Osteology and relationships of *Chirostenotes pergracilis* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada

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A partial skeleton of a small theropod found in the Judith River Formation of Dinosaur Provincial Park (Alberta) shows that *Chirostenotes pergracilis* is the same animal as "*Macrophalangia canadensis*" and probably "*Ornithomimus elegans*." New information on the skeleton suggests that *Chirostenotes* is closely related to *Elmisaurus* and *Oviraptor* and that these animals are derived from dromaeosaurid stock. Both robust and gracile forms are known from Alberta, and it is suggested that these correspond to the two "species" of *Caenagnathus* and represent sexual dimorphism. *Microvenator* from the Lower Cretaceous of Montana may represent an early caenagnathid. Specializations in the pelvic girdle and hind limb may indicate wading habits.

L'étude d'un squelette partiel d'un petit théropode trouvé dans la Formation de Judith River du Parc provincial des Dinosaures (Alberta) révèle que *Chirostenotes pergracilis* et « *Macrophalangia canadensis* » et probablement « *Ornithomius elegans* » sont en réalité le même animal. De récentes observations faites sur le squelette suggèrent que *Chirostenotes* est un proche parent de *Elmisaurus* et *Oviraptor* et que ces animaux dérivent d'une souche commune de dromaeosauride. La forme robuste et la forme gracile ont été reconnues en Alberta, et il apparaît que ces formes correspondent aux deux « espèces » de *Caenagnathus* et qu'elles représentent un dimorphisme sexuel. *Microvenator* des sédiments du Crétacé inférieur du Montana peut représenter un caenagnathide précoce. Les spécialisations dans la ceinture pelvique et du membre postérieur peuvent refléter les habitudes pataugeuses de ces animaux.

[Traduit par la revue]

Introduction

Chirostenotes pergracilis was described by Gilmore (1924) on the basis of two nearly complete mani of a single individual. Unfortunately, no other elements of the skeleton were found with the holotype (NMC 2367). Gilmore (1924) tentatively assigned a pair of dentaries to *Chirostenotes* but admitted that such a referral was arbitrary. The identification of the jaws will be discussed elsewhere (Currie *et al.*, in preparation).

Later the same year, the first specimen of *Oviraptor philoceratops* was described from the Djadochta beds of Mongolia (Osborn 1924). If only the skull had been found, identification would have been difficult because of its unusual appearance. Fortunately, the specimen included a partial skeleton that clearly showed *Oviraptor* to be a theropod. Osborn (1924) noted the similarity between the elongate second digit of the manus in both *Oviraptor* and *Chirostenotes*.

An isolated pes from the Judith River (Oldman) Formation of Alberta became the holotype of *Macrophalangia canadensis* (Sternberg 1932). The proximal end of metatarsal III was laterally compressed, which suggested to Sternberg that *Macrophalangia* may be closely related to the ornithomimids.

Parks (1933) described a metatarsus from the Judith River of Alberta as *Ornithomimus elegans*. C. M. Sternberg (1934) pointed out that this specimen was not from an ornithomimid, but he did not recognize the similarities between the new metatarsus and *Macrophalangia*. He did speculate on the possibility of this specimen being part of the foot of *Chirostenotes*. We now know that the type of "*Ornithomimus elegans*" is referable to *Macrophalangia* (Russell 1972). It differs from *Macrophalangia canadensis* in being more gracile.

Speculation on the association of *Chirostenotes* with other genera continued: Colbert and Russell (1969) wondered if it was congeneric with *Macrophalangia*, and Ostrom (1969) suggested that it might be *Dromaeosaurus*.

R. M. Sternberg (1940) described the lower jaws of a new specimen from the Judith River Formation of Alberta as *Caenagnathus collinsi*. He believed the edentulous jaws belonged to a bird, as did Cracraft (1971), who described a second species, *C. sternbergi*, from the same formation. Although Wetmore (1960) suggested *Caenagnathus* was a reptile, and Romer (1966) referred to it as a theropod, the identification remained uncertain until Osmolska (1976) compared it with a new specimen of *Oviraptor*. *Caenagnathus* is now generally considered to be related to but distinct from *Oviraptor* (Osmolska 1976; Olshevsky 1978; Barsbold 1981, 1983).

A new genus and species of small theropod was recently described from the Nemegt Formation of Mongolia (Osmolska 1981). *Elmisaurus rarus* is characterized by a fused tarsometatarsus. Aside from the fusion, the basic structure of the foot is similar to that of *Macrophalangia*, and the manus is hard to distinguish from that of *Chirostenotes*. Osmolska put the three genera in the family *Elmisauridae* and suggested that they may all be conspecific.

In 1979, staff of the Tyrrell Museum of Palaeontology, at that time working for the Provincial Museum of Alberta, collected a partial skeleton of a small theropod from Dinosaur Provincial Park. The specimen clearly shows that *Chirostenotes* and *Macrophalangia* are the same animal and suggests that Elmisauridae may be a junior synonym of Caenagnathidae. The foot is more gracile than the type of *Macrophalangia*

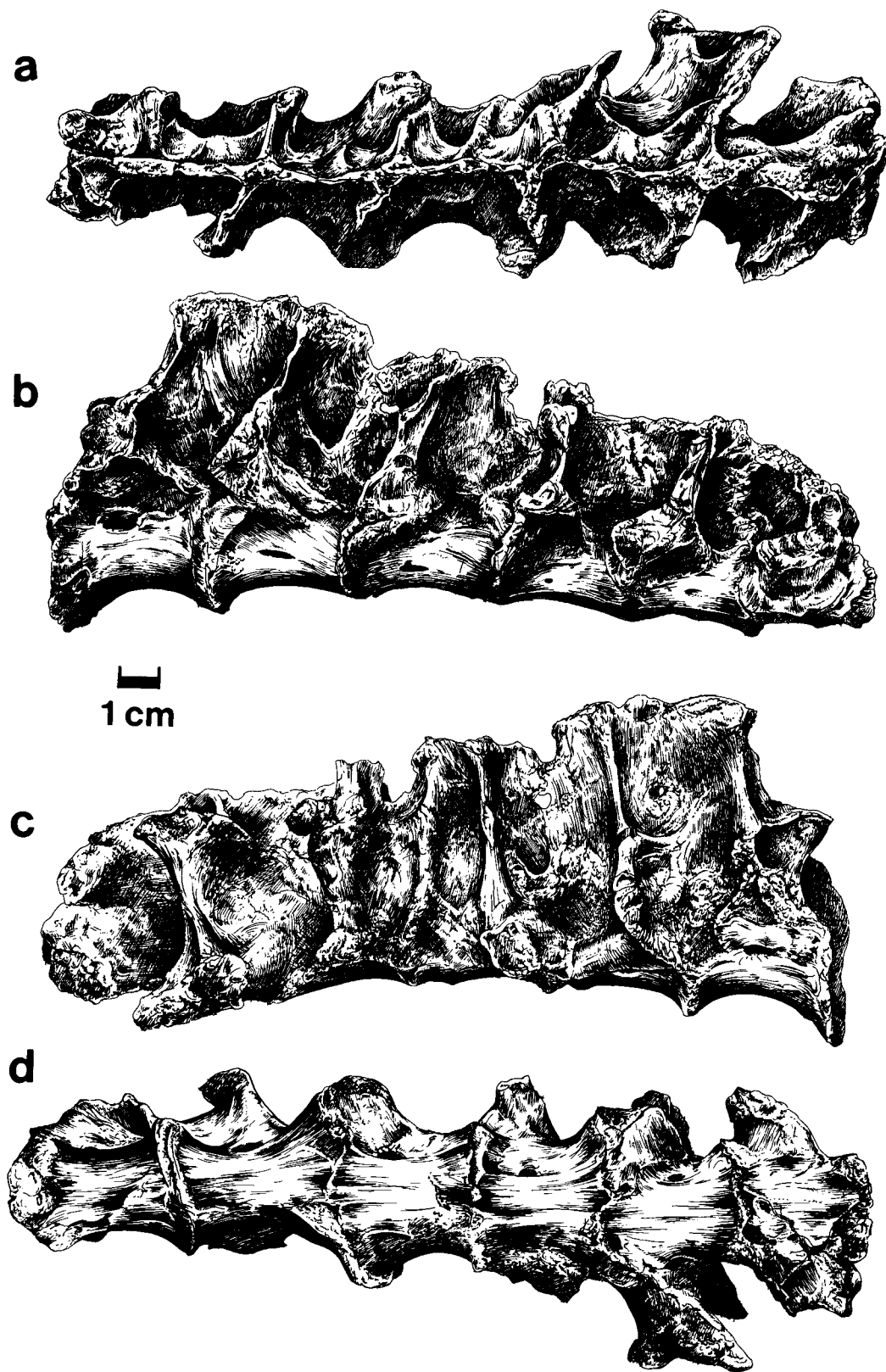FIG. 1. *Chirostenotes pergracilis.* Sacral vertebrate (TMP 79.20.1) in (*a*) dorsal, (*b*) left lateral, (*c*) right lateral, and (*d*) ventral views.

