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Original Article

A method for distinguishing dromaeosaurid manual unguals from pedal "sickle claws"

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Abstract：The manual unguals and pedal "sickle claws" of dromaeosaurid dinosaurs are easily confused. To find a method for distinguishing them, I compared the manual and pedal unguals of the dromaeosaurids *Microraptor zhaoianus, Bambiraptor feinbergi, Velociraptor mongoliensis* and *Deinonychus antirrhopus*. I found that the dorsal edge of a dromaeosaurid manual ungual arches higher than the articular facet when the latter is held vertically, whereas the same does not occur in a pedal "sickle claw". Also, the flexor tubercle of a dromaeosaurid manual ungual is much more pendant than that of a pedal "sickle claw". Application of these findings shows that disarticulated unguals of *Utahraptor* and *Pyroraptor* pertain to the foot, as does an ungual referred to *Dromaeosaurus*, whereas disarticulated unguals of *Achillobator* and *Unenlagia* pertain to the hand. This method is applicable only to Dromaeosauridae, because the unguals of other theropod taxa exhibit different morphologies.

Key Words：Theropoda, Dromaeosauridae, *Utahraptor, Achillobator, Unenlagia*

Introduction

In most theropod dinosaurs, it is easy to tell manual unguals from pedal unguals, because the former are strongly recurved, whereas the latter are not (Weishampel et al., 1990). However, members of the theropod family Dromaeosauridae exhibit a specialized ungual, often called the "sickle claw", on the second toe (Norell and Makovicky, 2005). The dromaeosaurid sickle claw is enlarged and strongly curved and resembles a dromaeosaurid manual ungual. The similarity is close enough to obscure the identity of an isolated or disarticulated dromaeosaurid ungual that exhibits strong curvature. For example, strongly curved unguals of *Utahraptor* and *Achillobator* have been thought to be manual unguals by some authors (Kirkland et al., 1993; Senter et al., 2004) and pedal unguals by others (Perle et al., 1999; Britt et al., 2001), and the describers of a strongly curved ungual of *Unenlagia* declined to take a stand as to its limb of origin (Calvo et al., 2004).

Ostrom (1969) used magnitude of ungual curvature to distinguish manual unguals from pedal sickle claws in *Deinonychus*, noting that curvature is greater in the latter. However, that method cannot be applied to most dromaeosaurid pedal unguals, because most are much less recurved than those of *Deinonychus* (Fig. 1). Kirkland et al. (1993) used the presence of a proximal ligament pit to infer whether or not an ungual came from the hand of *Utahraptor,* but Brinkman et al. (1998) showed that that method did not work with *Deinonychus*.

The ability to identify the limb from which an ungual came can be useful for a number of different types of studies. A researcher scoring character states for a phylogenetic data matrix that includes characters relating to unguals needs to know from which limb an ungual came. A researcher studying limb function needs to know whether a given ungual is from the limb under study. A researcher comparing two or more specimens to determine whether they are conspecific needs to know the limb of origin for each ungual that is used in the comparison, so as to avoid comparing the pedal unguals of one specimen with the manual unguals of another.

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Here, I describe a simple method for determining whether a strongly curved dromaeosaurid ungual belongs to the hand or the second toe, without reference to the magnitude of curvature or ligament pits, and apply the method to identification of disarticulated and isolated dromaeosaurid unguals. No functional or phylogenetic implications are discussed, because the purpose of this paper is simply to provide a method for identifying the limb of origin of dromaeosaurid unguals.

