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Stenonychosaurus inequalis (Saurischia: Theropoda) from the Judith River (Oldman) Formation of Alberta: new findings on metatarsal structure[1]

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A partial foot of *Stenonychosaurus* from the Judith River (Oldman) Formation, Dinosaur Provincial Park, Alberta, shows features in the metatarsus that have not previously been recognized. These include compression of metatarsal II and exclusion of the proximal half of metatarsal III from the anterior (= dorsal) surface of the metatarsus. Exclusion from the anterior surface of metatarsal III to this extent is unprecedented among theropods and further underscores the distinctiveness of the Saurornithoididae.

Une partie d'un pied de *Stenonychosaurus* trouvée dans la formation de Judith River (Oldman), dans le Parc provincial Dinosaur, en Alberta, exhibe des particularités dans le métatarse qui n'ont pas été reconnues antérieurement. Elles comprennent une compression du métatarsien II et une exclusion de la moitié proximale du métatarsien III de la surface antérieure (= dorsale) du métatarse. Une exclusion de la surface antérieure du métatarsien III de cette étendue est sans précédent parmi les théropodes et elle accentue la distinction des Saurornithoïdidés.

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Introduction

The small monotypic saurornithoidid theropod dinosaur *Stenonychosaurus inequalis* Sternberg is one of the rarest and most interesting species from the Cretaceous (Campanian) Judith River (Oldman) Formation of southern Alberta. When Russell (1969) reviewed the species, only 14 specimens were known, most complete of which was a skeleton comprising fragmentary cranial and postcranial material. The remainder were isolated elements or small groups of articulated bones. The type specimen, which included a fragmentary distal forelimb, a distal hind limb, and six caudal vertebrae (Sternberg 1932), was crushed and eroded. Since 1969 additional finds of *Stenonychosaurus* elements have been made (Currie 1985), but the skeleton is still incompletely known. *Stenonychosaurus inequalis* is of particular interest because of its large brain, possible stereoscopic vision, and the further possibility that an opposable digit was present in the manus (Russell and Séguin 1982).

In 1977, A. Kirkor brought to the first author a group of bones from the Judith River Formation. They included an *Aspideretes* carapace and small dinosaurian foot elements, mostly fragmentary, but all reportedly from the same general location. As the first author began to prepare the turtle carapace, news was received of Mr. Kirkor's untimely death. It was only after this that an attempt was made to reassemble the dinosaurian remains, tentatively identified as ornithomimid. It was found, surprisingly, that they were a mixture of ornithomimid phalanges along with three partial metatarsals referable to *Stenonychosaurus inequalis*. The metatarsals were uncrushed and matched one another closely in color and weathering pattern, differing in this respect from the ornithomimid material. It was concluded that the metatarsals had been collected as an articulated unit, and that although the other specimens came from the same area, they were not necessarily from the same site.

Mr. Kirkor had indicated that the collection was made near Dinosaur Provincial Park, southern Alberta. Once the metatarsals had been identified, efforts were made to locate friends with whom he had collected fossils, to obtain more specific information. This search met with success, and in 1982 the first author travelled to the park area with the J. Cran family. We concluded that the specimens were likely found near the southwest corner of the park, where a broad badlands tract extends southward from Little Sandhill Creek. It appears likely that Mr. Kirkor lost sight of park boundary markers and that the specimens were collected barely within its southern boundary (sec. 26, tp. 20, rge. 12, W 4th mer.), high in the Judith River Formation.

In 1979, a Provincial Museum of Alberta field party led by the second author revisited another locality in the northern part of Dinosaur Provincial Park where NMC 12340, a partial skeleton of *Stenonychosaurus*, had been collected (Russell 1969). As so often happens in the badlands, more of the skeleton had been exposed, and the distal ends of metatarsals II and III and fragments that fit onto parts of NMC 12340 were recovered. These were sent to the National Museum in Ottawa and catalogued with the original specimen.

Abbreviations

NMC, National Museums of Canada; TMP, Tyrrell Museum of Palaeontology.

