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The evolution of the manus of early theropod dinosaurs is characterized by high inter- and intraspecific variation

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Abstract

The origin of the avian hand, with its reduced and fused carpals and digits, from the five-fingered hands and complex wrists of early dinosaurs represents one of the major transformations of manus morphology among tetrapods. Much attention has been directed to the later part of this transition, from four- to three-fingered taxa. However, earlier anatomical changes may have influenced these later modifications, possibly paving the way for a later frameshift in digit identities. We investigate the five- to four-fingered transition among early dinosaurs, along with changes in carpus morphology. New three-dimensional reconstructions from computed tomography data of the manus of the Triassic and Early Jurassic theropod dinosaurs *Coelophysis bauri* and *Megapnosaurus rhodesiensis* are described and compared intra- and interspecifically. Several novel findings emerge from these reconstructions and comparisons, including the first evidence of an ossified centrale and a free intermedium in some *C. bauri* specimens, as well as confirmation of the presence of a vestigial fifth metacarpal in this taxon. Additionally, a specimen of *C. bauri* and an unnamed coelophysoid from the Upper Triassic Hayden Quarry, New Mexico, are to our knowledge the only theropods (other than alvarezsaurs and birds) in which all of the distal carpals are completely fused together into a single unit. Several differences between the manus of *C. bauri* and *M. rhodesiensis* are also identified. We review the evolution of the archosauromorph manus more broadly in light of these new data, and caution against incorporating carpal characters in phylogenetic analyses of fine-scale relationships of Archosauromorpha, in light of the high degree of observed polymorphism in taxa for which large sample sizes are available, such as the theropod *Coelophysis* and the sauropodomorph *Plateosaurus*. We also find that the reduction of the carpus and ultimate loss of the fourth and fifth digits among early dinosaurs did not proceed in a neat, stepwise fashion, but was characterized by multiple losses and possible gains of carpals, metacarpals and phalanges. Taken together, the high degree of intra- and interspecific variability in the number and identities of carpals, and the state of reduction of the fourth and fifth digits suggest the presence of a 'zone of developmental variability' in early dinosaur manus evolution, from which novel avian-like morphologies eventually emerged and became channelized among later theropod clades.

Key words: archosaur; birds; carpus; *Coelophysis bauri*; dinosaur; manus; *Megapnosaurus rhodesiensis*; theropod.

Introduction

The evolution of the theropod dinosaur hand and wrist is instrumental to understanding the acquisition and evolution of the derived avian manus. The homology of the avian hand elements was largely determined by a combination of studies of extinct theropod anatomy and evolutionary trends and extant reptile embryology. For instance, the homologies of the reduced and fused avian wrist elements with those of non-avian dinosaur carpals were provided by a combination of both extinct forms and embryology (Botelho et al. 2014). These two datasets have not always offered the same conclusions. For example, the identity of the digits, whether digits I-II-III (as traditionally evidenced by paleontology/comparative anatomy) or II-III-IV (as evidenced by embryology) compose the avian hand (see

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Young et al. (2011) for a review) remains a matter of debate. Although digit identity in birds remains contentious, the necessity of integrating embryological and paleontological information is widely recognized.

The importance of using extinct theropods to reconstruct the evolution of the avian hand from a plesiomorphically five-fingered hand with nine or 10 carpals to the much-reduced avian condition has long been recognized (e.g. Abel, 1911; Heilmann, 1927; Ostrom, 1976; Wagner & Gauthier, 1999). However, most studies that chronicle this evolution start well within theropods at Averostra, and consequently begin with a transition from a four-fingered to a three-fingered condition because of its relevance to the frameshift hypothesis of avian digit identities (Wagner & Gauthier, 1999). This restricted vision of the evolution of the hand negates early anatomical changes that may have influence over later modifications. Therefore, our current contribution focuses on the evolution of the theropod manus and carpus from its plesiomorphic form to the reduced hand present in averostrans. We accomplish this task through detailed anatomical study, combined with additional details from computed tomography of new specimens near the base of Theropoda. Understanding the pattern of reduction and loss of these carpals and digits starting with the plesiomorphic condition for dinosaurs (essentially the same as saurian reptiles) through the avian hand is critical to characterizing fully this rare evolutionary transition that may hold significant functional consequences for preserving the ancestral grasping function of the theropod manus (Sereno, 1997).

Early members of both major dinosaur clades, Ornithischia and Saurischia, have five manual digits, which were later further reduced independently in each clade. Our picture of the phylogenetic pattern of digit reduction in theropods changes with the discovery of new fossils. Previous studies of digit reduction in theropods (Wagner & Gauthier, 1999; Xu et al. 2009) typically make use of *Herrerasaurus ischigualastensis* Reig, 1963; *Coelophysis bauri* Cope, 1887, 1889; and/or *Dilophosaurus wetherilli* Welles, 1954; as outgroups. None has yet mapped the manus morphologies of more recently described taxa, such as *Tawa hallae* Nesbitt et al. 2009a; and *Eodromaeus murphi* Martinez et al. 2011, on a phylogeny.

Additionally, documentation of intraspecific variation within taxa known from large sample sizes [*C. bauri* and *Megapnosaurus* (= *Syntarsus*, = *Coelophysis*) *rhodesiensis* Raath, 1969; Ivie et al. 2001; Bristowe & Raath, 2004] is relevant to assessing whether the transition from five- to four-fingered taxa involved a great deal of within-population polymorphism, as hypothesized for the four- to three-fingered transition under the zone of developmental variability model (Bever et al. 2011). This model also posits that the loss of digit V was an important evolutionary event that made the later frame shift of avian digit identities possible. Thus, further study of the transition involving description of well-preserved specimens and documentation of interspecific and intraspecific differences among the earliest theropods is needed.

The majority of Triassic theropods are ‘coelophysoids’, a paraphyletic assemblage (Nesbitt et al. 2009a) of small-to-medium-sized carnivores that achieved a near global distribution during the Late Triassic and Early Jurassic (approximately 220–180 Ma). Among taxa within the more restricted Coelophysidae clade, two species, the aforementioned *C. bauri* and *M. rhodesiensis*, form an ideal case study for a comparative examination of intraspecific variation in manus morphology because they are known from large sample sizes (at least dozens of individuals). In some cases these may represent single populations (Colbert, 1989; Raath, 1990; Schwartz & Gillette, 1994). They are represented by many partial to complete articulated cranial and postcranial skeletons of different ontogenetic stages, including articulated carpi and digits. However, comparisons among these and other taxa are often hindered by the incomplete or incompletely prepared nature of the specimens. To facilitate broader comparisons, we present the first three-dimensional digital reconstruction of the manus of *Megapnosaurus*, and the second of the carpus and manus of *Coelophysis* (following Digimorph Staff, 2009). These reconstructions clarify aspects of carpal and manual anatomy among bones that would otherwise remain encased in matrix and would be difficult to manipulate by hand without magnification, and are hence more understandable in a virtual environment.

Materials and methods

Institutional abbreviations

AMNH FARB, American Museum of Natural History Fossil Amphibians, Reptiles, and Birds collection, New York, NY, USA; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; GPIT, Institute for Geosciences, Tübingen University, Tübingen, Germany; GR, Ruth Hall Museum of Paleontology, Ghost Ranch, NM, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MfN, Museum für Naturkunde Berlin, Berlin, Germany; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, NM, USA; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; QG, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe; SAM, Iziko South African Museum, Cape Town, South Africa; SMNS, Senckenburg Museum, Frankfurt, Germany.

We examined several specimens of *C. bauri* and *M. rhodesiensis* firsthand. *Coelophysis* and *Megapnosaurus* were compared with information from specimens, casts, and literature descriptions of other early theropod taxa (*H. ischigualastensis*, *E. murphi*, *Tawa hallae*, *D. wetherilli*), an early sauropodomorph (*Eoraptor lunensis* Sereno et al. 1993), and an early ornithischian (*Heterodontosaurus* *tucki* Crompton & Charig, 1962), for which articulated carpi and digits are known.

All *Coelophysis* specimens come from the Upper Triassic (Rhaetian) *Coelophysis* Quarry in the 'Siltstone member' of the Chinle Formation at Ghost Ranch, NM, USA (see Colbert, 1995). We assign all manus specimens to *C. bauri* despite the presence of another dinosaur, *Daemonosaurus chauliodus* (Sues et al. 2011), in the same bonebed, because (i) they all broadly resemble the morphology of the *Coelophysis* manus as described by Colbert (1989), (ii) *C. bauri* is by far the most common dinosaur taxon in the bonebed, and (iii) the manus of *Daemonosaurus* remains unknown but, based on its inferred phylogenetic position outside of Neotheropoda (Sues et al. 2011), digit V should be better developed. To be certain, only further recovery of an associated *Daemonosaurus* manus would help resolve the identity of all specimens described here, nevertheless we remain confident that all available information allows assignment of all Ghost Ranch specimens described here to *C. bauri*.

All *Megapnosaurus* specimens except QG 1 (the holotype) are from the Chitake River bonebed in the Lower Jurassic (Hettangian-Pliensbachian) Forest Sandstone, Zimbabwe. QG 1 is from a different Forest Sandstone locality along the Kwengula River, 20 miles northwest of Bulawayo, Zimbabwe (Raath, 1969, 1990). We follow the taxonomic reasoning of Griffin & Nesbitt (2016) in referring to these specimens as *Megapnosaurus* rather than '*Syntarsus*' or *Coelophysis.*

The description follows the terminology of Dilkes (2015), orienting the carpus and manus so that the palmar side of the hand faces ventrally, the side opposite to this is considered dorsal, the first digit is on the medial side of the hand, and the fifth digit is lateral to the other digits. These terms are used simply for ease of comparison with previous literature and are not intended to imply the actual anatomical position of the hand relative to the body during life. We retain the traditional identification of the digits and corresponding distal carpals of non-avian tetanuran theropods as I, II, and III for clarity when comparing them with earlier theropods that definitely possess digits I–III. For an alternative interpretation of the tetanuran manus, see Xu et al. (2009, 2014a).

AMNH FARB 27435 (Supporting Information Table S1, Figs S1–S4) is a small block from the *Coelophysis* Quarry that contains the remains of two or three *C. bauri* individuals, including an articulated left carpus and artificial casts of its accompanying complete, disarticulated manus elements, which had been prepared off of the block for histological sectioning while on loan to Museum of the Rockies, Bozeman, MT, USA.

AMNH FARB 30631 (Figs 1, 3, 4, 7E–H and 8A, Table S1) is a well-preserved articulated left carpus and manus from a small individual of *Coelophysis*. It is from a smaller block (#36) from the 1947 excavation of the *Coelophysis* Quarry. It was found with much of a foot, but this manus and pes cannot be connected to any other individual in the quarry.

AMNH FARB 7227 (Fig. 8G) is a *C. bauri* skeleton preserving a complete left manus on block IX from the *Coelophysis* Quarry.

AMNH FARB 7243 (Fig. 8D) is a partial skeleton of a single small individual of *C. bauri* from block V of the *Coelophysis* Quarry (Colbert, 1989). Its partial left carpus and manus and partial right manus are described here. The bones are larger than the corresponding elements of AMNH FARB 30631.

CM 81766 (Fig. 8H, Table S1) is an articulated partial skeleton from CM Block C-3-82 of the *Coelophysis* Quarry (Colbert, 1989) that preserves a complete left manus with carpus.

MCZ 4329 (Fig. 8B) is an articulated left forelimb of *C. bauri* from block X of the *Coelophysis* Quarry (Colbert, 1989).

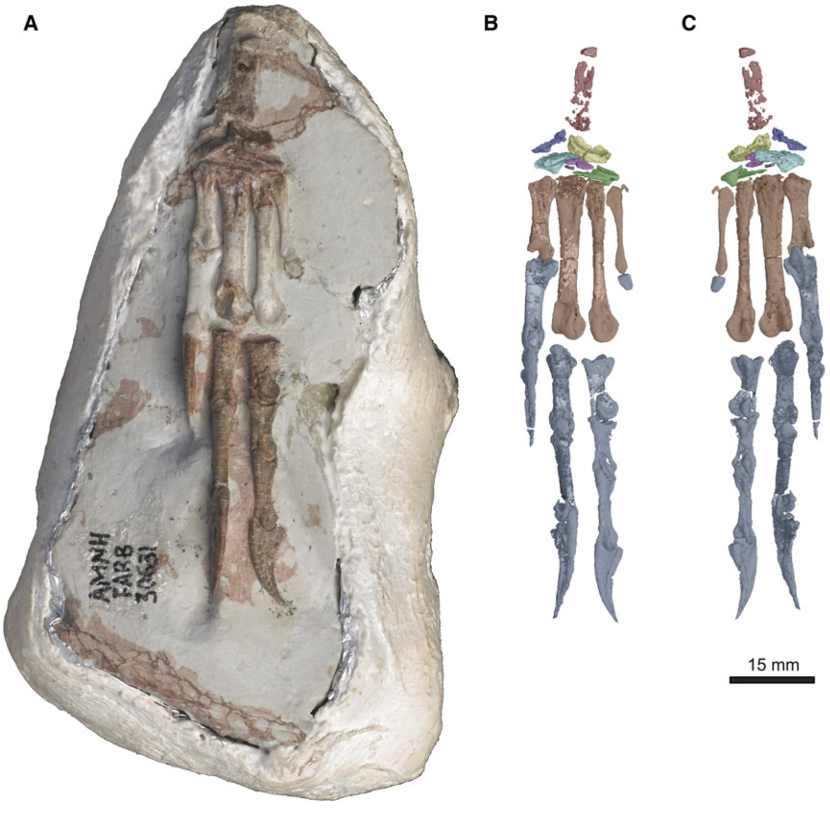

Fig. 1 *Coelophysis bauri* left manus. (A) AMNH FARB 30631. (B) 3D reconstruction in dorsal view. (C) 3D reconstruction in palmar view (B) and (C) © American Museum of Natural History.