canadensis and compares with the more delicate metatarsus of "*Ornithomimus elegans.*" There appear to be two distinct morphs, gracile and robust, with several specimens representing each. This is comparable with the two morphs of *Caenag-* *nathus*—*C. collinsi* and *C. sternbergi.*

Another recently discovered specimen (Currie, in preparation) from the Judith River Formation shows that *Elmisaurus* is closely related to but distinct from *Chirostenotes.*

For the first time, there appears to be enough articulated material to tie together many of the enigmatic small theropods of North America and Asia.

Systematic palaeontology

CLASS Reptilia Linnaeus 1758
DIVISION Archosauromorpha Huene 1946
ORDER Saurischia Seeley 1888
SUBORDER Theropoda Marsh 1881
INFRAORDER Oviraptorosauria Barsbold 1976
FAMILY Caenagnathidae Sternberg 1940
Chirostenotes pergracilis Gilmore 1924

Holotype

NMC 2367 (sec. 17, tp. 21, rge. 11, W 4th mer., Dinosaur Provincial Park; collected by G. F. Sternberg, 1914), nearly complete, articulated digits of both hands.

Referred specimens

NMC 8538 (type of "*Macrophalangia canadensis*," lsd. 7, sec. 20, tp. 21, rge. 12, W 4th mer., Dinosaur Provincial Park; C. M. Sternberg, 1928), distal extremity of right tibia with part of astragalus, two incomplete distal tarsals, and complete right pes. NMC 9570 (sec. 29, tp. 34, rge. 21, W 4th mer., C. M. Sternberg, 1926), second metatarsal. ROM 781 (type of "*Ornithomimus elegans*," Little Sandhill Creek, Dinosaur Provincial Park; 1926), left metatarsus. TMP 79.14.499, (Dinosaur Provincial Park), manual phalanx II-3. TMP 79.20.1 (lsd. 15, sec. 32, tp. 20, rge. 11, W 4th mer., Dinosaur Provincial Park; Gilles Danis, 1979), partial skeleton including sacrum, ribs, coracoid, partial left manus, ilium, ischium, femur, tibia, metatarsus, and pedal phalanges I-1 and III-1.

Abbreviations

NMC, National Museum of Natural Sciences, National Museum of Canada; ROM, Royal Ontario Museum; TMP, Tyrrell Museum of Palaeontology.

Stratigraphy

Judith River Formation (Campanian, Upper Cretaceous).

Diagnosis

Medium-sized carnivorous dinosaur, weighing between 35 and 40 kg at maturity. Six sacral vertebrae with pleurocoels. Digit III of manus longer than digit I, but with slender phalanges, having a diameter of less than half that of phalanges in other digits. Well-developed posterodorsal "lip" on manual unguals, as in *Elmisaurus* and *Oviraptor*. Dolichoiliac, prepubic pelvis; preacetabular portion of iliac blade longer than postacetabular. Metatarsal III is proximally pinched between metatarsals II and IV, but only the proximal tip is excluded from the anterior surface of the metatarsus, as in *Elmisaurus* and possibly *Oviraptor*. The tarsometatarsus may have fused in old individuals as in *Elmisaurus*.

Description

Six vertebrae have co-ossified to form the sacrum in TMP 79.20.1 (Fig. 1). Lines of fusion are still visible between the centra but not the neural arches. The longest sacral centrum is 36.9 mm long, and they decrease progressively to 29.9 mm in the last sacral. The entire sacrum is close to 200 mm in length and 89.5 mm high, including spine, in the first dorsosacral. Judging from the height of the ilium, the neural spine is incomplete and the total height of the vertebra may have been more than 100 mm. The ventral surface of the
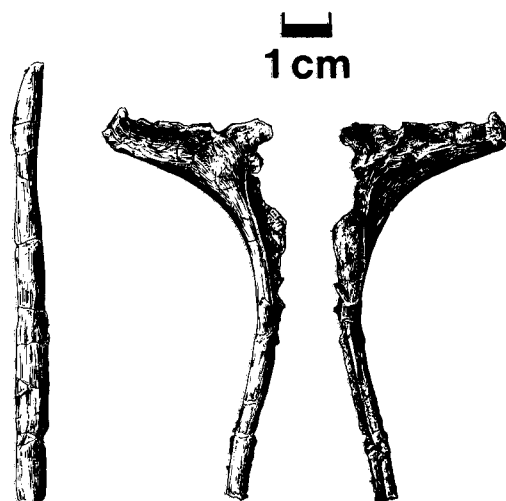

FIG. 2. *Chirostenotes pergracilis*. TMP 79.20.1, rib shaft and rib head (posterior and anterior views).

first centrum is rounded in section and is unquestionably derived from the thoracic series. There are a pair of longitudinal ridges on the ventral surfaces of the remaining centra (Fig. 1d), and these become more pronounced posteriorly. The centra are pierced by pleurocoels that have anteroposterior diameters of 9.5 mm in the first sacral but progressively decrease to 1.4 mm in the fourth and 1.7 in the last two sacrals. Ribs attach to the neural arches of the first two sacrals (Fig. 1b). The last four sacral ribs are intervertebral in position, each fusing to two centra. Both rib attachments and pleurocoels shift anteroventrally in the caudosacrals. The height of the sacral centra decreases posteriorly from 26 mm to 19 mm. The sacral vertebra preserved with the type of *Microvenator* is broad and low like the posterior sacrals of *Chirostenotes*. The sacral is not co-ossified with either its own neural arch or with other sacrals, showing that the type of *Microvenator* represents a juvenile.

