Homologies and homeotic transformation of the theropod 'semilunate' carpal

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The homology of the 'semilunate' carpal, an important structure linking non-avian and avian dinosaurs, has been controversial. Here we describe the morphology of some theropod wrists, demonstrating that the 'semilunate' carpal is not formed by the same carpal elements in all theropods possessing this feature and that the involvement of the lateralmost distal carpal in forming the 'semilunate' carpal of birds is an inheritance from their non-avian theropod ancestors. Optimization of relevant morphological features indicates that these features evolved in an incremental way and the 'semilunate' structure underwent a lateral shift in position during theropod evolution, possibly as a result of selection for foldable wings in birds and their close theropod relatives. We propose that homeotic transformation was involved in the evolution of the 'semilunate' carpal. In combination with developmental data on avian wing digits, this suggests that homeosis played a significant role in theropod hand evolution in general.

Avian wings are highly modified, fully foldable tetrapod forelimbs that typically function in flight. One part of the avian wing with an important role in both wing-folding and flight-related movements is the wrist, which is composed of two separate proximal carpals and two distal carpals that become fused to the metacarpals in early ontogenetic development[1–3]. Not only is the small number of carpal elements an evolutionary inheritance from ancestral theropods, but the unique shapes of these elements were gradually established in theropod evolution. From a functional perspective, a very important morphological feature of the avian wrist joint is a transversely trochlear articular facet (hereafter trochlear facet) on the lateral portion of the proximal surface of the carpometacarpus (Fig. 1c), which is inferred from ontogenetic data to be formed by the two lateral distal carpals (see electronic supplementary material)[2,3]. The trochlear facet plays a key role in folding the hand and flapping wing such as keeping the wing in place and preventing the manus from supinating during forward flight[4].

In adult non-avian theropods, a trochlear morphology occurs on a separate distal carpal, called the 'semilunate' carpal (Fig. 1a,b). The 'semilunate' carpal was first identified by Ostrom[5], who described this structure in the dromaeosaurid *Deinonychus* and listed it as one of the most significant features supporting the theropod hypothesis of avian origins based on the presence of a nearly identical element in *Archaeopteryx*[6]. The 'semilunate' carpal was subsequently identified in various other non-avian theropods, though with considerable variations in its shape, size, and position (e.g., ref. 7). The presence of the 'semilunate' carpal in non-avian theropods indicates that some morphological modifications that ultimately proved important for flight evolved early in theropod evolution, and that an avian-like mechanism for folding the wrist joint evolved before the origin of birds.

It should be noted that in most published literature the 'semilunate' carpal is homologized only with the medial portion of the trochlear facet of the carpometacarpus in living birds[7,8], without including the lateralmost portion which is formed by distal carpal 4 (Fig. 1c). Given that the 'semilunate' carpal is defined by a proximally transversely trochlear morphology, it is more appropriate to view the 'semilunate' carpal of extinct theropods as equivalent to the whole trochlear facet of the carpometacarpus in living birds.

The 'semilunate' carpal is clearly homologous to one or more of the small distal carpals in the wrists of primitive theropods, but the details are controversial. In *Deinonychus* and several other maniraptorans, the 'semilunate' carpal is an enlarged element covering the proximal ends of the two medialmost metacarpals[5,7]. Furthermore, a large distal carpal occupying the same position in the basal neotheropods *Syntarsus* and *Coelophysis* has been identified as a compound bone formed by fusion of distal carpals 1 and 2, leading Gauthier to suggest that these distal carpals were also homologous to the 'semilunate' carpal of non-avian maniraptorans[9]. However, this hypothesis is in conflict with
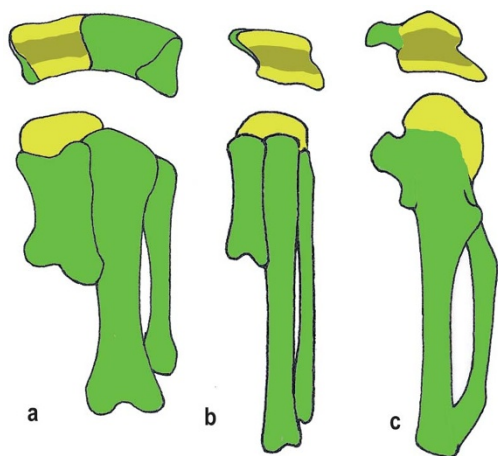
Figure 1 | Diagram showing the position and general morphology of the transversely trochlear proximal articular facet of the carpometacarpus in selected theropod hands with the phalanges omitted (upper: proximal view; lower: dorsal view; medial side of hand to left). (a) The basal coelurosaurian condition (based on *Guanlong*). (b) The basal paravian condition (based on *Sinovenator*). (c) The neornithine condition (based on *Crossoptilon*). Yellow indicates the 'semilunate' carpal; grey-yellow indicates the transverse groove; green indicates the metacarpals.