MCZ 4331 (Fig. 8C, Table S1) is a partial right forelimb with articulated carpus of *C. bauri* from block X of the *Coelophysis* Quarry (Colbert, 1989; Wagner & Gauthier, 1999).

MCZ 4334 is a portion of *Coelophysis* Quarry block X (Colbert, 1989) that preserves two articulated manus, one of which may be the right hand of the same individual as MCZ 4329, as they originally lay in close proximity before MCZ 4329 was prepared off of the block. The other manus catalogued under MCZ 4334 is part of an articulated left forelimb of a different individual.

NMMNH P-42576 (Fig. 8E) is a small *C. bauri* skeleton preserving both forelimbs, including a complete left manus. It is from block C-8-82 of the *Coelophysis* Quarry (Rinehart et al. 2009).

QG 1 (Table S1) is an artificial cast of the partial left manus (with carpus) of the holotype specimen of *M. rhodesiensis*.

QG 573 (Fig. 6, Table S1) includes partial disarticulated left and right manus of *M. rhodesiensis*.

QG 577 (Figs 2, 5 and 7A–D, Table S1) is a partial right radius and ulna with articulated manus of a small *M. rhodesiensis,* but the carpals are missing. As with most specimens in the quarry, it was found isolated from any other skeletal elements that could be assigned to a single individual.

Fig. 2 *Megapnosaurus rhodesiensis* right manus. (A) QG 577. (B) 3D reconstruction in dorsal view. (C) 3D reconstruction in palmar view.

QG 686 (Table S1) is a partial right forelimb of *M. rhodesiensis* including a partial manus that lacks the carpus.

GR 1033 (Fig. 8F) is a complete left manus with carpus of an undescribed coelophysoid from the Upper Triassic Hayden Quarry, NM, USA.

In addition to these, we personally examined casts and 3D prints derived from scan data of the manus of the following specimens: *H. ischigualastensis* (PVSJ 373), *T. hallae* (3D print of GR 242 and casts), and *E. murphi* (PVSJ 562). Other comparative information is derived from literature sources.

CT scanning

Computed tomography (CT) scanning was carried out with a GE Phoenix v|tome|x CT scanner. AMNH FARB 30631 was scanned at 220 kV, with a current of 280 μA, a 1.0-mm copper filter, and a voxel size of approximately 0.07 mm, to produce 1500 images. QG 577 was scanned at 220 kV, with a current of 280 μA, a 1.0-mm copper filter, and a voxel size of approximately 0.06 mm, to produce 1500 images. Reconstruction and image stitching were performed with Phoenix Datos X (GE Inspection Technologies, LP, Lewistown, PA, USA) and FIJI (IMAGEJ; Schindelin et al. 2012) software. VG STUDIO MAX (Volume Graphics, Inc., Charlotte, NC, USA) was used for segmentation of the bones from the surrounding matrix based on density differences.

MCZ 4329 was CT-scanned using a custom-built BIR scanner at the University of Texas at Austin High Resolution X-Ray CT Facility (Department of Geological Sciences) by Matthew Colbert in 2007. This specimen was scanned at 180 kV, with a current of 0.16 mA, with voxel dimension of 0.056 mm (*x* and *y* axes) by 0.1216 mm (*z* axis, = slice thickness). There are 1125 slices in the final dataset. We imported the 16-bit TIFF images contained within this dataset directly to VG STUDIO MAX for segmentation. An earlier 3D reconstruction of this specimen is viewable at the Digital Morphology website (http://digimorph.org/specimens/Coelophysis_bauri/).

Description

Carpals

AMNH FARB 30631 preserves five carpal elements displaced only slightly from their life positions (Figs 1, 3, and 8A). *Coelophysis bauri* was previously described as possessing five carpals (Colbert, 1989); however, a centrale (Fig. 3C) is preserved, the first and second distal carpals are fused into a single unit, the third and fourth distal carpals are similarly fused, the intermedium may be fused to the ulnare or absent in this specimen, and an uncertain pisiform-like element may be present in others (see below), suggesting that *C. bauri* had five to nine total carpals. In contrast, *M. rhodesiensis* (QG 573, QG 1) likely lacks a centrale but possesses a possible pisiform (Raath, 1969; Botelho et al. 2014), the 'flexor sesamoid' of Raath (1969).

The radiale of *C. bauri* (AMNH FARB 30631, Fig. 3A) is poorly preserved; this element is more complete in MCZ 4329 (Fig. 8B). In AMNH FARB 30631, MCZ 4329, and AMNH FARB 7243 (Fig. 8D), the radiale is shallowly concave proximally, and its lateral half is rectangular in dorsal view, as in

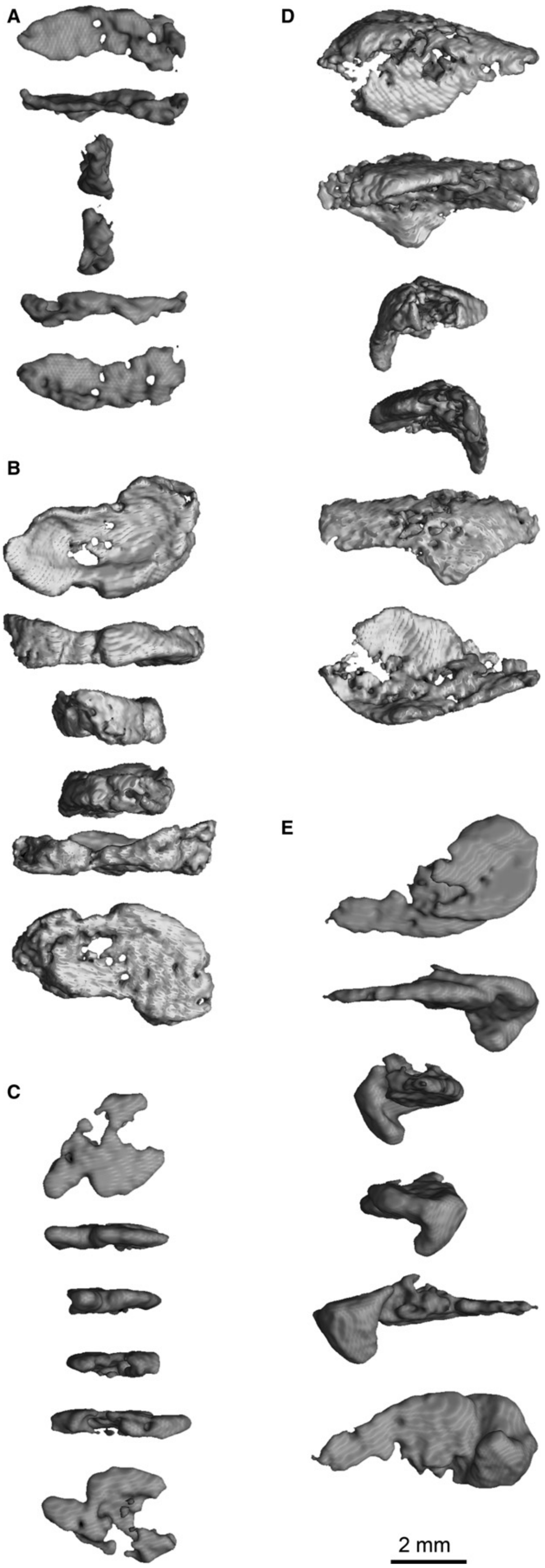

Fig. 3 AMNH FARB 30631 *Coelophysis bauri* carpals. (A) Radiale. (B) Fused intermedium (?) and ulnare. (C) Centrale. (D) Fused distal carpals 1 and 2. (E) Fused distal carpals 3 and 4. All carpals are shown (respectively from top to bottom) in proximal, dorsal, medial, lateral, ventral/palmar, and distal views © American Museum of Natural History.

E. murphi (PVSJ 562) and *H. ischigualastensis* (Sereno, 1993). In MCZ 4329, the dorsal surface of the radiale is expanded to nearly twice the proximodistal height of the palmar surface.

The ulnare of AMNH FARB 30631 (Fig. 3B) is reniform with a proximal articular surface that is more concave than that of the radiale. The distal surface of the ulnare is slightly concave as well. It is similar in most respects to the ulnare of *E. murphi* (Martinez et al. 2011), with both showing a thickened rim bordering the dorsomedial side of the proximal concavity. In contrast to the ulnare of *C. bauri*, the *H. ischigualastensis* ulnare (Sereno, 1993) is more square than reniform in proximal view, and possesses an additional pair of knob-like processes on the palmar surface.

A rectangular element situated primarily between the radiale and ulnare in *C. bauri* (MCZ 4331, AMNH FARB 7243; Fig. 8C,D) is consistent in position and shape with the intermedium of other archosaurs. It primarily underlies the ulna in AMNH FARB 7243 (exposed in dorsal view) and is situated between the radius and ulna in MCZ 4331 (exposed in palmar view). In both specimens, this element appears separated from the other carpals by natural borders, being slightly offset from the ulnare and separated from it by a deep cleft, suggesting that it is a separate element and not part of the ulnare. The medial edge of this intermedium is proximodistally thicker in dorsal view than the lateral edge, with its border projecting proximally between the radius and ulna. In AMNH FARB 30631, the large, lateralmost proximal carpal (Fig. 3B) contains a thin-floored, perforated depression. A broad valley divides the medial and lateral portions of the element in dorsal view. We propose that this element is an incipiently coossified intermedium and ulnare (Fig. 3B). Alternatively, an intermedium is not present in AMNH FARB 30631, and the element (Fig. 3B) is the ulnare alone (with the perforations representing foramina or weathered holes). Despite the lack of a line between the two elements, we tentatively favor the fusion interpretation on the basis of the blocky shape of the medial side of this element, which resembles the intermedia of AMNH FARB 7243 in dorsal view (Fig. 8D), MCZ 4331 in palmar view (Fig. 8C), and *T. hallae* (Burch, 2013), and its inferred position primarily distal to the ulna as in AMNH FARB 7243. The lateral portion of this element resembles the ulnare of other *C. bauri* (Fig. 8C,D,G,H), and it is plausible that the thin, perforated bony sheet connecting them is an area of incomplete ossification. In another *C. bauri* (MCZ 4329), the lateral side of the element is incomplete and it lacks the large perforations in the depression that received the ulna;

however, it does preserve a thick, proximally projecting medial edge, as in AMNH FARB 30631. The intermedium may be fused to the ulnare or absent in AMNH FARB 30631 and MCZ 4329, and free in AMNH FARB 7243 and MCZ 4331, in contrast to *M. rhodesiensis*, for which only a free intermedium has been described (Raath, 1969). *Dilophosaurus wetherilli* (Welles, 1984) and *T. hallae* (Burch, 2013) also possess intermedia. Santa Luca (1980) posited that apparent loss of the intermedium in the early diverging ornithischian *H. tucki* is a result of (i) true loss, (ii) fusion of the intermedium to the ulnare, (iii) fusion of the intermedium to the radiale or (iv) displacement to the position of a centrale. The medial half of the *H. tucki* ulnare is proximodistally thick and projects proximally between the ulna and radius, as in *C. bauri*, suggesting that this portion of the bone may indeed represent a fused intermedium. Additionally, Colbert (1989, fig. 68C) labeled a free, square-shaped carpal element in AMNH FARB 7227 as 'I(?)', probably indicating a questionable intermedium. We note the similarity in shape in dorsal view of this element to the intermedium of AMNH FARB 7243, but consider its identity uncertain given its state of preparation and apparent displacement (Fig. 8G).

A small, discoid carpal situated distal to the ulnare (Figs 3C and 8A) is likely the centrale, based on its positional similarity to the centrale in *H. tucki* (Santa Luca, 1980). In both *C. bauri* and *H. tucki*, the majority of this bone is overlain by the ulnare. The presence of a centrale in AMNH FARB 30631 is curious, given that Colbert (1989) considered this bone to be absent in *C. bauri*. Although it is possible that taphonomic distortion has moved a different carpal into the place of the centrale in AMNH FARB 30631, the otherwise good preservation of topologic relationships among the carpal and manual elements in this specimen (e.g. the delicate metacarpal V, see below) argues against this. Curiously, we found no trace of a centrale in MCZ 4329 (Fig. 8B). Therefore, we suggest that either the presence of an ossified centrale is individually variable in *C. bauri*, that its presence has been overlooked in other specimens, or that it is not visible as a result of incomplete or overpreparation of several *C. bauri* specimens. A centrale is known for most other basal theropod taxa, including *T. hallae* (Burch, 2013), so its presence in some *C. bauri* is not unusual. Its position differs from that of *H. ischigualastensis* (Sereno, 1993) and *E. murphi* (Martinez et al. 2011), in which it primarily underlies the radiale. No centrale is known for *E. lunensis*, though the poor preservation of the carpi of the holotype hampers the identification of individual carpal elements (Sereno et al. 2012). A small piece of bone just distal to the centrale ('?' in Fig. 8A) is probably a fragment of another manus bone and not a distinct carpal element.