Description

The Kirkor find (TMP 84.65.1) consists of distal portions of left metatarsals II–IV. Metatarsal II in medial aspect displays an interosseous ridge for attachment of ligaments for reduced metatarsal I, and the distinctive structure and proportions described by Russell (1969) for *Stenonychosaurus* are clearly evident. The uncrushed nature of these elements allowed the second author to make detailed comparisons with the two pre-

[1] Dedicated to the memory of Andrew Kirkor.

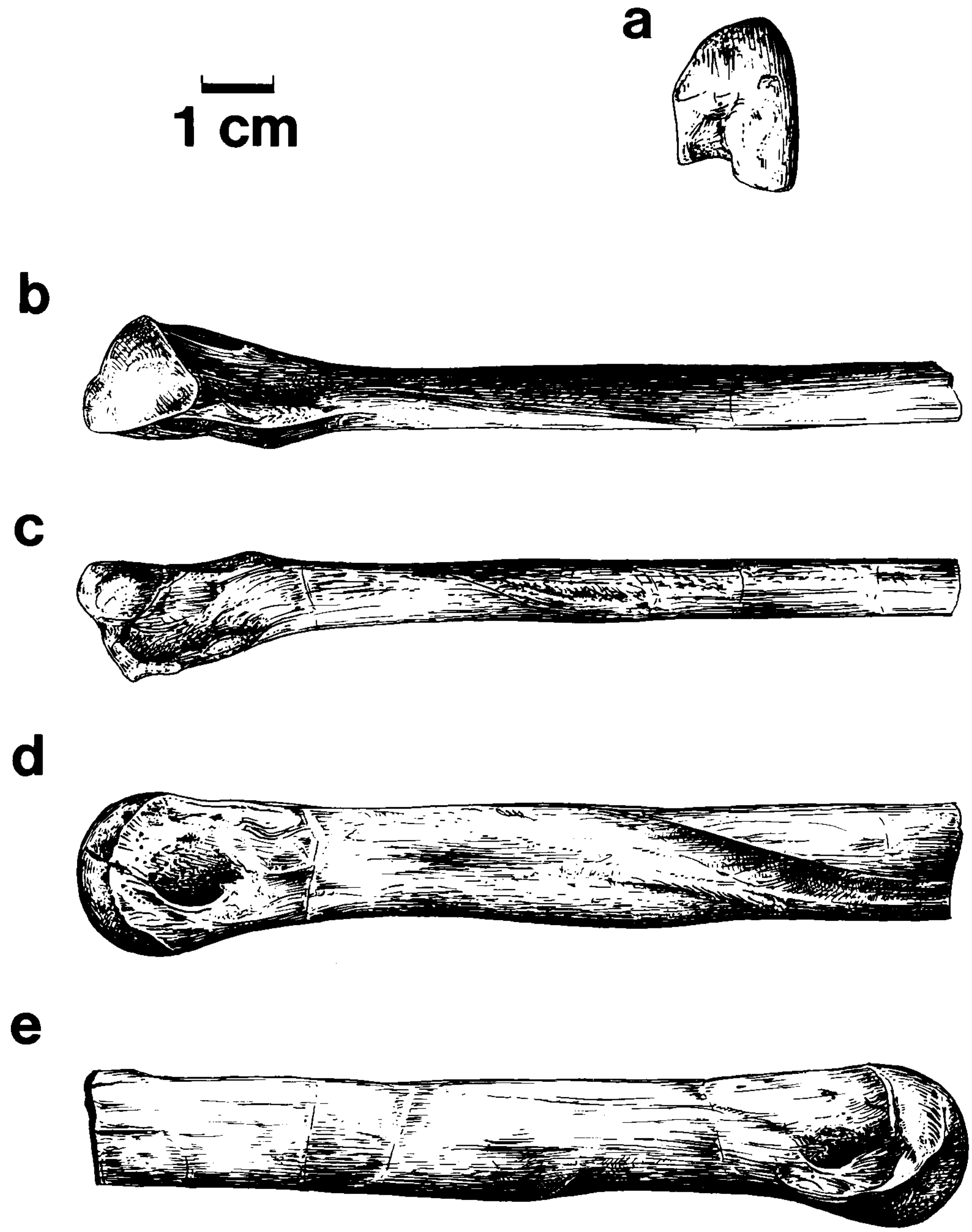

FIG. 1. *Stenonychosaurus inequalis*, distal three quarters of left metatarsal II (TMP 84.65.1). (*a*) Distal aspect. (*b*) Anterior aspect. (*c*) Posterior aspect. (*d*) Lateral aspect, showing trough for metatarsal III. (*e*) Medial aspect.

viously known *Stenonychosaurus* metatarsi, both in the collection of the National Museum of Natural Science (National Museums of Canada). Directional terms used in the ensuing discussion are based on inferred adult posture and follow Russell (1969). Appropriate developmental (embryonic limb bud) equivalents are as follows, in parentheses: anterior (dorsal), posterior (ventral), medial (anterior), and lateral (posterior). The terms in parentheses are useful in comparisons involving reptiles of a variety of limb forms, whereas postural terms have been used in specific discussions of morphogenetically similar forms.

Metatarsal II (Fig. 1) is the longest preserved fragment, being represented by the distal 123.4 mm, approximately three quarters of the overall length of the element. The distal condyle is 17.0 mm in maximum breadth and 22.7 mm in antero-posterior diameter, as compared with 17.7 mm by 22.8 mm in NMC 12340 and 19.1 mm by 25.4 mm in the type specimen, NMC 8539. The shaft describes a compressed ovoid in cross section, with maximum breadth of 8.3 mm and antero-posterior diameter of 16.5 mm. An unfigured fragment of right metatarsal II of NMC 12340 has a maximum breadth of 8.3 mm in the same region. Narrowness of this element also appears to be indicated in NMC 8539. The medullary cavity running through the shaft is relatively small (2.5 mm × 6 mm) in section. A shallow, longitudinal trough on the lateral surface of this specimen (Fig. 1*d*) and NMC 12340 marks the contact with the third metatarsal. This trough tapers dorsally and indicates that the proximal half of the third metatarsal was set back from the anterior (embr. dorsal) surface of metatarsal II by at least 12 mm. Examination of a cast of the metatarsus of the type

