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Claw retraction and protraction in the Carnivora: the cheetah (*Acinonyx jubatus*) as an atypical felid

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Abstract

The cheetah *Acinonyx jubatus* is the most cursorial felid and has been described as somewhat dog-like in both the shape and the diminished degree of retraction of the claws. In this study we evaluate and investigate the osteological correlates associated with claw retraction in the cheetah through a comparison of the morphology of its middle phalanges with those of other felids and of the wolf *Canis lupus*. Compared to other felids, the middle phalanges of the cheetah have better-developed grooving of the distal articular facets in both the manus and pes, reduced to absent angulation to the distal articular facets in the inner and outer digits, less marked asymmetry of the shaft, and a mid-shaft cross-section that is less triangular and more circular. In all of these features, the morphology of the cheetah is intermediate between that of other felids and that of the wolf. The cheetah's distinctive morphology is autapomorphic within Felidae and similarities between the cheetah and the wolf are the result of convergence. Study of an ontogenetic series of specimens of the domestic cat suggests that the morphology of the cheetah can be explained, at least in part, as a product of heterochrony in which the development of the middle phalanx is truncated at an earlier stage than is typical of the adults of other felids. Some of the morphological differences in the middle phalanges of the cheetah can be associated with its distinctive hunting behaviour. The reduced manipulative capabilities of the forelimb associated with the evolution of cursorial adaptations seem to have limited the roles of the forepaws in both the subduing of prey and feeding.

Key words: Felidae, *Acinonyx*, claws, hunting, heterochrony

INTRODUCTION

The cheetah *Acinonyx jubatus* is arguably the most distinctive extant member of the Felidae. This distinctiveness is reflected taxonomically in its referral to a monospecific genus and its separation from other extant species at higher taxonomic levels by some authors (e.g. Pocock, 1917; de Beaumont, 1964; Martin, 1980; Stains, 1984; Wozencraft, 1993; McKenna & Bell, 1997). Over short distances the cheetah is the fastest terrestrial vertebrate (Hildebrand, 1959; Sharp, 1997). Unlike other felids that typically pounce on prey at close range, the cheetah usually runs down its prey using a high-speed chase that may cover up to several hundred metres (Kruuk & Turner, 1967; Eaton, 1970; Neff, 1982; Turner & Anton, 1997). This difference in hunting behaviour is reflected in many aspects of its anatomy (Neff, 1982). For example, the claws are considered to

have a diminished range of motion as compared to other cats and have been described as dog-like (Ewer, 1973).

The claws of members of the Felidae are more highly retractile than those of most other carnivores (Ewer, 1973; Neff, 1982; Hunt, 1987), a condition that was termed hyper-retraction by Bryant *et al.* (1996). In felids, the morphology of the phalanges and the arrangement of the interphalangeal ligaments allow the distal phalanx to retract to the lateral side of the middle phalanx, rather than onto the dorsal surface of that phalanx as in most other carnivores (Gonyea & Ashworth, 1975; Bryant *et al.*, 1996). It is sometimes stated that the claws of the cheetah are not hyper-retractile; this claim may have started with Mivart (1882; see Neff, 1982), and can be found in the recent literature (e.g. Eisenberg, 1981; Taylor, 1989). The cheetah's claws are straighter than those of other felids and are always visible because the sheaths of skin that cover the claws in other felids are absent. This visibility of the claws has probably contributed to the hypothesis that the retractile system differs from that of other

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felids. Pocock (1916) and Gonyea & Ashworth (1975) demonstrated, however, that phalangeal morphology and the functioning of the interphalangeal ligaments of the cheetah are similar to those of other felids. None the less, despite these fundamental similarities in the retractile mechanism between cheetahs and other felids, the degree of hyper-retraction in the cheetah is putatively less than in other felids (Neff, 1982). However, possible osteological correlates for reduced hyper-retraction in the cheetah and the degree to which differences in the anatomy and functioning of its claw retraction mechanism are directly associated with its distinctive hunting behaviour among felids do not seem to have been rigorously investigated.

Bryant *et al.* (1996) demonstrated that various morphological features that have been associated with claw retraction vary considerably among the digits within the manus and pes in felids. These features include the lateral projection and orientation of the distal head and the asymmetry of the shaft of the middle phalanx, and the orientation of the articular surface on the distal phalanx. In felids the distal articular surface of the middle phalanges of the digits on the manus lacks the dorsoventrally oriented groove that is characteristic of other carnivorans. Although these features are associated with hyper-retraction of the claws, some of the interdigital variation is associated with the spreading of the claws during claw protraction. The sample of domestic cats ($n=10$) used in this study provides our assessment of variation within a single species (as documented by Bryant *et al.*, 1996: 294–295), and consistent patterns of phalangeal morphology of felid species (exclusive of *Acinonyx*) permits broad-scale comparisons for the cheetah. This study provides a comparative framework for investigating the phalangeal morphology of the cheetah, a taxon that was not included in our initial study.

In this study we investigate the phalangeal anatomy of the cheetah to determine whether differences in hunting behaviour are associated with differences in morphology. Building on our previous work on claw retraction in other felids (Bryant *et al.*, 1996), we compare the morphology of the middle phalanx of the cheetah with those of other felids and canids. The anatomy is interpreted within a phylogenetic and functional context, and the ontogenetic development of phalangeal morphology in the domestic cat is examined in order to determine whether ontogeny provides a possible explanation for the cheetah's morphology.

MATERIALS AND METHODS

Primary comparisons were made of skeletal morphology in adults of the wolf *Canis lupus*, lion *Panthera leo* and cheetah *A. jubatus*). Data for only digits 2–5 of the manus and pes are reported because digit 1 of the manus has a different articular configuration to the other digits and its claw is not retractile (Bryant *et al.*, 1996). The first digit of the pes is absent in felids.