No pisiform is preserved in AMNH FARB 30631, but its presence is unclear in other *C. bauri* specimens (MCZ 4329 and AMNH FARB 7243, see below). A pisiform is present in *H. tucki*, *T. hallae*, and possibly in *M. rhodesiensis* (Sereno, 2012; Burch, 2013; Botelho et al. 2014). Yet Raath (1977) explicitly considered this bone in *M. rhodesiensis* to be a flexor sesamoid distinct from the pisiform (which he interpreted as absent or not preserved), as he considered the possibility of displacement of a pisiform to the position seen in the specimen highly unlikely. Given that some of the other carpals in QG 1 are slightly displaced from their presumed life positions, we are unable to rule out either interpretation of the possible pisiform at this time. The carpal element of *C. bauri* specimen MCZ 4329 labeled 'pisiform' by Tarsitano (1991) might instead correspond to a fragment of the ulnare or a third or fourth distal carpal, but the elements on the lateral side of the wrist have been shifted from their original positions, rendering interpretation of their homologies difficult (Fig. 8B). One wedge-shaped fragment lateral and proximal to the ulnare in MCZ 4329 does resemble in shape and orientation the possible pisiform of the coelurosaur *Struthiomimus altus* (Osborn, 1917; Nicholls & Russell, 1985). However, because of the fragmentation and displacement of other elements on the lateral side of the carpus, and our uncertainty as to the homology of the element in *S. altus* with the pisiform of other dinosaurs, [given that no other non-avian tetanuran theropods possess a pisiform (Botelho et al. 2014)], it would be premature to conclude that this fragment in MCZ 4329 is a pisiform at this time. For the same reasons, we also tentatively interpret a bone or bone fragment of similar shape and position in AMNH FARB 7243 as a potential pisiform.

The distal carpals of *C. bauri* (AMNH FARB 30631) largely match the pattern described by Colbert (1989). We follow Gauthier (1986), Colbert (1989), and Nesbitt (2011) in identifying the compound element overlying metacarpals I and II as a fused distal carpal 1 and distal carpal 2 (Fig. 3D), as this element caps both the first and second underlying metacarpals, and there is no evidence for loss or shifting of the other distal carpals in *C. bauri* compared to earlier diverging theropods. This element is likely not entirely homologous to the derived 'semilunate' carpal of later theropods and birds (Xu et al. 2014a). The proximal surface of the fused first and second carpals is flat to slightly convex, and the bone appears disc-shaped in proximal view. On the palmar surface of this element, a triangular flange extends distally. This flange appears to have inserted between the proximal ends of metacarpals I and II in life, and is similar to, though more pronounced than, a similar triangular extension of this bone in *M. rhodesiensis* (Raath, 1969). Though Raath (1969) described distal carpals 1 and 2 fused in QG1 and his original illustration of the specimen reflects that, we observe from recent photographs of QG 1 and Raath's (1977, 1990) photographs that the two carpals are separated by a space that gives the appearance in dorsal view that the elements are unfused. No separation between these carpals is present in the cast of QG 1 that we examined, nor in Galton's (1971) photographs. This suggests that the separation results from a crack that damaged the specimen at some point after the cast was made.

In *C. bauri* (AMNH FARB 30631), a mediolaterally broad discoidal bone that overlies metacarpals II and III likely represents distal carpal 3 (Fig. 3E). An additional distal carpal tightly overlaps this element proximally and partially overlies metacarpal IV (Figs 3E and S4). Dorsally, it resembles the mediolaterally broad, discoid third distal carpal, but the palmar surface is relatively massive and triangular as in the fourth or fifth (Ezcurra, 2010) distal carpal of *H. ischigualastensis* (Sereno, 1993) and the fourth distal carpals of *Tawa* (Burch, 2013) and *E. murphi* (Martinez et al. 2011). As questioned by Burch (2013), the bone identified as the fifth distal carpal of *E. murphi* by Martinez et al. (2011) may more plausibly be interpreted as a fourth distal carpal, given its position overlying the fourth metacarpal, its blocky, triangular shape, and that the specimen would otherwise lack a third distal carpal under the interpretation of Martinez et al. (2011). This lends support to our interpretation of this element as a fourth distal carpal in *C. bauri*. The third and fourth distal carpals appear to be fused in AMNH FARB 30631, given that there is no matrix separating these elements and a continuous density of bone joins them in the CT slices. This fusion has not been reported in other *C. bauri* specimens. In contrast to *C. bauri*, the fourth distal carpal of *M. rhodesiensis* (QG 1) is a smaller, more round element in palmar view. The fourth distal carpal of *H. tucki* is similar in size to the other distal carpals and subspherical (Santa Luca, 1980; Sereno, 2012). Curiously, distal carpals 1–3 and possibly 1–4 are completely fused in one *C. bauri* specimen (NMMNH P-42576, Fig. 8E), as well as an undescribed coelophysoid from Hayden Quarry (GR 1033, Fig. 8F). This unique morphology is not seen in other *C. bauri* individuals or any other non-alvarezsaur, non-avian theropod we are aware of. *Heterodontosaurus tucki*, *E. lunensis*, and possibly *H. ischigualastensis* (Ezcurra, 2010) retain distal carpal V. It is absent in *C. bauri* and *M. rhodesiensis*.

Metacarpals

Metacarpal I is the shortest metacarpal of *M. rhodesiensis* (QG 577), and the second-shortest in *C. bauri* (AMNH FARB 30631; after metacarpal V, see below; Table S1). The presence of asymmetric distal condyles (or ginglymi) of the metacarpals (particularly the first metacarpal) of some saurischian dinosaurs and the non-archosaur archosauriform *Euparkeria capensis* has been cited as functionally significant, allowing for opposability of the first digit (Ewer, 1965; Galton, 1971). In both *C. bauri* and *M. rhodesiensis*, the distal articular surface of metacarpal I is proximomedially-laterodistally inclined because of the asymmetry of the distal condyles (Figs 4A and 5D). In *M. rhodesiensis* (QG 577), this is matched by the parallel inclination of the proximal joint surface of phalanx I-1, so that digit I remains roughly parallel to the long axis of the hand overall. In an

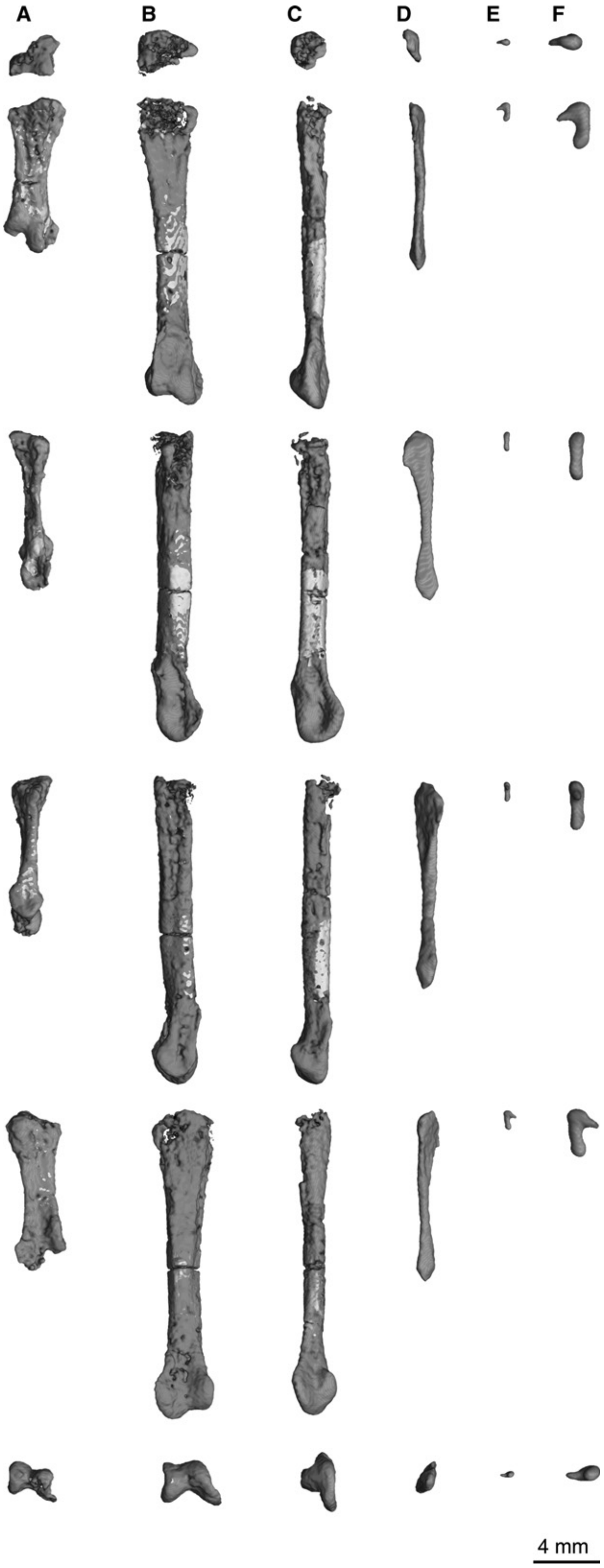

Fig. 4 AMNH FARB 30631 *Coelophysis bauri* metacarpals (MCs). (A) MC I. (B) MC II. (C) MC III. (D) MC IV. (E) MC V. (F) Enlargement of (E) to show detail. All metacarpals are shown (from top of page to bottom) in proximal, dorsal, lateral, medial, ventral/palmar, and distal views © American Museum of Natural History.

individual of *C. bauri* (AMNH FARB 30631), however, the proximal joint surface of phalanx I-1 is less inclined (condyles more symmetrical). This suggests that there may have been more offset between digit I and the other digits in some *C. bauri* specimens than in *M. rhodesiensis*, as both QG 577 and QG 1 (Galton, 1971) show a more parallel inclination of the two joint surfaces than AMNH FARB 30631 does. *Eoraptor lunensis* and *E. murphi* both have highly offset first digits as in *C. bauri* (Martinez et al. 2011); the first digits of *H. tucki* and *H. ischigualastensis* show an intermediate level of offset between that of *C. bauri* and *M. rhodesiensis* (Sereno, 1993, 2012). In both *C. bauri* (AMNH FARB 30631, Fig. 4A) and *M. rhodesiensis* (QG 577, Fig. 5D) the proximal end of metacarpal I is roughly triangular, with cross-sections flattening into ellipsoids distally. The lateral surface of metacarpal I is flattened along its proximal two-thirds for articulation with metacarpal II. This is more evident in *M. rhodesiensis* (QG 577) than *C. bauri* (AMNH FARB 30631). An individual of *M. rhodesiensis* (QG 573, Fig. 6D) exhibits more extensive flattening, with nearly the entire lateral surface of metacarpal I flattened and appressed to metacarpal II. Raath (1990) described QG 1 and QG 573 as robust morphs and QG 577 as a gracile morph of *M. rhodesiensis* based on differences in overall shape and proportions of their metacarpals and phalanges. This difference is particularly evident in metacarpal I, with those of QG 1 and QG 573 having proportionally slightly thicker shafts (Raath, 1990). All metacarpals bear deep ovoid collateral ligament pits distally. The lateral and medial collateral ligament pits are very similar in shape.

Particularly evident on the dorsal surface of metacarpals II and III of both *C. bauri* and *M. rhodesiensis* is a region of 'unfinished' bone surface between the proximal end and the shaft that suggests the bone was thinner and/or less well ossified there (Figs 4B,C and 5B,C). This is near the insertions of extensor digitorum longus in extant turtles, lepidosaurs and crocodylians (Miner, 1925; Haines, 1939; Meers, 2003; Burch, 2014). Metacarpal II bears the deepest distal extensor depression in *C. bauri* and *M. rhodesiensis*. This is less pronounced on metacarpal III. The extensor depressions of *C. bauri* and *M. rhodesiensis* are narrower and deeper than in *E. lunensis* (Sereno et al. 2012) and *H. ischigualastensis* (Sereno, 1993), being more similar in shape to those of *H. tucki* (Sereno, 2012; Galton, 2014). Metacarpals II and III are nearly the same length in *C. bauri* and *M. rhodesiensis* (Table S1), with III being slightly longer, as in *E. murphi* (Martinez et al. 2011) and *H. ischigualastensis* (Sereno, 1993). The distal articular surface of the third metacarpal is twisted somewhat medially, so that its phalanges projected laterally when the digits were flexed (Galton, 1971). This twist is much more evident in metacarpal III than metacarpal II in *C. bauri* and *M. rhodesiensis*, and neither element is laterally twisted in *H. tucki*, *E. lunensis*, *H. ischigualastensis* or *E. murphi*. The metacarpal shafts of

Fig. 5 QG 577 *Megapnosaurus rhodesiensis* metacarpals (MCs). (A) MC IV. (B) MC III. (C) MC II. (D) MC I. All metacarpals are shown (from top of page to bottom) in proximal, dorsal, lateral, medial, ventral/palmar, and distal views.

Fig. 6 QG 573 *Megapnosaurus rhodesiensis* metacarpals (MCs). (A) Left MC IV. (B) Right MC III and IV. (C) Right MC II. (D) Right MC I. All metacarpals are shown (from top of page to bottom) in proximal, dorsal, lateral, medial, ventral/palmar, and distal views.

C. bauri (AMNH FARB 30631) and *M. rhodesiensis* (QG 577) are straight, in contrast to the bowed shaft of the second metacarpal of *H. ischigualastensis* (Sereno, 1993). In *C. bauri* and *M. rhodesiensis*, metacarpal II is roughly square-shaped in proximal view, with flat surfaces for articulation with metacarpals I and III proximomedially and proximolaterally. The proximal end of metacarpal III is narrower and somewhat trapezoidal. In *C. bauri* and *M. rhodesiensis*, as in the other early dinosaurs examined, metacarpal II either does not overlap metacarpal III, or overlaps it only slightly, in contrast to some tetanuran theropods (Tykoski & Rowe, 2004).