ontogenetic data from both Mesozoic birds[10] and living birds[2,3], which show that the distal carpal proximal to the medialmost metacarpal is absent in birds and the lateralmost carpal is involved in the formation of the transversely convex and trochlear proximal articular surface. This conflict has been repeatedly cited as evidence against the theropod hypothesis of avian origins (e.g., ref. 11,12).

In the present study, we describe the detailed morphology of the 'semilunate' carpal in several non-avian theropods, discuss changes in 'semilunate' carpal morphology during theropod evolution, comment on the conflicting primary homology hypotheses that have been proposed for this element, and propose a new scenario for the evolutionary history of the 'semilunate' carpal.

Methods

Most descriptions presented in this paper are based on direct observation of specimens, although some morphological information is derived from published literature. Although our focus is the evolution of the 'semilunate' carpal of tetanuran theropods, we also refer to *Herrerasaurus*[13] and *Coelophysis*[14], which exemplify the primitive theropod condition. The 'semilunate' carpal present in some theropods is distinguished from the other distal carpals by three critical features: large size, transverse convexity of the proximal surface, and a transversely oriented trochlea on the proximal surface. However, these features evolved incrementally in theropod evolution, and in extant adult birds no separate distal carpal element is present although the fused carpometacarpus bears a transversely trochlear proximal articular surface comparable to that of the 'semilunate' carpal of non-avian theropods. Consequently, our goal in the present paper is to trace the evolutionary history of this unique articular surface, rather than that of any single carpal element.

Positional relationships, special features, and continuity with intermediate forms have been widely accepted as the three operational criteria for primary homology, with the first often considered to be the main operational criterion[15], but dissenting opinions have been expressed[16]. Although the tetanuran metacarpals are identified as I-II-II (-IV) in many studies[17–20], the majority of the embryological data from living birds and alligators suggest that the three manual digits of living birds are digits II-III-IV based on positional criteria[17–22]. A recent study suggests that the metacarpals of extinct tetanuran theropods are most parsimoniously identified as metacarpals II-III-IV(-V) if the avian metacarpals are II-III-IV[23,24], and this scheme is adopted in the present paper. Here primary homologies of distal carpal elements are postulated on the basis of how they are positioned relative to the metacarpals. Ontogenetic data from living birds indicate that there are two ossification centers proximal to metacarpals III and IV, respectively[2,3,10], which develop into the transversely trochlear proximal articular surface of the carpometacarpus. These two distal carpals are thus identified as distal carpals 3 and 4. For extinct tetanuran theropods, we identify the medialmost distal carpal as distal carpal 2 rather than distal carpal 1 because we identify the medialmost metacarpal of the tetanuran theropods as metacarpal II, a view consistent with most ornithological literature (e.g., ref. 11).