The number of vertebrae incorporated into the sacrum of *Chirostenotes* is high for a theropod, especially for such a small, lightweight animal. There are three primary vertebrae in the saurischian sacrum (Romer 1956). The number increased to four in primitive theropods like *Compsognathus* (Ostrom 1978) and *Dilophosaurus* (Welles 1984) and to five in *Ceratosaurus* (Gilmore 1920), *Allosaurus* (Madsen 1976), ornithomimids (Osmolska et al. 1972), and tyrannosaurids (Lambe 1917; Osborn 1906). The sacrum of *Deinonychus* includes five vertebrae, but another dorsal is in the process of being incorporated (Ostrom 1976). *Saurornithoides* (AMNH 6516), *Garudimimus* (Barsbold 1983), and *Oviraptor* (Barsbold 1983) have six sacral vertebrae as in *Chirostenotes*. *Ingenia* may actually have seven sacrals (Barsbold 1983). Sacral pleurocoels are found in *Chirostenotes*, *Oviraptor*, ?dromaeosaurids, *Archaeornithomimus* (P. M. Galton, personal communication, 1986), and tyrannosaurids. They are not present in *Garudimimus*.

The head of a right mid-dorsal rib and the shafts of three other ribs are preserved with TMP 79.20.1 (Fig. 2). Tubercular and capitular heads are separated by 35 mm on the rib head, and all shafts are oval in cross section.

The single right coracoid (Fig. 3) is higher (58 mm) than it is long (52 mm). At the time of death, the coracoid had
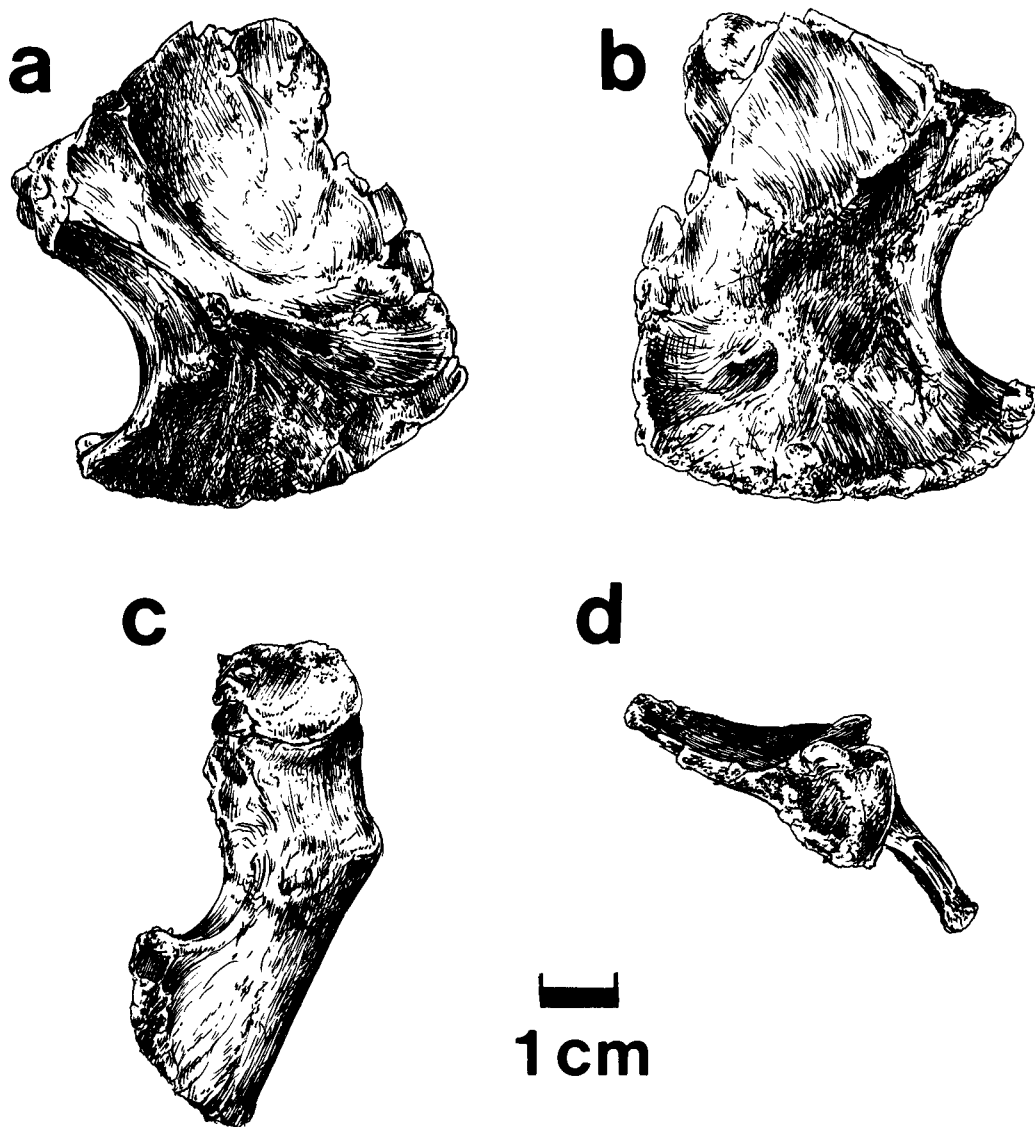
FIG. 3. *Chirostenotes pergracilis*. Coracoid (TMP 79.20.1) in (*a*) lateral, (*b*) medial, (*c*) posterior, and (*d*) dorsal views.

not fused to the scapula. The presence of a powerful biceps tubercle does suggest that the animal was mature, however. The coracoid foramen has a maximum diameter of 3.9 mm. In outline, the coracoid is similar to that of *Deinonychus* (Ostrom 1969, 1974), but it has a relatively longer contact with the scapula. As near as can be seen from Barsbold's (1983) figures, there are no significant differences between the coracoids of *Chirostenotes* and *Oviraptor*. The coracoid of *Microvenator* (Ostrom 1970), because the animal was so young and much of the element would have been cartilaginous, has a poorly defined shape, especially along the scapular margin.

Only the distal end of metacarpal I from the left manus is preserved (Figs. 4, 5). It is identical to the distal end of a left metacarpal I preserved with the type specimen of *Chirostenotes*. The distal articulation of metacarpal I is a mechanically simple, ginglymoid joint that is turned slightly medially from the longitudinal axis of the shaft to separate digits I and II. Although the bone is incomplete, it obviously had a straight, more slender shaft, comparable with that of *Elmisaurus* (Osmolska 1981) and in contrast with the stouter, shorter first

metacarpal of *Oviraptor* (Barsbold 1983), *Deinonychus* (Ostrom 1969), *Ornitholestes* (Osborn 1917), *Dilophosaurus* (Welles 1984), and tyrannosaurids (Lambe 1917). The first metacarpal of ornithomimids is relatively longer and stouter (Osborn 1917; Osmolska *et al.* 1972). Osmolska (1981) noted that *Microvenator celer* has a long, slender first metacarpal, comparable with that of *Elmisaurus* (longer and more slender than that of most theropods but relatively shorter than that of ornithomimids).