In *C. bauri* and *M. rhodesiensis*, metacarpal IV is a slender, rod-like element about 50–60% the length of metacarpal III (Figs 4D, 5A and 6A). In all specimens of *C. bauri*, metacarpal IV articulates with metacarpal III laterally and slightly ventrally (Fig. 1), whereas it articulates more ventrally with metacarpal III in all articulated *M. rhodesiensis* hands (Figs 2 and 6B). The fourth metacarpals of *H. ischigualastensis*, *E. murphi*, and *D. wetherilli* (Xu et al. 2009) have at least a slightly palmar articulation with metacarpal III. Metacarpal IV is triangular (QG 577) or elliptical (AMNH FARB 30631) in proximal cross-section and lacks collateral ligament pits on its distal end in *C. bauri*, in contrast to *M. rhodesiensis*, *H. tucki*, *E. lunensis*, and *E. murphi*, which all have them (Martinez et al. 2011; Sereno, 2012). A further discrepancy of note between the current state of QG 1 and the cast we examined is that digit IV has been straightened out relative to the other metacarpals in the actual specimen, as depicted by Raath (1977, 1990), whereas it seems to have been angled across the palmar surface of the other digits originally (Raath, 1969; Galton, 1971).

A small element lateral or ventral to metacarpal IV in a number of *C. bauri* specimens [AMNH FARB 30631 (Fig. 4E, F), AMNH FARB 7223 (Colbert, 1989), NMMNH P-42576 (Fig. 8E), and MCZ 4329) was previously identified as a fifth metacarpal (Gauthier, 1986; Padian, 1992; Wagner & Gauthier, 1999; Langer & Benton, 2006; Xu et al. 2009; Young et al. 2011). This assessment is supported by its position in articulation relative to the other metacarpals and the proximal articulation with metacarpal IV (Fig. 1). In addition to AMNH FARB 30631, this element was figured but not named or described for AMNH FARB 7223 by Colbert (1989). Gauthier (1986) makes reference to what we assume to be this illustration, and notes that Colbert interpreted the nubbin of bone as the fifth metacarpal, though Colbert seems to have never published this observation. A fifth metacarpal is also present but slightly displaced in NMMNH P-42576 (Fig. 8E), and is definitively present in a fourth *C. bauri* specimen, MCZ 4329. In AMNH FARB 30631, the fifth metacarpal is a slightly bowed cylindrical element. It is similarly elongate, but wider, in NMMNH P-42576 (Fig. 8E), and shorter and more rounded in AMNH FARB 7223 (Colbert, 1989). The fifth metacarpal is relatively elongate in *H. tucki, E. lunensis,* and *E. murphi*, even bearing a single phalanx in *E. murphi* (Martinez et al. 2011) and two in *H. tucki* (Santa Luca et al. 1976; Sereno, 2012). It is more splint-like in *H. ischigualastensis* (Sereno, 1993), and is reduced to a small rounded element in *D. wetherilli* (Xu et al. 2009). No fifth metacarpal is present in any of the *M. rhodesiensis* specimens examined here.

Gauthier's (1986) assertion in character nine of his phylogenetic analysis that the proximal ends of the fourth and fifth metacarpals were plesiomorphically situated on the palmar surface of the manus in saurischians, remains plausible, although interpretations are complicated by the possibility of postmortem shifting of these elements in even well-preserved, articulated specimens. In *C. bauri* (AMNH FARB 7223; Colbert, 1989), the proximal end of the fourth metacarpal is slightly palmar to that of the third metacarpal, and the fifth metacarpal is entirely palmar to the fourth. These elements have the same orientations in MCZ 4329. In contrast, the fourth and fifth metacarpals of AMNH FARB 30631 are nearly in the same plane as the others. However, slight crushing and rotation of some elements of AMNH FARB 30631 may have altered the orientation of these metacarpals. The fourth and fifth metacarpals are lateral and palmar to the other digits in *H. tucki*, but they are separated by matrix from one another and the other metacarpals in the complete left hand of SAM-PK-K1332, lacking any contact with these elements (Sereno, 2012; Galton, 2014). The right hand of this specimen has a third metacarpal that overlaps the fourth proximally, but a fifth digit is not preserved on the right hand. In *E. lunensis*, the third and fifth metacarpals both slightly overlap the fourth, but given the displacement of other manus elements in this specimen, caution is warranted in interpreting this as the life articulation of these elements (Sereno et al. 2012). In *H. ischigualastensis, E. murphi*, and *D. wetherilli* (Sereno, 1993; Xu et al. 2009; Martinez et al. 2011), the fourth and fifth metacarpals lie on the palmar surface of the hand, whereas the fourth metacarpal is not overlapped by the others in *T. hallae* (Nesbitt et al. 2009a). Given these interspecific differences and preservational factors, it remains difficult to assess whether early diverging dinosaurs retained a single plesiomorphic pattern of metacarpal arrangement, or whether this character was more variable.

Phalanges

As is the case for the distal ends of the metacarpals, all of the phalanges of *C. bauri* and *M. rhodesiensis* bear deep collateral ligament pits (Fig. 7). These pits have the same shape on both the lateral and medial sides of the phalanges. In both AMNH FARB 30631 and QG 577, the first phalanges of digits I and II are the broadest in mediolateral width of all the phalanges. In *C. bauri*, the distal surface of metacarpal I and the proximal surface of the first phalanx of digit I have opposite inclinations, forcing the first digit to point medially, whereas the two surfaces have complementary inclinations in *M. rhodesiensis,* keeping digit I more nearly in line with the other digits of the hand. This indicates that the first digit of *C. bauri* was perhaps more opposable than that of *M. rhodesiensis*. However, the distal end of phalanx I-1 is slightly twisted laterally in *M. rhodesiensis*, possibly allowing the first ungual (phalanx I-2) to still have the ability to draw in towards the midline of the hand when the digits were flexed.

The first ungual is the longest in *C. bauri* (Colbert, 1989). The second and third unguals of *M. rhodesiensis* (QG 577) are incomplete and cannot be directly compared with the first ungual. In another specimen of *M. rhodesiensis* (Raath, 1969) the second ungual is slightly longer than the first, in contrast to *C. bauri*. All unguals are extremely narrow transversely; the first ungual is the most strongly curved. Overall, the unguals are proportionally more elongate and less curved distally than those of *H. tucki* and *H. ischigualastensis*. The unguals of *E. lunensis* (Sereno et al. 2012) are relatively shorter and less curved than any of these taxa. The flexor tubercles on the ventral surface of the unguals of *C. bauri* are prominent and rounded in cross section.

Phalanx 1 of digit II of *C. bauri* and *M. rhodesiensis* (Fig. 7B,F) exhibits a deep, narrow extensor depression on its distal end, bordered by raised ridges extending off of the distal condyles. This matches the well-developed depression on the distal end of the corresponding metacarpal II.

Phalanx 2 of digit II is the longest phalanx in both *C. bauri* (AMNH FARB 30631) and *M. rhodesiensis* (QG 577; Fig. 7B,F, Table S1). It is very narrow mediolaterally. Like *C. bauri* and *M. rhodesiensis*, *H. tucki* and *E. murphi* show a relatively greater elongation of phalanx II-2 than phalanx II-1, in contrast to the more equal lengths of the two elements in *E. lunensis* and *H. ischigualastensis* (Sereno, 1993; Sereno et al. 2012). Phalanx II-2 and II-1 are relatively equal in length in *D. wetherilli* and *Allosaurus fragilis* (Madsen, 1976; Welles, 1984), but phalanx II-2 is elongated in most non-avian coelurosaurs (Gishlick & Gauthier, 2007). This suggests that the elongation of phalanx II-2 in both coelophysids and coelurosaurs is convergent.

In *C. bauri* (AMNH FARB 30631, Fig. 7G) and *M. rhodesiensis* (QG 577, Fig. 7C), the first two phalanges of digit III are the shortest, except for the first phalanx of digit IV. These two phalanges are very similar in shape, both being shorter and narrower than II-1, with III-2 slightly narrower mediolaterally than III-1. In *C. bauri* both have triangular proximal articular surfaces, and wider, more rounded triangular proximal articular surfaces are present in *M. rhodesiensis*. Phalanx III-3 in *C. bauri* and *M. rhodesiensis* is highly elongate, as is typical of the elongation of the penultimate phalanges in most theropods (Tykoski & Rowe, 2004). In *C. bauri*, phalanx IV-1 is a highly reduced, mediolaterally flattened nub of bone lacking a well-developed proximal articular surface and a distal articular surface entirely (Fig. 7H). This phalanx is somewhat better developed in *M. rhodesiensis*, as it is longer, with a more defined proximal articular surface but only a simple distal surface (Fig. 7D). Both taxa appear to possess faint collateral ligament pits on phalanx IV-1. However, there is no trace of a hypothesized ungual phalanx on digit IV (Padian, 1992) in any *C. bauri* and *M. rhodesiensis* specimens. Metacarpal V lacks phalanges in *C. bauri*.

Comparisons with partial manus from other coelophysoids

In addition to the more complete, articulated manus of early diverging dinosaurs with which comparisons were

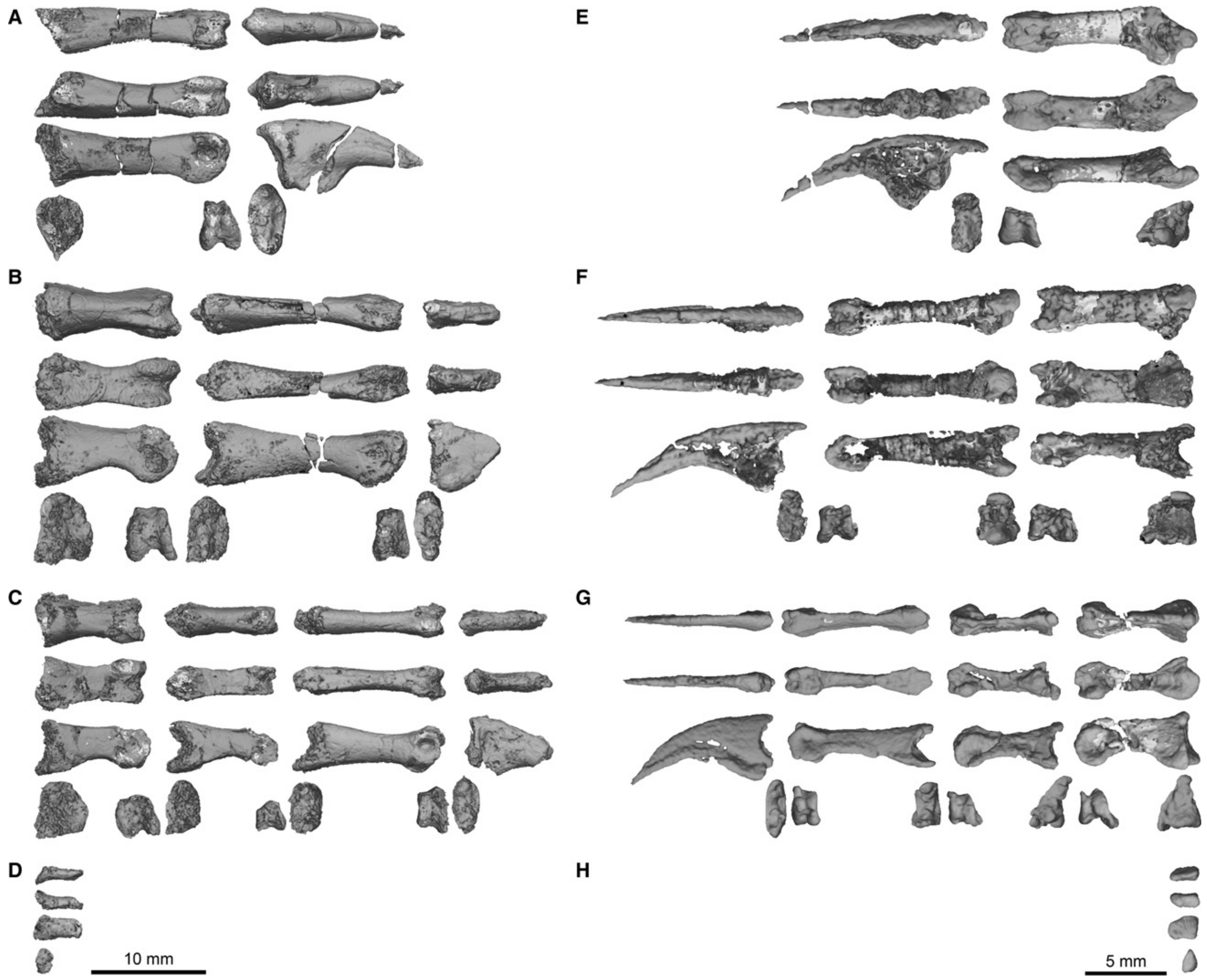

Fig. 7 QG 577 *Megapnosaurus rhodesiensis* (A–D) and AMNH FARB 30631 *Coelophysis bauri* (E–H) manual phalanges. (A) *M. rhodesiensis* right phalanges I-1 and I-2. (B) *M. rhodesiensis* right phalanges II-1, II-2, and II-3 (partial). (C) *M. rhodesiensis* right phalanges III-1, III-2, III-3, and III-4 (partial). (D) *M. rhodesiensis* right phalanx IV-1. (E). *C. bauri* left phalanges I-1 and I-2. (F) *C. bauri* left phalanges II-1, II-2, and II-3. (G) *C. bauri* left phalanges III-1, III-2, III-3, and III-4. (H) *C. bauri* left phalanx IV-1. Each phalanx is shown (from top of page to bottom) in dorsal, ventral/palmar, lateral, and articular surface views (E)–(H) © American Museum of Natural History.

made above, other coelophysoids *sensu* You et al. (2014) that are typically recovered outside the *M. rhodesiensis* + *C. bauri* clade also preserve manual elements which can be compared with these taxa. These include *Liliensternus liliensterni* von Huene, 1934; *Segisaurus halli* Camp, 1936*;* '*Syntarsus*' *kayentakatae* Rowe, 1989*; Panguraptor lufengensis* You et al. 2014; and *Dracoraptor hanigani* Martill et al. 2016. A manus previously assigned to the coelophysoid *Procompsognathus triassicus* Fraas, 1913 is actually that of a crocodylomorph associated with the specimen (Ostrom, 1981; Welles, 1984; Sereno & Wild, 1992; Knoll, 2008), hence the carpus and manus of this taxon remains unknown. Of these taxa, only the *P. lufengensis* holotype possesses a complete articulated manus. The manus of the other taxa are disarticulated and incomplete.

