megaraptor* (Calvo et al., 2004) and *Australovenator* (White et al., 2012) two carpal elements are documented: a disk-shaped radiale, and an enlarged distal carpal described as distal carpal 1 by White et al. (2012). Because the homology of this bone among theropods is difficult to interpret (e.g., Xu et al., 2006, 2009, 2014), we will informally describe it as a "semilunate carpal", based on its proximally arched profile in dorsal view.

Semilunate carpals of *Megaraptor* and *Australovenator* resemble *Allosaurus* (Madsen, 1976) in being gently convex proximally (figs. 3, 4, 5). As in the latter taxon, the semilunate carpal is in contact with most of the proximal end of metacarpal I, and also the medial half of the proximal end of metacarpal II. The semilunate carpal of megaraptorids bears a pair of distal projections for articulation with metacarpal bones, also present in *Allosaurus*, *Acrocanthosaurus* and the basal coelurosaur *Guanlong* (Madsen, 1976; Currie and Carpenter, 2000; Xu et al., 2006). One of these projections is visible in ventral view, and wedges between metacarpals I and II. The other projection is seen in dorsal view, and lodges into a socket on the proximal end of metacarpal I. Such interlocking among the semilunate carpal and metacarpals I and II probably constitutes a tetanuran feature, apomorphically lost among derived coelurosaurs (e.g., oviraptorosaurs, paravians) in which the distal surface is flat or slightly concave, without projecting between metacarpals I and II (Rauhut, 2003).

Aside from the general similarities noted with *Allosaurus*, the semilunate carpal of megaraptorids exhibits a proximodistally deep profile, mainly due to the bulged condition of the distal projection that lodges into the proximal end of metacarpal I. In this regard, the semilunate carpal of *Megaraptor* and *Australovenator* differs from the

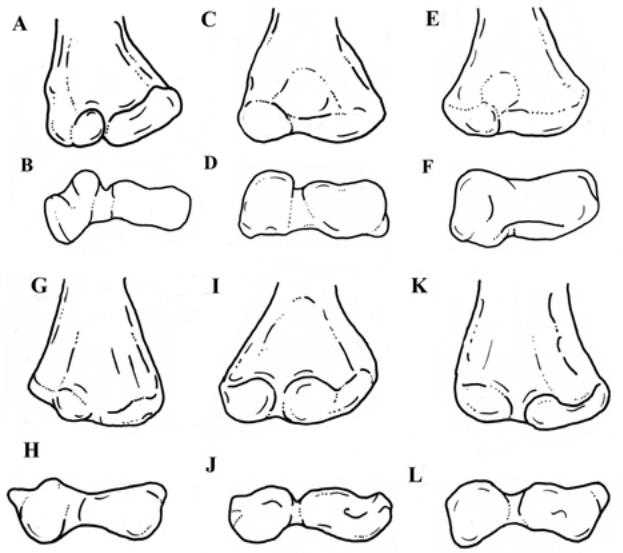

Figure 2. Distal end of humerus in anterior (A,C,E,G,I,K,) and distal (B,D,F,H,J,L) views of *Australovenator* (A,B), *Allosaurus* (C,D), *Xuanhanosaurus* (E,F), *Chilantaisaurus* (G,H), *Guanlong* (I,J), and *Coelurus* (K,L). Not to scale. A,B, modified from White et al. (2012). G,H, modified from Benson and Xu (2008).

proximodistally shallower semilunate carpal of basal tetanurans (e.g., *Allosaurus, Acrocanthosaurus*) and basal coelurosaurs, such as *Tanycolagreus* (Carpenter et al., 2005), *Sinosauropteryx* (Currie and Chen, 2001), *Scipionyx* (Dal Sasso and Maganuco, 2011), *Coelurus*, and ornithomimosaurs (Kobayashi and Lü, 2003).

In sum, megaraptorids retained a carpal morphology diagnostic at the level of Tetanurae. No derived features shared with coelurosaurs are identified. The distally convex condition of the semilunate carpal probably represents a synapomorphic feature for Megaraptoridae.

Metacarpus. Comparing the forearms of *Megaraptor* with those of *Allosaurus* and *Acrocanthosaurus* (equaling the length of the ulna), permits recognition that the manus of the first taxon is much more elongate and slender than in those basal tetanurans. In particular, metacarpal I of *Megaraptor* is less massive than the block-like Metacarpal I of *Allosaurus, Acrocanthosaurus,* and *Torvosaurus* (figs. 3, 6; Madsen, 1976; Galton and Jensen, 1979; Currie and Carpenter, 2000). In *Megaraptor* the ratio between transverse diameter and total length of the metacarpal I results in, approximately 40, whereas in *Allosaurus* the same ratio is of 50 (Novas, 1998). Digits II and III of *Megaraptor* are considerably elongate, in particular their respective ungual phalanges. The exception is digit III, which is not proportionally longer with respect to *Allosaurus.* In this regard, the shortness of digit III was considered as a derived feature shared by megaraptorids and tyrannosaurids (Novas et al., 2013). Moreover, the ungual phalanx of digit III of *Megaraptor* is less curved and trenchant than its homologue in *Allosaurus*. *Australovenator* also exhibits slender metacarpals as in *Megaraptor*, as well as an enlarged ungual on digit I. However, proportions of the remaining phalanges are intermediate between those of *Allosaurus* and *Megaraptor.*

Metacarpal I. As pointed out by Rauhut (2003), metacarpal I in most coelurosaurs is much longer than broad. Rauhut (2003) proposed that a length:width ratio greater than 2.2 is diagnostic for derived coelurosaurs (e.g., *Ornitholestes,* troodontids, oviraptorids, dromaeosaurids), and that was <2 in other theropods. Metacarpal I of megaraptorids exhibits slender proportions resembling those of coelurosaurs, contrasting with most non-coelurosaurian theropods in which the metacarpal is approximately as broad as long (e.g., *Allosaurus, Torvosaurus, Acrocanthosaurus*; fig. 7). In megaraptorids the metacarpal I has a length:width ratio of 1.85 for *Megaraptor,* and 2 for *Australovenator.* This contrasts with non-coelurosaurian theropods, such as *Allosaurus, Acrocanthosaurus,* and *Xuanhanosaurus,* in which the relationship between length:width is 1.52, 1,24 and 1,67 respectively (Madsen, 1976; Dong, 1984; Currie and Carpenter, 2000). In addition, the elongation of metacarpal I is also shared by the Australian "*Rapator"* (see White et al., 2013). On the other hand, in coelurosaurians like *Deinonychus* and *Guanlong*, the ratio is 1,89 and 1,86 respectively (Ostrom, 1076; obs. pers.), resembling in this aspect the megaraptoran condition.