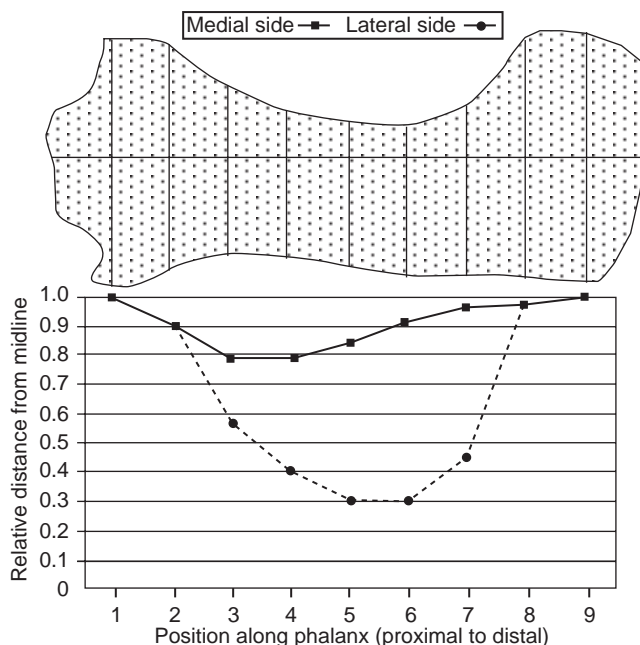


Fig. 1. Method used to document the degree of symmetry of the middle phalanx. This drawing represents the middle phalanx of the third manual digit of a lion *Panthero leo*, with the lateral margin at the top of the figure and the distal end to the right. The phalanx has been divided into 10 equal parts by the series of nine perpendiculars to its mid-line axis. The relative lengths of the lateral and medial portions of the perpendiculars are used to construct the graph (after Bryant *et al.*, 1996; see reference for details).

Secondary comparisons were made with the leopard *P. pardus*, tiger *P. tigris*, snow leopard *P. uncia* and lynx *Lynx canadensis*; only data for the third digit of the manus and pes are reported for these taxa. This digit acts as the exemplar for the morphology in these taxa, providing comparisons with the primary models. Skeletal specimens of *A. jubatus*, *L. canadensis*, *P. leo*, *P. pardus*, *P. tigris*, *P. uncia*, and *C. lupus* were obtained from the University of Calgary Museum of Zoology (UCZM).

Foetal domestic cat *Felis catus* material was obtained from the uteri of commercially purchased pregnant cats (Boreal Scientific, Mississauga, Ontario) after previous dissection in anatomy courses. A series of individuals encompassing crown–rump lengths of 52–185 mm was examined, the latter size representing near-term individuals.

The shape of the middle phalanges of the above-mentioned species was determined after the method described by Bryant *et al.* (1996; Fig. 1). The middle phalanx was divided into 10 equal parts by a series of 9 perpendiculars to its midline axis (Fig. 1). The relative lengths of the lateral and medial perpendiculars were used to construct graphic representations of asymmetry. Camera lucida drawings were made of the isolated elements of skeletal specimens; drawings of the foetal material were made from cleared and stained specimens (Wassersug, 1976).

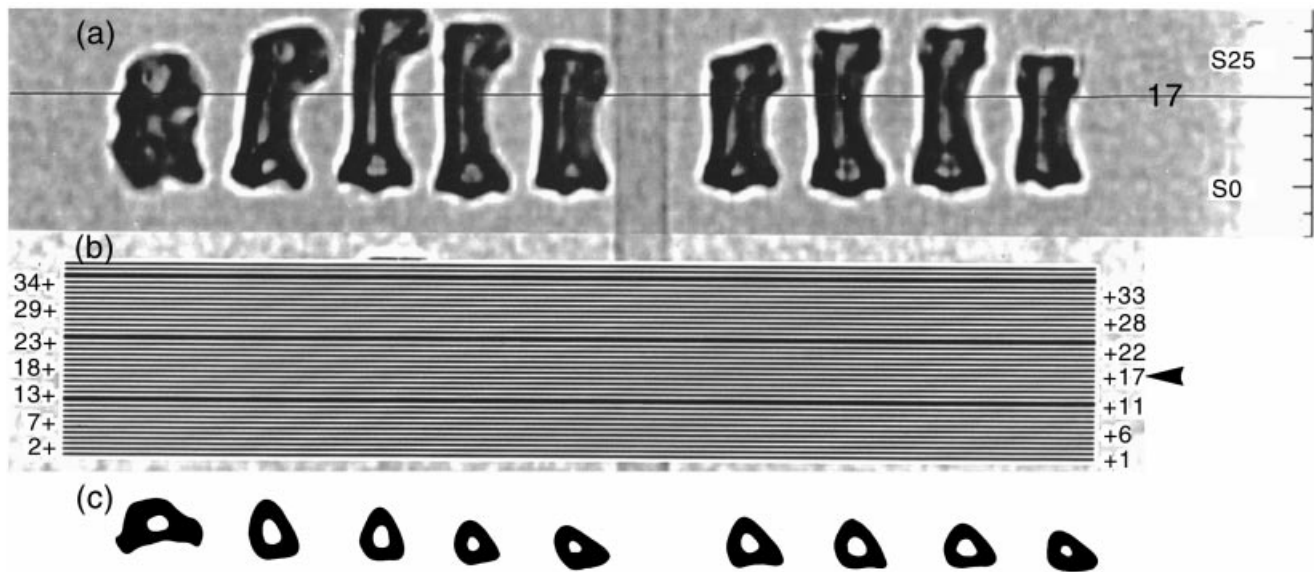


Fig. 2. Computed tomography cross-sections of the middle phalanges: (a) the layout image of the phalanges of the right manus (left of the vertical bar) and pes (right of the vertical bar) of the lion *Panthera leo* on the tomographic platform, with the horizontal line corresponding to sectioning line 17; (b) 1-mm sectioning grid used to obtain the tomographic imaging; sectioning line 17 highlighted with arrowhead; (c) representative tomographic section of the phalanges of the manus and pes of the lion as depicted in (a) and sectioned at line 17, the mid-shaft area for the longest phalanges, as indicated in (b).