Description

In the basal tetanuran *Xuanhanosaurus*[25], distal carpal 2 is significantly enlarged and covers the proximal ends of both metacarpal II and metacarpal III, while a separate, tiny distal carpal 3 also contacts the proximal end of metacarpal III (Fig. 2a). The proximal surface of distal carpal 2 is somewhat convex in the dorsoventrally direction, as well as mediolaterally, but lacks a transverse groove. This differs from the condition in basal neotheropod coelophysids such as *Coelophysis*, in which an enlarged distal carpal is present but lacks a convex proximal surface[14].
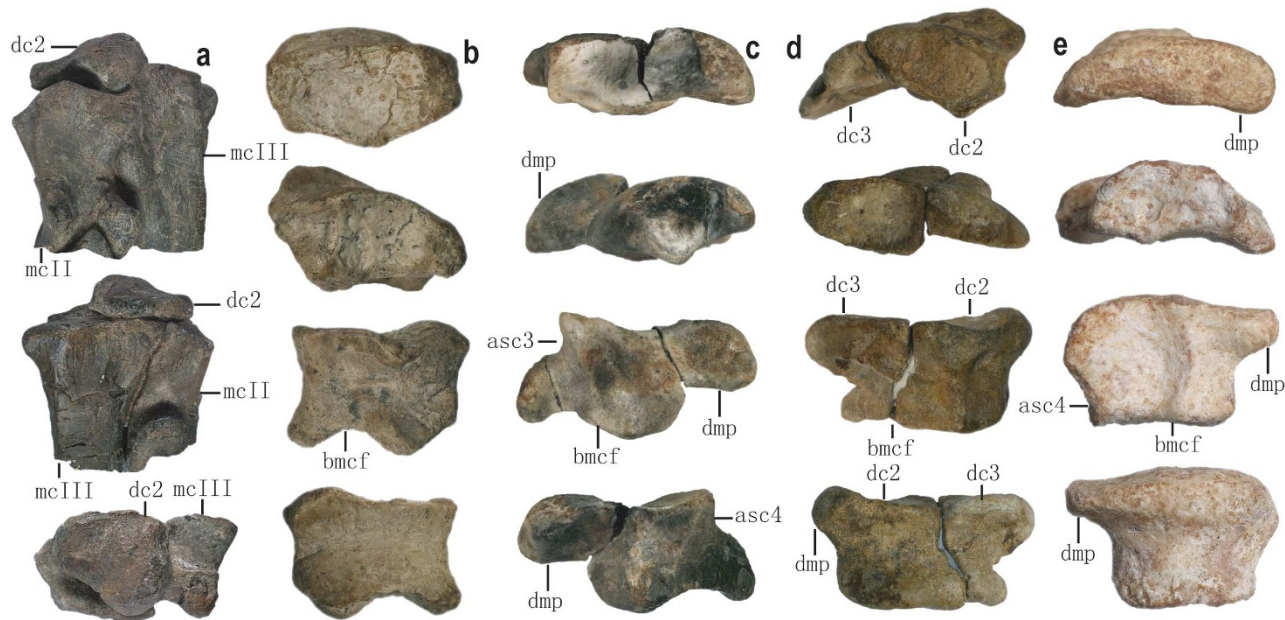

Figure 2 | 'Semilunate' carpals of selected non-avian theropods in (from top to bottom) dorsal, ventral, distal, and proximal views. (a) The basal tetanuran *Xuanhanosaurus* (without distal view). (b) The basal tyrannosauroid *Guanlong*. (c) The basal alvarezsauroid *Haplocheirus*. (d) The basal therizinosauroid *Alxasaurus*. (e) The dromaeosaurid *Linheraptor*. Abbreviations: asc3: articular surface for distal carpal 3; asc4: articular surface for distal carpal 4; bmcf: boundary between two metacarpal facets; dc2-4, distal carpals 2-4; dmp, mediodorsal process; mcII-IV, metacarpals II–IV; Not to scale.

In the basal tyrannosauroid *Guanlong*[26], an enlarged distal carpal with a transversely trochlear, slightly convex proximal surface mainly contacts the proximal end of metacarpal II, but also has a substantial contact with that of metacarpal III (Fig. 2b). This distal carpal is similar in general morphology to distal carpal 2 of the allosauroid *Allosaurus*[7], but is proportionally deeper proximodistally and has a more convex proximal surface.

In the basal alvarezsauroid *Haplocheirus*[27], distal carpal 2 is proportionally larger than in more basal theropods, and also bears a larger articular facet for metacarpal III and a proximal surface with a greater degree of transverse convexity (Fig. 2c). A prominent mediodorsal process is present for articulation with metacarpal II. As in *Allosaurus*[7], a separate, tiny distal carpal 3 fits into a notch on the lateral margin of distal carpal 2 (Fig. 2c). In the derived alvarezsauroid *Linhenykus*, the 'semilunate' carpal is fused with metacarpal II, and a transversely convex, trochlear facet occupies the central part of the proximal surface of this compound structure[28]; in some other parvicursorines, the three metacarpals are fused together and also to the 'semilunate' carpal to form a carpometacarpus, but a similar facet is present in the same position[29].