As already said, the proximal end of metacarpal I bears a deep embayment to lodge the semilunate carpal. This proximal concavity of metacarpal I is also present in basal tetanurans (e.g., *Allosaurus*) as well as basal tyrannosauroids (e.g., *Guanlong*), but in megaraptorids it is emphasized by the presence of a prominent proximal projection on the medial corner of the bone. Huene (1932), in the original description of *Rapator ornitholestoides,* pointed out the peculiar proximomedial process of metacarpal I (figs. 7, 8). This feature was usually considered as a probable autapomorphic trait diagnostic for this taxon (e.g., Molnar, 1980, 1990). However, Agnolín et al. (2010) recognized that a similar process is also present in *Australovenator* and *Megaraptor*, thus suggesting that it may constitute a synapomorphy of Megaraptoridae (see also White et al., 2012). The proximal concavity on metacarpal I and its associated proximomedial process are less well developed in basal coelurosaurs (e.g., *Scipionyx*; Dal Sasso and Maganuco, 2011), basal tyrannosauroids (e.g., *Tanycolagreus*; Carpenter, Miles and Cloward, 2005), and paravians (e.g., *Deinonychus*; Ostrom, 1976), in which the proximal margin of metacarpal I is almost straight and a proximomedial process is lacking. The only possible exception among basal coelurosaurs is the compsognathid *Sinosauropteryx*, which appears to posseses a metacarpal I that is proximally notched and bears an associated proximomedial process (Figure 6; Currie and Chen, 2001).

In the Australian megaraptorids *Australovenator* and "*Rapator"* the lateral margin of metacarpal I is straight (in dorsal and ventral views), and the lateral surface for articulation with metacarpal II is slightly faced dorsally (fig. 8). This morphology resembles metacarpal I of basal tyrannosauroids (e.g., *Guanlong*; Xu et al., 2006) and derived coelurosaurs (e.g., *Deinonychus*; Ostrom, 1969), and differs from basal tetanurans (e.g., *Torvosaurus*, *Allosaurus, Acrocanthosaurus*; Madsen, 1976; Currie and Carpenter, 2000; Galton and Jensen,

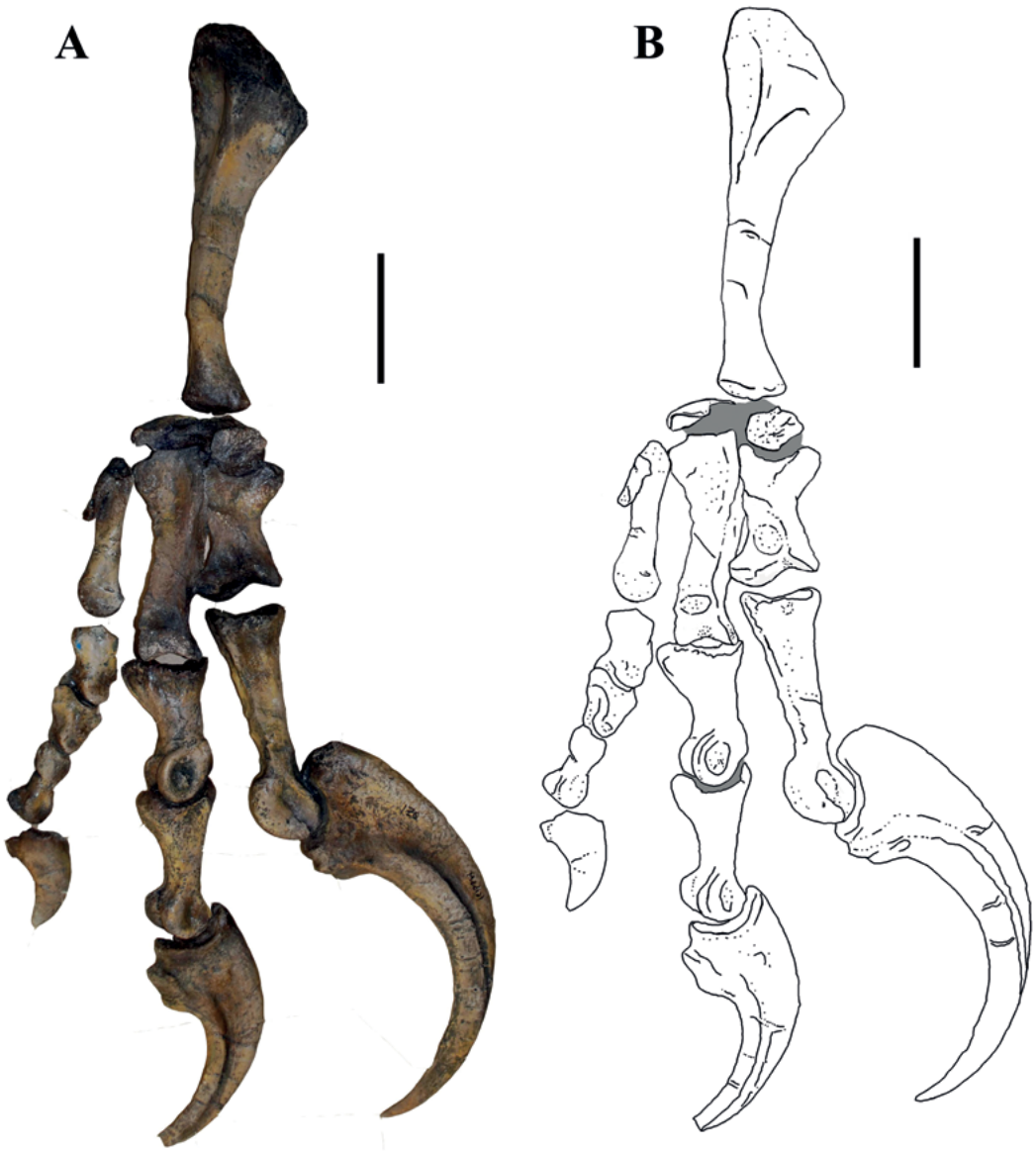

Figure 3. Left manus of *Megaraptor namunhuaiquii* (MUCPv 341) in dorsal view (A) and schematicrepresentation (B) . Scale bar: 1 cm.