Cross-sectional data of the middle phalanges of adults were obtained using computed tomography. Phalanges were aligned on the scanner bed (Fig. 2a) with their long axes parallel to one another. With the sectioning frequency set at 1 mm intervals (Fig. 2b), cross-sectional images were obtained (Fig. 2c). These images were aligned with the graphic representations of asymmetry to illustrate the cross-sectional morphology at each point of measurement (see Fig. 1). No tomographic cross-sectional images were obtained of the developing phalangeal shafts in the foetal domestic cats because of their extremely small size.

RESULTS

Comparisons of adult osteology

In the wolf the distal articular facets of the middle phalanx of both the manus and pes are distinctly grooved (Fig. 3a). In the lion, the distal articular facets of the manus lack grooves (Fig. 3b), while those of the pes have shallow grooves (Fig. 3c). The cheetah displays slight grooving on the distal articular facets of the middle phalanges of the manus (Fig. 3d) that is equivalent to the condition seen in the pes of the lion, and distinct grooving in the pes (Fig. 3e), to a degree equivalent to the situation found in the manus of the wolf. The pattern observed in the secondary comparative taxa (leopard, tiger, snow leopard and lynx) is essentially the same as that described above for the lion, and is consistent with that reported for the domestic cat (Bryant *et al.*, 1996).

In the wolf the distal articular facets of the middle phalanges are essentially normal to the long axis of the

phalanges (Fig. 3a). In the lion (and in the other cats examined, except for the cheetah) the distal articular facets of digit 2, and to a lesser extent digit 5, are angled with reference to the long axes of the phalanges, especially in the manus (Fig. 3b), a condition also evident in the domestic cat (Bryant *et al.*, 1996). In the cheetah there is no angulation of the distal articular facets in the inner and outer digits of the pes (Fig. 3e), and in the manus, angulation is only evident in the second digit (Fig. 3d).

The phalangeal shafts of the middle phalanges of the wolf display little or no asymmetry and the emargination of the medial and lateral borders is essentially equal (Figs 3a & 4). In the lion the shafts exhibit marked asymmetry (Figs 3b, c & 5), with the lateral border being much more extensively emarginated than the medial border. This pattern is also evident in the domestic cat (Bryant *et al.*, 1996) and in the secondary comparative taxa in this study (leopard, tiger, snow leopard, lynx; Fig. 6). In the cheetah (Figs 3d, e & 7) an intermediate condition occurs, with the lateral border of the shaft being more extensively emarginated than the medial border, so that the degree of lateral emargination is more extensive than that in the wolf, but less than that displayed by the lion. The degree of asymmetry of the lateral and medial emarginations is less than that displayed by the lion, but considerably greater than that evident in the wolf (Figs 3, 4, 5 & 7).

At mid-shaft, the middle phalanges of the wolf are essentially circular in cross-section (Fig. 4); this position represents the narrowest portion of the shaft. The circularity of the cross-sections at this point, and their essentially symmetrical (although not circular) cross-sections at points proximal and distal to mid-shaft

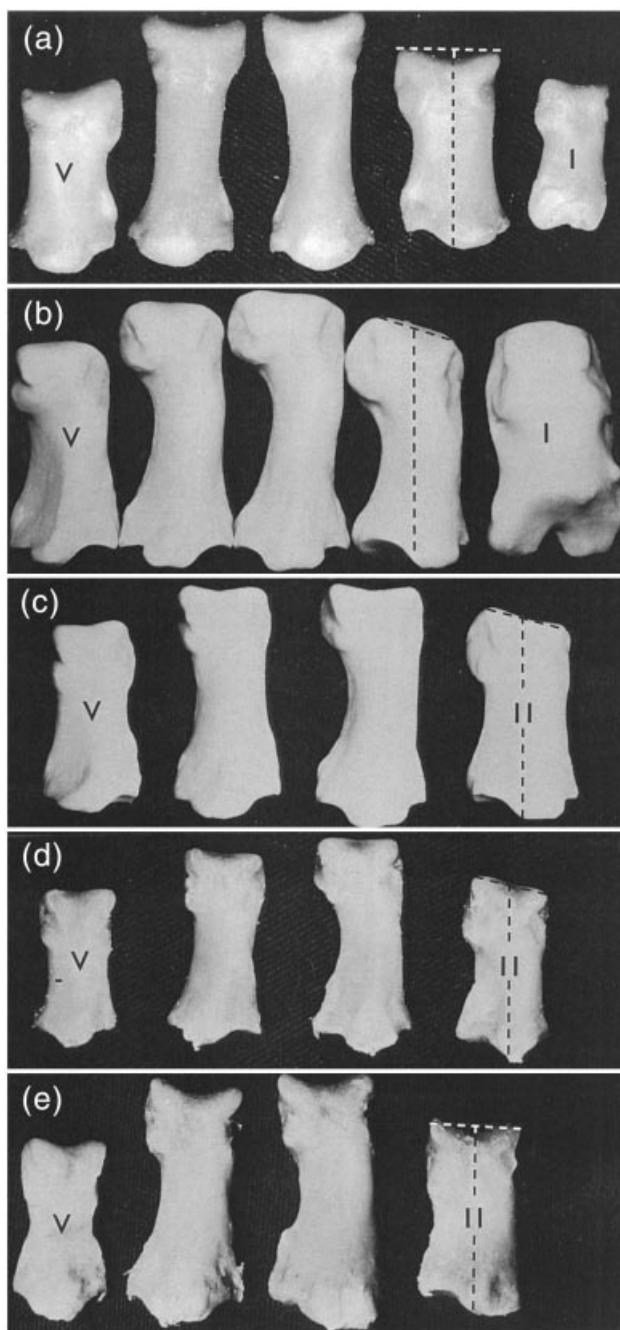


Fig. 3. Dorsal views of the proximal (first digit) and middle (digits 2–5) phalanges of: (a) right manus of the wolf *Canis lupus*; (b) left manus of the lion *Panthera leo*; (c) left pes of the lion; (d) left manus of the cheetah *Acinonyx jubatus*; (e) left pes of the cheetah. Dashed lines trace the long axis of the second phalanx and the inclination of the distal articular facet of this phalanx. Wolf phalanges (a) have been printed in reverse format to accord with the felid phalanges (b–e) that are from the opposite side of the body. Lateral, left of the figure.