Abbreviations

AMNH, American Museum of Natural History, New York City, New York, USA. CAGS, Chinese Academy of Geological Sciences, Beijing, China. IGM, Mongolian Institute of Geology, Ulaan Baator, Mongolia. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China. MNHN, Muséum National d'Histoire Naturelle, Paris, France. MNUFR, Mongolian National University, Ulaan Baator, Mongolia. MUCP, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina. NMC, Canadian Museum of Nature, Ottawa, Ontario, Canada. YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Materials and Methods

The dromaeosaurids ***Deinonychus antirrhopus, Velociraptor mongoliensis, Bambiraptor feinbergi***, and ***Microraptor zhaoianus*** (which is here considered to include "***M. gui***", for reasons given in Senter et al., 2004) are all taxa for which both manual and pedal unguals are known. Here, ***Microraptor*** is considered a dromaeosaurid; in one published phylogeny it falls outside Dromaeosauridae sensu stricto (Senter et al., 2004), but in most others it falls within the family (Xu et al., 2000; Hwang et al., 2002; Xu and Wang, 2004; Makovicky et al., 2005; Novas and Pol, 2005). I compared the shapes of manual unguals and pedal sickle claws of these four taxa, using outlines that were traced from my own photographs of casts in some cases and from illustrations in the literature in others (sources listed in caption of Fig. 1), to test the following two hypotheses: (1) The shape of a dromaeosaurid manual ungual is distinguishable from that of a dromaeosaurid pedal sickle claw. (2) The shape of a dromaeosaurid manual ungual is not distinguishable from a dromaeosaurid pedal sickle claw. The first hypothesis predicts that consistent shape differences between dromaeosaurid manual and sickle claws will be found across all examined taxa, whereas the second hypothesis predicts that they will not.

I compared unguals in a standardized orientation: with the articular facet vertical, as determined by a vertical line connecting the dorsal and palmar extremities of the facet (Fig. 1). I also used a pair of lines perpendicular to the vertical line—one at the level of the dorsal extremity of the articular facet, the other at its palmar/plantar extremity—as a standard of reference for how far above or below the articular facet the parts of the ungual extended. Using those standards of reference, I noted differences between manual and pedal unguals and used the differences to determine the limb of origin for disarticulated unguals attributed to the dromaeosaurids ***Utahraptor*** (Kirkland et al., 1993), ***Achillobator*** (Perle et al., 1999), ***Unenlagia*** (Calvo et al., 2004), ***Pyroraptor*** (Allain and Taquet, 2000), and ***Dromaeosaurus*** (Colbert and Russell, 1969). The generic identity of the ungual referred to ***Dromaeosaurus*** is dubious, because neither the holotype nor other referred specimens exhibit unguals with which to compare it (Colbert and Russell, 1969; Sues, 1977; Currie et al., 1990). Nevertheless, the method described here allows determination of the limb from which each ungual came, if not the genus.

Results and Conclusions

Dromaeosaurid manual unguals consistently exhibit certain traits that distinguish them from pedal sickle claws in all examined taxa. This supports the hypothesis that the shape of a dromaeosaurid manual ungual is distinguishable from that of a dromaeosaurid pedal sickle claw.

One consistent difference between dromaeosaurid manual unguals and pedal sickle claws is that in the manual unguals, the dorsal margin arches high above the articular facet when the articular facet is oriented vertically (Fig. 1). The dorsal margin of the pedal sickle claw exhibits no such arch (Fig. 1). The dorsal margin of the pedal sickle claw of ***Deinonychus*** extends a little above the articular facet (Fig. 1K), but only barely so and only proximally; in contrast, the excursion of the dorsal edge of each examined manual ungual above the articular facet extends much further distally (for example, in Fig. 1A length AC is greater than length AB). A second consistent difference is that the flexor tubercles of dromaeosaurid manual unguals extend far palmar to the articular facet, whereas the flexor tubercles of the sickle claws do not (Fig. 1). A third difference is that dromaeosaurid manual unguals often exhibit a proximodorsal lip, whereas the