Seven of the nine phalanges of the left manus are preserved. On the average, the manual phalanges are only about 3% longer than those of the type specimens of *Chirostenotes* and *Elmisaurus*. In all three individuals, the longest phalanx is II-2, although it is only 5% longer than II-1. The third digit is approximately 30% longer than digit I, but it is 30% shorter than digit II. The longest phalanx in *Oviraptor* (AMNH 6517) and ornithomimids (Osborn 1917) is I-1, followed by II-2. The third digits of these animals are also 30% longer than the first digits, but they are subequal with the second. As the proportions of the hand of *Chirostenotes* are close to those of the Jurassic *Ornitholestes* (Osborn 1917), it is assumed that the
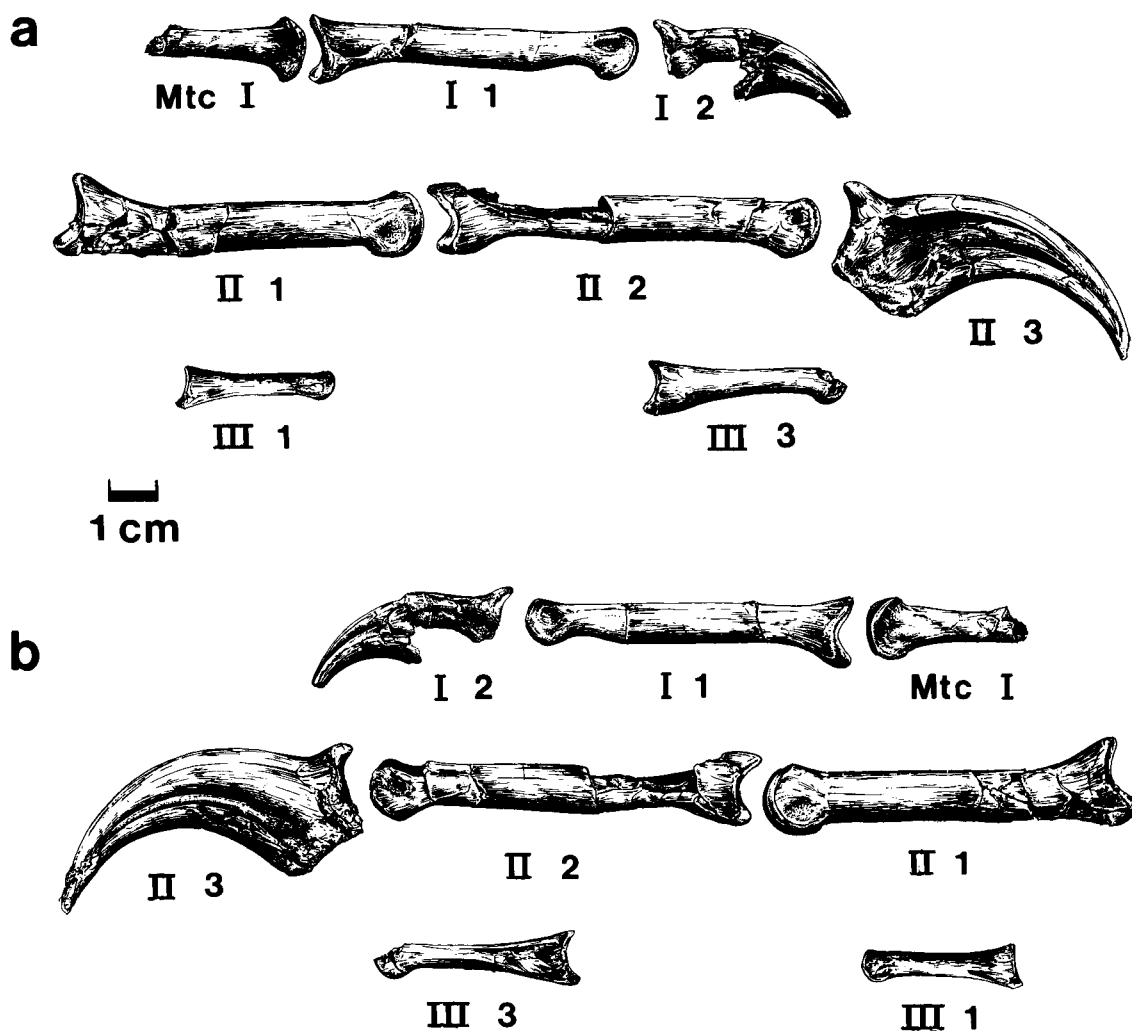
FIG. 4. *Chirostenotes pergracilis*. Manal elements (TMP 79.20.1) in (*a*) medial and (*b*) lateral views.

condition seen in *Oviraptor* and ornithomimids is the derived character state.

It is evident from the metacarpal–phalangial joint that the longitudinal axis of phalanx I-1 diverges 10% laterally from the longitudinal axis of the metacarpal. The first two digits therefore were parallel and could not have been opposable. The shaft of phalanx I-1 curves away from the longitudinal axis of the second digit, showing that these digits did diverge distally.

It is not as easy to interpret phalanx III-1 in the absence of the metacarpal. The proximal articulation is a concave, modified ovoid joint surface, in contrast with the sellar joint surfaces of all other metacarpophalangial and interphalangial joints of *Chirostenotes*. The angle between the proximal articulation and the shaft of phalanx III-1 is acute, which would bring the digit medially towards the second finger. However, the shaft curves laterally to partially compensate for the proximal articulation. It is suggested that the first phalanx is well adapted for giving the third digit capability of abduction and adduction in addition to flexion and extensión. The angle of the proximal surface and curvature of the shaft would allow the third digit to lie close to the second when not in special use.

The two preserved phalanges of digit III are long, slender bones. The minimum shaft width of III-1 is 3.0 mm, with a

shaft height of 4.8 mm. The same dimensions in II-1 are 8.5 and 9.9 mm. Although III-3 is only slightly shorter than that of the type specimen of *Chirostenotes*, the minimum shaft width is 4.0 mm, compared with 4.9 mm in the holotype. The same specialized third digit can be found in *Elmisaurus* (Osmolska 1981), and, to a lesser extent, in *Ornitholestes* (Osborn 1917). In contrast, the third digit of *Oviraptor* is as well developed as the second finger.