reflect the overall symmetrical shape of the middle phalanges in this taxon. In contrast, the lion exhibits a distinctly triangular outline to the cross-section of the shaft at its mid-point (Fig. 5), with the apex being directed dorsomedially. This shape is reflective of the

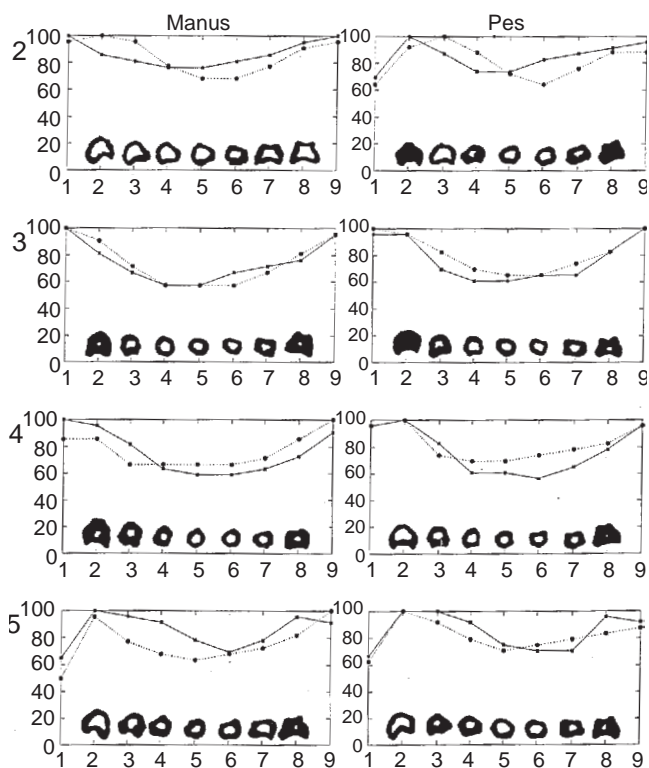


Fig. 4. Graphical (upper) and tomography-derived (lower) cross-sectional representations of the morphology of the middle phalanx of digits 2–5 of the manus and pes of the wolf *Canis lupus*. Plot of the medial margin of each phalanx is represented by a solid line and squares that demarcate the measurement points as outlined in Fig. 1. Dotted line with circles, plot for the lateral margin; vertical axis, percentage of greatest distance between the margin and the midline; horizontal axis, position along the long axis of the phalanx (from proximal to distal) as depicted in Fig. 1. The tomography-derived cross-sections are aligned with the proximal to distal positional demarcation points. Mid-shaft is represented by demarcation point 5. Numbers 2, 3, 4 and 5 to the left of the manual panels refer to digit number.

more pronounced lateral emargination at mid-shaft, and becomes even more pronounced in the more distal cross-sections (Fig. 5). The more proximal cross-sections are less asymmetrical and lack the pronounced lateral shelf (Fig. 5). The morphology in the lion is repeated in the leopard, tiger and snow leopard (Fig. 6; no tomographic cross-sections of the lynx were obtained). The chamfered shelf evident on the lateral side of the distal and mid-shaft cross-sections of the middle phalanges of these felids receives the hyper-retracted ungual phalanges. In the cheetah, the cross-sectional shape of the middle phalanges at mid-shaft (Fig. 7) is essentially intermediate between that of the wolf and the morphology displayed by the other felids described herein. The triangularity of the mid-shaft sections is less marked and is evident only on digits 2 and 3 of the manus, and 3 and 4 of the pes (Fig. 7). The remaining digits display a more circular or rectangular cross-sectional shape at this point. The chamfering associated

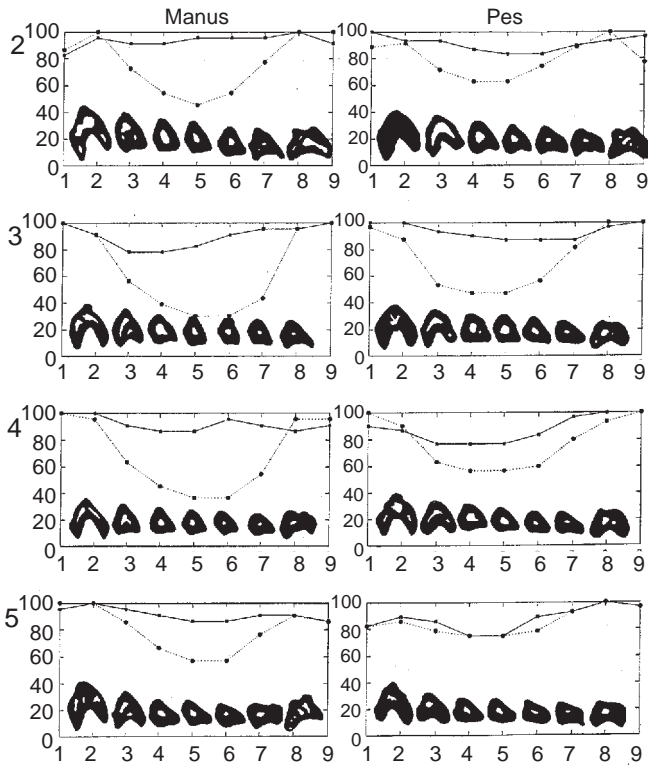


Fig. 5. Morphology of digits 2–5 of the middle phalanx of the manus and pes of the lion *Panthera leo*. All details as in Fig. 4.