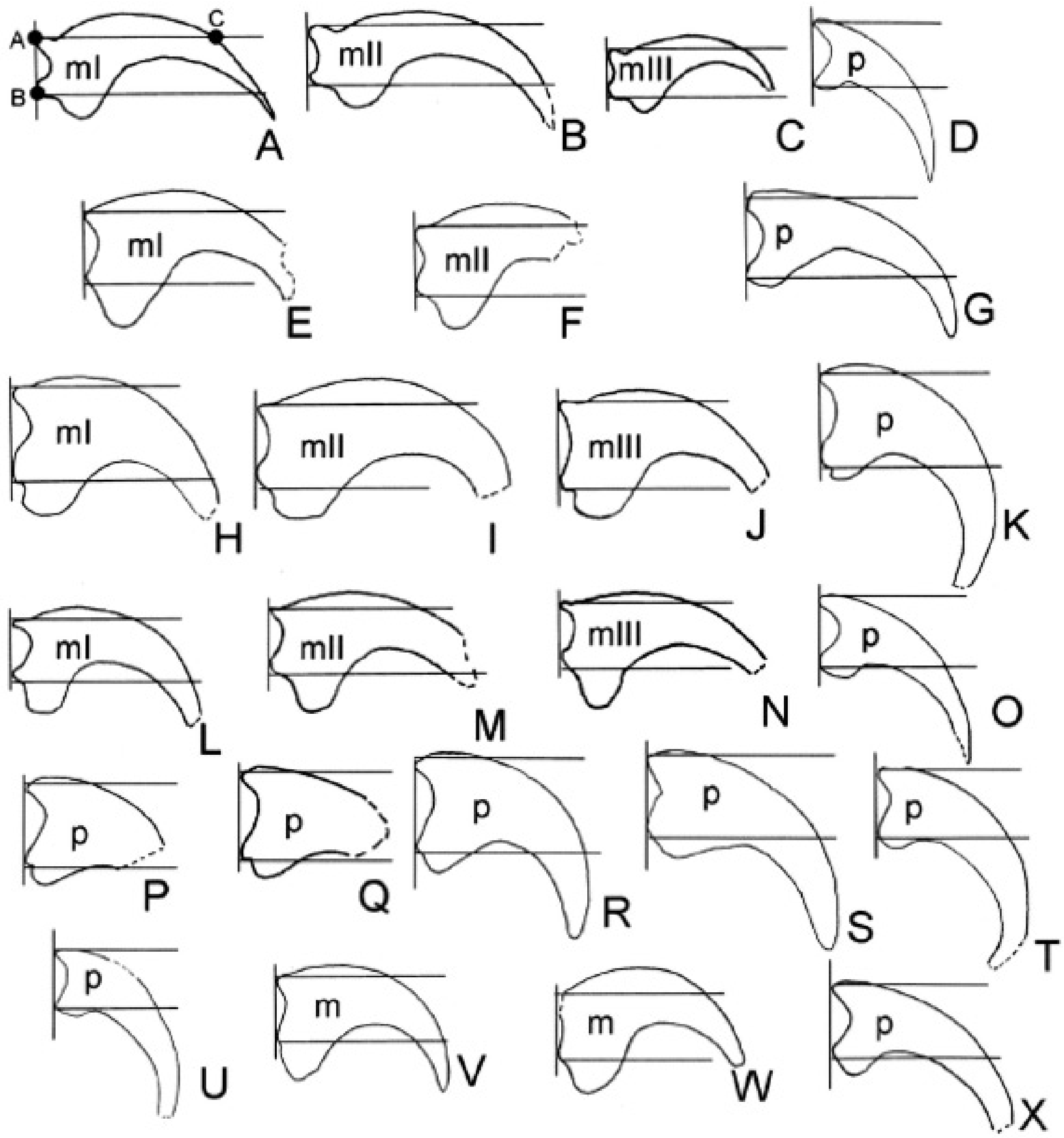

Figure 1 Outlines of dromaeosaurid unguals (not to scale). A − C. Manual unguals I (A), II (B) and III (C) of IVPP V 13352 (***Microraptor***). D. Pedal ungual II of CAGS 20-8-001 (***Microraptor***). E − G. Manual unguals I (E) and II (F) and pedal ungual II (G) of AMNH FR 30556 (***Bambiraptor***). H − I. Manual unguals I (H) and II (I) of YPM 5206 (***Deinonychus***). J. Manual ungual III of YPM 5209 (***Deinonychus***). K. Pedal ungual II of YPM 5205 (***Deinonychus***). L − N. Manual unguals I (L), II, (M), and III (N) of IGM 100/982 (***Velociraptor***). O. Pedal ungual II of NMC 34828 (***Velociraptor***). P. Isolated ungual, BYU 13068 (***Utahraptor***). Q. Isolated ungual, BYU 9438 (***Utahraptor***). R. Isolated ungual, CEU 184v294 (***Utahraptor***). S. Isolated ungual, CEU 184v86 (***Utahraptor***). T. Isolated ungual, MNHN BO001 (***Pyroraptor***). U. Isolated ungual, MNHN BO004 (***Pyroraptor***). V. Disarticulated ungual of MNU FR 15 (***Achillobator***). W. Disarticulated ungual of MUCP v-43 (***Unenlagia***). X. Isolated ungual, NMC 12240 (referred to ***Dromaeosaurus***). A − C after Xu et al. 2003, fig. 2. D after Hwang et al., 2002, fig. 30. L − N after Norell and Makovicky, 1999, fig. 8. P and Q after Kirkland et al., 1993, fig. 12. R after Kirkland et al., 1993, fig. 11. S after Kirkland et al., 1993., fig. 9. T and U after Allain and Taquet, 2000, fig. 1. V after Perle et al., 1999, fig. 16. W after Calvo et al., 2004, fig. 38. X after Colbert and Russell, 1969, fig. 15. E − K and O drawn from photos of casts. m = manual ungual, mI − III = manual unguals I − III, p = pedal ungual II.

pedal sickle claw does not. This difference should be treated with caution, however, because it is not consistent across Dromaeosauridae (for example, it is absent in ungual I of *Bambiraptor*). In this inconsistency Dromaeosauridae resembles Oviraptorosauria and Therizinosauoidea, in both of which lipped manual unguals and unlipped manual unguals are known (Makovicky and Sues, 1998; Clark et al., 1999; Zhou et al., 2000; Xu et al., 2002; Zanno, 2006).