The manus of *Chirostenotes* bears three distinctive, well-developed unguals. The unguals are strongly recurved and laterally compressed and bear large, well-developed flexor tubercles. When found, the second ungual of TMP 79.20.1 still had a remnant of the epidermal sheath preserved distally. This extended 5 mm beyond the end of the ungual and was thicker along the extensor edge. Unfortunately the sheath disintegrated shortly after collection. The dorsal edge of the proximal articulation is raised into a distinct "lip," which is not as pronounced in other theropods except *Elmisaurus* (Osmolska 1981), *Oviraptor* (Barsbold 1981), and *Microvenator* (one of three manual unguals only). The length of II-3 of TMP 79.20.1 along the outside curvature is 82.5 mm, compared with 76 mm in the type. TMP 79.14.499 is an incomplete ungual of *Chirostenotes* that appears to be almost 20% larger than II-3 of TMP 79.20.1. In *Chirostenotes* and
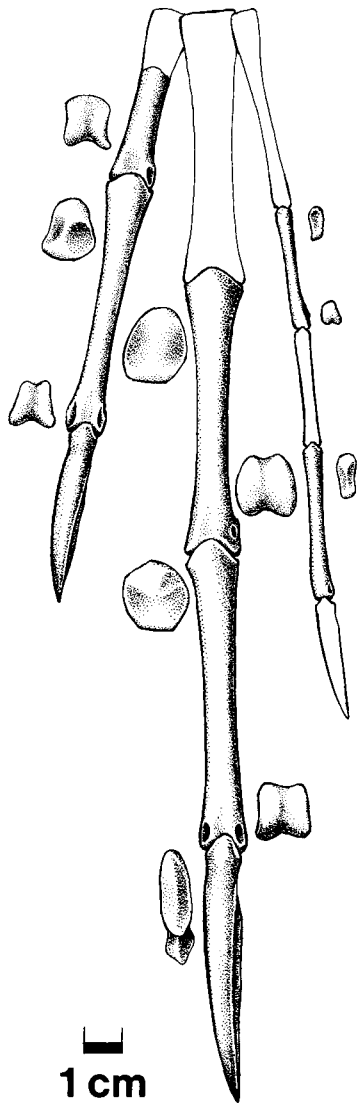
FIG. 5. *Chirostenotes pergracilis*. Manus (TMP 79.20.1) reconstructed in dorsal view.

Elmisaurus, I-2 is as well developed proximally as II-3, but it is shorter and more strongly curved. The ungual of digit 3 is both lower and shorter than the other manual unguals (Gilmore 1924). The proportions of the unguals of *Microvenator* are similar (Ostrom 1970). In contrast, the unguals of digits I and II are subequal in *Oviraptor* (Barsbold 1981) and *Deinonychus* (Ostrom 1969), and III-4 is also well developed in ornithomimids (Osborn 1917).

Most of the left ilium is preserved (Fig. 6), and it appears to be lacking only the thin, anterior margin of the iliac blade. Like most theropods, it is dolichoilic, having an elongate preacetabular blade that is squared off anteriorly. The postacetabular blade is bluntly pointed and surprisingly short, its total length being less than 70% the length of the preacetabular blade. The only other theropods known with similar preacetabular—postacetabular proportions are the opisthopubic dromaeosaurids *Adasaurus* (Barsbold 1983) and *Deinonychus* (Ostrom 1969). The ilia of *Microvenator* are incomplete, but that of *Oviraptor* is prepubic (Barsbold 1983). Segnosaurids, which also have a short postacetabular blade, are not theropods (Paul 1984).

The iliac blade is high, 90.9 mm above the acetabulum, compared with the total length of 255 mm. The dorsal edge is convex and curves gently throughout its length, like that of *Oviraptor* (Barsbold 1983). In most theropods, the dorsal margin of the ilium tends to be either straight or slightly concave. A rugose area on the posterolateral surface of the ilium marks the origin of the caudofemoralis. On the medial surface, the fossa for the caudofemoralis brevis is well defined by a strong ridge, but it is oriented more medially than posteroventrally. Striations along the medial surface of the dorsal margin would have strengthened the attachments of the M. longissiumus dorsi and M. iliocostalis. Six rugose areas on the medial surface mark the synarthroses with the sacral ribs. Strong ridges separate the areas of attachment of the third, fourth, and fifth ribs.

In comparison with other theropods, including *Microvenator*, the pubic peduncle is short. The pubic suture faces anteroventrally rather than ventrally, showing that the pubis was oriented anteroventrally as in all theropods except for dromaeosaurids.

The right ischium (Fig. 7) is similar to the ischia of troodontids, *Oviraptor* (Barsbold 1983), and *Deinonychus* (Ostrom 1969) in having a strong obturator process that is well separated from the pubic synarthrosis. Like more primitive forms, however, the ischium still extends for most of its length behind the obturator process. The overall length of the ischium is short, about 45% the length of the femur, compared with 55% in *Deinonychus* and 65−73% in large theropods (Ostrom 1969). The proximal end of the ischium is crushed, so that the iliac and pubic sutures cannot be distinguished.

The ratio of tibia to femur is 1.18 in TMP 79.20.1, which is comparable with that of the more cursorial theropods like *Compsognathus* (1.23−1.31, Ostrom 1978), *Deinonychus* (1.09, Ostrom 1969), and ornithomimids (1.08−1.30, Osborn 1917; Parks 1933; Russell 1972; Osmolska *et al.* 1972). *Microvenator* also has a high tibia/femur ratio (1.27), which may be a juvenile characteristic. More primitive theropods like *Ornitholestes* (0.71, Osborn 1917) and *Dilophosaurus* (0.99, Welles 1984) and large forms such as the tyrannosaurids (0.87−0.96; Lambe 1917; Russell 1970) have relatively shorter tibias.

The metatarsus is elongate in TMP 79.20.1, the ratio of metatarsal III to femur being 0.67. In the highly cursorial ornithomimids, the same ratio ranges between 0.71 and 0.80 (Russell 1972; Osmolska *et al.* 1972). The ratio is also high in *Compsognathus* (0.74−0.83, Ostrom 1978), but it is less than 0.6 in other theropods, including *Deinonychus* (0.49, Ostrom 1976), *Ornitholestes* (0.56, Osborn 1917), and *Dilophosaurus* (0.54, Welles 1984). The situation in *Microvenator*, *Oviraptor*, and troodontids is presently unknown or undescribed.