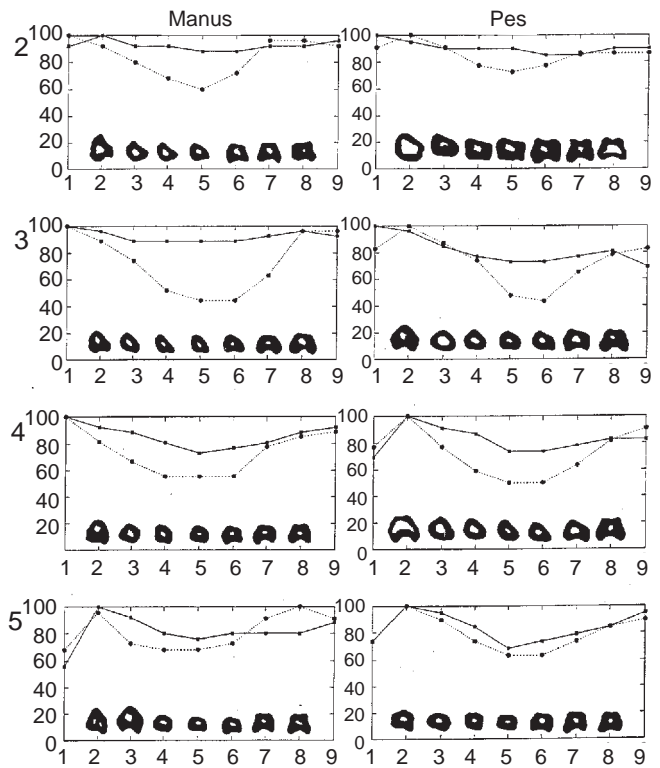


Fig. 7. Morphology of digits 2–5 of the middle phalanx of the manus and pes of the cheetah *Acinonyx jubatus*. All details as in Fig. 4.

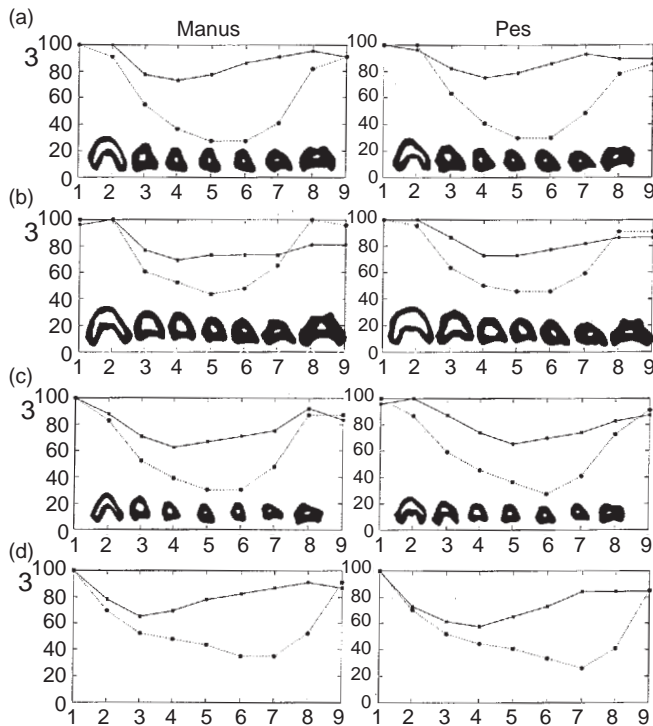


Fig. 6. Morphology of digit 3 of the middle phalanx of the manus and pes of: (a) leopard *Panthera pardus*; (b) tiger *P. tigris*; (c) snow leopard *P. uncia*; (d) lynx *Lynx canadensis* as exemplars of the form of this phalanx in other felids. Conventions as for Fig. 4. Note that no tomography-derived cross-sections were obtained for the lynx.

with emargination of the lateral margin of the middle phalanges is much less evident in the cheetah and the phalanges are more gracile than those of the other felids examined (Figs 5 & 6).

Development of phalangeal asymmetry in the domestic cat

The morphology of the middle phalanges of the manus and pes of foetal domestic cats was examined in an attempt to understand the pattern of development of the asymmetry evident in adult felids (Figs 3b, c, 5 & 6). As the middle phalanges develop, there is a transient appearance of grooving to the distal articular facet in both the manus and pes that is most evident in the 55, 83 and 95 mm embryos (Figs 8 & 9). The grooving begins to disappear in later developmental stages and this disappearance is concomitant with the elongation of the shaft and the beginnings of its lateral and medial emargination. The emargination itself increases with growth (Figs 8, 9: 155, 163 and 185 mm embryos). Initially the emargination is more or less equally developed on the medial and lateral borders, but in the latest stages of intrauterine development the lateral border seems to become more extensively emarginated (Figs 8 & 9: 185 mm embryo). The marked asymmetry seen in adult domestic cats (similar to that shown by the lion; see Fig. 5) develops post-natally. Angulation of the distal articular facet is not evident in this series of embryos and may represent a post-natal transformation.

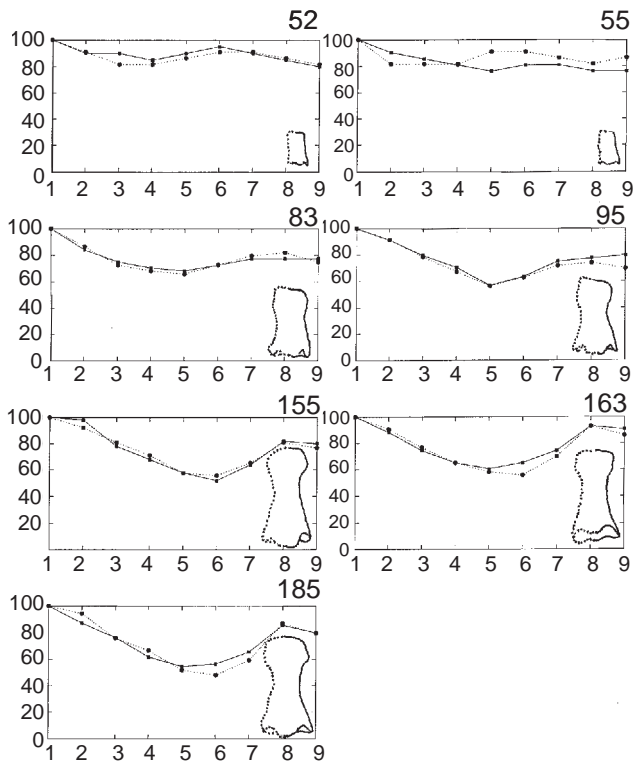


Fig. 8. Development of asymmetry and emargination of the middle phalanx of digit 3 of the manus of the foetal domestic cat *Felis catus*. Conventions as in Fig. 4. Insets: dorsal views of this phalanx at each of the developmental stages examined (crown-rump lengths for each specimen at upper right of each panel); dotted line, lateral border; solid line, medial border. The morphology of this phalanx in the adult domestic cat is essentially the same as that depicted for the lion (Fig. 5, manus, 3).

