

# THE HAND STRUCTURE OF *CARNOTAURUS SASTREI* (THEROPODA, ABELISAURIDAE): IMPLICATIONS FOR HAND DIVERSITY AND EVOLUTION IN ABELISAURIDS

by JAVIER RUIZ<sup>1</sup>, ANGÉLICA TORICES<sup>2</sup>, HUMBERTO SERRANO<sup>2</sup> and VALLE LÓPEZ<sup>3</sup>

<sup>1</sup>Departamento de Geodinámica, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, 28040 Madrid, Spain; e-mail: jaruiz@geo.ucm.es

<sup>2</sup>Departamento de Paleontología, Universidad Complutense de Madrid, 28040 Madrid, Spain

<sup>3</sup>Instituto de Geología Económica, CSIC-Universidad Complutense de Madrid, 28040 Madrid, Spain

---

**Abstract:** *Carnotaurus sastrei* is an abelisaurid dinosaur from the Late Cretaceous of Argentina that has very reduced, but robust, forelimbs and derived hands with four digits, including a large, conical-shaped metacarpal IV lacking an articulation for a phalanx. The analysis presented in this work highlights a series of additional autapomorphies of *C. sastrei*. For example, the proximal phalanges are longer than the metacarpals in digits II and III, and digit III

includes only one phalanx besides the ungual. The hand of *Carnotaurus* shares several features with those of *Aucasaurus* and *Majungasaurus*, but the hands of the latter genera also display autapomorphies, indicating that the diversity in abelisaurid hand structure is similar to the diversity of cranial protuberances of these dinosaurs.

**Key words:** Dinosauria, Theropoda, abelisaurids, *Carnotaurus*.

---

*CARNOTAURUS SASTREI*, known from a fairly complete and articulated skeleton from the Late Cretaceous of the Argentinean Patagonia, was the first abelisaurid specimen discovered that preserved a nearly complete forelimb (see Bonaparte *et al.* 1990). The abelisaurids are theropod dinosaurs typical of Gondwana characterized by a short, high skull, textured maxillae, frequent presence of frontal bulking or protuberances of diverse morphologies, and highly reduced forelimbs (Sampson *et al.* 1998; Coria *et al.* 2002, Sereno *et al.* 2004; Carrano and Sampson 2008; Novas 2009). Abelisaurids are included in the clade Ceratosauria (Bonaparte 1991); we follow recent works that exclude coelophysoids from Ceratosauria, which is therefore considered to be the sister group of Tetanurae (for a review see Carrano and Sampson 2008).

*Carnotaurus* has very reduced forelimbs that display a highly derived morphology. The radius and ulna are very robust and are roughly one-fourth the length of the humerus. The hand has four digits, with the elongate and conical-shaped metacarpal IV being the largest bone in the hand (Bonaparte *et al.* 1990). The hands of *Carnotaurus sastrei* were recovered partly articulated, but several bones are lost or displaced. Presumably based on their study of the right hand of the only available specimen of

*Carnotaurus*, Bonaparte *et al.* (1990) proposed that the hand is characterized by short metacarpals (except metacarpal IV) and first phalanges, similarly to *Ceratosaurus nasicornis*, a ceratosaur from the Late Jurassic Morrison Formation of the United States. Bonaparte *et al.* (1990) interpreted several small bones found on the manus or forearm bones as carpals.

The discovery of *Aucasaurus garridoi* (Coria *et al.* 2002), from the Campanian of Patagonia, provided a second example of an abelisaurid forelimb with better preserved articulation than that of *Carnotaurus*, and Burch and Carrano (2008) recently gave a preliminary report of the recovery of a nearly complete forelimb of the Malagasy abelisaurid *Majungasaurus crenatissimus*. The hand of *Aucasaurus* also has four digits, but the largest bone is metacarpal I, and metacarpal IV, although conical in shape and apparently lacking an articulation for a phalanx, is comparable in size to metacarpals II and III. The metacarpals of *Aucasaurus* articulate directly with the forearm bones, and for this reason, Coria *et al.* (2002) suggested that the small bones of *Carnotaurus* interpreted as carpals by Bonaparte *et al.* (1990) could be phalanges. In this context, it is important to note that the hands of *Ceratosaurus* and *Majungasaurus* lack ossified carpals

(Gilmore 1920; Burch and Carrano 2008), and this is also the case for the Chinese very basal ceratosaur *Limusaurus inextricabilis* (Xu *et al.* 2009).