In the basal therizinosauroid *Alxasaurus*[30], distal carpals 2 and 3 combine to form a single 'semilunate' unit with a convex, transversely grooved proximal surface (Fig. 2d) as in several other therizinosauroids[31,32]. In contrast to the condition in more basal theropods, the composite structure displays a semilunate outline in both dorsal and ventral views, and the articular facet for metacarpal III is larger than the one for metacarpal II. However, the composite 'semilunate' carpal is variable in relative size among therizinosauroids, being largest in *Falcarius* and smallest in *Therizinosaurus*. Similarly, distal carpal 2 is sub-equal in size to distal carpal 3 in *Falcarius*, but considerably larger than the latter in *Alxasaurus* and *Therizinosaurus*[30,32]. In *Beipiaosaurus*[33], distal carpal 3 is the largest carpal and has a transversely grooved proximal surface, but a transverse groove is lacking in distal carpal 2.

In the deinonychosaurian *Linheraptor*[34], the 'semilunate' distal carpal is a single hypertrophied element (Fig. 2e) as in other deinonychosaurians[5–7]. The 'semilunate' carpal has a more convex proximal surface than in more basal theropods. The articular facet for metacarpal III is larger than the one for metacarpal II, and contacts metacarpal II mainly via a mediodorsal process. The boundary between the two metacarpal facets is nearly vertical (Fig. 2e), rather than oblique as in *Guanlong* (Fig. 2b) and *Haplocheirus* (Fig. 2c).

Several other paravian specimens representing different ontogenetic stages provide significant information on the homologies of the 'semilunate' carpal in this group (Figs 3 and S1). In a sub-adult individual of the basal troodontid *Sinovenator* (IVPP V12583), a large distal carpal primarily contacts metacarpal III and achieves a secondary contact with metacarpal II mainly via a mediodorsal process (Fig. 3a). In ventral view, however, this element has only an incomplete semilunate outline and is separated from the proximal end of metacarpal IV by a distinct notch. A separate distal carpal 4 is located proximal to the distally displaced metacarpal IV, a feature seen in a number of young derived maniraptoran specimens including some basal birds[10,35,36]. Distal carpal 4 contacts the ventral part of the distally inclined lateral surface of the large distal carpal, and combines with the latter bone to form a full semilunate shape in ventral view (Fig. 3a). In a larger and thus presumably older individual of *Sinovenator* (IVPP V14009), a single distal carpal articu-
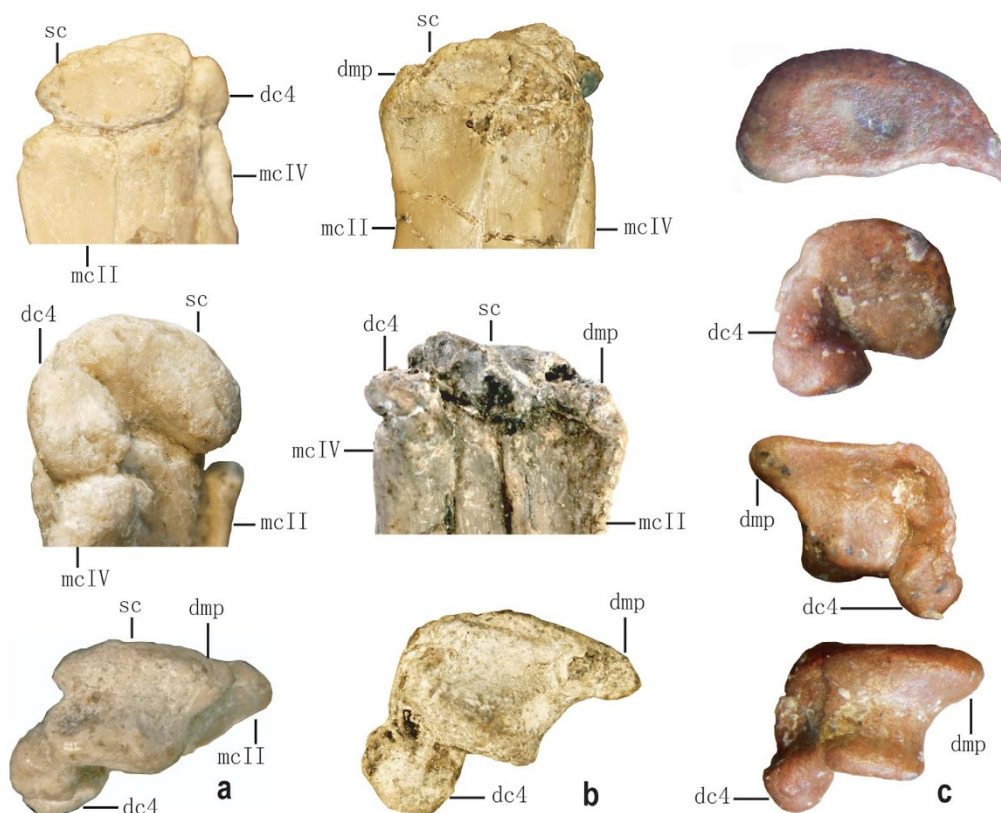