DISCUSSION

Phylogenetic context

Although the cheetah has often been separated taxonomically from other extant felids on the basis of its unique features, and various phylogenetic schemes have suggested that the cheetah was an early offshoot of the modern felid radiation (e.g. Thenius, 1967; Hemmer, 1978; Martin, 1980), most recent phylogenetic analyses suggest that the cheetah is deeply embedded within the extant felid radiation. The outgroup position of the cheetah in the composite felid tree generated using matrix representation using parsimony by Bininda-Emonds *et al.* (1999) is probably a result of the disproportionate influence of the mostly earlier studies that focused on the cheetah's phenetic distinctiveness, outweighing the more recent phylogenetic studies discussed below.

Based on immunological distance, Collier & O'Brien (1985) identified three major radiations within the Felidae, the ocelot, domestic cat and pantherine lineages. The pantherine lineage, which included *Panthera*, *Puma*, *Lynx* and *Acinonyx*, was considered

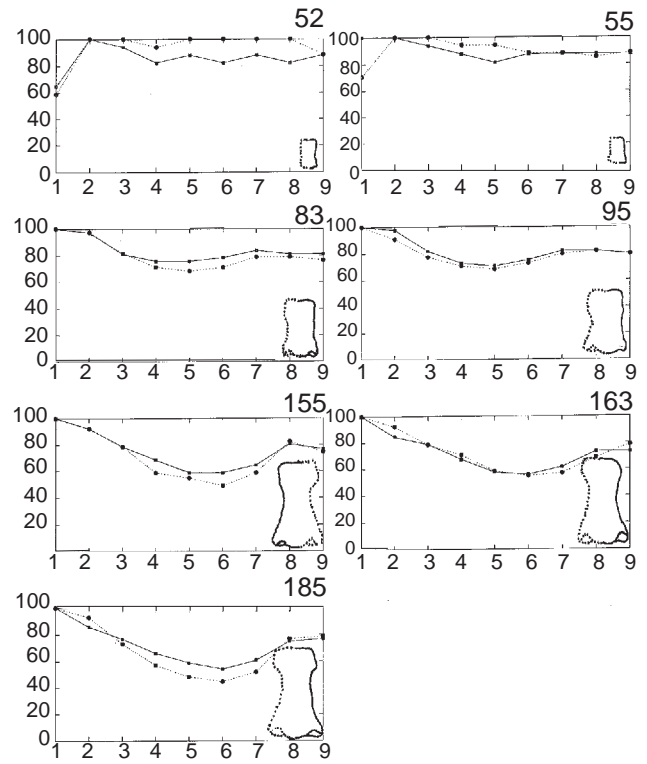


Fig. 9. Development of asymmetry and emargination of the middle phalanx of digit 3 of the pes in the foetal domestic cat *Felis catus*. All details as for Fig. 8. The morphology of this phalanx in the adult domestic cat is essentially the same as that depicted for the lion (Fig. 5, pes, 3). Note that for all stages except 155 mm, the phalanx depicted is from the left pes, hence the reversal of dotted and solid lines for the 155 mm example.

the last of the three major lineages to radiate. Based on a cladistic analysis of morphological data, Salles (1992) also placed the cheetah closest to *Panthera* and *Puma*; this clade also included *Herpailurus* and was part of a large polytomy within Felidae that included, among others, the small cats, *Lynx* and the ocelot (Fig. 10a). The analyses of Janczewski *et al.* (1995) using mitochondrial 12S RNA and cytochrome *b* sequence data also found strong support for a sister group relationship between the cheetah and the puma and placed this clade within the felid radiation closest to the lynxes and golden cats (Fig. 10b). A close relationship between *Acinonyx* and *Puma*, and also *Herpailurus* in some analyses, has been confirmed by most subsequent molecular studies (Masuda *et al.*, 1996; Johnson & O'Brien, 1997). One exception is a maximum parsimony analysis of cytochrome *b* data that placed the cheetah in an outgroup position (Masuda *et al.*, 1996); in contrast, a neighbour joining analysis of the same data supported the closest relationship to *Puma* and *Herpailurus*. Despite the differences in detail among these recent studies, most conclude that the cheetah is not in an outgroup position relative to the rest of the extant Felidae. This phylogenetic framework (Fig. 10) provides the context for our evolutionary and develop-