TMP 79.20.1 includes a badly crushed right femur (Fig. 8) that is 310 mm long, with a midshaft circumference of 92 mm. The lateral margin of the femur is almost straight, with a stronger concavity along the medial edge of the shaft. The head of the femur is separated from the greater trochanter by a narrow, shallow, saddle-shaped concavity. The base of the lesser trochanter is more than 40 mm distal to the proximal margin of the greater trochanter, in contrast with *Deinonychus*, where the lesser trochanter occupies a more proximal position (Ostrom 1976). Although the lesser trochanter may have been extended by a lamella of bone separate from the main body of the femur, as in *Microvenator* (Ostrom 1970), ornithomimids (Osmolska *et al.* 1972), allosaurids (Madsen
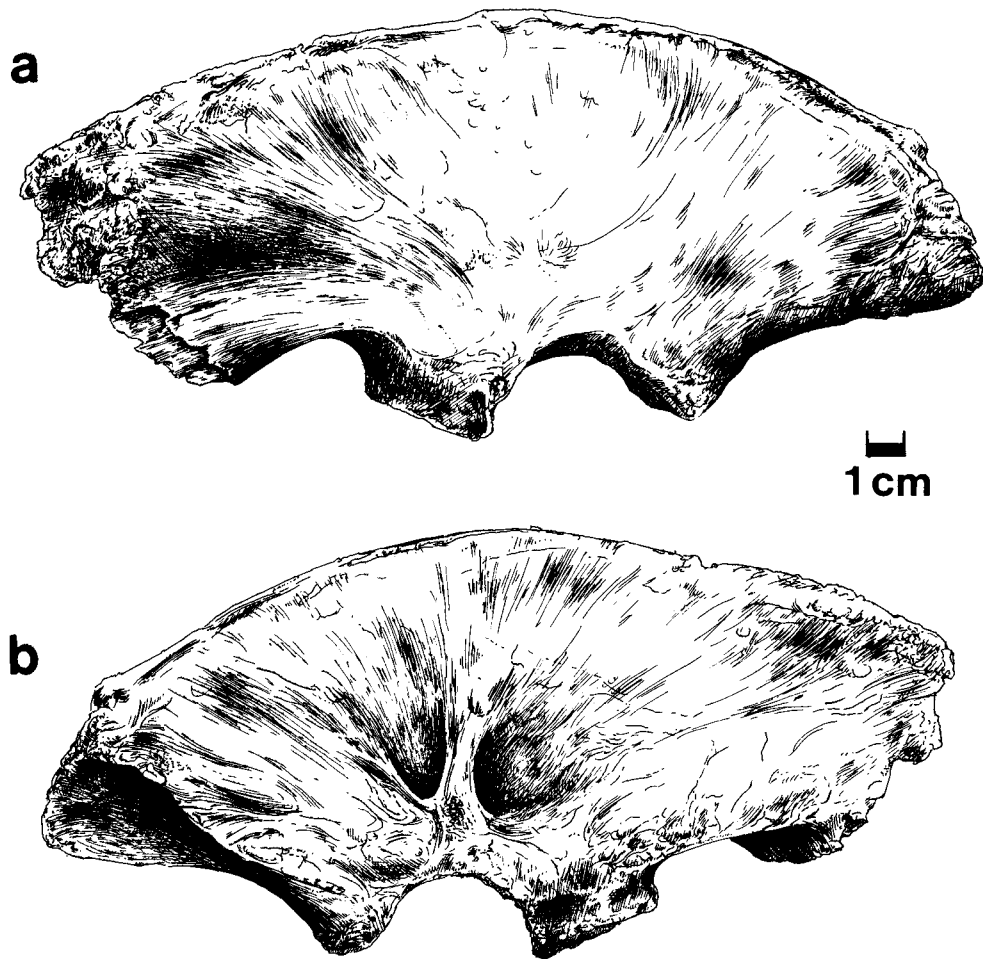
FIG. 6. *Chirostenotes pergracilis*. Left ilium (TMP 79.20.1) in (*a*) lateral and (*b*) medial views.
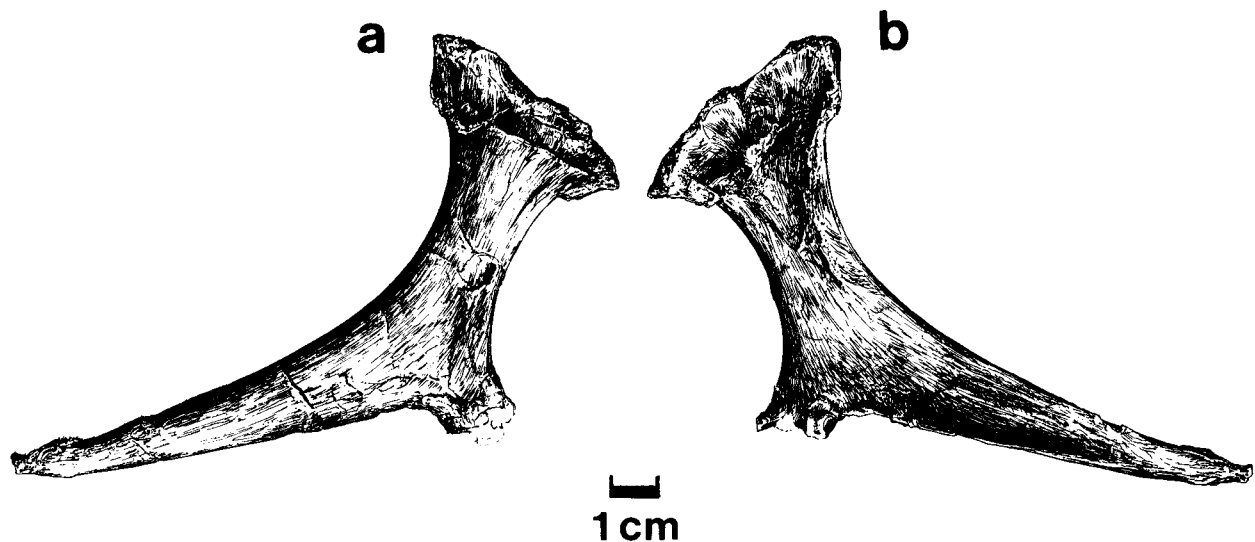

FIG. 7. *Chirostenotes pergracilis*. Right ischium (TMP 79.20.1) in (*a*) lateral and (*b*) medial views.

1976), tyrannosaurids (Lambe 1917), and other theropods, the base is more distally located than all other theropods known from the Cretaceous. There is no evidence of a fourth trochanter, although it may have been obliterated when the bone was crushed. *Microvenator* has a depression in this area