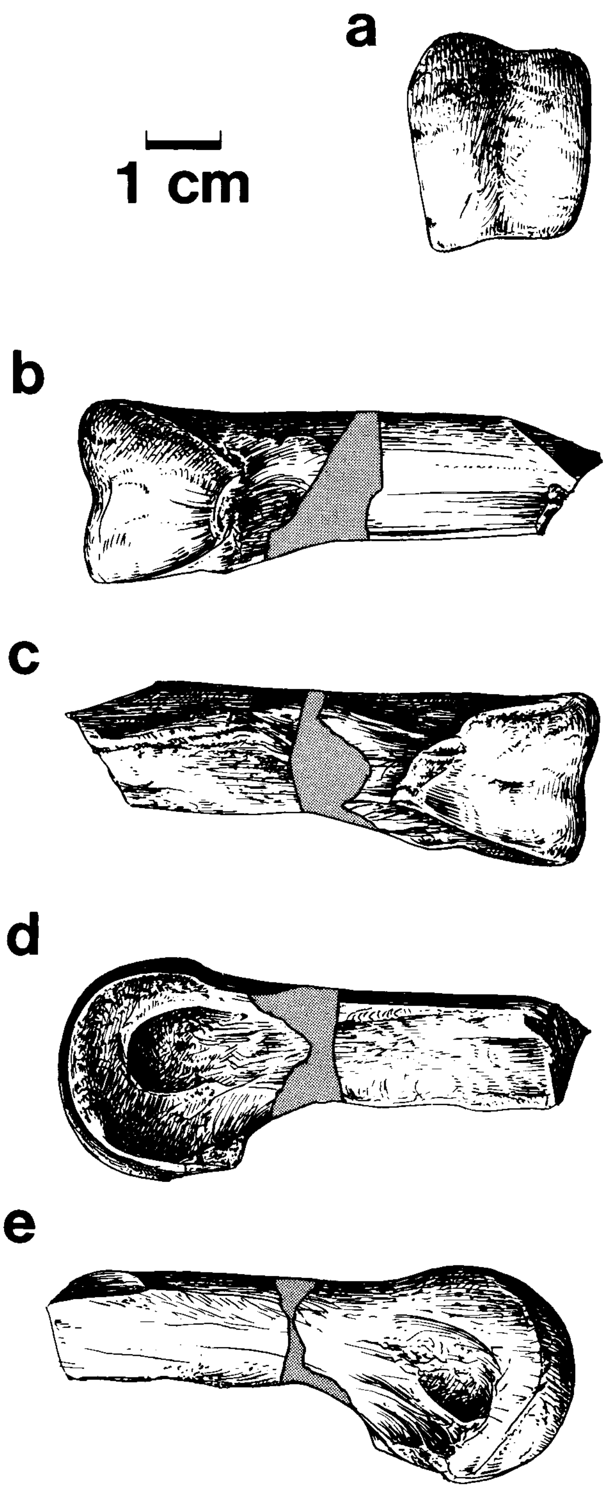

FIG. 2. *Stenonychosaurus inequalis*, distal half of left metatarsal III (TMP 84.65.1; missing portion shaded). (*a*) Distal aspect. (*b*) Anterior aspect. (*c*) Posterior aspect. (*d*) Lateral aspect. (*e*) Medial aspect. Note postero-proximal extension of distal condyle as a prominent tongue of bone.

specimen (NMC 8539) of *Stenonychosaurus inequalis* also suggests that this is the case. Surface scarring in the trough shows that there were strong ligamentous attachments between metatarsals II and III.

Metatarsal III of TMP 84.65.1 (Fig. 2) is represented by half of the overall length of the element. It was found in two pieces that lacked a good contact. Reconstruction of the intervening portion was fashioned in plaster on the assumption that the two fragments contacted at one point. Comparison with the same element in NMC 12340 suggests that this may not have been the case, however, and the two fragments should have been separated by 3–5 mm. The distal condyle of the third metatarsal is 23.4 mm in maximum breadth and 29.1 mm in antero-posterior diameter, compared with 24.8 mm by 28.6 mm in NMC 12340 and about 26 mm by 31.2 mm in NMC 8539. As in NMC 8539, the distal condyle of the third metatarsal is extended posteroproximally into a long, broad tongue of bone, a feature unique to saurornithoidids (Russell 1969). In distal aspect, there are minor differences between TMP 84.65.1 and NMC 12340, related to the fact that the maximum breadth of the latter is about 10% greater relative to the antero-posterior diameter. Differences of this magnitude can be accounted for by individual variation and postmortem distortion. In both specimens, the outline (Fig. 2*a*) tapers posteriorly by 10% in mediolateral breadth; the antero-posterior length of the lateral aspect of the condyle is also 90% that of the medial aspect of the condyle. The shaft is slender and prismatic, with flat to broadly concave faces. The circular medullary cavity in NMC 12340 has a diameter of about 6 mm distally but tapers proximally, disappearing about 70 mm from the distal end of the bone.

A fragment of right metatarsal III of NMC 12340 is from the region of maximum constriction of this element. The fragment covers the interval between 125 and 165 mm from the distal end of the bone, as near as can be estimated, and fits perfectly into the articular trough of metatarsal II. The cross-sectional outline of the bone changes dramatically as it passes dorsally between metatarsals II and IV (Fig. 4). Distally the fragment is triangular in section (Fig. 4*b*) and probably was only minimally exposed in the posterior view of the metatarsus. Proximally, metatarsal III has receded so far from the anterior face of the metatarsus that the bone is only 3.1 mm antero-posteriorly and 4.5 mm wide. Above this point, scarring on metatarsals II and IV indicates that the third metatarsal would have been excluded from the anterior aspect of the metatarsus as its neighbors came into contact.