1979) in which metacarpal I possesses a well-developed posterolateral surface (also partially faced proximally) for articulation with metacarpal II. The latter bone has a transversely expanded its proximal head, embracing metacarpal I ventrally. The morphology of the proximolateral portion of metacarpal I and the way it articulates with metacarpal II is not uniform among megaraptorids, as shown by *Megaraptor* in which the proximolateral corner of metacarpal I is truncated in a similar condition to that described for *Allosaurus* (Madsen, 1976). In other words, *Megaraptor* exhibits the ancestral tetanuran condition, but its close relative *Australovenator* developed an articulation of metacarpal I that is morphologically closer to that of coelurosaurian theropods. This suggests that character transformation within Megaraptoridae has been more complex than we expected.

In megaraptorids (i.e., *Australovenator, Megaraptor, "Rapator"*) the medial edge of metacarpal I is transversely rounded and dorsoventrally deep (as seen in proximal view; fig. 8). This prominent medial margin resembles *Allosaurus*, being different from the dorsoventrally depressed and sharp medial margin present in some coelurosaurs, such as *Guanlong* and *Deinonychus* (Ostrom, 1976; Xu et al., 2006).

In megaraptorids (e.g., *Megaraptor, Australovenator, "Rapator"*) the medial distal condyle of metacarpal I is more distally placed than in other theropods (Calvo et al, 2004;

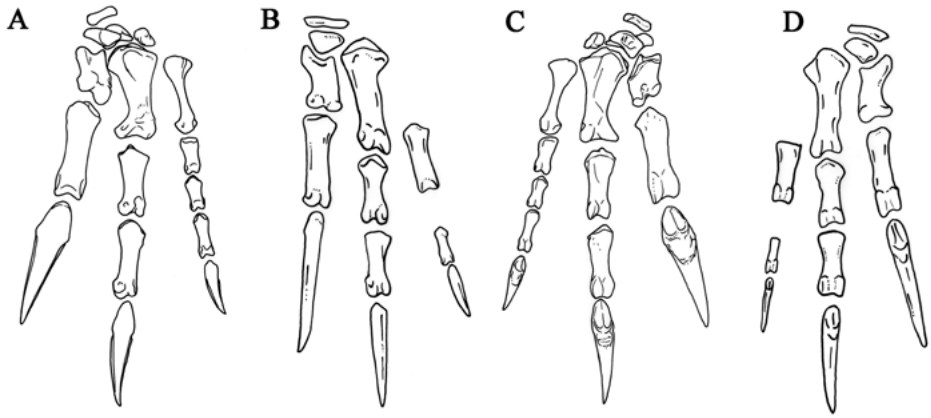

Figure 4. Left manus of (A,C), *Allosaurus fragilis*, and (B,D), *Australovenator wintonensis* in (A,B) dorsal, and (C,D) ventral views. Not to scale. B,D, mofied from White et al. (2012).

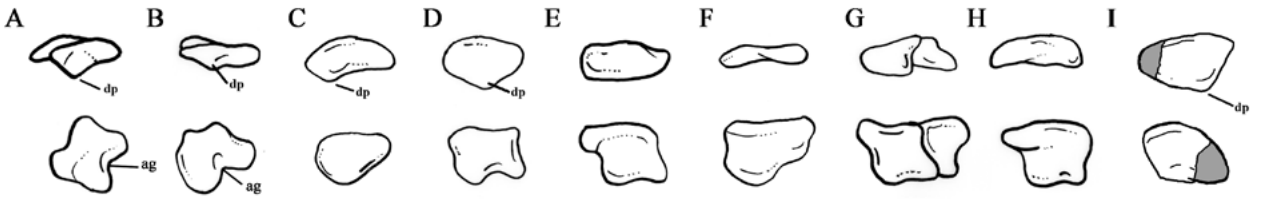

Figure 5. Left "semilunate" carpal in proximal (upper row) and dorsal (lower row) of A, *Allosaurus*, B, *Acrocanthosaurus* (modified from Currie and Carpenter, 2000); C, *Megaraptor*; D, *Guanlong* (modified from Xu et al., 2014); E, *Ornitholestes* (mofiied from Carpenter et al., 2005); F, *Tanycolagreus* (modified from Carpenter et al., 2005); G, *Alxasaurus* (modified from Xu et al., 2014); H, *Deinonychus* (modified from Ostrom, 1969); and I, *Australovenator* (modified from White et al., 2012). Not to scale. **Abbreviations**: ag, anterior groove; dp, distal projections.

White et al., 2012; fig. 8). In addition, the distal end of metacarpal I in megaraptorids is distally oriented, lacking a medial tilting (Calvo et al., 2004; Agnolin et al., 2010; White et al., 2012, 2013). This morphology results in a metacarpal I that is distally less asymmetrical than in other theropods, with the exception of derived paravians, including *Archaeopteryx,* dromaeosaurids and troodontids, in which the distal end lacks the medial twisting present in other theropods (Rauhut, 2003).

In most saurischians, including theropods, the distal end of the first metacarpal I shows asymmetrically developed articular condyles, in which the lateral condyle is larger than the medial condyle (Galton, 1971). This pattern is also present in all known megaraptorids (Calvo et al., 2004; White et al., 2012, 2013). However, the distal end of metacarpal I shows some minor distinctions among megaraptorids: in *Megaraptor* metacarpal I differs from *Allosaurus* and *Australovenator* in the presence of a greatly developed lateral distal condyle, which is ventrally wider than in the above mentioned taxa. In *Australovenator*, the medial distal condyle is prominently projected ventrally (as seen in distal view; see White et al., 2012, fig.13C), constituting a condition hitherto unreported among theropods, with the exception of of *Guanlong* in which the medial condyle projects incipiently ventrally. Differences between *Megaraptor* and *Australovenator* may reveal subtle variations in the way digit I functioned. Contrasting with *Acrocanthosaurus* and *Allosaurus* (Madsen, 1976; Currie and Carpenter, 2000), *Megaraptor* has a metacarpal I that bears distal articular condyles that are little-developed dorsally and lack the globe-shaped morphology characteristic of the aforementioned allosauroids. In the same way, *Xuahanosaurus* has a poorly developed distal articular surface in both views (Dong, 1984). The extensor ligament pit of metacarpal I in *Megaraptor* is roughly triangular in outline, unlike the transversely elongate and elliptical form of this feature *Acrocanthosaurus* and *Allosaurus* (Madsen, 1976; Currie and Carpenter, 2000; fig. 7). *Guanlong* has a similar condition to *Megaraptor* (Xu et al., 2014).