The dorsal surfaces of the unguals of *Utahraptor* and *Pyroraptor* and the ungual referred to *Dromaeosaurus* do not arch above the articular facet when it is oriented vertically (Fig. 1). In all these unguals, the flexor tubercle does not extend much further palmarly than the articular facet. These unguals are therefore pedal sickle claws. As previously claimed (Britt et al., 2001), this is true even for the *Utahraptor* unguals that were originally attributed to the hand (Kirkland et al., 1993). In *Utahraptor,* the depth of the flexor tubercle of the sickle claw differs from specimen to specimen (Fig. 1P — S), but even in specimens with relatively deeper flexor tubercles (Fig. 1 R, S) the tubercle is not as deep relative to the articular facet as it is in a dromaeosaurid manual ungual.

The dorsal surfaces of the unguals of *Achillobator* and *Unenlagia* arch high above the articular facets (Fig. 1V, W). Their flexor tubercles extend far palmar to the articular facets. These unguals are therefore manual unguals. The lack of a proximodorsal lip on the *Achillobator* ungual does not preclude its assignment to the hand, because the first ungual of *Bambiraptor* also lacks the lip. Proximodorsal breakage of the *Unenlagia* ungual precludes determination of whether a lip was present.

Discussion

The differences between manual unguals and pedal sickle claws in the taxa examined here are consistent with manual and pedal ungual morphology in dromaeosaurids for which only manual unguals or only pedal unguals are known (Sues, 1978; Novas and Pol, 2005). They are also consistent with the pedal sickle claw morphology of *Rahonavis* (Forster et al., 1998), which was thought to be a basal bird (Forster et al., 1998; Chiappe, 2002) but may instead be a basal dromaeosaurid (Makovicky et al., 2005).