In this work, we examine the hand structure of *Carnotaurus sastrei*, taking into account the bones preserved in both hands. Indeed, the consideration of the right and left hands together offers an image sharply different from that previously obtained from the study of the right hand alone. We also discuss the implications of our observations on forelimb diversity and evolution in abelisaurid theropods.

*Institutional abbreviations.* MACN-CH, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' - Colección Chubut, Buenos Aires, Argentina.

## MATERIAL

MACN-CH-894, holotype of *Carnotaurus sastrei* (Bonaparte, 1985), was collected from the Late Cretaceous (Campanian–Maastrichtian) La Colonia formation (Lamanna *et al.* 2002), Chubut Province, Central Patagonia, Argentina. The specimen preserves nearly complete forelimbs, including an important proportion of both hands, which are partly articulated, partially embedded in matrix and physically joined to the respective forearms (Pl. 1). Many of the preserved bones, particularly those of the right hand, have suffered some degree of post-mortem displacement, and some are broken and/or incomplete.

## DESCRIPTION AND COMPARISON

The hand of *Carnotaurus* has four metacarpals. Metacarpal IV is the largest bone in the hand of *Carnotaurus*. It is well preserved in the right hand, whereas it is broken into two fragments in the left hand and its distal end is lost (Pl. 1, figs 1–2, 4). This bone is enlarged and has a conical and relatively acute distal end without an articular facet for a phalanx. The proximal part of this bone is rounded and includes a concave surface for the articulation with the ulna on its palmar side; in fact, the left metacarpal IV is preserved articulated to the ulna (Pl. 1, fig. 1), which is a configuration unique among the known theropods that retain a fourth metacarpal. Indeed, in contrast to the condition in *Carnotaurus*, metacarpal IV is

short and very thin, with an articulation for a small phalanx, in coelophysoids, *Ceratosaurus* (e.g. Gilmore 1920; Tykoski and Rowe 2004) and *Limusaurus* (Xu *et al.* 2009). In *Aucasaurus*, metacarpal IV is conical and without articulation for a phalanx, but short and of similar size to the metacarpals II and III (Coria *et al.* 2002). So, although the metacarpal IV of *Carnotaurus* presents a more derived condition than that of *Aucasaurus*, both genera share a conical metacarpal IV that is of similar width to metacarpals II and III.

Metacarpals I, II and III are robust, relatively short and generally resemble one another (Pl. 1, figs 1–4). These bones display concave and mostly smooth proximal articulation surfaces, suggesting that they should articulate directly with the forearm. In fact, metacarpals II and III are preserved in the left hand in connection with the radius and ulna, respectively, and the proximal end of metacarpal II is dorsolaterally expanded to provide an ample surface of articulation with the radius (Pl. 1, figs 1–2). Metacarpals directly articulated with the forearm are also exhibited by *Aucasaurus* (Coria *et al.* 2002), and ossified carpals are not present in *Ceratosaurus*, *Limusaurus* and *Majungasaurus*.

The length of metacarpal III of *Carnotaurus* is roughly 80 per cent of that of the metacarpal II. By contrast, in coelophysoids, *Ceratosaurus* (Tykoski and Rowe 2004) and basal Tetanurae (Holtz *et al.* 2004), metacarpal III is similar in length to metacarpal II. Thus, with respect to this feature, *Carnotaurus* is more derived. Metacarpal I of *Carnotaurus* has a similar length to metacarpal III, whereas metacarpal I is roughly as long as half of metacarpal II in herrerasaurs (see Langer 2004; Novas 2009), coelophysoids, *Ceratosaurus* (Tykoski and Rowe 2004) as well as in the majority of Tetanurae (Holtz *et al.* 2004), although in ornithomimosaurs, metacarpals I and II are usually of similar length (e.g. Makovicky *et al.* 2004).