Metatarsal IV (Fig. 3) is represented only by a partial distal condyle in TMP 84.65.1. Useful measurements cannot be taken, although it is almost identical in size to that of NMC 12340. As pointed out by Russell (1969), the shaft of the fourth metatarsal is massive in comparison with the others (Fig. 4). A shallow but distinct trough along the medial surface of NMC 12340 was the articular surface for the third metatarsal.

Discussion

From the structure of metatarsals II–IV and indirectly from the evidence for metatarsal I, it is clear that TMP 84.65.1 represents *Stenonychosaurus inequalis*. Although not as complete as the type specimen (NMC 8539), it is uncrushed and provides new information on the structure of the second and third metatarsals. The new specimen came from an animal approximately the same size as that represented by NMC 12340, and both were slightly smaller than the type.

Examination of TMP 84.65.1 and restudy of NMC 12340 indicates diagnostic characters for the Saurornithoididae that have not been noted previously in *Stenonychosaurus*. Compression of the second metatarsal is distinctly different from the situation in dromaeosaurids (Ostrom 1969), elmisaurids (Sternberg 1932; Osmolska 1981), and ornithomimids (Osborn 1917;

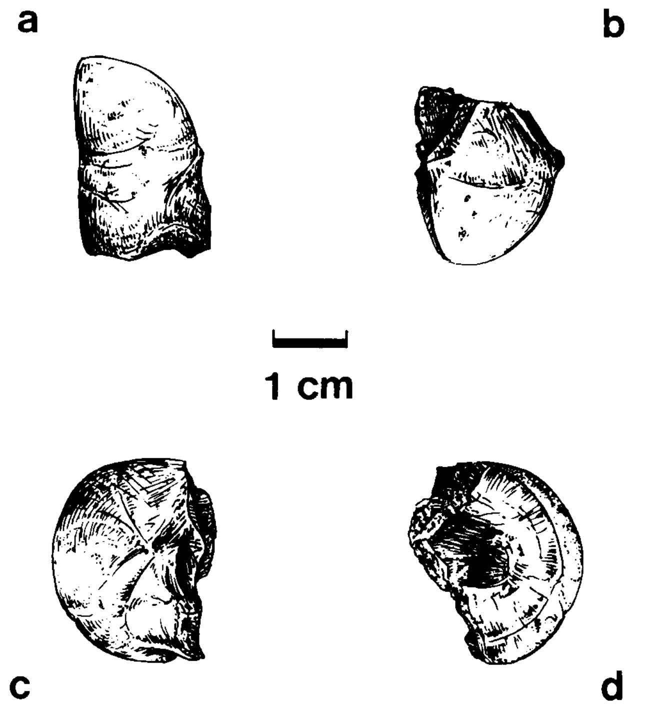

FIG. 3. *Stenonychosaurus inequalis*, distal fragment of left metatarsal IV (TMP 84.65.1). (*a*) Distal aspect. (*b*) Anterior aspect. (*c*) Lateral aspect. (*d*) Medial aspect.

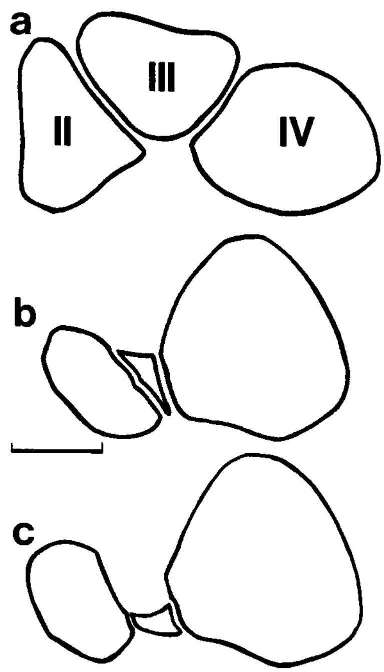

FIG. 4. *Stenonychosaurus inequalis*, cross sections of right metatarsus (NMC 12340). Sections are approximately (*a*) 50 mm, (*b*) 130 mm, and (*c*) 160 mm from the distal end of the metatarsus. Anterior surface is up in all drawings. Scale bar = 10 mm.