Figure 3 | 'Semilunate' carpals of three basal troodontid specimens representing different ontogenetic stages. Wrist region in dorsal, ventral, and proximal views (from top to bottom) in the sub-adult IVPP V12583 (a) and the adult IVPP V14009 (b), both of which are specimens of the basal troodontid *Sinovenator*; (c), wrist region in dorsal, ventral, distal, and proximal views (from top to bottom) in a sub-adult specimen of the basal troodontid *Mei long* (IVPP V12744). Abbreviations: dc4, distal carpal 4; dmp, mediodorsal process; mcII-IV, metacarpals II-IV; sc, 'Semilunate' carpal. Not to scale.
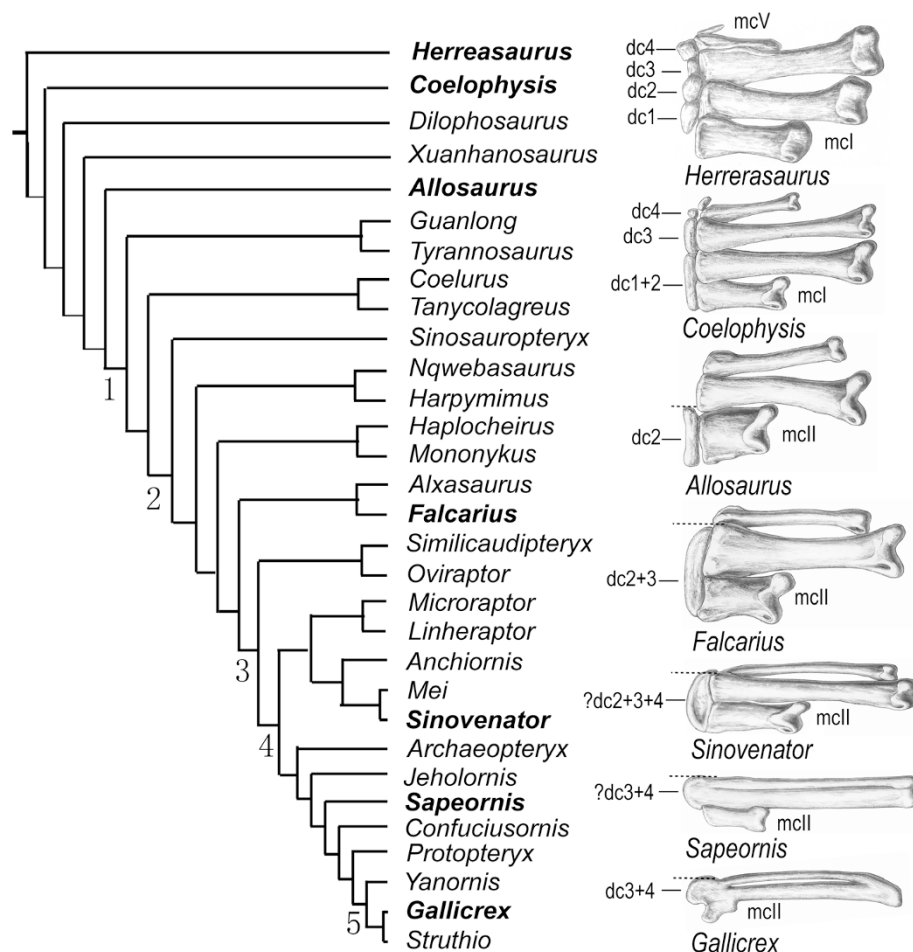
Figure 4 | Distribution of major morphological features pertaining to the trochlear facet across theropod phylogeny. The ancestral character states pertaining to the trochlear facet for major theropod nodes are reconstructed using the Mesquite software package (see Supplementary information for details) and they are summarized below: 1, distal carpal 2 with transversely trochlear proximal articular surface; 2, 'semilunate' carpal with a prominent mediodorsal process; 3, 'semilunate' carpal covering proximal end of metacarpal III; 4, distal carpal 4 incorporated into 'semilunate' carpal to form a ventrolateral process; 5, 'semilunate' carpal with a prominent ventrolateral process and fused to two lateral metacarpals. Note the lateral shift in the position of the trochlear articular facet on the proximal surface of the carpometacarpus. Movement of the trochlear facet upon the proximal carpals is constrained by a mediodorsal process in basal maniraptorans including *Archaeopteryx*, and by a ventrolateral process (formed by distal carpal 4) in derived birds. The lateral shift could have increased the range of abduction (ulnar deflection) by preventing the proximal end of metacarpal IV from protruding laterally beyond the distal carpals, a position in which it would tend to lock against the ulna (or cartilaginous ulnare, if one was present) during abduction. Abbreviations: dc1-4, distal carpals 1–4; mcI-V, metacarpals I–V; Not to scale.