Metacarpal I of *Carnotaurus* has a conservative appearance, with a distal articulation for a phalanx (Pl. 1, fig. 4). This bone is conical but very reduced, and it does not carry phalanges, in *Limusaurus* (Xu *et al.* 2009). The metacarpal I of *Ceratosaurus* is also small, but not conical, showing a groove in its distal end, indicating the presence of at least one phalanx in digit I. In contrast, metacarpal I is the longest bone of the hand of *Aucasaurus*, and it has a conical appearance resembling that of metacarpal IV, albeit none is as derived as the metacarpal IV of *Carnotaurus*; also, the metacarpal I of *Aucasaurus* apparently did not bear phalanges (Coria *et al.* 2002).

---

### EXPLANATION OF PLATE 1

Figs 1–4. Hands of MACN-CH-894. 1, Right hand, dorsal view. 2, Right hand, palmar view. 3, Left hand, dorsal. 4, Left hand, palmar view.



2 cm



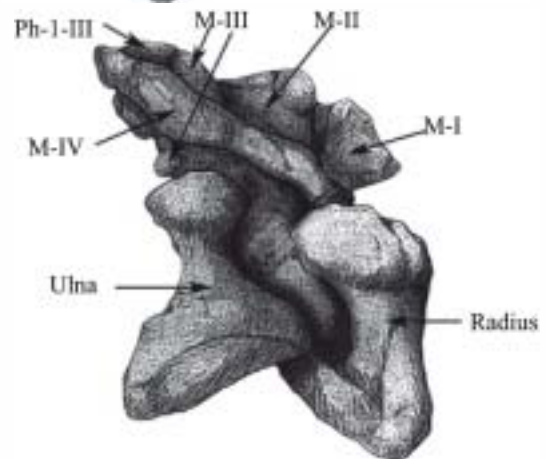
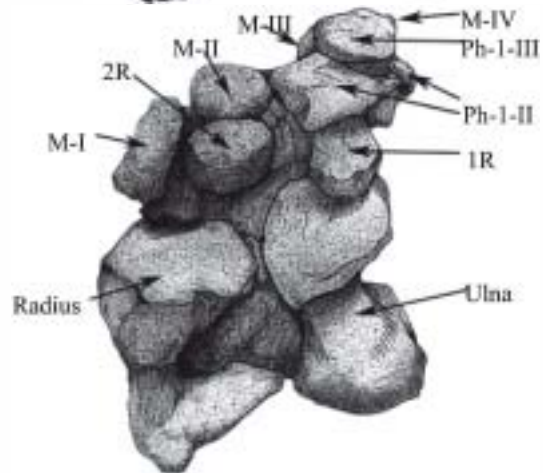
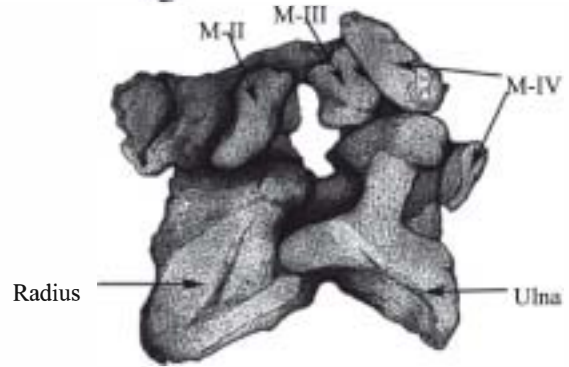
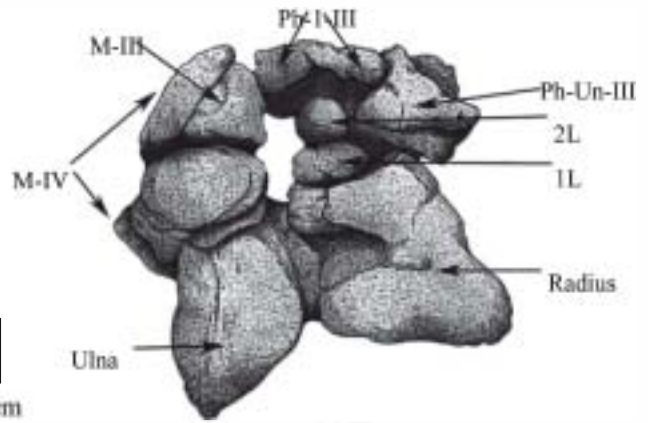
2 cm