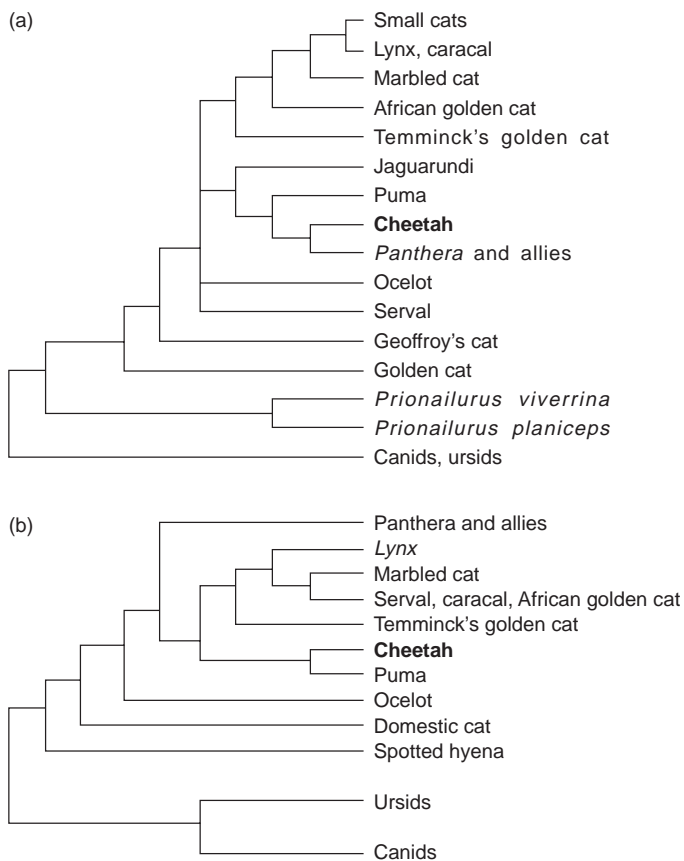


Fig. 10. Recent hypotheses of phylogenetic relationships within the Felidae: (a) cladistic analysis based upon skull morphology (simplified from Salles, 1992: fig. 52); (b) maximum parsimony analysis based upon combined mitochondrial 12S RNA and cytochrome *b* DNA sequences (simplified from Janczewski *et al.*, 1995: fig. 5).

mental interpretations of the cheetah's distinctive morphology.

The cheetah's anatomy

This study has shown that the middle phalanges of the cheetah differ from those of other felids in: (1) the more marked grooving of the distal articular facets in the manus and pes; (2) the reduced to absent angulation to the distal articular facets of the inner and outer digits; (3) the less marked asymmetry; (4) the tendency for the cross-section at mid-shaft to be less triangular and more circular. Given the phylogenetic context in Fig. 10, these features are interpreted as autapomorphies for the cheetah, at least among extant felids. This interpretation is consistent with the analysis of Van Valkenburgh, Grady & Kurten (1990) of the morphology of the phalanges in *Miracinonyx inexpectatus* and *M. trumani*, Pliocene and Pleistocene fossils that seem to be most closely related to *Acinonyx*. These authors argued that in *Miracinonyx* the degree of claw retractility was comparable to that of typical extant felids, rather than the more limited retractility of *Acinonyx jubatus*.

Our investigation of the ontogenetic development of the middle phalanx in the domestic cat indicates that early in ontogeny the morphology of this element more closely resembles that of other carnivorans and that the features characteristic of felids appear at later developmental stages. Early in ontogeny there is the transient appearance of grooving of the distal articular facet and the initial emargination of the shaft is symmetrical. Later in intrauterine development the distal grooving disappears and the asymmetry of the shaft begins to appear as emargination becomes more extensive on the lateral margin. Thus, features of the middle phalanx in adult cheetahs, such as the distal grooving and the less extensive emargination, more closely resemble the morphology at early developmental stages, rather than that of the adults, of other felids. Given that the cheetah's adult features are interpreted as autapomorphies within Felidae, the ontogeny of these features in the domestic cat suggests that heterochrony provides a plausible mechanism to explain the cheetah's distinct morphology. We hypothesize that through the truncation at a sub-terminal stage of the ontogenetic sequence characteristic of other felids, the morphology of the middle phalanges of adult cheetahs is intermediate between that of most felids and that of other carnivorans. One obvious assumption that we make here is that the cheetah goes through a similar ontogenetic sequence to that seen in the domestic cat. Further data are required to test this, but it is noteworthy that certain fossil cheetahs display a morphology of the middle phalanges that is more akin to that of other extant felids than it is to that of *Acinonyx* (Van Valkenburgh *et al.*, 1990).

The claws and retractile mechanism of the cheetah differ from those of other felids in features in addition to those investigated in this study. Compared to those of other felids, the claws on digits 2–5 are straighter, thicker and more elongated, resembling those of canids (Gonyea & Ashworth, 1975). Gonyea & Ashworth (1975) reported that, although the cheetah has the large lateral dorsal elastic ligament between the middle and distal phalanges that is typical of felids, this species also has the pair of proximal dorsal elastic ligaments that characterize most non-felid carnivorans. The authors suggested that the former retracts the claw, whereas the latter provide additional support for the distal phalanx during terrestrial locomotion. The phylogenetic context in Fig. 10 suggests that, although the occurrence of a pair of dorsal elastic interphalangeal ligaments is probably plesiomorphic for the Carnivora, its occurrence in the cheetah is probably an autapomorphy relative to the absence of these ligaments in other extant felids.

Pocock (1916) noted that the digital pads of the cheetah are tilted slightly upward anteriorly, and are harder, more pointed and more strongly ridged than those of other felids; this morphology probably improves traction during running (Neff, 1982). Neff (1982) also suggested that the blunting typical of the claws on digits 2–5 in the cheetah is associated with their use in gaining additional traction, a function for which there is no evidence in other felids and for which their phalan-

geal morphology and claws are not suited. Indeed, when the claws are protracted the manus and pes of felids with hyper-retractile claws are precluded from weight-bearing.

Some features associated with the long bones of the cheetah also differ from those of other felids and approach the morphology in canids, including the orientation of the olecranon fossa with respect to the long axis of the humerus and the orientation of the radial notch on the ulna (Gonyea, 1978). Both of these features are associated with the fact that in the cheetah the forelimb travels in a more nearly parasagittal plane, as in canids, whereas in most felids the forelimb arches away from the parasagittal plane. The latter is associated with the greater degree of mobility in the elbow and wrist in felids that is required for the manipulative capabilities of the forelimb. Stein & Casinos (1997: 188) proposed that 'cursorial mammals are those terrestrial quadrupeds that possess vertically-oriented limbs which move in a parasagittal plane, regardless of the gait being employed.' By this criterion the cheetah is certainly the most cursorial felid, at least for the forelimb.