(Ostrom 1970), as in *Syntarsus* (M. A. Raath, personal communication, 1984). The fourth trochanter of *Oviraptor* is located near the middle of the bone, but it is very weak (Barsbold 1983). The distal condyles slope medially, the angle between the shaft and the distal end being 76°, so that the feet
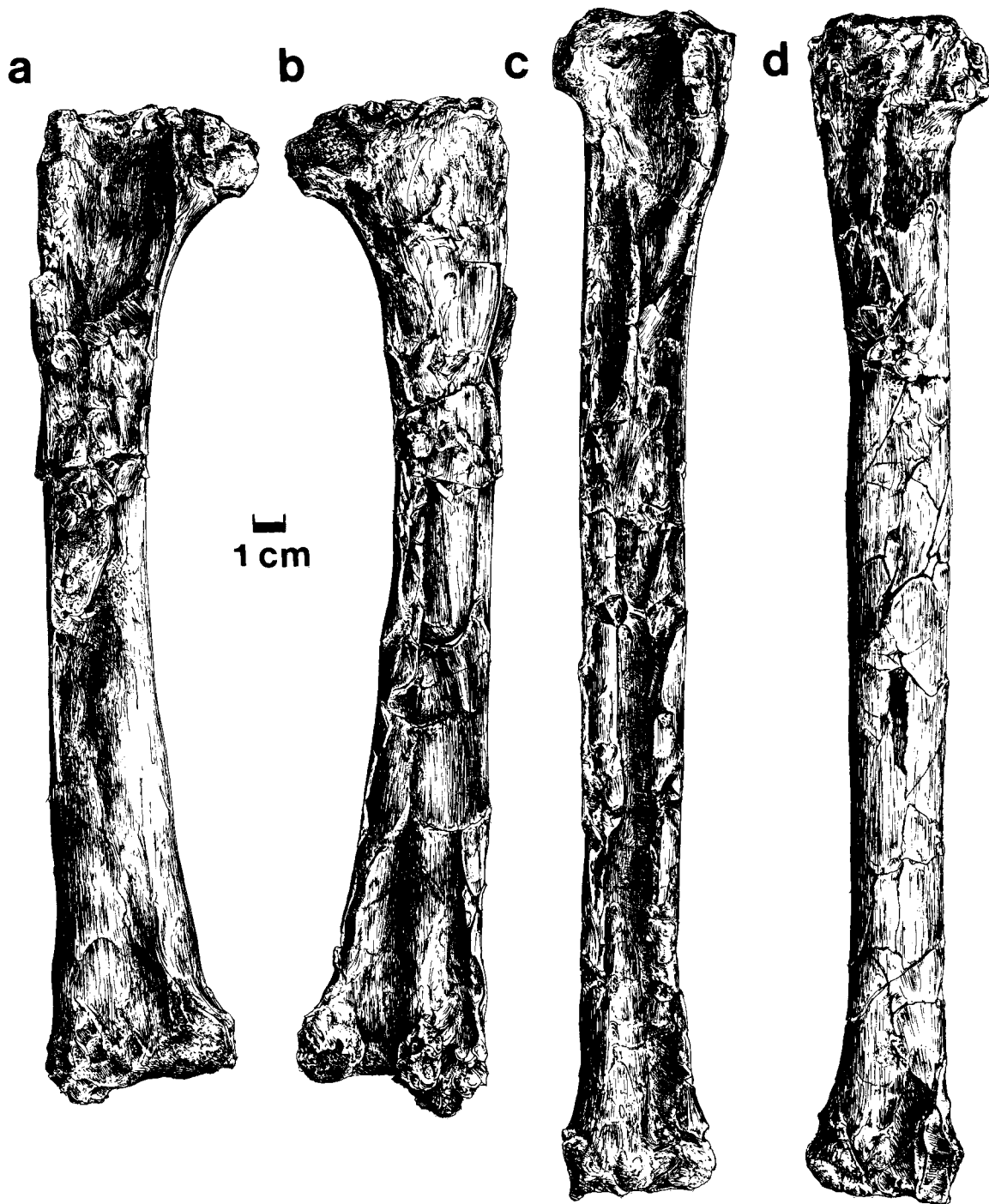
FIG. 8. *Chirostenotes pergracilis*. TMP 79.20.1. Right femur in (*a*) anterior and (*b*) posterior aspects. Right tibia in (*c*) anterolateral and (*d*) posteromedial views.

normally would have been positioned directly beneath the body. The lateral condyle, like that of most theropods including *Microvenator* (Ostrom 1970), has a well-defined ectocondylar tuber and a crescentic articular surface for the fibula. The ectocondylar tuber does not seem to be present in *Deinonychus* (Ostrom 1976).

The right tibia of TMP 79.20.1 (Fig. 8) has been flattened into a single plane. The shaft is almost perfectly straight over its entire length of 367 mm, and the proximal and distal articular surfaces are perpendicular to the longitudinal axis. The

proximal head is made up of two distinct condyles for articulation with the femur. The lateral condyle is small but pronounced and has a distinct lateral area of unfinished bone for the gliding articulation with the fibula. The cnemial crest is crushed and broken, but it could not have extended distally very far. As in Deinonychus (Ostrom 1969) and ornithomimids (Osmolska *et al.* 1972), there is a sharp ridge along the anterolateral edge of the shaft for contact with the fibula. The ridge ends about a third of the way down the shaft. The distal end of the tibia is flat. A distinct facet on the anterior surface
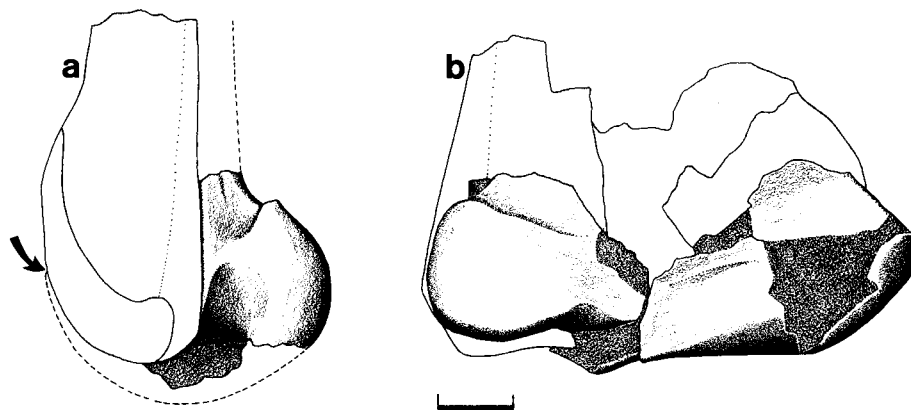
FIG. 9. *Chirostenotes pergracilis*. Astragalus (NMC 8538) in (*a*) lateral and (*b*) anterior views. Arrow indicates posterodorsal limit of astragalus on tibia.

shows the position of part of the synarthrosis (synostosis) with the ascending process of the astragalus. The ascending process extended at least 58 mm up the shaft of the tibia. Distolaterally, there is a distinct facet on the tibia for contact with the fibula.

Two pieces of the distal end of the tibia are preserved with the type specimen of "*Macrophalangia canadensis.*" Most of the anterior face of the distal end is a shallow concavity for contact with the astragalus. However, near the lateral margin, a low, ascending ridge seems to separate the synarthrosis with the astragalus from that of the calcaneum. A knob-like thickening near the centre of the distoanterior edge continues dorsally as a low ridge. The tibial – astragular synarthrosis covers the entire ventral surface of the tibia and even extends onto the posterior aspect of the tibia laterally (Fig. 9*a*).

Fragments of the right astragalus are found with NMC 8538, but they were not put in proper association when the specimen was prepared (Fig. 9). The width of the medial condyle is about 40 mm, compared with 25 mm in the lateral condyle. In contrast with the "albertosauroid" and "ornithomimoid" types of astragali (Welles and Long 1974), there is no pronounced horizontal groove separating the lateral and medial condyles from the ascending process (Fig. 9*a*). Only the dorsal portion of the lateral condyle is preserved, but it appears to have been separated from the rest of the condyle by a shallow, horizontal groove. The lateral margin is deeply excavated, indicating that there was a small but separate calcaneum, in contrast with *Troodon* (= "*Stenonychosaurus*"), in which the calcaneum is lost as a discrete element (Russell 1969). Nevertheless, the overall morphology of the astragalus is closest to the "ornithomimoid" types of Welles and Long (1974). *Microvenator* has a tall astragalus, with condyles of similar proportions to those of *Chirostenotes*, and a shallow horizontal groove above the condyles. Also it is similar in having only a small but separate calcaneum (Ostrom 1970).

With the exception of the proximal portion of metatarsal I, all of the right metatarsus of TMP 79.20.1 is preserved (Fig. 10) and compares closely with NMC 8538 and ROM 781 (Fig. 12). In all specimens, metatarsal II is slightly shorter than metatarsal IV, which in turn is shorter than metatarsal III.

Metatarsals II to IV have not co-ossified proximally in TMP 79.20.1, as they have in *Elmisaurus* (Osmolska 1981; Currie, in preparation). However, the fact that the central parts of the shafts of the third metatarsals of both NMC 8538

and ROM 781 were eroded away but left the proximal ends of the same metatarsals in proper association with the second and fourth metatarsals suggests that these three elements were closely associated and may have co-ossified in old individuals.