2 cm



2 cm



On the right hand, only a c. 1 cm fragment of the proximal part of phalanx 1–III is preserved (Pl. 1, fig. 3); this fragment is articulated with the metacarpal III. On the left hand, phalanx 1–III is longitudinally broken, its palmar part is lost, and a fracture separates the proximal part of the bone (which remains articulated with metacarpal III) from the distal part, which is longer but with a lesser preserved transversal section (Pl. 1, fig. 1); the distal fragment has been displaced and slightly rotated with respect to the proximal one. Because of this, the total length of this phalanx is difficult to measure exactly (we estimate it to be 40 mm), although it is clearly larger than metacarpal III, a condition unique among the known theropods.

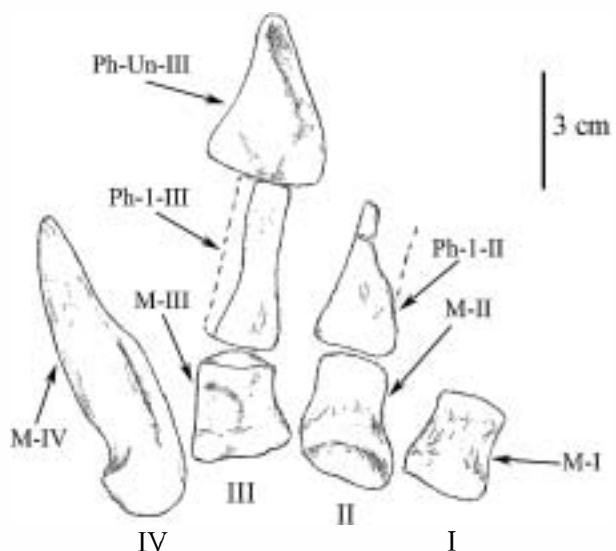
On the left hand, there is a bony piece articulated with the distal end of phalanx 1–III, which we tentatively interpret as the unguis phalanx of digit III (Pl. 1, fig. 1). This element has a roughly textured surface, an approximately conical shape and a somewhat acute end, although it is not clear whether it was sharp. Thus, digit III of *Carnotaurus* had only one phalanx besides the unguis.

On the right hand, a large portion of a phalanx is preserved in contact with the lateral side of metacarpal II, although its major axis is oriented perpendicular to the metacarpal (Pl. 1, fig. 3). This phalanx was interpreted by Bonaparte *et al.* (1990) as the phalanx 1–II. This interpretation is accepted here because metacarpal II is located between this phalanx and metacarpal I. This putative phalanx 1–II of the right hand is fractured and includes a small fragment that has been moved slightly distal to the larger fragment. Bonaparte *et al.* (1990) suggested that the first phalanx of digit II is relatively short, and they interpreted the minor fragment as a portion of the proximal part of a second phalanx of digit II. However, the more distal portion of the larger fragment is clearly fractured and without indications of an articulation, which supports our interpretation. The total length (around 39 mm) of the preserved portion of this phalanx is difficult to estimate precisely (because of the displacement of the minor fragment), but it is comparable to the length of phalanx 1–III preserved in the left hand. Similar to the condition exhibited by digit III, phalanx 1–II is longer than metacarpal II, which is also unique among the theropods.

Two small bones have been recovered in each of the two hands of MACN-CH 894, although it is not clear that they represent the same elements (Pl. 1, fig. 1, 3). Bonaparte *et al.* (1990) interpreted these small bones as carpals, which were tentatively placed by these authors between the metacarpals II and III and the forearms. In contrast, Coria *et al.* (2002) suggested that these bones were probably phalanges, on the basis of the structure observed in *Aucasaurus*, in which carpals were not recovered and the metacarpals were directly articulated on the forearm.

All of these four small bones are preserved on the dorsal side of the hand (which may or may not be indicative of their original position), have a subcylindrical shape and are short, with a wide transverse section (Pl. 1, figs 1, 3). We have denoted these bones with a number and the initial of the hand side, but this terminology does not have implications for bone interpretation. On the right hand, one of these elements (1R) is placed on the ulna, whereas the other (2R) is on the metacarpal II, in equal distance from the ulna and from the radius (Pl. 1, fig. 3). In the left hand, a small bone (1L) is preserved on the radius, and another (2L) lies between 1L and phalanx 1–III (Pl. 1, fig. 1). These bones resemble, to a certain degree, the comparatively short and featureless phalanges II-2, III-1 and III-2 of *Limusaurus*, which would support their interpretation as phalanges of digit I and/or II. However, preserved phalanges of the closer *Carnotaurus*-relatives *Ceratosaurus* and *Aucasaurus* are not as featureless as those of *Limusaurus* or the small bones of *Carnotaurus*.