The dorsal surface of metacarpal I in non-coelurosaurian theropods (e.g., *Allosaurus, Acrocanthosaurus, Torvosaurus;* Madsen, 1976; Galton and Jensen, 1979; Currie and Carpenter, 2000) is longitudinally grooved. This groove is contiguous with a similar trough on the dorsal surface of the semilunate carpal (fig. 5). By contrast, in coelurosaurs (e.g., *Scipionyx, Tyrannosaurus, Falcarius, Gallimimus*, *Deinonychus*; Ostrom, 1979; Brochu, 2003; Zanno, 2010; Dal Sasso and Maganuco, 2011) the dorsal surface of metacarpal I and its

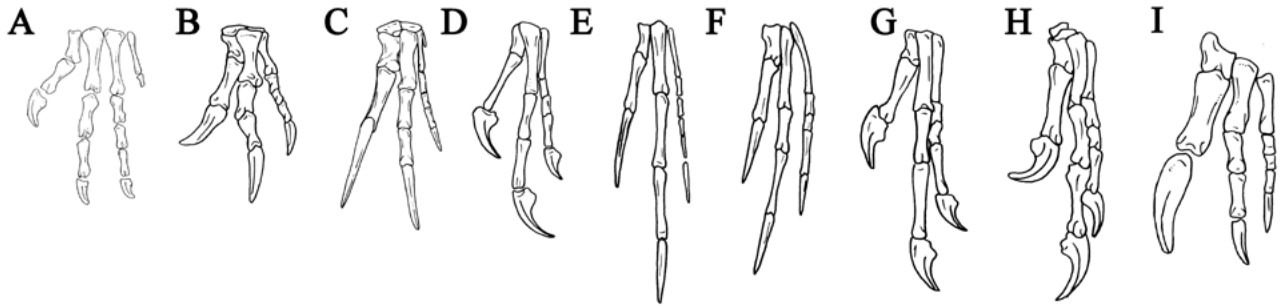

Figure 6. Left manus in dorsal view of A, *Dilophosaurus* (modified from Welles, 1980); B, *Allosaurus*; C, *Megaraptor*; D, *Sinocalliopteryx*; E, *Tanycolagreus* (modified from Carpenter et al., 2005); F, *Deinonychus* (modified from Ostrom, 1969); G, *Scipionyx* (modified from Dal Sasso and Maganuco, 2011); H, *Guanlong* (modified from Xu et al., 2009); and I, *Sinosauropteryx* (modified from Currie and Chen, 2001). Not to scale.

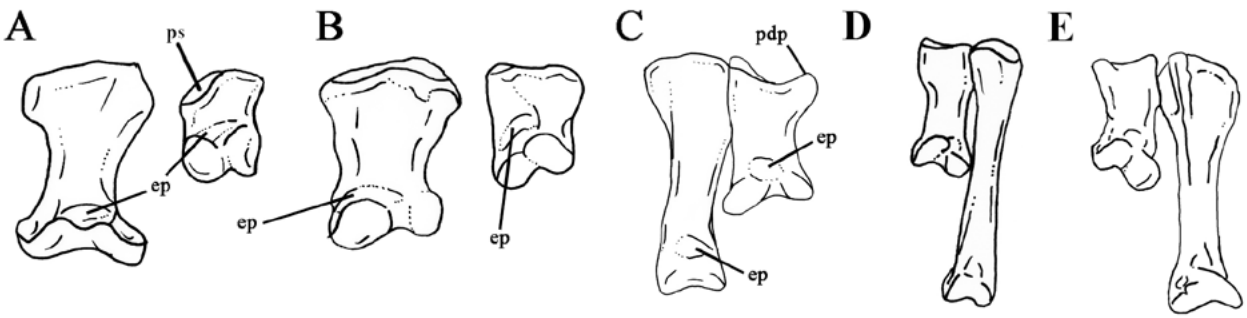

Figure 7. Right metacarpals II and I in dorsal view of A, *Acrocanthosaurus* (modified from Currie and Carpenter, 2000); B, *Torvosaurus* (modified from Galton and Jensen, 1979); C, *Megaraptor*; D, *Deinonychus* (modified from Ostrom, 1969); E, *Guanlong* (modified from Xu et al., 2009). Not to scale. **Abbreviations**: ep, extensor pit; pdp, proximomedial process; ps, proximolateral surface.

corresponding carpal is almost flat or slightly concave. In *Australovenator* the dorsal surfaces of both metacarpal I and the semilunate carpal are almost flat, resembling the condition described for coelurosaurs. In *Megaraptor* the metacarpal I is slightly concave, and although the semilunar carpal is damaged, its dorsal surface is flattened. A similar condition to *Megaraptor* is retained in other basals coelurosaurs like *Guanlong, Ornitholestes* and *Tanycolagreus* which possesses a deep groove in dorsal view (Carpenter et al., 2005; Xu et al., 2006). In sum, the absence of a continuous proximodistal groove on metacarpal I and semilunate carpal may constitute a sinapomorphic trait uniting megaraptorids with coelurosaurs retained in some basals coelurosaurs.