lates with and partially fuses to the proximal ends of metacarpals II-IV (Fig. 3b), and this element is nearly identical in shape and position to the compound 'semilunate' structure of IVPP V12583.

Formation of a compound, fully fused 'semilunate' carpal late in deinonychosaur ontogeny is further supported by data from the basal troodontid *Mei*. In a sub-adult individual of *Mei* (IVPP V12744), a single 'semilunate' carpal is present, but a visible line of fusion indicates that this bone is a compound element comprising a large distal carpal attached to a small one. The small distal carpal is identical in shape and position to distal carpal 4 of IVPP V12583 (Fig. 3c). Two individuals of the basal dromaeosaurid *Microraptor* (IVPP V17749 and 17750) representing different ontogenetic stages also exhibit the same pattern as the troodontid specimens. The 'semilunate' structure is formed by a large medial distal carpal and a small distal carpal 4 in the younger individual, and by a single large, presumably compound distal carpal in the older individual (see electronic supplementary material, fig. S1).

Discussion

Our analysis demonstrates that morphological features pertaining to the unique trochlear facet of the carpometacarpus evolved in an incremental way, developed on different distal carpals in different theropods, and shifted their position from the medial side to the lateral side of the hand during theropod evolution (Fig. 4). The first modification related to the formation of the 'semilunate' carpal was present in basal neotheropod coelophysoids, which have an enlarged medial distal carpal formed by fusion of distal carpals 1 and 2[9]. The basal tetanuran *Xuanhanosaurus* documents the second stage in the evolution of the 'semilunate' carpal, namely the appearance of a convex proximal surface on distal carpal 2. Allosauroids and several other tetanuran groups have a compound structure formed by a large distal carpal 2 and a tiny distal carpal 3, which probably became fused to each other very late in ontogeny[7,30,32]. This compound structure has a transversely trochlear proximal surface, and this surface is asymmetrical in basal maniraptorans (e.g., the basal alvarezsauroid *Haplocheirus*) due to the presence of a long mediodorsal process. As the result of a further modification, distal carpal 3 makes a larger contribution to the compound 'semilunate' carpal in therizinosauroids and other derived maniraptorans[30,32,33] than in other theropods.

Basal paravians including *Archaeopteryx* document another important stage. In these taxa, a hypertrophied distal carpal possibly formed by fusion of a small distal carpal 2 and a large distal carpal 3,

together with a small distal carpal 4 that contacts the distally displaced metacarpal IV[37,38,39], forms a compound 'semilunate' carpal that covers the proximal ends of the three metacarpals. In at least some species, the small distal carpal 4 becomes integrated with the large distal carpal late in ontogeny (e.g. *Sinovenator* and *Mei*). The proximal articular surface is asymmetrical in that the mediodorsal process forms a facet facing proximoventrally and distal carpal 4 forms a facet facing proximodorsally.