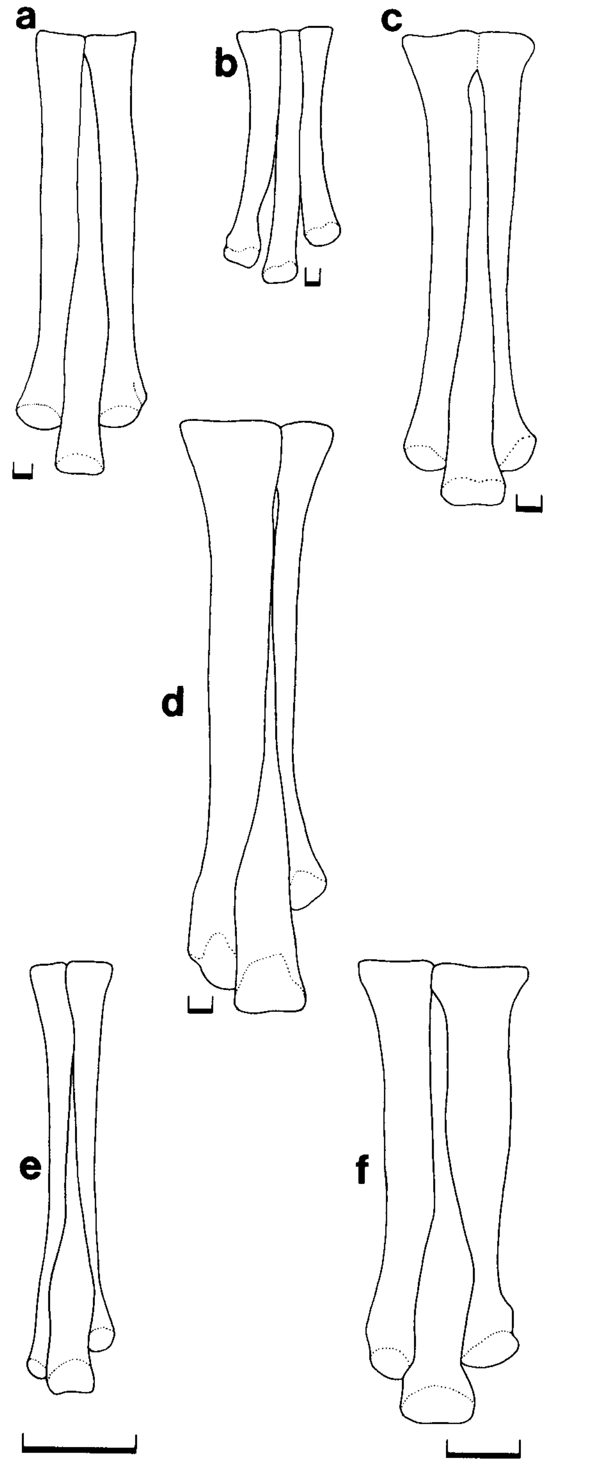

FIG. 5. Right metatarsals II, III, and IV of (*a*) *Macrophalangia*, (*b*) *Deinonychus*, (*c*) *Elmisaurus*, (*d*) *Stenonychosaurus*, (*e*) *Struthiomimus*, and (*f*) *Albertosaurus*. *Stenonychosaurus* reconstruction based on specimens described in this paper and the proximal end of a metatarsus described by Barsbold (1974). *Macrophalangia* based on TMP 79.20.1, *Deinonychus* after Ostrom (1969), *Elmisaurus* after Osmolska (1981), *Struthiomimus* after Osborn (1917), and *Albertosaurus* after Lambe (1917). (*a*, *b*, *c*, *d*) Scale bar = 10 mm. (*e*, *f*) Scale bar = 100 mm.