Metacarpal II. In *Megaraptor* and *Australovenator* the metacarpal II is long and slender, with a distal ginglymoid transversely narrower than the proximal end of the bone. This condition differs from that of *Syntarsus, Dilophosaurus, Allosaurus*, and *Acrocanthosaurus*, in which the distal end of metacarpal II bears a prominent ginglymus that flares on both sides, with a transverse diameter equals to that of the proximal end. The just condition described for megaraptorids resembles that of *Compsognathus* (Ostrom, 1969) and *Sinocalliopteryx* (Ji et al., 2007). An intermediate step between the allosauroid and the megaraptorid condition is seen in *Guanlong* (Xu et al., 2006). Scaled at the same size, the distal ginglymoid of metacarpal II of *Megaraptor* is considerably narrower than that of *Allosaurus*, representing half the transverse diameter of the latter taxon´s metacarpal II. Another condition is seen in derived coelurosaurids *(Deinonychus;* Ostrom, 1969) which has a slender metacarpal I with equally developed extremities. In congruence with the narrow condition of distal ginglymus, the extensor ligament pit of metacarpal II in *Megaraptor* has a proximodistally extended sub-triangular contour, similar to *Sciurumimus* (Rauhut et al., 2012), but different from the proximodistally short and transversely wide ligament pit of *Allosaurus* (Madsen, 1976).

As mentioned above, in *Megaraptor* the proximal head of metacarpal II is medially expanded, ventrally embracing metacarpal I**.** This condition differs from that of most coelurosaurs, including *Compsognathus,* tyrannosauroids (e.g., *Guanlong, Tanycolagreus, Tyrannosaurus;* Xu et al., 2009; Carpenter et al., 2005; Brochu, 2003), and more crownward forms (e.g., *Ornitholestes, Deinonychus, Velociraptor*; Carpenter et al., 2005; Ostrom, 1976), in which

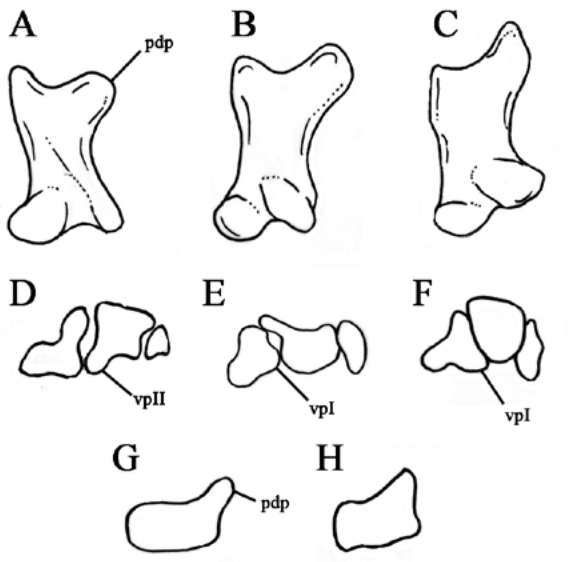

Figure 8. A-C, left first metacarpal in dorsal view of A, *Megaraptor,* B, *Australovenator*, and C, *Rapator*; D-F, proximal view of left metacarpus of D, *Guanlong* (modified from Xu et al.,2009), E, *Tanycolagreus* (modified from Carpenter et al., 2005), and F, *Deinonychus* (modified from Ostrom, 1969); G-H, proximal view of right first metacarpal of G, *Rapator*, and H, *Australovenator.* Not to scale. **Abbreviations**: pdp, proximomedial process; vpI, ventral process of metacarpal I; vpII, ventral process of metacarpal II.

the lateroventral margin of metacarpal I is laterally projected, thus embracing the ventral surface of metacarpal II.

Metacarpal III. Among megaraptorans, this bone has been solely recorded in *Megaraptor.* Calvo et al. (2004) described the metacarpal III of *Megaraptor* as transversally compressed, its distal end being narrower than its proximal end. This condition is also present in most tyrannosaurids (e.g., *Daspletosaurus, Tyrannosaurus, Albertosaurus*; Russell, 1970; Lipkin and Carpenter, 2008), in which metacarpal III is extremely slender. This condition has been interpreted as diagnostic of advanced tyrannosauroids (Holtz, 2004).

The reduction of metacarpal III is correlated with the reduction of the entire digit III. In *Megaraptor* the phalanges of digit III are proximodistally shortened and transversely compressed, thus resulting in a digit III shorter and more slender than in basal tetanurans (e.g., *Allosaurus, Acrocanthosaurus*; Madsen, 1976; Currie and Carpenter, 2000). This peculiar morphology may be regarded as autapomorphic for *Megaraptor.*

In *Megaraptor*, the length of metacarpal III represents 71% of metacarpal II, a ratio that matches that of specialised tyrannosauroids (Russell, 1970; Barsbold, 1982; Rauhut, 2003; Holtz, 2004). This proportion, as well as the short length of the entire digit III may be a condition shared between both groups.

Megaraptor retained a small and rod-like metacarpal IV, and no evidence of phalanges of digit IV have been found in the preserved manus (Calvo et al., 2004), thus it is probable that digit IV was completely lost. The only available specimen of *Australovenator* does not preserve metacarpal IV (Hocknull et al., 2009; White et al., 2012). Presence of metacarpal IV in *Megaraptor* is here interpreted as an apomorphic reversal from the neotetanuran ancestral state, in which metacarpal IV is absent (e.g., *Sciurumimus, Allosaurus, Acrocanthosaurus;* Rauhut, 2003). This conclusion agrees with Rauhut et al. (2012) who recognized a high level of homoplasy in this characteristic, given that the basal allosauroid *Sinraptor* (Currie and Zhao, 1993) and the basal tyrannosauroid *Guanlong* (Xu et al., 2006) retained a rudimentary fourth metacarpal.

Manual phalanges. In *Megaraptor* and *Australovenator*, manual phalanges exhibit shallow and triangular-shaped extensor ligament pits, which lack well-defined margins and are not proximally delimited by a transverse ridge (fig. 7). Rauhut (2003) pointed out that coelurosaurs lack well-defined extensor pits on manual phalanges. In contrast, in non-coelurosaurian theropods, extensor ligament pits are deep and transversely extended, as shown for example in *Eoraptor, Dilophosaurus, Syntarsus, Xuanhanosaurus, Torvosaurus, Allosaurus, Acrocanthosaurus, Sinraptor,* and *Baryonyx* (Raath, 1969; Madsen, 1976; Galton and Jensen, 1979; Welles, 1984; Dong, 1984; Currie and Zhao, 1993; Sereno et al., 1993; Charig and Milner, 1997; Currie and Carpenter, 2000; Rauhut, 2003). In contrast most coelurosaurian theropods have shallow or absent extensor pits (e.g. *Deinonychus, Nothronychus, Tyrannosaurus, Troodon*; Ostrom, 1969; Currie and Russel, 1987; Bochu, 2003; Zanno et al., 2009; Zanno, 2010).