Liliensternus liliensterni

The holotype of *L. liliensterni* (von Huene, 1934) preserves a single carpal, which, based on its relative size and position in articulation with the proximal ends of metacarpals III and IV, may be distal carpal 3 but this is difficult to verify from the illustrations of von Huene (1934). As in both *C. bauri* and *M. rhodesiensis*, the proximal end of metacarpal II in the *L. liliensterni* holotype possesses an extensive fossa for the insertion of extensor digitorum longus (von Huene, 1934; Burch, 2014). Also similar to *C. bauri* and *M. rhodesiensis* is an asymmetry of the distal condyles, where the lateral condyle is larger than the medial one. A deep dorsal extensor depression is also present on the distal end of metacarpal II as in *C. bauri* (AMNH FARB 30631). The single preserved phalanx I-1 of the *L. liliensterni* holotype likely belongs to the left manus, though this was not stated by von Huene (1934). If correctly identified as a left phalanx, its shaft would bow medially, which is typical among early neotheropods. Given this identification, the medial distal condyle is larger than the lateral, similar to *D. wetherilli* (Xu et al. 2009) and *E. murphi* (Martinez et al. 2011), but opposite to that seen in *M. rhodesiensis*.

Segisaurus halli

No carpals are known for *S. halli* (Carrano et al. 2005). Manual elements of this taxon consist entirely of partial phalanges and unguals. Although their identities are difficult to determine, it is likely that they include phalanges II-2, II-3, III-2, III-3, and III-4 of the left manus (Camp, 1936). Overall, these elements differ little in their morphology from those of *C. bauri* and *M. rhodesiensis*.

'Syntarsus' kayentakatae

As first described by Rowe (1989) and figured by Tykoski (2005), a partial manus is known for this taxon. No carpals are preserved. Metacarpals III and IV appear to be in partial articulation. The main difference between *'S.' kayentakatae* and *C. bauri* and *M. rhodesiensis* is its possession of two phalanges in digit IV, in contrast to the single phalanx of the other two taxa. The element tentatively identified as a first metacarpal by Tykoski (2005) appears more similar to phalanx I-1 or II-1, given its strongly curved proximal articular surface and anteroposteriorly shorter, dorsoventrally wider dimensions compared with the first metacarpals of *C. bauri* and *M. rhodesiensis*. The phalanx tentatively identified as II-2 by Tykoski (2005) does not resemble this element in *C. bauri* or *M. rhodesiensis*, as this phalanx is the longest of all in both species, and is longer than metacarpal IV, instead of shorter as in the *'S.' kayentakatae* holotype. This element corresponds better with either phalanx III-3 or a more proximal phalanx of digit II or III.

Panguraptor lufengensis

The carpals, if present, are obscured in the articulated, partially prepared holotype of this taxon (You et al. 2014). The phalangeal formula is presumably the same as *M. rhodesiensis*, as there is no evidence of a fifth metacarpal as in *C. bauri*, and though no ungual is preserved on digit III, its absence would be highly unusual among theropods. You et al. (2014) note the possible presence of a second phalanx on digit IV, as in *'S.' kayentakatae*, but this is not clearly visible in their Fig. 4. Phalanx II-2 is relatively shorter and more robust than in either *C. bauri* or *M. rhodesiensis*. Otherwise, the proportions of all manus elements are similar to *C. bauri* or *M. rhodesiensis*. CT scanning of this specimen may provide important information.

Dracoraptor hanigani

No carpals are known for this taxon. The manus is disarticulated and represented by a metacarpal and several phalanges of uncertain position (Martill et al. 2016).

Discussion

Difficulties in interpreting carpals

Before discussing our results, it is necessary to provide caveats for the study of fossil vertebrate carpals, given difficulties arising from the conditions of preservation and preparation of this delicate, complex anatomical region. Attempts to identify carpals and other components of the dinosaur manus are complicated by their varying degrees of ossification (possibly reflecting ontogenetic stage) within and between specimens and species, and postmortem disarticulation of the elements. Articulation or near-articulation of elements preserving their topological relationships is necessary for confident identification in most cases. Even slight disarticulation, as in QG 1, the only *M. rhodesiensis* with an articulated carpus, can impede accurate assessment. Additionally, weathering and diagenetic alteration of specimens (particularly along poorly ossified portions of elements) also impedes identifications, as is the case for *E. lunensis* (Sereno et al. 2012). It is important to consider that future discoveries of less-altered specimens of this and other taxa may change interpretations of carpal evolution.

Additionally, the amount and style of specimen preparation can influence interpretations of carpal elements. For example, if all elements are left in articulation, small bones such as the centrale may be obscured by other bones or entirely encased in matrix, leading one to conclude that they are absent. Specimens left on large blocks of matrix and obscured by the overlying bones of other individuals in bonebeds (such as the majority of the Ghost Ranch *C. bauri* specimens) cannot be rotated to view other preserved surfaces. Situations such as these encourage the use of digital preparation methods using CT scans (see Abel et al. 2012 for a review of these methods) to examine carpal morphology more fully, while requiring no or little additional mechanical preparation.

Considering variation, some taxa, such as *E. lunensis* (PVSJ 512) and *T. hallae* (GR 242), possess more uniform rounded carpals. Others, such as *H. ischigualastensis* and *C. bauri*, have carpals with a variety of distinctive and interlocking shapes. It is tempting to hypothesize that this represents ontogenetic variation, with the simple, rounded carpals representing early growth stages and the more complex bones representative of the later or adult growth stages. This interpretation cannot be ruled out; however, it is also important to consider the complexity of the ontogenetic trajectories of the earliest dinosaurs known from more than a single skeleton, which apparently varied widely among individuals (Griffin & Nesbitt, 2016). Thus, it is difficult to know how accurately morphology reflects the actual age of the individuals without further histological evidence.

A major difficulty in studying the evolution of dinosaur hands and wrists is that no close outgroup comparison is possible, as no manual elements are known for any non-dinosaurian dinosauromorph, pterosaur hands are highly modified, and even pseudosuchian and stem archosaur hands and wrists are poorly known (Nesbitt, 2011). Thus, it is not currently possible to assess whether any of the features common to most early dinosaurs (e.g. reduced digits IV and V and 'grasping' modifications) represent synapomorphies of Dinosauria or whether they are distributed more widely outside the clade (Langer & Benton, 2006; Brusatte et al. 2010; Langer et al. 2010). Thus, dinosaurs preserve the only substantial record of major transitions in ornithodiran manus evolution during the Triassic Period thus far.

Intraspecific variation

Carpus

The main variable characters within the Ghost Ranch specimens of *C. bauri* are the separation or fusion of the intermedium and ulnare (or alternatively the presence or absence of an intermedium altogether), presence or absence of an ossified centrale, and the degree of fusion among the distal carpals (Fig. 8). These could result from biological polymorphism, including ontogenetic change, or from pathologies or variable preservation of elements. The delicate nature and frequent displacement of these elements renders a taphonomic explanation for their absence in some specimens plausible. However, the generally excellent state of articulation of AMNH FARB 30631 makes any homology interpretations predicated on element displacement less likely.

Comparing two CT reconstructions of *C. bauri* reveals the presence of a centrale in AMNH FARB 30631 (Fig. 8A) and its absence in MCZ 4329 (Fig. 8B). No intermedium is visible in MCZ 4329, whereas the intermedium may be coossified with the ulnare in AMNH FARB 30631, and free in MCZ 4331 (Fig. 8C) and AMNH FARB 7243 (Fig. 8D). If a pisiform

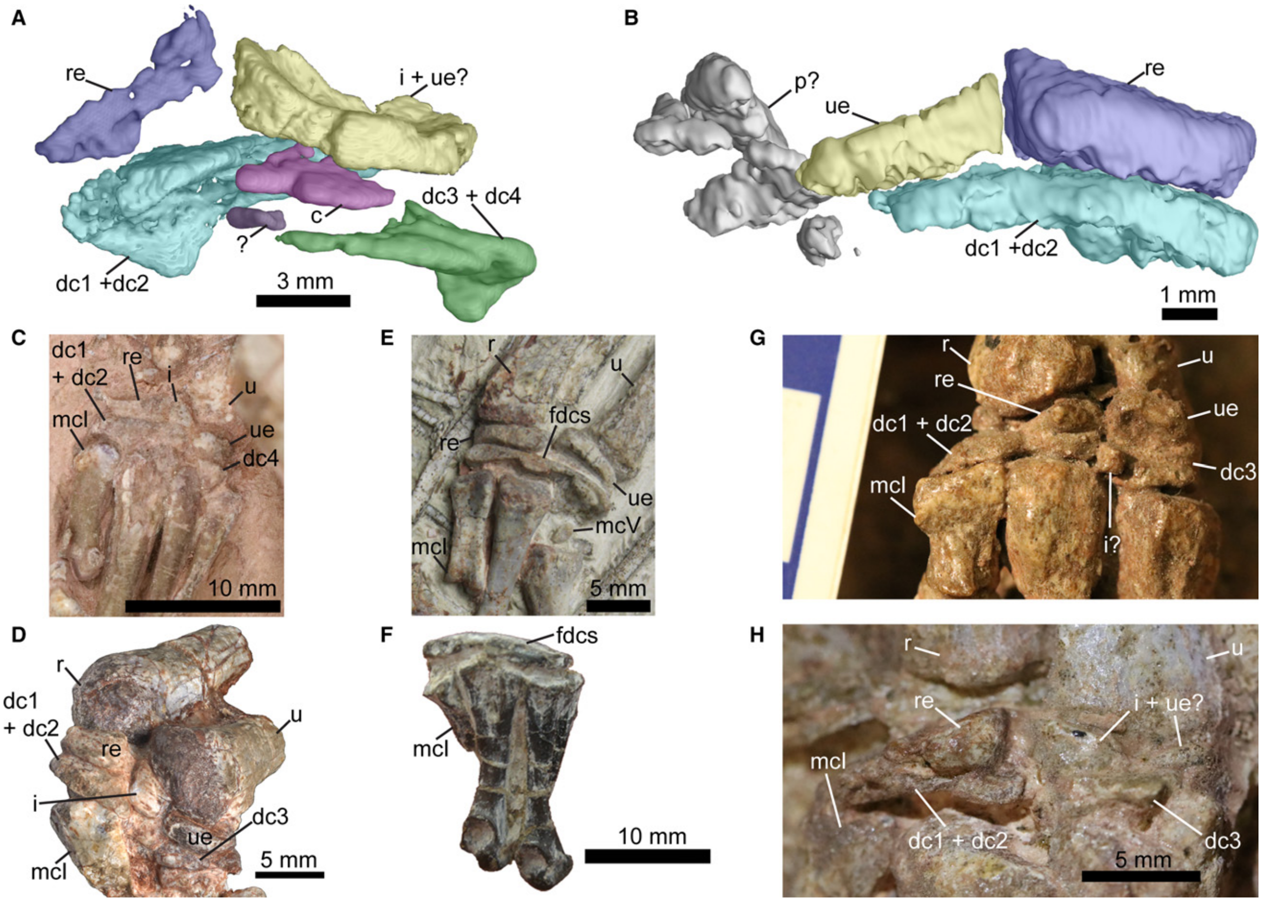

Fig. 8 Variation among carpi. All except (F) are *Coelophysis bauri*, and all are shown in dorsal view except (C), which is shown in palmar view. (A) AMNH FARB 30631. Note the presence of a centrale and possible coossification of the intermedium and ulnare © American Museum of Natural History. (B) MCZ 4329. Note the lack of a centrale and the possible pisiform. (C) MCZ 4331. Note the presence of a free intermedium. (D) AMNH FARB 7243. Note the presence of a free intermedium. (E) NMMNH P-42576. Note the fused row of distal carpals and a fifth metacarpal. (F) Unnamed Hayden Quarry coelophysoid GR 1033. Note the fused row of distal carpals. (G) AMNH FARB 7227. Note a possible free intermedium. Scale bar increment is 10 mm. (H) CM 81766. Note a possible coossified intermedium and ulnare, a possibly free third distal carpal. c, centrale; dc, distal carpal; fdcs, fused distal carpals; i, intermedium; mcl, metacarpal I; mcV, metacarpal V; p, pisiform; r, radius; re, radiale; u, ulna; ue, ulnare. Image credit for (B) and (C): Museum of Comparative Zoology, Harvard University, © President and Fellows of Harvard College.

similar to that found in *Struthiomimus altus* (Nicholls & Russell, 1985) is present in some *C. bauri* (MCZ 4329, Fig. 8B; AMNH FARB 7243), then these would differ from all other *C. bauri* specimens examined, none of which preserve a pisiform. However, as we noted above, the fragmentation and displacement of other carpal elements near the possible pisiform in MCZ 4329 makes determining its identity difficult.