Osmolska *et al.* 1972). The articular surface on the lateral aspect of the shaft of the second metatarsal indicates that the proximal end of metatarsal III was excluded from the anterior (embr. dorsal) surface of the metatarsus as in *Saurornithoides* (Barsbold 1974). For the first time, however, the degree of exclusion is evident. Although proximal constriction of the third metatarsal is seen in ornithomimids and tyrannosaurids (Fig. 5 *e* and *f*), this element remains visible in anterior view for almost its entire length. Metatarsal III is excluded from the anterior surface of the metatarsus in *Macrophalangia* (Fig. 5*a*) and *Elmisaurus* (Fig. 5*c*) but only at its proximal extremity. The fact that only the distal position of the third metatarsal is exposed anteriorly therefore appears to be another sauronithoidid characteristic unique among theropods. Other derived characters of the metatarsus shared by *Stenonychosaurus* and *Saurornithoides* include the presence of a posteroproximally extended tongue of the distal condyle and the relatively massive size of the fourth metatarsal (Russell 1969; Barsbold 1974).

Constriction of metatarsal III characterizes avimimids (Kurzanov 1981), *Macrophalangia* (Fig. 5*a*), *Elmisaurus* (Fig. 5*c*), saurornithoidids (Fig. 5*d*), ornithomimids (Fig. 5*e*), and tyrannosaurids (Fig. 5*f*), whereas the more primitive unconstricted metatarsal III (Fig. 5*b*) is found in all other theropods. Although this specialization may indicate common ancestry for all theropods that possess it, other skeletal features suggest that it developed independently in the avimimid, *Macrophalangia–Elmisaurus*, saurornithoidid–ornithomimid, and tyrannosaurid lineages. There can be little doubt that proximal reduction of metatarsal III could have developed as often as necessary as a functional adaptation for improved cursorial locomotion. Reduction of the proximal end of metatarsal III allowed development of an oblique area of contact on each side to enhance transmission of force to metatarsals II and IV. The proximal ends of metatarsals II and IV in *Stenonychosaurus* were tightly bound together and even coossified in *Avimimus* (Kurzanov 1981) and possibly *Macrophalangia* (Currie and Russell, in preparation). Force transmitted from metatarsal III in these forms was thereby effectively spread across the mesotarsal joint. The shape of the third metatarsal is such that it could have rotated in relation to the other metatarsals about an axis near the midpoint of the metatarsus, the proximal end pulling postero-distally and the distal end antero-proximally. The metatarsus would, despite this, have been bound tightly throughout by interosseous ligaments, which would have absorbed much of the shock of impact with the ground when the animal was running, thereby reducing stress on the tarsal joints. The robust nature of metatarsal IV and narrowness of metatarsal II in *Stenonychosaurus* are related to the fact that the animal was functionally didactylous, with digit II specialized as an offensive weapon that probably touched the ground only rarely (Russell and Séguin 1982).

Tendencies toward metatarsal binding or even fusion in various theropods call to mind the fused tarsometatarsus of birds, and detailed comparisons have recently been made by Brett-Surman and Paul (1985). In both groups the adaptations could relate to cursorial ability, though given the variety of adaptations in birds this need not be the only factor involved. Similar reduction in number of metatarsals and fusion of remaining elements are seen in such cursorial groups as gracile ungulate mammals. Flexibility within the metatarsus is sacrificed in favor of efficient transmission of force along the central axis of the appendage, with compensatory adaptations to allow the distribution of force widely over articular surfaces. However, in juvenile ratite and carinate birds examined by the authors, the proximal half of metatarsal III is not reduced in diameter as in the theropods considered here. In birds, the element does become constricted at midshaft, but the proximal end is expanded and remains an important part of the articular surface. Metatarsal III is pinched proximally to the extent that it is usually not visible in anterior aspect at the proximal end, but despite this the proximal articular surface in birds is often as large as that of metatarsal II or metatarsal IV. The combination of traits involved here could be useful in discriminating birds from theropods (Brett-Surman and Paul 1985). It would seem at this time premature to draw anything more than convergence between saurornithoidids and birds in terms of metatarsal structure.

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