Phalanges of digit I. Megaraptor is distinguished from the remaining theropods, including *Australovenator*, in the remarkable elongation of the internal bones of the manus (i.e., metacarpal I, phalanx 1.I, and especially the ungual phalanx). The tip of digit I ungual ends at the level of the mid-length of the second ungual digit (fig. 3).

Phalanx 1 of digit I of *Megaraptor* exhibits a proximodorsal lip. In most basal theropods (e.g., coelophysoids, *Torvosaurus, Spinosaurus, Allosaurus, Acrocanthosaurus;* Rauhut, 2003; Ibrahim et al., 2014) the phalanx I.1 bears a transversely wide proximodorsal lip on phalanx 1 of digit I. Such a wide lip appears to be related with a transversely extended, deep, and well-defined extensor ligament pit on distal metacarpal I, a condition regarded as plesiomorphic among theropods (Sereno et al., 1993; Rauhut, 2003). However, among coelurosaurs (e.g., *Tanycolagreus, Guanlong, Tyrannosaurus*, *Gallimimus*, *Deinonychus*; Ostrom, 1976; Brochu, 2003; Carpenter et al., 2005; Xu et al., 2006) the proximodorsal lip of phalanx 1 is narrower. In *Megaraptor* and *Australovenator* the proximal surface of the proximal phalanx presents a pointed proximodorsal lip, which is different from the condition described for the remaining theropods. This pointed process appears to be related with a reduction in the distal extensor pits of the metacarpals, as diagnostic of coelurosaurs (Rauhut, 2003).

In *Megaraptor* and *Australovenator* the proximal end of phalanx I.1 is sub-quadrangular in outline (fig. 9). It shows robust and thickened lateral, medial, and dorsal margins, conforming to an expanded articular surface for metacarpal I. The lateral margin is even more thickened than the medial one and is strongly proximally expanded. This set of features

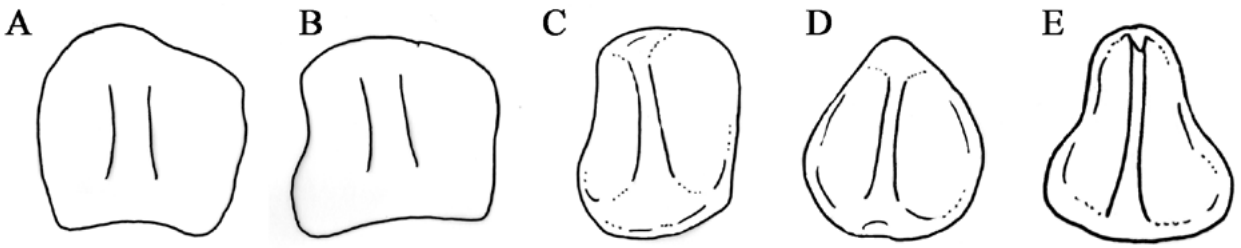

Figure 9. Proximal end of right phalanx I.1 of A, *Megaraptor*; B, *Australovenator*; C, *Allosaurus*; D, *Tyrannosaurus* (modified from Brochu, 2003); and E, *Deinonychus* (modified from Ostrom, 1969). Not to scale.

appears to be unique to megaraptorids: in other theropods, the proximal end is transversely narrow and dorsoventrally deep, being sub-rectangular in shape (e.g., *Allosaurus, Acrocanthosaurus, Torvosaurus, Tyrannosaurus*; Galton and Jensen, 1979; Madsen, 1976; Currie and Carpenter, 2000; Brochu, 2003) or subtriangular in outline (as in *Guanlong* and *Deinonychus*; Ostrom, 1976; Xu et al., 2006). Furthermore, in *Megaraptor* the proximal articular surface is transversely wider dorsally than ventrally (Novas, 1998). This condition is unknown in other theropods, including *Australovenator* (White et al., 2012), in which the proximal end is transversely wider on its ventral margin than on its dorsal edge.

Phalanx 1 of digit I in *Megaraptor* shows a deep and wide furrow along its ventral surface (Novas, 1998). As a result, both lateral and medial margins of this surface acquired the form of sharp longitudinal ridges (fig. 10). These features are also documented in *Australovenator* (White et al., 2012). In other theropods, phalanx 1.I is ventrally excavated, but the furrow is restricted on the proximal half of the bone, and it is not as deep as in megaraptorids. No longitudinal ridges are present. It is interesting to note that in megaraptorids, the ventral margin of the proximal articular surface of phalanx 1.I is concave, reflecting the deep furrow present along the ventral surface of the bone. This is in contrast with other theropods, in which this margin is straight (e.g., *Allosaurus*; Madsen, 1976) or convex (e.g., *Guanlong, Deinonychus*; Ostrom, 1976; Xu et al., 2006).

The distal ginglymus of phalanx 1.I of *Megaraptor* is dorsoventrally deeper and transversely narrower than in other theropods (including *Australovenator*), and the dorsoventral sulcus is much more incised.

Megaraptor is well-known by its extremely large and elongate manual ungual on digit I (Calvo et al., 2004), which is subequal in length to the ulna**.** This condition is unusual among theropods, being absent among basal tetanurans (e.g., *Allosaurus*; Madsen, 1976), basal coelurosaurs (e.g., *Scipionyx, Tanycolagreus, Chilantaisaurus*; Dal Sasso and Maganuco, 2011; Carpenter et al., 2005; Benson and Xu, 2008), ornithomimosaurs (e.g., *Gallimimus*), oviraptorosaurs, basal therizinosaurs (e.g., *Falcarius, Nothronychus*; Zanno, 2010; Zanno et al., 2009), and paravians (e.g., *Deinonychus*; Ostrom, 1969). Furthermore, in the megaraptorans *Australovenator* and *Fukuiraptor*, the ungual of digit I is much shorter than the ulna, representing approximately half of its length. Basal tetanurans that evolved an enlarged ungual in manual digit I are the compsognathid *Sinosauropteryx* (Currie and Chen, 2001), and the megalosauroids *Baryonyx* and *Torvosaurus* (Galton and Jensen, 1979; Charig and Milner, 1997).