Distal carpals 1 and 2 are fused in all *C. bauri* specimens examined. In at least two specimens (AMNH FARB 7223, CM 81766, Fig. 8H) distal carpals 3 and 4 are probably separate. Because the lateral side of the carpus of MCZ 4329 is distorted (Fig. 8B), we cannot identify distal carpals 3 and 4 with any certainty to assess their condition. AMNH FARB 30631 is currently unique in preserving the two fused distal carpal blocks (1 + 2 and 3 + 4) as separate elements. All distal carpals appear to be fused into a single block in NMMNH P-42576 (Fig. 8E). Fusion of all distal carpals to one another is also present in the unnamed coelophysid from the Hayden Quarry (GR 1033, Fig. 8F), bolstering our interpretation that the condition in *C. bauri* (NMMNH P-42576) is not taphonomic or pathologic. Furthermore, the manus of NMMNH P-42576 is well-preserved overall, with little shape distortion or surface modification of bones, and clearly defined separations between them. This suggests that extensive merging of the distal carpals through diagenesis is unlikely.

The observed variations in *C. bauri* carpus morphology do not obviously correlate to manus size among the examined specimens (Table S1). We caution against making conclusions about how manus size correlates to total body size or whether either correlates with age, as it is often difficult to connect *C. bauri* manus to the rest of their corresponding skeletons, and external morphological indicators of maturity have been shown not to be closely correlated with body size in *C. bauri* (Griffin & Nesbitt, 2016). The lack of preserved articulated wrists (other than that of QG 1) of *M. rhodesiensis* does not allow us to comment on individual variation in the carpus of the taxon. QG 577 lacks a carpus and it does not preserve the possible pisiform that adheres to the ulna of QG1.

As discussed above, the low sample size of carpi for many fossil reptile taxa prevents study of intraspecific variation in this region. Two for which this can be assessed for comparison with *C. bauri* are the thalattosaur *Askeptosaurus italicus* Nopcsa, 1925 and the sauropodomorph dinosaur *Plateosaurus engelhardti* von Meyer, 1837. Müller (2005) notes variation in the presence or absence of a centrale as well as in the relative sizes of distal carpals 1 and 4 to the others in two specimens of *A. italicus*. The variable presence of a centrale possibly mirrors the condition in *C. bauri*. However, this element may easily be obscured in *C. bauri* specimens in their current state of preparation (see above). Additionally, comparison of the terrestrial *C. bauri* with the aquatic *A. italicus* may not be fair, given that the carpi and tarsi of aquatic taxa are typically highly modified in other ways (Osburn, 1906; Caldwell, 2002).

Plateosaurus engelhardti is a basal sauropodomorph dinosaur known from a large number of specimens from European Triassic bonebeds. *Plateosaurus* specimens from the Trossingen bonebeds in Germany come from two bone layers separated by several meters (Seeman, 1933; Sander, 1992) that represent the remains of individuals from presumably multiple populations accumulated over an unknown duration (Sander, 1992).

Considering variation in these populations, the presence of a radiale and ulnare in the Trossingen *Plateosaurus* may vary among individuals. Neither element is preserved in SMNS 91297, SMNS 58958, AMNH FARB 6810, and most other specimens for which this anatomical region is reasonably complete and undistorted. Galton & Upchurch (2004) suggested that these elements may have remained cartilaginous, noting their rare occurrence among Triassic and Jurassic sauropodomorphs as a whole. GPIT 1 may have a radiale and ulnare (Mallison, 2011), though these are not clearly visible in the original quarry illustration (von Huene, 1928) of this specimen, which only shows distal carpals 1 and 2 and a large, flat element not comparable to any distal carpal known from other specimens. Perhaps this element is one of the proximal carpals that Mallison (2011) describes. A *P. engelhardti* specimen from the Halberstadt locality (MfN Skelett XXV) was also claimed to have a radiale and ulnare (Mallison, 2010a, 2011), but neither element is present in the original illustration of this specimen (Jaekel, 1913, fig. 20), which only show three elements resembling distal carpals. The carpal ossification interpreted as an intermedium in other early sauropodomorphs (Cooper, 1981; Sertich & Loewen, 2010) is variably preserved in *P. engelhardti*. When present, it is a small, rounded or triangular element between the radius and ulna, proximal to the distal carpals. It is clearly visible in SMNS 58958 and AMNH FARB 2595 (= AMNH FARB 6810; Fig. 9A,B). The position of this element relative to the radius and ulna supports its identification as the intermedium; however, it could also be a centrale or a different proximal carpal. We consider either identification plausible at this time.

Most well-preserved specimens have three distal carpals, although there are only two in SMNS 58958 (= F33; Mallison, 2010a; Schoch, 2011), and four in SMNS F61 (Bonnan & Senter, 2007). A *P. engelhardti* carpus (SMNS 13200k) figured by von Huene (1932) comprises three major distal carpals (dc 1, 2, and 3) and includes three smaller, round ossifications of uncertain homology. The two elements lateral and proximal to the third distal carpal in this specimen may be the fourth and fifth distal carpals (Galton & Upchurch, 2004), but the other element, being medial to the first distal carpal, does not match the position of any known carpal in other dinosaur taxa. The ‘fourth distal carpal’ of the mounted skeleton AMNH FARB 6810 is almost certainly a different element that was displaced during

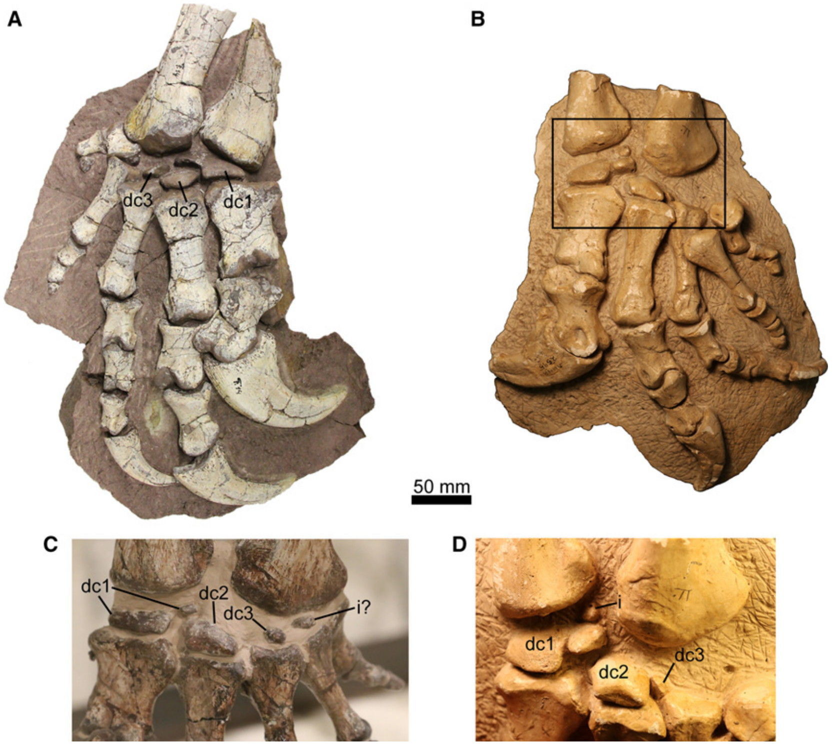

Fig. 9 Variation in *Plateosaurus engelhardti* carpi. (A) SMNS 91297 in dorsal view. Note the absence of an intermedium. (B) AMNH FARB 2595 (cast of AMNH FARB 6810) in dorsal view. Note the presence of an intermedium. Rectangle shows region in (D). (C) AMNH FARB 6810 in dorsal view. Compare with (B) and (D) and note the 'absence' of the intermedium, which may have been moved to a position over the fourth metacarpal prior to mounting of the specimen. The third distal carpal was also shifted slightly, and the dorsal notch in the first distal carpal was filled with plaster, giving the appearance of two separate elements in the final mounted skeleton. (D) Close-up of AMNH FARB 2595 (= AMNH FARB 6810) carpus in dorso-proximal view. dc, distal carpal; i, intermedium. Scale bar: (A,B) 50 mm.

mounting (Fig. 9C). There was no element above the fourth metacarpal at the time of initial preparation of the specimen, as revealed by a cast (Fig. 9B,D; given the separate number AMNH FARB 2595), drawing (redrawn by Galton, 2001; Fig. 1C), and photograph (AMNH Library Archives Negative #311538) made prior to its mounting for exhibition. The 'fourth distal carpal' of the mounted skeleton (Fig. 9C) may actually be the intermedium placed over the fourth metacarpal, as the intermedium is visible in the cast (Fig. 9B), photograph, and illustration of AMNH FARB 6810, but not in the mounted wrist. Alternatively, it could be some other bone fragment added to the carpus. It is also possible that a true fourth distal carpal was discovered upon further preparation, but this would not explain why the intermedium is missing from the mount. A notch in the first distal carpal was also filled with plaster before mounting, erroneously giving the appearance of two separate elements in this position in the finished mount (Fig. 9C).

Plateosaurus engelhardti shows similarly high variation in carpal number to *C. bauri*. The reason for variation in *P. engelhardti* is not immediately discernible, but a high degree of intraspecific variability in body size and neurocentral suture closure has been described previously for this taxon (Sander & Klein, 2005; Hofmann & Sander, 2014), so perhaps this developmental polymorphism extends to the carpus and other characters as well. Though a reduced carpus is often associated with quadrupedality in large sauropod and ornithischian dinosaurs (Maidment et al. 2012), abundant evidence suggests *P. engelhardti* was an obligate biped (Mallison, 2010a,b, 2011; Reiss & Mallison, 2014). Therefore, reduction of the wrist relative to the ancestral dinosaur condition likely occurred under a different set of functional constraints in *P. engelhardti* than quadrupedal dinosaurs.

Digits

The major variation among specimens in the digits of *C. bauri* is the presence or absence of the remnant fifth metacarpal. As with the carpal characters, it is difficult to ascertain whether the absence of this bone is biological, preparational or taphonomic in nature. The variable shape and occasional displacement of the fifth metacarpal, as in NMMNH P-42576 (Fig. 8E), also complicate efforts at identifying it when the element is present. It shows great differences in shape, from rounded to more elongate, although all of the fifth metacarpals known for *C. bauri* are approximately the same size relative to the other metacarpals.

Raath (1990) considered *M. rhodesiensis* to represent two morphs: 'gracile' and 'robust'. He observed these differences based on metacarpal morphology, with QG 577 an example of 'gracile' metacarpals and QG 1, the holotype, an example of 'robust' metacarpals. This is apparent in our examination as well. QG 577 does have proportionally longer and thinner metacarpals with narrower distal and proximal ends than QG 1. These differences may be ontogenetic in nature, as Raath (1977) described QG 577 as a juvenile. However, this hypothesis remains to be tested with size-independent ontogenetic criteria (e.g. bone histology).

An additional difference between QG 1 and QG 577 is the relatively larger and better-developed phalanx IV-1 in the latter specimen. This may not be an ontogenetic difference, as one would expect the less complex bone to be present in the 'juvenile' instead.

Differences between *C. bauri* and *M. rhodesiensis*

It is clear that there are many differences in manus morphology between these two otherwise very similar taxa (Table 1). These differences are summarized in Table 1, taking into account information on other specimens of these taxa described by Raath (1969) and Colbert (1989) in addition to the specimens reconstructed for this paper.

Evolution of the archosauromorph carpus

We briefly review the evolutionary history and relatively poor fossil record of archosauromorph carpals, expanding on the discussion presented by Nesbitt et al. (2015), to better contextualize what can be inferred about plesiomorphic conditions in successive outgroups to Dinosauria, and to highlight an anatomical region that has historically received less attention from phylogenetic studies than the tarsus (Dyke, 1998). The relationships of the taxa discussed below are illustrated in Fig. 10. We focus largely on terrestrial forms, as the carpi of specialized aquatic taxa are typically highly specialized (Osburn, 1906; Caldwell, 2002). Owing to the generally low sample size for each of the taxa discussed, as well as difficulties in identifying elements once a carpus even partially disarticulates (Nesbitt et al. 2015), these comparisons remain necessarily generalized, and such attempts at generalization should be viewed with additional caution in light of the potential for a great deal of intraspecific variation in the carpus (as discussed above for *C. bauri*, *A. italicus*, and *P. engelhardti*).

Non-archosaur archosauromorphs such as *Trilophosaurus buettneri* and *Azendohsaurus madagaskarensis* likely possessed 10 (*Trilophosaurus*) or nine (*Azendohsaurus*) carpals. This is reduced from the plesiomorphic amniote condition of eleven carpals, exemplified by 'pelycosaur' synapsids (Romer & Price, 1940), the early eureptile *Paleothyris acadiana* (Carroll, 1969), and the diapsid *Petrolacosaurus kansensis* (Reisz, 1981). The carpi of *Hovasaurus bouli* and *Thadeosaurus colcanapi*, non-saurian diapsids (Reisz et al. 2011), also contain 11 carpals (Currie, 1981; Currie & Carroll, 1984); however, *Youngina capensis* appears to lack a pisiform (Gow, 1975). Pritchard et al. (2016) discussed the extreme modifications to the manus of drepanosaurs; therefore, we choose not to repeat their thorough discussion here. The carpus of rhynchosaurs consists of up to three ossified proximal carpals (radiale, intermedium, and ulnare) and at least four distal carpals (Carroll, 1976; Benton, 1990; Dilkes, 1998). The carpus of *Protorosaurus speneri* consists of the same nine elements as those of *A. madagaskarensis* (Gottmann-Quesada & Sander, 2009; Nesbitt et al. 2015) and rhynchosaurs (Carroll, 1976), and the carpals appear to be reduced in number in the more aquatic 'protorosaurs' *Dinocephalosaurus orientalis* and *Tanystropheus* cf. *longobardicus* (Renesto, 2005; Rieppel et al. 2008; Nesbitt et al. 2015).