An alternative interpretation, similar to that proposed by Bonaparte *et al.* (1990) although not exactly equivalent, would be that these bones are ossified carpals located on the dorsal side of the hand, because the metacarpals are directly articulated with the radius or the ulna. The interpretation of these bones as ossified carpals would be supported by the disposition of all the small bones on the dorsal side of the hand, by the position of 1R and 1L near the ulna and radius, respectively, and by our observation that the only two unambiguous phalanges are relatively long. Based on these uncertainties, the correct interpretation of those small bones preserved on both hands of



**TEXT-FIG. 1.** Reconstruction of the left hand (dorsal view) of *Carnotaurus sastrei*, based on the identified bones in both hands of MACN-CH-894 (see text for details).

MACN-CH 894 is therefore an open question, but if they are ossified carpals, their emplacement would be extremely unusual.

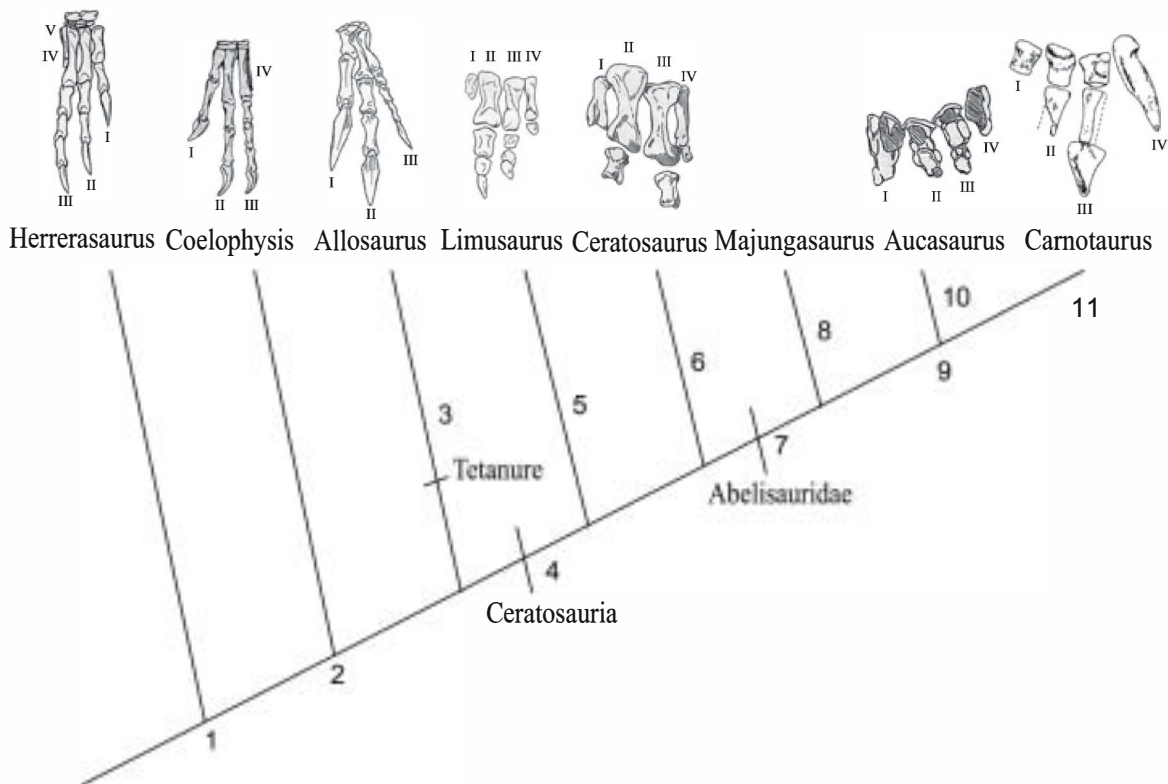
The examination of the left hand of MACN-CH 894, along with a re-evaluation of the right hand, gives a new interpretation of the structure of the hand of *Carnotaurus* with respect to the preliminary reconstruction of Bonaparte *et al.* (1990, fig. 29). Indeed, metacarpals are directly articulated with the forearms, and the first phalanges in digits II and III are larger than the respective metacarpals.