In the original description of *Megaraptor* (Novas, 1998), it was remarked that the ungual phalanx bore a sharp longitudinal ventral keel. This trait was later considered as a synapomorphy of Megaraptoridae (Novas et al., 2013). In *Megaraptor*, towards the proximal end of the claw, the ventral keel gradually displaces laterally, joining the lateral margin of the claw on its most proximal portion, a condition also reported in *Australovenator* (White et al., 2012; fig. 11). Other theropods, including *Fukuiraptor* (Azuma and Currie, 2000), basal tyrannosauroids (e.g., *Guanlong*; Xu et al., 2006), megalosauroids (e.g., *Baryonyx*, *Torvosaurus*; Galton and Jensen, 1979; Charig and Milner, 1997) and the problematic *Chilantaisaurus* (Benson and Xu, 2008) have unguals with a transversely rounded expanded ventral surface, without traces of a ventral keel. In sum, such a transverse compression of the enlarged ungual constitutes a distinctive feature of Megaraptoridae.

In addition, the manual ungual I of *Megaraptor* and *Australovenator* share very deep and well-defined flexor facets on the lateral and medial surfaces of the flexor tubercle. These facets are deep, wide, and more well-defined than in other theropods, including *Allosaurus, Baryonyx* and *Torvosaurus* (Madsen, 1976; Galton and Jensen, 1979; Charig and Milner, 1997). Furthermore, in *Megaraptor* such facets are delimited by acute ridges of bone (Figure 12). It is worth nothing that similar facets were described for *Fukuiraptor* (Azuma and Currie, 2000).

Digit II. In *Megaraptor*, phalanx 1.II is shorter than phalanx 2.II, a condition similar to that of some allosauroids, such as *Allosaurus* (Gilmore, 1920; Madsen, 1976) and *Acrocanthosaurus* (Currie and Carpenter, 2000), and selected coelurosaurs, as for example *Sinocalliopteryx* (Ji et al., 2007), *Sinosauropteryx* (Currie and Chen, 2001), *Scipionyx* (Dal Sasso and Maganuco, 2011), *Guanlong* and *Deinonychus*. Distribution of this feature (i.e., length ratio of pre-ungual phalanges of digit II) is not uniform among tetanurans. For example, in the megaraptorid *Australovenator* and the basal tyrannosauroid *Tanycolagreus* (Carpenter et al., 2005), phalanges 1 and 2 of

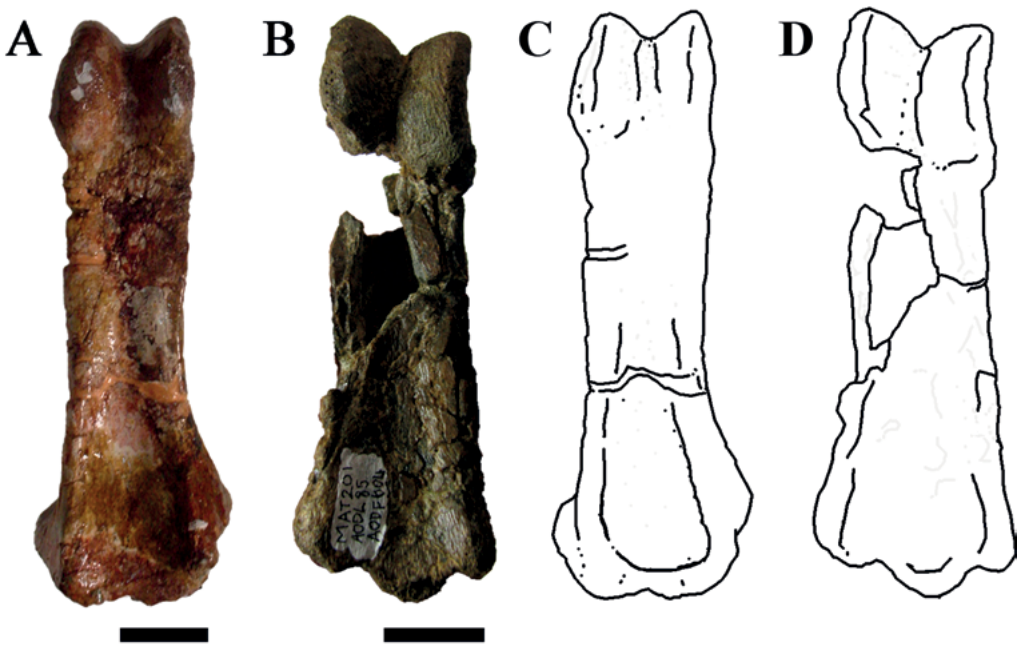

Figure 10. Right manual phalanx 1 of digit I in ventral view and schematic representations of *Megaraptor* (A, C), *Australovenator* (B,D). Scale bar: 2 cm. Note the well-developed longitudinal ventral furrow.

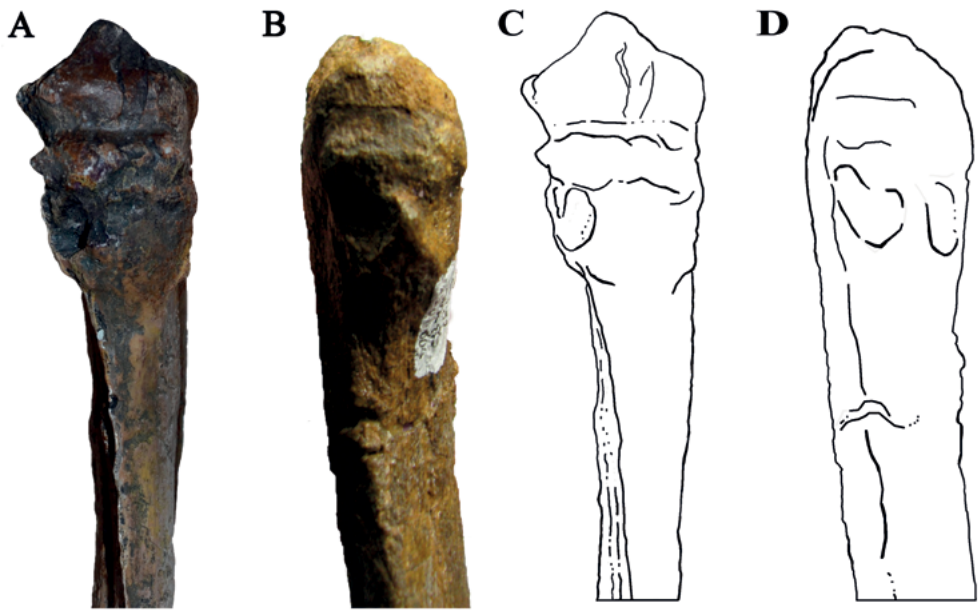

Figure 11. Right manual ungual phalanx of digit I in ventral view and schematic representation of *Megaraptor* (A,C); and *Australovenator* (B,D). Not to scale.