Carpals are similarly rarely preserved among non-archosaur archosauriforms. Gow (1975) reconstructed *Prolacerta broomi* with the typical basal archosauromorph carpal number of 10; however, he notes that the number and identities of elements missing from the figured specimen remains uncertain. Cruickshank (1972) speculatively reconstructed the carpus of *Proterosuchus fergusi* as containing three proximal carpals (including a large, blocky ulnare) and four distal carpals. The carpus of erythrosuchids is very poorly known. Two carpals of uncertain identity are known for *Vancleavea campi* (Nesbitt et al. 2009b). The carpus of proterochampsians is unknown (Trotteyn et al. 2013). Likewise, no carpals are known for *Euparkeria capensis*, and Ewer (1965) hypothesized that they were mostly cartilaginous. The carpus of phytosaurs remains unknown despite an otherwise extremely good fossil record for this clade.

The fossil record of non-dinosaurian archosaur carpals is as depauperate as that of other archosauriforms, and what few carpi are available tend to confuse, rather than clarify, interpretations of the origin of the extant crocodylian carpal pattern. The proximal carpals of the ornithosuchid pseudosuchian *Riojasuchus tenuisceps* are large and blocky, and the intermedium remains unfused to either the radiale or ulnare (Ezcurra, 2016). Up to four carpals have been described for *Ornithosuchus woodwardi* (Walker, 1964), but it is difficult to ascertain their identities. Two carpals of uncertain identity are present in the holotype of the shuvosaurid pseudosuchian *Effigia okeeffeae* (Nesbitt, 2007). The rauisuchid pseudosuchians *Postosuchus kirkpatricki* and *P. alisonae* have blocky proximal carpals similar to those of *Riojasuchus*; however, the intermedium is fused to the ulnare in at least *P. alisonae* (Peyer et al. 2008). The

Table 1 Comparison between manus features of *Coelophysis bauri* and *Megapnosaurus rhodesiensis*.

	Coelophysis bauri	*Megapnosaurus rhodesiensis*
Centrale	Present in AMNH FARB 30631, not in others	Absent
Pisiform	Absent in most, possibly present in MCZ 4329 and AMNH FARB 7243?	Present in QG 1? (Botelho et al. 2014)
Intermedium	Free in AMNH FARB 7243 and MCZ 4331, fused to ulnare or absent in AMNH FARB 30631 and others	Free in QG 1
Metacarpal V	Present	Absent

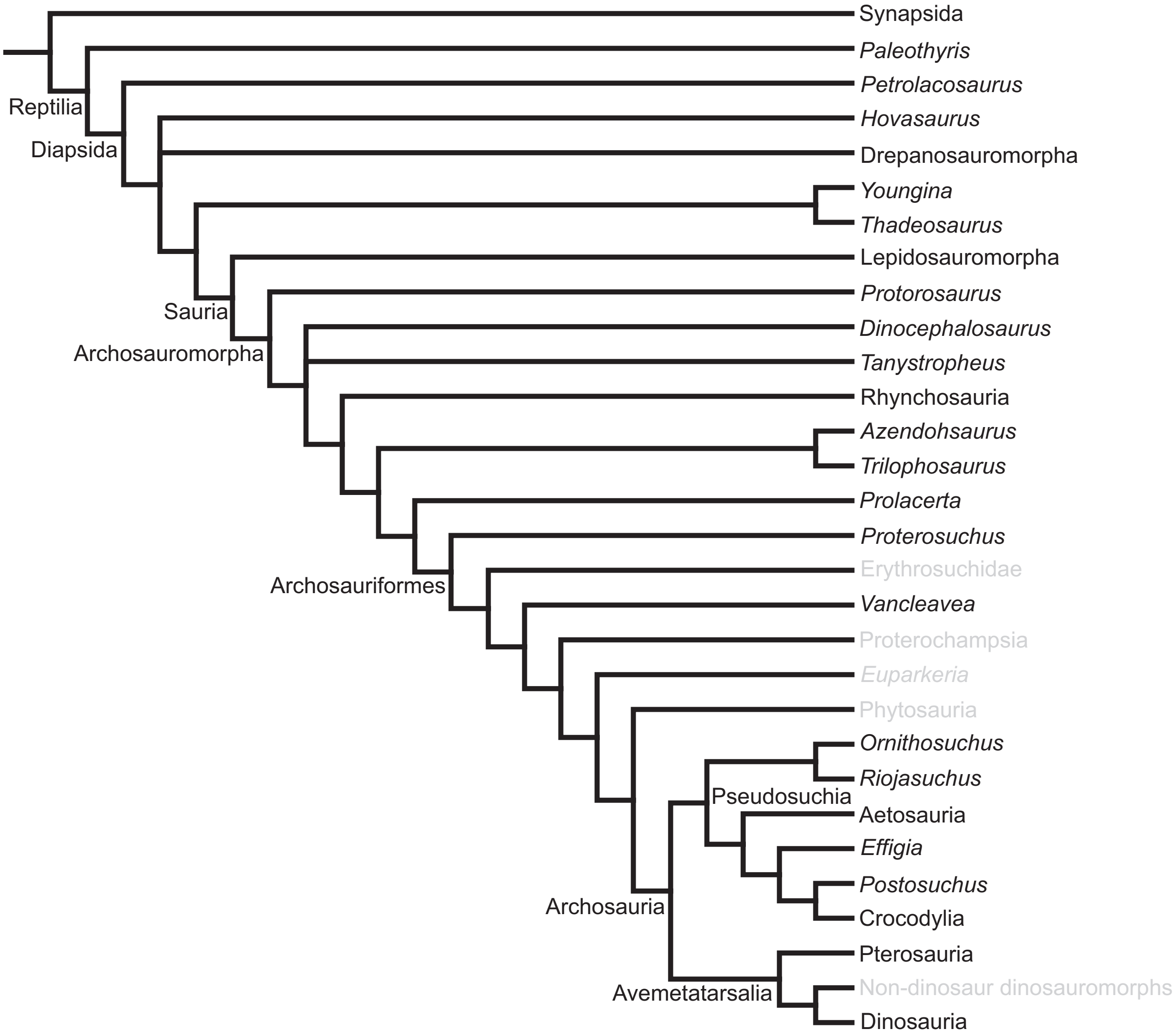

Fig. 10 Composite cladogram illustrating the approximate relationships of select amniote taxa discussed in the text. No preserved carpi are known for the taxa listed in faded gray text. The tree topology is based on those of Müller & Reisz (2006), Nesbitt (2011), Reisz et al. (2011), Pritchard et al. (2016), Nesbitt et al. (2015), and Ezcurra (2016).

identities of the two fused carpals are less clear for *P. kirkpatricki*, as either the labels or orientation of the bones presented by Weinbaum (2013, fig. 14) may be reversed, with the radiale apparently on the lateral side of the manus instead of the medial. Weinbaum (2013, p. 536) does state that the intermedium and ulnare are fused in *P. kirkpatricki.* Interestingly, this fusion contrasts with the condition in *Alligator mississippiensis*, where the intermedium fuses with the radiale early in development (Müller & Alberch, 1990; Burke & Feduccia, 1997). It is unclear whether other crocodylians form this cartilaginous precursor of the intermedium (Lima et al. 2011; Vieira et al. 2016). Fusion of the intermedium to the ulnare in at least some *Postosuchus* (along the crocodylian stem) and *C. bauri* (along the avian stem) suggests that the fusion of intermedium to radiale in both *Alligator* and extant birds (Botelho et al. 2014) evolved independently. Further complicating this picture, Sawin (1947) and Walker (1961) identified possible fusion of the intermedium to the radiale in the stem crocodylians aetosaurs. Little can be said about the evolution of the centralia or distal carpals of pseudosuchians, owing to a lack of specimens.

Pterosaurs have four carpals: a medial carpal and the pteroid bone it supports, a proximal element consisting of two fused proximal carpals, and a distal element made up of two or three fused distal carpals (Wellnhofer, 1984; Bennett, 1993; Unwin et al. 1996). The specific identities of the carpals comprising these two syncarpals remain somewhat uncertain, given that there are currently no fossils that shed light on the origin of the modified pterosaur forelimb in general. As previously stated, the carpus of non-dinosaur dinosauromorphs is unknown.

Other than the aforementioned taxa, dinosaurs exhibit some of the best-preserved hands and wrists from any early Mesozoic archosaurs. *H. tucki* shares the primitive number of nine carpals with early archosauromorph taxa such as *A. madagaskarensis*. In *H. tucki* and *C. bauri*, the intermedium probably fuses to the ulnare in at least some individuals, and in the ornithischian *Stegosaurus sulcatus*, the pisiform additionally fuses to the coossified ulnare and intermedium (Gilmore, 1914). Within theropods, the intermedium switches from either occasionally fusing to the ulnare (or being absent) to merging with the radiale while both are still cartilaginous in coelurosaurs (scapholunare; Botelho et al. 2014). The ulnare trends from being a dominant bone in early archosaurs and early dinosaurs to disappearing completely in tetanurans (Botelho et al. 2014). The radiale of early dinosaurs is typically smaller than the ulnare or combined intermedium plus ulnare. Saurischians appear to lose the pisiform, with the exceptions of its possible reappearance in *C. bauri*, *M. rhodesiensis* (Botelho et al. 2014), *Harpymimus okladnikovi* (Kobayashi & Barsbold, 2005), and *S. altus* (Osborn, 1917; Nicholls & Russell, 1985).

If the observed individual or ontogenetic variation in fusion of the intermedium and ulnare in *C. bauri* is present in other taxa, extensive polymorphism could complicate using the presence or absence of fusion as a phylogenetic character for this part of the dinosaur tree. Likewise, the presence or absence of the centrale and pisiform are probably less useful phylogenetic characters for establishing lower clade level relationships, owing to difficulties in preparing and uncertainty in identifying these elements. Establishing the extent of polymorphism in carpal character states preserved among fossil taxa is essential before incorporating these characters into a phylogenetic data matrix. Furthermore, it is difficult to differentiate individual differences among skeletally mature individuals from ontogenetic variation between skeletally immature and mature individuals given the presence of large amounts of ontogenetic sequence polymorphism within the Ghost Ranch *C. bauri* population (Griffin & Nesbitt, 2016) and the lack of well-constrained histologically derived ages for *C. bauri* specimens.

Despite the similar resulting morphologies of the elements, the enlarged distal carpal 1 of early branching sauropodomorphs is distinct from the element produced from the fusion of distal carpals 1 and 2 in some theropods (Nesbitt, 2011), an alternative interpretation to the hypothesis that the two clades show a homologous enlargement of the medial-most distal carpal (Langer & Benton, 2006). Fusion of distal carpals 1 and 2 persists to varying degrees within Tetanurae, resulting in the semilunate carpal of coelurosaurs (Botelho et al. 2014). Madsen (1976) notes that 14 of 18 *Allosaurus* specimens he examined from the Cleveland Lloyd Quarry exhibit fusion of distal carpals 1 and 2, and that this fusion does not correspond to the maturity of the specimens [maturity was assumed to correspond to size throughout Madsen's (1976) study]. Most early diverging members of the major coelurosaur clades and later non-avian maniraptorans have an avian-like carpus with at least distal carpals 1 and 2 eventually fusing into a 'semilunate' carpal, occasionally a third distal carpal, and one proximal carpal, the scapholunare, which ossifies from a composite radiale and intermedium cartilage (these elements form separate ossifications in the earliest coelurosaur taxa; Botelho et al. 2014; Xu et al. 2014a). In contrast to this, some coelurosaur groups that deviate greatly in manus morphology from both the ancestral tetanuran condition and the derived avialan condition exhibit a variety of accompanying modifications to their carpi. Both the tyrannosaurid *Gorgosaurus libratus* (Lambe, 1917; Holtz, 1994) and the ornithomimosaurs *Struthiomimus altus* and *Harpymimus okladnikovi* (Osborn, 1917; Nicholls & Russell, 1985; Kobayashi & Barsbold, 2005) exhibit distal carpals lacking well-defined articular surfaces and an increase in carpal number to a minimum of five. Because of their small and poorly ossified nature, Gauthier (1986) suggested that the carpals of ornithomimids and tyrannosaurs 'appear to be arrested at a juvenile stage of development'. Fusion of a semilunate-like carpal to metacarpal I (and sometimes metacarpal II) to form a blocky carpometacarpus occurred in alvarezsaurids (Perle et al. 1994; Xu et al. 2013). In contrast to the reduced but well-ossified wrist of tetanurans, ceratosaurs other than *Eoabelisaurus* and an undescribed noasaurid (Keillor & Sereno, 2010; Pol & Rauhut, 2012) apparently lack any ossified carpals (Ruiz et al. 2011). Distal carpal 4 is consistently large and the most robust of the distal carpals among early saurischians, often exhibiting a roughly triangular shape. This contrasts with *H. tucki*, where the fourth distal carpal is similar in size and shape to the other distal carpals (Santa Luca, 1980). *Heterodontosaurus tucki*, *E. lunensis*, and possibly *H. ischigualastensis* (Ezcurra, 2010) exhibit the plesiomorphic character state of possessing a fifth distal carpal. The loss of distal carpal 5 within later theropods and sauropodomorphs ('prosauropods') seems an important event, as this element does not reappear throughout the evolution of either group (Langer & Benton, 2006).

Phylogenetic context of digit reduction

In all early dinosaurs, digit I is the shortest of the three non-vestigial digits. The relative lengths of digits II and III show a marked change across early theropods, with *H. ischigualastensis* and *T. hallae* sharing with *H. tucki* the presumably plesiomorphic condition of a longer digit III, and these digits becoming subequal in length in *E. murphi* and neotheropods. Digits II and III are approximately equal in length in the sauropodomorph *E. lunensis* as well. In tetanurans, digit III is much shorter than digit II. These changes in length seem to be driven by a shortening of metacarpal III, and in tetanurans, shortening of the individual phalanges of digit III (Fig. 11).