## DISCUSSION AND CONCLUSIONS

The structure of the hand of *Carnotaurus* is very peculiar, characterized by a series of features unique among the theropods (Text-fig. 1). The most obvious feature (Bona-

parte *et al.* 1990) is the lengthened metacarpal IV, which is the largest element in the hand, with a length more than two times that of metacarpal II and which ends in a conical and relatively acute distal extremity without an articulation for a phalanx. Also, the first phalanges of digits II and III are longer than the metacarpals with which they articulate, and digit III presents only one phalanx besides the ungual. Ossified carpals are either absent or placed on the dorsal side of the hand.

*Aucasaurus* shares with *Carnotaurus* metacarpals directly articulated with the forearm, and a conical metacarpal IV without an articulated phalanx and a similar width to those of metacarpals II and III. However, the largest element in the hand of *Aucasaurus* is the metacarpal I, whose shape is also conical. Otherwise, the highly derived hand of *Carnotaurus* has a metacarpal I with a conservative appearance, similar to the metacarpals II and



**TEXT-FIG. 2.** Simplified phylogeny including the left-hand anatomy of the most representative genera discussed in the text: *Herrerasaurus* (based on Sereno 1994), *Coelophysis* (based on Colbert 1989), *Allosaurus* (based on Norman, 1985), *Limusaurus* (based on Xu *et al.* 2009), *Ceratosaurus* (modified from Gilmore 1920), *Aucasaurus* (modified from the right hand in Coria *et al.* 2002) and *Carnotaurus* (this work). Currently, there are not available illustrations of the hand of *Majungasaurus*. Hands are not a scale, but shown in a similar size to facilitate comparisons. The presented phylogeny is based on Xu *et al.* (2009), for taxa not included in Abelisauridae, whereas for genera included in Abelisauridae, the shown relations derive from Coria *et al.* (2002), Canale *et al.* (2009) and the present work. Characters denoted by numbers: 1, elongate hand, five digits, with digit V much reduced; 2, M-II and M-III of similar length, digit IV reduced, digit V lost; 3, digit I robust, digit III thinned, digit IV lost; 4, reduction of the forearm, no ossified carpals; 5, M-I conical and much reduced; 6, first phalanges in digits II and III proportionally small; 7, M-II and M-III shortened; 8, certain degree of fusion of bones; 9, M-IV conical and of similar width to M-II and M-III; 10, M-I large, conical and without articulation for a phalanx; 11, enlargement of M-IV, P-1-II and P-1-III. There is a general trend to lost phalanges in ceratosaurs, although it cannot be exactly traced on the phylogeny.



III. Digits II and III of *Aucasaurus* preserve one and two small phalanges, respectively, but it is unknown whether there were claws on these digits. The recently found forelimb material of *Majungasaurus* has not been formally described, but a preliminary report (Burch and Carrano 2008) described a hand with four digits, short metacarpals, one phalanx on digits I and IV, two phalanges on digit II and two fused phalanges on digit III; the metacarpal and phalanx of digit IV are fused. The presence of a conical metacarpal IV implies a closer relation between *Carnotaurus* and *Aucasaurus* than with *Majungasaurus*, in accordance with previous works by Coria *et al.* (2002) and Canale *et al.* (2009).