The lateral shift in both composition and position of the 'semilunate' carpal continued during avian evolution. In adult avialans other than *Archaeopteryx*, a separate 'semilunate' carpal is absent. In many specimens of various early birds, including confuciusornithids[40], *Jeholornis*[41], *Sapeornis*[42], and enantiornithines[10], the 'semilunate' carpal is fused to the proximal ends of metacarpals III and IV but not to that of metacarpal II (see electronic supplementary material, fig. S2). In *Jeholornis* the 'semilunate' carpal has a large contact with metacarpal II, but does not fuse with the latter element. In ornithuromorphans such as *Yanornis*[43], the 'semilunate' carpal is fused to the proximal ends of all three metacarpals to form a carpometacarpus of modern aspect, though its fusion to the proximal end of metacarpal II is only partial (see electronic supplementary material, fig. S1). In adult living birds, a transversely trochlear articular facet is present on the lateral portion of the proximal surface of the carpometacarpus, but does not extend onto the proximal end of metacarpal II (see electronic supplementary material, fig. S1). Ontogenetic data from both Mesozoic and living birds indicate that this facet is formed by fusion of a single ossification center proximal to metacarpal III and a small element proximal to metacarpal IV[2,3,10], which are respectively identifiable as distal carpals 3 and 4 (see electronic supplementary material). In enantiornithines and ornithuromorphans, the mediodorsal process of the 'semilunate' carpal is lost and distal carpal 4 becomes fused to distal carpal 3 relatively early in ontogeny. The trochlear facet is restricted to the lateral half of the carpometacarpus, and continues a short distance distally along the lateral margin of the carpometacarpus (Figs 1 and S1).

Our observations have several implications, including clarifying the homology of the 'semilunate' carpal, shedding new light into the evolution of distal carpal 4, providing new information for phylogenetic analyses, and suggesting a possible homeotic transformation. Each of these implications is discussed below.

Homology of the 'semilunate' carpal. Our morphological data from various ontogenetic stages of several deinonychosaurian taxa remove the conflict between evidence from avians and evidence from non-avian theropods concerning the homology of the 'semilunate' carpal. The new data suggest that, in at least some basal deinonychosaurians (e.g., *Mei* and *Microraptor*), the transversely trochlear proximal surface of the carpometacapus (the 'semilunate' carpal) is formed partly by the lateralmost distal carpal (distal carpal 4) as in both Mesozoic and living birds[2,3,10]. Consequently, the involvement of the lateralmost distal carpal (distal carpal 4) in forming the 'semilunate' carpal within the carpometacarpus of Mesozoic and modern birds is an inheritance from their non-avian theropod ancestors, like many other salient avian features such as flight feathers.

Evolution of distal carpal 4. Distal carpal 4 deserves special mention here. In most tridactyl tetanuran theropods, a separate distal carpal 4 seems to be absent, which is consistent with the invariable absence of an ossified distal carpal proximal to the lateralmost metacarpal in specimens of more basal theropods[13,14,44]. The lack of preservation of the lateralmost distal carpal suggests that a cartilaginous lateralmost distal carpal was sufficient because there is a functional emphasis on the medial side of the theropod hand[22] and the lateralmost digit was not being subjected to large forces (e.g. forces introduced by struggling prey during predation). Consequently, the preservation of distal carpal 4 in some specimens of deinonychosaurians[45], *Archaeopteryx* and certain other avialans[10,35,36] might represent a

derived feature associated with a functional shift toward the lateral side of the hand. However, it should be noted that all of the specimens in which distal carpal 4 is preserved as an element separate from the other carpals and the metacarpals are small individuals and/or clearly show a lack of fusion in other parts of the skeleton (e.g., metacarpals not fused to each other or to semilunate carpal, proximal tarsals not fused to tibia, and metatarsals not fused to distal tarsals or to each other), suggesting a relatively early ontogenetic stage. This pattern implies that distal carpal 4 probably fused to the metacarpals late in the ontogeny of basal birds, as was evidently also true in basal deinonychosaurs. In fact, an evolutionary trend toward ontogenetically earlier occurrence of skeletal fusion, particularly of basipodial elements to the autopod, is apparent on the line to modern birds.