Digit IV is always shorter than I and possesses three phalanges in *H. tucki* and *Plateosaurus*, presumably reflecting the basal dinosaurian condition, although no phalanges are preserved for this digit in *E. lunesis*. *Herrerasaurus ischigualastensis* and all taxa closer to Aves, except for *T. hallae* and possibly *Ceratosaurus nasicornis* (Carrano & Choiniere, 2016), developed only a single phalanx on digit IV. In ceratosaurs, the length of all digits is greatly reduced compared with other theropods, with shortening of the distal phalanges and marked reduction of metacarpal I in *Limusaurus inextricabilis* (Xu et al. 2009). Similar shortening of the distal phalanges, reduction of the number of phalanges on each digit, and further reduction of the length of the metacarpals is seen in abelisaurids (Ruiz et al. 2011; Burch & Carrano, 2012). *Aucasaurus garridoi* and *Carnotaurus sastrei* uniquely exhibit a conical, elongated fourth metacarpal that lacks phalanges (Ruiz et al. 2011). As our data describe variation in the fourth and fifth digits before their ultimate loss in later diverging theropods, they do not directly concern the debate (Xu et al. 2009; Vargas et al. 2009; Bever et al. 2011; Carrano & Choiniere, 2016) over the ancestral digit identities of tetanuran theropods sparked by the description of *Limusaurus inextricabilis*. The four hypotheses of the timing and pattern of digit reduction and identity shifts in tetanurans summarized by Xu et al. (2014b, Fig. 4) remain plausible.

Digit IV is lost entirely in tetanurans, with only a nubbin of a fourth metacarpal reappearing in *Sinraptor dongi*, *Megaraptor namunhuaiquii*, and *Guanlong wucaii* (Currie & Zhao, 1993; Calvo et al. 2004; Xu et al. 2006; Rauhut et al. 2012), and in AMNH FARB 587, which Brusatte (2013) states may belong to either *Tanycolagreus topwilsoni* (Carpenter et al. 2005) or *Ornitholestes hermanni* (Osborn, 1903). This element is morphologically similar to the remnant fifth metacarpal of some *C. bauri* and *D. wetherilli*. The reappearance of the fourth metacarpal in AMNH FARB 587, despite its absence in most other tetanurans and other coelurosaurs, suggests that the developmental pathway for forming this element had not been fully suppressed. Thus, a high level of homoplasy in the absence of a fourth digit among tetanuran groups represents either multiple losses of this element or multiple atavistic gains (Rauhut et al. 2012). The vestigial fifth metacarpal of *D. wetherilli* is the most crown-ward occurrence of digit V within Theropoda (Fig. 11), and the remnant fourth metacarpal of AMNH FARB 587 may be the most crownward occurrence of digit IV, depending on the precise taxonomic assignment and phylogenetic position of this specimen.

The zone of developmental variability in theropod manus evolution

The reduction or loss of the fifth digit is common among reptiles, and in dinosaurs occurs in concert with reduction of the fourth digit (Shapiro et al. 2007). Interestingly, theropods and some salamanders are the only tetrapods where loss of digits IV and V occurs without any accompanying loss of digits I–III (Shapiro et al. 2007). This lateral reduction is hypothesized to maintain the ancestral grasping role of the

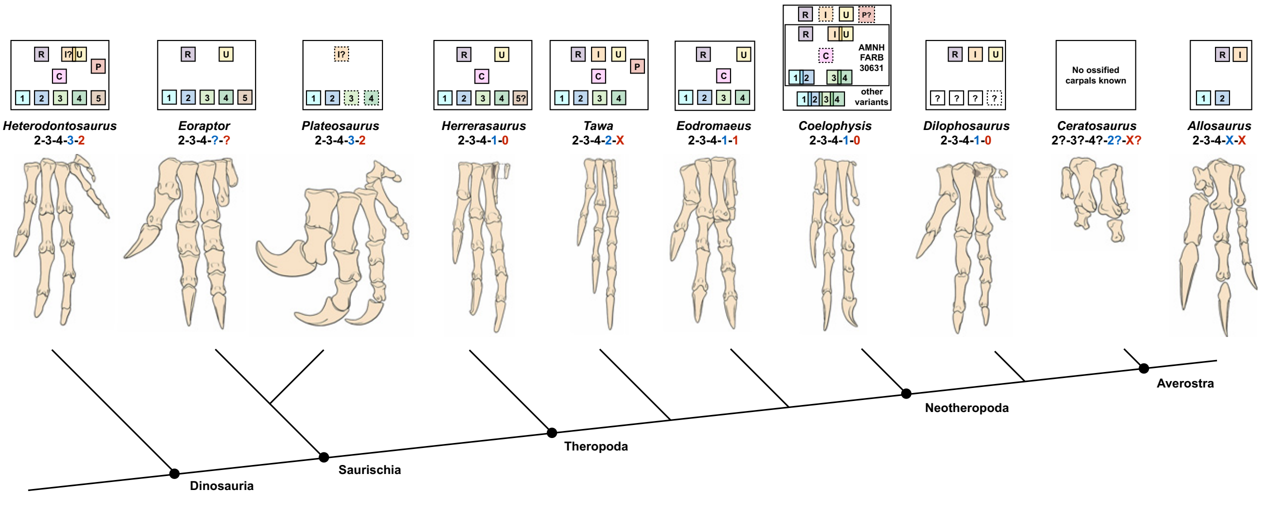

Fig. 11 Cladogram of early dinosaur left hands in dorsal view with phalangeal formulas and simplified diagrams of ossified carpals. Tree topology from Nesbitt & Ezcurra (2015). Illustrations by Nicole Wang, redrawn and modified from (L-R) Santa Luca (1980), Sereno et al. (2012), this study, Sereno (1993), Burch (2014), Martinez et al. (2011), this study, Xu et al. (2009), Gilmore (1920), and Madsen (1976). R, radiale; I, intermedium; U, ulnare; C, centrale; P, pisiform; 1–5, distal carpals 1–5. Dashed lines around carpals in *Coelophysis* and *Plateosaurus* indicate the variable presence of those elements. Question marks after a carpal name indicate uncertainty in the identification of that element. Overlapping blocks indicate fused elements. Identifications of *Tawa* carpals follow Burch (2013). No ossified carpals are known for *Ceratosaurus* (Carrano & Choiniere, 2016). The number and identities of *Dilophosaurus* distal carpals remain uncertain (Welles, 1984).

manus in dinosaurs (Sereno, 1997). Given that they are reduced in size and likely lacked a great deal of grasping function, the fourth and fifth digits of dinosaurs are considered vestigial structures (Senter, 2010). It has been suggested that reduced selection on vestigial structures may allow for high levels of intraspecific variability (e.g. Darwin, 1859, 1871; Fong et al. 1995; Tague, 1997, 2002; Maxwell & Larsson, 2007; Moch & Senter, 2011; Xu et al. 2011). Although very difficult to test empirically, from this variation a variety of character combinations within and among taxa can emerge, predicting a complex pattern of character state gains and losses (a zone of developmental variability) on a phylogenetic tree that precedes the 'fixation' of the eventual character combination (Shubin et al. 1995; Bever et al. 2011). Indeed, among non-avian theropods such interspecific variability has been noted for the presence or absence of a vestigial fourth metacarpal in tetanurans (Rauhut et al. 2012) and for both the number of phalanges on digit II and presence or absence of digit III among alvarezsauroids (Xu et al. 2011). The zone of developmental variability model predicts that evolutionary transitions are accompanied by an increased likelihood that individuals in a population will produce either a derived or ancestral state during their development, leading to a high degree of polymorphisms in populations before the transition can be seen as 'accomplished' at a coarser phylogenetic resolution (Bever et al. 2011). We investigate morphological changes in manus and carpus morphologies towards the base of the theropod tree in an effort to determine the extent of such a zone of developmental variability within theropods.

Examination of phalangeal formulas mapped onto a recent phylogenetic tree topology of the earliest theropods (Nesbitt & Ezcurra, 2015) reveals a more complex pattern of digit reduction among this grade than previously recognized, complicating an understanding of the outgroup condition for studies of digit reduction in later diverging theropods (Fig. 11). For example, the complete loss of digit V in *T. hallae* is most parsimoniously convergent with the loss in later theropods such as allosauroids. *Tawa hallae* is also unique among the studied theropod taxa in possessing two tiny phalanges on its fourth digit. Similarly, *E. murphi* may have independently gained a single phalanx on its fifth digit, a feature not present in any other theropod. *Megapnosaurus rhodesiensis* also exhibits independent loss of the fifth metacarpal, convergent in both *T. hallae* and allosauroids.

This phylogenetic distribution of digit reduction shows that early theropods independently lost or gained portions of the fourth and fifth digits at least three times before these features disappeared completely (at least post-hatching) within later tetanurans including birds. Previous studies (e.g. Wagner & Gauthier, 1999; Xu et al. 2009) that only made use of *H. ischigualastensis*, *C. bauri*, and *D. wetherilli* as outgroups for studying digit reduction in tetanurans, could not resolve the complexity of the transition between five- and four-fingered theropods, as the three taxa have the same phalangeal formula.

The carpus of early dinosaurs also exhibits a great deal of inter- and intraspecific variation. The intermedium, centrale, and pisiform are variably present or absent along the entire grade, and within *C. bauri* (Fig. 11). From the available evidence, there is no clear stepwise reduction in carpal number between the complex wrist of *C. bauri* and the greatly reduced (and in some cases likely unossified) wrists of early averostrans.

The degree of variation in digits IV and V and the carpus observed within and between *C. bauri* and *M. rhodesiensis* and the grade of early theropods as a whole may reflect an earlier 'zone of developmental variability' that preceded the frameshift of theropod digit identities, which likely occurred along the averostran or tetanuran stems (Bever et al. 2011). Under this idea, that a high degree of developmental variability among populations will persist through at least the early portion of character state transitions on a phylogeny, one may speculate that the developmental pathways governing the production of ossified fourth and fifth digits and their associated phalanges were not lost completely within Theropoda until some point within Tetanurae, and that many such losses may have occurred independently among basal theropods. This is supported by the multiple independent losses and/or gains of an ossified fourth metacarpal among tetanurans (Rauhut et al. 2012). The carpus may exhibit similar interspecific variation within Coelurosauria, with, for example, the possible reappearance of a pisiform in ornithomimosaurs and birds (Botelho et al. 2014). Intraspecific differences already noted within *C. bauri* and *M. rhodesiensis* may similarly be indicative of variation in developmental pathways of the carpus and manus. Only documentation of individual variation within an ontogenetic framework constrained by bone histology will shed more light on this issue.

It seems clear that both a homeotic transformation of digit identities and a significant reduction in the number of ossified carpals took place at or near the Averostra node (Bever et al. 2011; Botelho et al. 2014). Future developmental and paleontological studies should focus on whether these transformations in the wrist and digits are directly linked. The sparse fossil record of early ceratosaurs and tetanurans hinders further resolution of the ancestral Averostran condition and these subsequent transformations. Nevertheless, our data show that digit and carpal characters were highly variable among dinosaurs before the frameshift occurred, and that significant variation (e.g. reappearance of the fourth digit, reappearance of the pisiform) persisted after this homeotic transformation, throughout later tetanuran evolution (Rauhut et al. 2012; Botelho et al. 2014). Understanding how these zones of developmental variability are related necessitates future developmental work and the discovery of fossils that fill phylogenetic gaps in the record of theropod manus evolution.

In summary, ancestral state reconstructions of manual characters for major clades (e.g. Saurischia, Theropoda) are complicated by the degree of intraspecific variability observed in only a small subset of the total individuals of *C. bauri*, as well as the complex distribution of gains and losses of digits, phalanges, and carpals among early dinosaurs. The uncertain positions recovered for many key early dinosaur taxa among different phylogenetic analyses (e.g. Martinez et al. 2011; Nesbitt & Ezcurra, 2015; Cabreira et al. 2016; Baron et al. 2017) further complicates such reconstructions, but under all recovered tree topologies, the pattern of carpal and digit reduction is similarly complex.

Conclusion

Through description of new three-dimensional digital reconstructions of the carpus and manus of *C. bauri* and *M. rhodesiensis* and comparative anatomical study with the carpus of other archosauromorphs, we present the first evidence of an ossified centrale in a *C. bauri* specimen and a completely fused distal carpal row in another. We also found several differences between *C. bauri* and *M. rhodesiensis* (including the presence of a fifth metacarpal in *C. bauri*), and a complex, non-stepwise reduction of carpals and manual digits IV and V in early dinosaurs. The independent gain and loss of metacarpals and phalanges from these digits in *T. hallae*, *E. murphi*, and *M. rhodesiensis* demonstrates that the loss of these elements within Tetanurae was not a unique loss within the history of Theropoda, as previously considered. Thus, the manus was highly variable among dinosaurs before the hypothesized frameshift in theropod digit identities. Future integration of developmental data and new fossil discoveries along this grade will surely further elucidate this important but little-studied evolutionary transition.

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Author contributions

D.E.B. conceived and designed the research, acquired the data, performed the analyses, and drafted and revised the manuscript. S.J.N. conceived and designed the research, assisted with data acquisition and analysis, and revised the manuscript. M.A.N. assisted with data analysis and revised the manuscript.

Conflict of interest

The authors declare no conflicts of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figs S1–S4. Photographs of the manus and carpus of AMNH FARB 27435 *Coelophysis bauri* provide additional documentation of the morphology of this taxon.

Table S1. Manus measurements of selected *Coelophysis bauri* and *Megapnosaurus rhodesiensis* specimens.