The noteworthy reduction of the abelisaurid forelimb seems to have started in basal ceratosaurs (Carrano 2007; Carrano and Sampson 2008; Xu *et al.* 2009). The hand of basal ceratosaurs *Limusaurus* and *Ceratosauros* is reduced with respect to those of herrerasaurs and coelophysoids (see Text-fig. 2), with shorter metacarpals in digits II and III, and a very slender metacarpal I. Metacarpal IV of basal ceratosaurs is also slender, but proportionally longer and wider (which correlates with the higher robustness of the hand) than in herrerasaurs and coelophysoids. The metacarpal II of *Ceratosauros* and *Berberosaurus liassicus*, from the Early Jurassic of Morocco, interpreted as either a basal abelisauroid (Allain *et al.* 2007) or a basal ceratosauros (Carrano and Sampson 2008), and the metacarpal III of *Austrocheirus isasii*, from the Maastrichtian of Patagonia (Ezcurra *et al.* 2010), is proportionally (and absolutely) much longer than in *Carnotaurus* or *Aucasaurus*. So, the large relative size of metacarpal I relative to metacarpal II in *Carnotaurus* and *Aucasaurus* is related to the shortening of metacarpals II and III in abelisauroids. Basal Tetanurae such as *Allosaurus* (e.g. Gilmore, 1920; Text-fig. 2) retain longer metacarpals and phalanges, metacarpal III is shorter than metacarpal II, and digit IV is lost. The only possible nonungual phalanx of digit III of *Carnotaurus* is consistent with a loss of manual phalanges in ceratosaurs, which also seems to be the case for *Aucasaurus* and *Majungasaurus*, although the first phalanges of digits II and III as well as metacarpal IV have increased their length in *Carnotaurus* (Text-fig. 2).

The forelimbs of *Carnotaurus*, considered as a whole, show an extreme reduction, proportionally greater than the reduction observed in tyrannosaurids (Middleton and Gatesy 2000), although the radius, ulna and humerus are very robust. The forelimbs of *Aucasaurus* and *Majungasaurus* exhibit similar features, although the humerus, radius and ulna are less robust and the proportional shortening of the forearms bones is less extreme. The ulna and radius are one-fourth the length of the humerus in *Carnotaurus*, whereas they are about one-third the length of the humerus in *Aucasaurus* and *Majungasaurus* (Coria *et al.* 2002; Burch and Carrano 2008). Similarly, the

humerus of *Carnotaurus* is relatively shorter and more robust than those of its two relatives. Thus, following the divergence from the *Aucasaurus* lineage, the *Carnotaurus* lineage shortened the forearm and increased the robustness of the entire forelimb.

Xu *et al.* (2009) have analysed the question of manual digital identities in avian and nonavian theropods, supporting the shift in phalangeal identities from the ancestral digits I, II and III to digits II, III and IV in early Tetanurae proposed by Wagner and Gauthier (1999). Xu *et al.* (2009) cite the much reduced digit I (limited to a very short and conical metacarpal I) and the short phalanges in digits II and III of *Limusaurus* as evidence for both digit I reduction and hand shortening before the divergence of Ceratosauros and Tetanurae. The metacarpal I of *Limusaurus* is, however, more reduced than in latter ceratosaurs, making it unrepresentative, and therefore not providing relevant clues for the frameshift hypothesis.

The morphological diversity of the hand of abelisauroids suggested by the present work is reminiscent of the diversity of structures found in the skull roof of these dinosaurs. However, there are not clear evolutionary trends or homologies in cranial protuberances of abelisauroids (Canale *et al.* 2009), and a correlation with hand morphology is not evident.

*Acknowledgements.* JR thanks Alejandro Kramarz for facilitating the access to the MACN-CH 894 specimen and for their kind help, the personnel of the Sección de Paleontología de Vertebrados of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Buenos Aires) and Guillermo Rougier for their hospitality, and Javier García-Guinea and María T. Alberdi for logistical help. We thank Michael Benton, Rodolfo Coria and the editor Kenneth Angielczyk for their reviews and suggestions, Nieves López-Martínez and Fernando Novas for their comments on this work, and Nita Lawson and Jean-Pierre Williams for language assistance.

*Editor.* Kenneth Angielczyk

## REFERENCES

- ALLAIN, R., TYKOSKI, R., AQUESBI, N., JALIL, N., MOUNBARON, M., RUSSELL, D. and TAQUET, P. 2007. An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. *Journal of Vertebrate Paleontology*, 27, 610–624.
- BONAPARTE, J. F. 1991. The Gondwanian theropod families Abelisauridae y Noasauridae. *Historical Biology*, 5, 1–25.
- NOVAS, F. E. and CORIA, R. A. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the middle Cretaceous of Patagonia. *Contributions in Science*, 416, 1–41.
- BURCH, S. and CARRANO, M. 2008. Abelisauroid forelimb evolution: new evidence from *Majungasaurus crenatissimus*