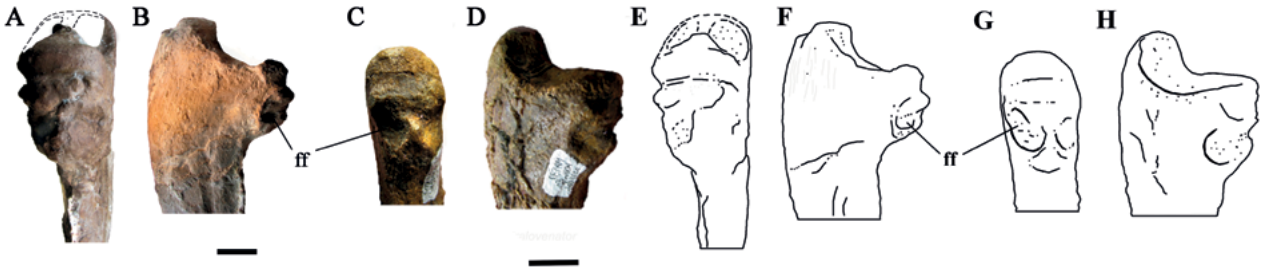

Figure 12. Right manual ungual phalanx of digit I in A,C, ventral, and B,D, lateral views. A-B, *Megaraptor*; C-D, *Australovenator* and schematic representation in E,G, ventral, and F,H, lateral views. E-F, *Megaraptor;* G-H, *Australovenator.* Scale bar: 2 cm. **Abbreviations**: ff, flexor facets.

digit II are subequal in length, and the megalosauroid *Sciurumimus* (Rauhut et al., 2012) shows coelurosaur-like proportions, with phalanx 1.II shorter than phalanx 2.II.

In *Megaraptor*, the proximal articular surface of phalanx 1.II describes a dorsoventrally deep ovoid contour. Its ventral margin bears a rounded process that projects proximomedially, a feature shared with *Australovenator* (White et al., 2012) and *Fukuiraptor* (Azuma and Currie, 2000). This results in a relatively narrow ventral margin of the proximal end of phalanx 1.I. This shape is in contrast with other theropods, such as *Allosaurus* and *Tyrannosaurus* (Madsen, 1976; Brochu, 2003), in which the ventral margin is straight. Furthermore, in *Megaraptor*, and probably also in *Australovenator* and *Fukuiraptor*, the proximal articular surface phalanx 1.II is obliquely oriented with respect to the distal articular trochlea, a condition unknown in other theropods, in which the main axes of both proximal and distal ends are sub-parallel.

In *Megaraptor*, metacarpal II and its corresponding non-ungual phalanges have respective distal articular trochleae with a medial condyle more ventrally projected than the lateral one. In probable correlation with this shape, it is seen that non-unguals of digit II exhibit a longitudinal keel that runs along their ventromedial margins. Such strong asymmetry of distal condyles and longitudinal ridges appear to be absent in other theropods, including *Australovenator*, although in the available phalanx 1.II of *Fukuiraptor* (Azuma and Currie, 2000) a similar ventromedial ridge seems to be present.

Digit III. In *Megaraptor* phalanges of this digit look similar in proportions to those of *Allosaurus* (Gilmore, 1920; Madsen, 1976), except for the ungual, which is proportionally shorter and smaller. The pre-ungual phalanx of digit III of *Megaraptor* is longer than phalanges 1 and 2 of the same digit, as generally occurs among tetanurans, although it does not reach the elongation that characteristically occurs in coelurosaurs (e.g., *Sinocalliopteryx, Dilong, Guanlong, Deinonychus*; Ostrom, 1976; Xu et al., 2006; Ji et al., 2007).

Conclusions

Shared presence of a longitudinal groove along the medial side of humeral shaft in megaraptorans and tyrannosaurids conforms a novel feature supporting close relationships between these theropod families. Comparison of the manus in *Megaraptor* and *Australovenator* allowed the recognition of several features that may shed light on the phylogenetic relationships of megaraptorids. The manus of *Megaraptor* exhibits the following unique traits that are not present in other theropods, and are here interpreted as autapomorphies of this genus: 1) metacarpal I with an acute medial condyle on distal gynglimus; 2) phalanges of digit II with ventromedial ridges; and 3) an extremely elongate manual ungual on digit I, approximating the length of the ulna.

Manual characters here interpreted as diagnostic of Megaraptoridae include: symmetrical-shaped metacarpal I, proximal end of phalanx 1.I transversally expanded, phalanx 1.I with a longitudinal ventral furrow, and ungual phalanx of digit I with a laterally displaced sharp ventral margin. Manual characters diagnostic of Megaraptora are more difficult to recognize because the manus of the basal megaraptoran *Fukuiraptor* is poorly known. Nevertheless, two possible derived features have been identified: asymmetrical phalanx 1. II; and first digit ungual with deep facets on the flexor tubercle.

After comparing carpal, metacarpal and phalangeal morphology, it becomes evident that megaraptorids retained several of the manual features present in basal tetanurans, such as *Allosaurus*. In this regard, *Megaraptor* and *Australovenator* are devoid of several manual features that the basal tyrannosauroid *Guanlong* shares with more derived coelurosaurs (e.g., *Deinonychus*). However, there are some manual characters that support Megaraptora as members of Coelurosauria, including the elongate and slender shaft of metacarpals I and II, and the presence of separated flexor and extensor distal end of the humerus, and the absence of a longitudinal furrow on the dorsal surface of metacarpal I, and a semilunar carpal. Furthermore, megaraptorans are similar to specialised members of Tyrannosauroidea in having a transversely narrow metacarpal III that represents 0.75 the length of metacarpal II, a set of features previously interpreted as synapomorphies uniting both clades (Novas et al., 2013; Porfiri et al., 2014).

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