The criteria found here for determining the limb of origin of an ungual apply only to Dromaeosauridae. The strong arching of the dorsal surface of a manual ungual, as found in Dromaeosauridae, is rare in other theropods. It is found in some therizinosauroids (Xu et al., 2002) and basal birds (Wellnhofer, 1974), but is absent in most other theropods, including coelophysoids (Welles, 1984; Colbert, 1989), carnosaurs (Madsen, 1976; Currie and Zhao, 1993), tyrannosaurids (Lambe, 1917), ornithomimosaurs (Osmólska et al., 1972; Nicholls and Russell, 1985), and oviraptorids (Barsbold et al., 1990; Clark et al., 1999). As in Dromaeosauridae, large, pendant flexor tubercles are common in oviraptorids (Barsbold et al., 1990; Clark et al., 1999) and troodontids (Barsbold et al., 1987; personal observation of cast of IVPP V 9612, *Sinornithoides youngi*). However, they are absent in most other theropods, including coelophysoids (Welles, 1984; Colbert, 1989), carnosaurs (Madsen, 1976; Currie and Zhao, 1993), tyrannosaurids (Lambe, 1917), and ornithomimosaurs (Osmólska et al., 1972; Nicholls and Russell, 1985).

In the sickle-clawed family Troodontidae, the sickle claws exhibit dromaeosaurid morphology but the manual unguals do not. Troodontid manual unguals exhibit neither the typical dromaeosaurid arch nor a proximodorsal lip (Barsbold et al., 1987; personal observation of cast of IVPP V 9612). However, as in dromaeosaurids, troodontid manual flexor tubercles extend far palmar to the articular facets (Barsbold et al., 1987; personal observation of cast of IVPP V 9612), whereas the flexor tubercles of troodontid pedal sickle claws do not (Barsbold et al., 1987; Xu and Wang, 2004; personal observation of cast of IVPP V 9612). Using flexor tubercle morphology as a guide, one can conclude that the isolated unguals of *Troodon* figured by Russell (1969, fig. 9) are pedal unguals. Because dromaeosaurid and troodontid manual unguals are so different, it is important to ascertain to which family a specimen belongs before applying the method described here for identifying the limb of origin of a strongly curved ungual.

The case of the non-dromaeosaurid theropod *Megaraptor* also illustrates that the criteria found here for distinguishing dromaeosaurid manual from pedal unguals do not apply to other taxa. A *Megaraptor* ungual that was once thought to be a pedal sickle claw lacks a proximodorsal lip, a pendant flexor tubercle, and a dorsal surface that arches over the level of the dorsal extremity of the articular facet (Novas, 1998). However, despite its resemblance to a dromaeosaurid pedal sickle claw, the bone is now known to be a manual ungual (Calvo et al., 2004). It is therefore important to apply the criteria found here only to unguals of Dromaeosauridae. Interestingly, the collateral grooves of the *Megaraptor* ungual are asymmetrical, which was cited as evidence that the ungual was from the foot (Novas, 1998). The finding that the ungual came from the hand demonstrates that collateral groove asymmetry is not a reliable indicator of limb of origin in theropods.

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ドロマエオサウルス科の前肢と後肢の末節骨（“鎌状の爪”）の識別方法

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要旨：ドロマエオサウルス科恐竜の手（前肢）の末節骨と足（後肢）の末節骨（“鎌状の爪”）は極めて混同しやすい. それらの識別する方法を見出すために, 筆者はドロマエオサウルス科に分類される 4 種, ***Microraptor zhaoianus, Bambiraptor feinbergi, Velociraptor mongoliensis, Deinonychus antirrhopus*** の前肢と後肢の末節骨を比較した. その結果, ドロマエオサウルス科の前肢の末節骨では, 関節面を垂直に置いた場合, 弓形をなすその背側縁が関節面より高くなること, そして後肢の末節骨では背側縁は関節面よりも高くならないことが確認された. またドロマエオサウルス科の前肢の末節骨では, 屈筋結節の腹側への発達が後肢の末節骨より顕著であった. これらの発見を適用することによって, ***Utahraptor*** や ***Pyroraptor*** の非交連状態で発見された末節骨が後肢のものであること, 同様に ***Dromaeosaurus*** に分類された末節骨, ならびに非交連状態で発見された ***Achillobator*** と ***Unenlagia*** の末節骨は前肢のものであることが判明した. 獣脚類の他の分類群の末節骨では異なった形態的特徴を有するため, この方法はドロマエオサウルス科のみに適用可能である.

キーワード：獣脚類, ドロマエオサウルス科, *Utahraptor, Achillobator, Unenlagia*