Associations between the cheetah's anatomy and its hunting behaviour

The differences in the morphology of the middle phalanges, claws, interphalangeal ligaments and long bones between the cheetah and the other felids in this study can be associated with differences in the hunting behaviour of the cheetah and that of other felids. In general, the morphology in the cheetah tends to be intermediate between that of most felids and that of canids such as the wolf. Given the phylogenetic position of the cheetah (Fig. 10), features of the cheetah that are unique within Felidae are autapomorphies within this clade and the similarities between the cheetah and the wolf are the result of convergence. This convergence between the cheetah and canids may be associated with the functional requirements of hunting behaviours that rely more on pursuit, and less on stalking and ambush as is more typical of most felids.

Prey capture by the cheetah usually involves a high-speed chase in open terrain, often preceded by little or no stalking (Neff, 1982). The cheetah does not crouch like other felids, but will often approach prey slowly initially to reduce the distance to the prey at the start of the chase (Eaton, 1970). In other instances the cheetah will approach and move through a herd without attempting to hide itself (Kruuk & Turner, 1967). At the beginning of the chase the cheetah is usually further from its prey than is typical of felids and it relies on its acceleration and speed to overtake prey within 200–300 m (Neff, 1982). The cheetah brings down prey by causing it to lose its balance, usually by hooking one of its sharp dew claws into the animal's hide and shifting its own weight posteriorly; death is usually by strangulation, using a bite to the ventral region of the neck (Eaton, 1974; Neff, 1982).

As many authors (e.g. Pocock, 1916; Eaton, 1974; Gonyea & Ashworth, 1975; Neff, 1982) have noted, a number of the cheetah's morphological features that are unique among felids can be associated with its distinctive hunting behaviour. Of these features, the presence of the proximal dorsal interphalangeal elastic ligaments, the ridged digital pads, and the dog-like claws are probably associated with the need for greater support and traction during running. The enhanced grooving of the distal articular surface of the middle phalanges and the reduced angulation of the distal articular facets on the middle phalanges of the inner and outer digits, identified in this study, can probably be added to this list. The reduced asymmetry and more circular shape of the shaft of the middle phalanges that reduce the degree of hyper-retractility of the claws may be associated with the absence of selective pressure for the protection of the claws from blunting because they are protracted to gain traction during running.

The cheetah's increased cursorial ability was acquired at the expense of the manipulative capabilities of the forelimb. Grasping and manipulation of the prey using the forelimbs play important roles in prey capture in most felids (Gonyea & Ashworth, 1975). This role for the forelimbs is especially important in the larger felids because they typically take prey with a body size that is equal to, or greater than, their own. The spreading of the digits on the manus, with their sharp, strongly hooked claws, during protraction (Bryant *et al.*, 1996), is an important part of this functional complex. The importance of claw-equipped forelimbs in the manipulation of prey may have limited adaptations associated with speed (Gonyea 1976). This morphological and functional complex is probably plesiomorphic for extant felids and provides the frame of reference for interpreting the evolution of the cheetah's autapomorphic morphology and the role of the forepaws in the animal's hunting behaviour.

The more dog-like morphology of both the middle phalanges of digits 2–5 of the manus and the shape of the keratinous claw sheath, together with less spreading of the digits during protraction resulting from the reduced angulation of the distal surfaces of the middle phalanges, has diminished the manipulative capabilities of the manus. Whereas other felids use the spread, protracted claws of all five digits on the manus to grab the prey, the dog-like claws on digits 2–5 on the manus of the cheetah are not well designed for this function. Only the dew claw (digit 1), which is not in contact with the ground during running, retains the short, hooked, laterally compressed claw sheath that is typical of other felids. This morphology is essential for the role of the dew claw in bringing down fleeing prey.

Gonyea (1976) noted that among the large felids, the cheetah is the only species that regularly kills prey with a body weight that is less than its own. This tendency to take smaller prey has been associated with the relatively small head and canines of the cheetah and the fact that the animal is often near exhaustion at the end of a chase, limiting the size of prey that can be subdued

(Turner & Anton, 1997). However, the modifications to the anatomy of the phalanges and the retractile claw mechanism that provide better traction and stability during the high-speed chase reduced the manipulative abilities of the forelimb. The inability of the cheetah to manipulate prey with its forelimbs may be an additional factor that limits the relative size of its prey. This loss of manipulative capabilities is also reflected in the fact that, unlike other large felids, the forepaws do not seem to be involved in the feeding behaviour of the cheetah (Van Valkenburgh, 1996; Iwaniuk, Pellis & Whishaw, 1999).

Much of the literature has been devoted to the consideration of the forelimbs and their claws, probably because of their dual roles in locomotion and prey manipulation. The hindlimbs and their claws are not confronted with this duality of function and are responsible for the greater proportion of thrust production in locomotion. Comparison of the grooving and angulation of the distal articular facets and the asymmetry of the shaft of the middle phalanges of the manus and pes indicates that hyper-retractility of the claws is better developed in the forelimb of all felids (Fig. 3b–e). In the absence of this functional compromise, hyper-retraction is less well developed in the pes. The fact that this difference also occurs in the cheetah, despite the diminished role of the forelimbs in prey capture and feeding, may reflect its ancestry or the retention of some manipulative capabilities in the forelimb.

CLOSING REMARKS

This comparative study of the morphology of the middle phalanges of the cheetah, other felids, and the wolf has confirmed that osteological correlates can sometimes be found for the behaviour of carnivorans, especially when the variation in morphology and behaviour is viewed within a phylogenetic context. Given the phylogenetic position of the cheetah, it is evident that similarities in its morphology to that of the wolf reflect convergence associated with similarities in their hunting behaviours. The presence of these osteological correlates provides some optimism that the study of the phalanges of fossil carnivorans may yield useful information regarding the lifestyle of these taxa. However, much detailed investigation of the range of manual and pedal morphology throughout the extant Carnivora is a necessary prerequisite to making these inferences in fossils. Only through further studies on extant taxa will it become evident as to whether the broad range of function and behaviour associated with the manus and pes within Carnivora is consistently reflected in distinct osteological morphologies.

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