'Semiluante' carpal and theropod phylogenetic analyses. The 'semiluante' carpal is often used as a simple binary character in theropod phylogenetic studies[9,27,46–51], but our analysis suggests that the trochlear facet is developed on different distal carpals in different theropods. Accordingly, a new and more complex set of characters pertaining to the trochlear facet is needed for theropod phylogenetic studies. We formulated 18 characters with a total of 46 states describing different possible configurations of the proximal surface of the theropod carpometacarpus (Supplementary text), and scored these characters for 31 species representing major theropod subgroups (Supplementary Table S1). We incorporated the information into an analysis that aimed to reconstruct the ancestral states of these 18 characters for the major nodes across a widely accepted theropod phylogeny (Figs. 4 and S3). The analysis was performed using Mesquite, a software package that offers a variety of functions for ancestral state reconstruction and other phylogeny-based analyses[52]. Although the results are admittedly tentative due to the relative paucity of data available from the poorly known theropod wrist region, the analysis does suggest an incremental evolutionary pattern for the morphological features pertaining to the trochlear facet (Supplementary Table S2). The theropod wrist evolution is featured by the sequential occurrences of the following major modifications: enlargement of distal carpal 2 together with reduction of distal carpal 3 and loss of distal carpal 4, development of a transverse groove on a composite distal carpal composed of large distal carpal 2 and small distal carpal 3, development of a transverse trochlea on a large distal carpal composed of distal carpal 2 and enlarged distal carpal 3, development of a prominent transverse trochlea on a large distal carpal composed of distal carpals 2, 3, and the reappeared distal carpal 4, and development of a prominent transverse trochlea on the proximolateral portion of the metacarpus composed of distal carpals 3 and 4 (Fig. 4).

Homeotic transformation of 'semilunate' carpal. Homeosis refers to the ectopic development of a structure or organ, and it has been suggested to contribute to the success and diversity of some major eukaryotic groups[53–55]. The distribution of the morphological features pertaining to the trochlear facet across theropod phylogeny is consistent with a partial and gradual homeotic transformation of the 'semilunate' carpal. Although no direct developmental data are available to support the occurrence of a homeotic transformation, this interpretation is suggested by the positional shift of the topologically unique articular surface from the medial side of the wrist to the lateral side (i.e. the trochlear facet shifts from medial carpals to lateral carpals). Future research into avian wrist development may eventually demonstrate the existence of a positional shift of the developmental program contributing to the formation of the trochlear facet of the carpometacarpus in living birds. The shift in the position of the 'semilunate' carpal parallels the lateral shift in digital morphology that took place in theropod hand evolution (in which digits II–IV of the tetanuran hand took on a phalangeal formula of 2-3-4, which characterizes digits I-III of basal

theropods). Increasing evidence supports the hypothesis that stepwise homeotic changes altered the morphology of the manual digits of theropods, particularly in contributing to the evolution of the tridactyl hand seen in birds and other tetanuran dinosaurs[23]. Particularly, several genes have been shown to have shifted their spatial pattern of expression in living birds[17,22,56,57]. The morphological data presented in this paper suggest that piecemeal, partial homeotic transformation also occurred in theropod wrist evolution, and contributed to the formation of a fully foldable wrist joint. The two shifts differ in that the lateral shift of the 'semilunate' carpal occurred later, and in an even more piecemeal fashion, than the lateral shift in digit morphology. Interestingly, a key event in the carpal lateral shift appears to have been the reappearance of distal carpal 4 to contribute to the 'semilunate' articular surface in derived maniraptorans. Interestingly, a key modification in theropod digit evolution is the reappearance of a fully functional digit IV in tetanurans[24], and the reappearance of distal carpal 4 is thus analogous to the former event.

Fusion, expansion, or reduction of basipodial elements is common in vertebrate evolution. However, it is rare for a shift in position and composition of a unique, functionally significant carpal or tarsal structure to occur without greatly disrupting the structure's topology (Fig. 4). The progressive changes in the composition and position of the 'semilunate' carpal during the evolution of theropods possibly resulted from strong selection for foldable wings in avialans and their close relatives, though some modifications particularly those occurring in early theropod evolution might have been just random. The strong positional nature of the shift suggests that homeotic transformation, which accounts for much of the existing diversity among vertebrate body plans[55], affected the theropod carpus. In combination with both morphological and developmental data indicating that the manual digits underwent a homeotic transformation on the line to birds[22,23], morphological data from the theropod 'semilunate' carpal suggest that homeosis played a significant overarching role in theropod hand evolution.

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Author contributions

X.X. designed the project. X.X., Q.Z. and F.L.H. performed the research. X.X., Q.Z. and F.L.H. wrote the manuscript.

Additional information