- (Abelisauridae: Theropoda) from the late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 22 (Suppl. 3), 58A.
- CANALE, J. I., SCANFERLA, C. A., AGNOLIN, F. L. and NOVAS, F. E. 2009. New carnivorous dinosaurs from the Late Cretaceous of NW Patagonia and the evolution of the abelisaurid theropods. *Naturwissenschaften*, 96, 409–414.
- CARRAN, M. T. 2007. The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir*, 8, 163–179.
- and SAMPSON, S. D. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Paleontology*, 6, 183–236.
- COLBERT, E. H. 1989. The Triassic dinosaurs *Coelophysis*. *Museum of Northern Arizona Bulletin*, 53, 1–69.
- CORIA, R. A., CHIAPPE, L. M. and DINGUS, L. 2002. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, 22, 460–465.
- EZCURRA, M. D., AGNOLIN, F. L. and AND NOVAS, F. E. 2010. An abelisauroid dinosaurs with a non-atropied manus from the Late Cretaceous Pari Aike Formation of southern Patagonia. *Zootaxa*, 2450, 1–25.
- GILMORE, C. W. 1920. Osteology of the carnivorous Dinosaurs in the United State National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum*, 110, 1–154.
- HOLTZ, T. R., MOLNAR, R. E. and CURRIE, P. J. 2004. Basal Tetanurae. 71–110. In WEISHAMPEL, D. B., DOBSON, P. and SMÓLSKA, H. (eds). *The Dinosauria*, Second edition. University of California Press, Berkeley, CA, 861 pp.
- LAMANNA, M. C., MARTÍNEZ, R. D. and SMITH, J. B. 2002. A new abelisauroid theropod from northwestern Patagonia. *Journal of Vertebrate Paleontology*, 22, 58–69.
- LANGER, M. C. 2004. Basal Saurischia. 25–46. In WEISHAMPEL, D. B., DOBSON, P. and SMÓLSKA, H. (eds). *The Dinosauria*, Second edition. University of California Press, Berkeley, CA, 861 pp.
- MAKOVICKY, P. J., KUBAYASHI, Y. and CURRIE, P. J. 2004. Ornithomimosauria. 137–150. In WEISHAMPEL, D. B., DOBSON, P. and SMÓLSKA, H. (eds). *The Dinosauria*, Second edition. University of California Press, Berkeley, CA, 861 pp.
- MIDDLETON, K. M. and GATESY, S. M. 2000. Theropod forelimb design and evolution. *Zoological Journal of the Linnean Society*, 128, 149–187.
- NORMAN, D. 1985. *The illustrated encyclopaedia of dinosaurs*. Salamander Books, London, 208 pp.
- NOVAS, F. E. 2009. *The age of dinosaurs in South America*. Indiana University Press, Bloomington, IN, xxi + 452 pp.
- SAMPSON, S. D., WITMER, L. M., FORSTER, C. A., KRAUSE, D. W., COHEN, P. M., DOBSON, P. and RAVAVY, F. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science*, 280, 1048–1051.
- SEREN, P. C. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology*, 14, 53–73.
- WILSON, J. A. and CONRAD, J. L. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society of London, Series B*, 271, 1325–1330.
- TYKOSKI, R. S. and ROWE, T. 2004. Ceratosauria. 47–70. In WEISHAMPEL, D. B., DOBSON, P. and SMÓLSKA, H. (eds). *The Dinosauria*, Second edition. University of California Press, Berkeley, CA, 861 pp.
- WAGNER, G. P. and GAUTHIER, J. A. 1999. 1,2,3 = 2,3,4: a solution to the problem of the homology of the digits in the avian hand. *Proceedings of the National Academy of Sciences, USA*, 96, 5111–5116.
- XU, X., CLARK, J. M., MO, J., CHENIERE, J., FORSTER, C. A., ERICKSON, G. M., HONE, D. W. E., SULLIVAN, C., EBERTH, D. A., NESBITT, S., ZHAO, Q., HERNANDEZ, R., JIA, C., HAN, F. and GUO, Y. 2009. A Jurassic ceratosaurs from China helps clarify avian digital homologies. *Nature*, 459, 940–944.