As in many theropods, the first metatarsal was divided into proximal and distal segments as the intervening shaft failed to ossify. The proximal segment is absent in even the well-articulated NMC 8538 (C. M. Sternberg 1932), and its persistant absence leads one to speculate that this element may have failed to ossify or been lost in *Chirostenotes* specimens. There is a large, triangular articular facet on the proximolateral half of the distal segment of the first metatarsal, showing the nature of the articulation with metatarsal II. This strongly suggests that the shaft of metatarsal I did not continue dorsally as a cartilaginous rod but had become totally suported by the second metatarsal. The point of contact between the two bones can be seen in NMC 8538, which was articulated when discovered (C. M. Sternberg 1932), and the distal end of metatarsal I was about 20% of the length of the second metatarsal from the end of the same. The articular facet for metatarsal I can be seen on the posteromedial corner of NMC 9570 (Fig. 11*c*), and it ends 53 mm (20%) from the end of the bone. The longitudinal axis of metatarsal I diverged about 25° from the metatarsus.

The second, third, and fourth metatarsals of TMP 79.20.1 are more slender distally than their equivalents in NMC 8538 (Figs. 12, 13), even though they are only about 10% shorter. The type specimen of "*Ornithomimus elegans,*" ROM 781, is almost 20% shorter than the metatarsus of TMP 79.20.1 and is even more gracile (Fig. 12*b*). The correlation between size and gracility suggests that the differences may be related to age at time of death, but it seems more likely to us that it is a combination of age and sexual differences.

Metatarsal II is crushed like the other metatarsals of TMP 79.20.1, and many anatomical details are obscured. As in ROM 781 (Parks 1933), the shaft diameter seems to have been slightly less than that of the fourth metatarsal, in contrast with *Troodon* (Wilson and Currie 1985), where the fourth is much more massive than the second. Although preservation again makes it uncertain, it appears as if the second and fourth metatarsals contacted each other proximally for about 5 mm along the anterior surface of the metatarsus. This contact can be seen in ROM 781, and it may also have been present in NMC 8538. The lateral surface of the second metatarsal of TMP 79.20.1 has a slightly rugose area for interosseous con-
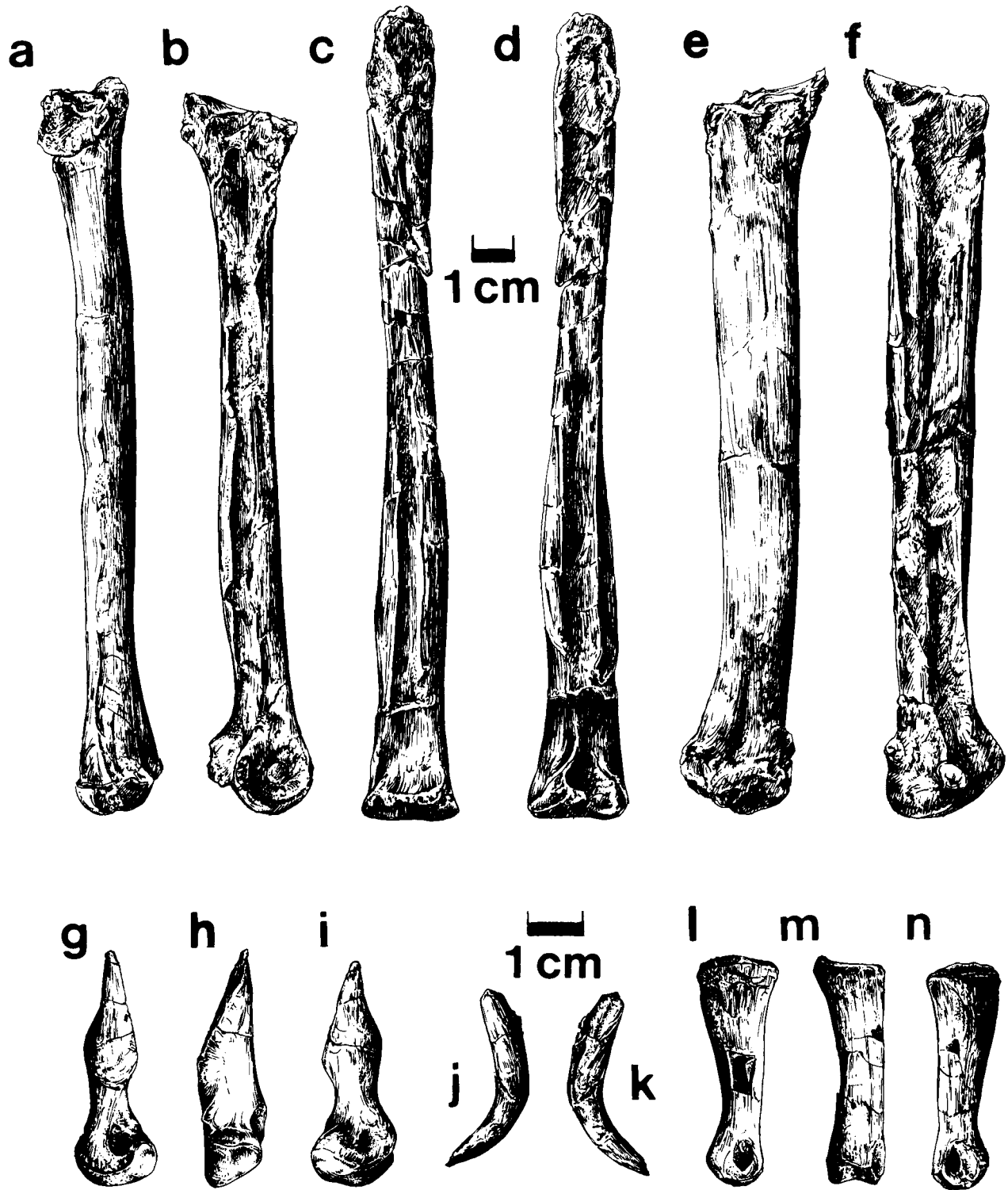
FIG. 10. *Chirostenotes pergracilis*. Pes elements of TMP 79.20.1, including metatarsal II in (*a*) extensor and (*b*) lateral views; metatarsal III in (*c*) anterior and (*d*) posterior views; metatarsal IV in (*e*) extensor and (*f*) flexor views; metatarsal I in (*g*) lateral, (*h*) extensor, and (*i*) medial views; metatarsal V in (*j*) anterior and (*k*) posterior views; and phalanx I-1 in (*l*) medial, (*m*) extensor, and (*n*) lateral aspects.

tact with the third metatarsal. The synarthrosis starts 24 mm from the distal end of the bone and shows that the distal end of the second metatarsal was excluded from the anterior surface of the metatarsus by the third. Approximately 70 mm from the distal end of the bone, however, it is evident that the relationship between the two bones is changing and that the proximal half of the second metatarsal excludes the third from the anterior surface of the foot.

Russell (1984) briefly described a left second metatarsal (NMC 9570, Fig. 11) from the Horseshoe Canyon Formation of Alberta. It is well preserved and has suffered little from crushing. The proximal end evidently did contact metatarsal IV,
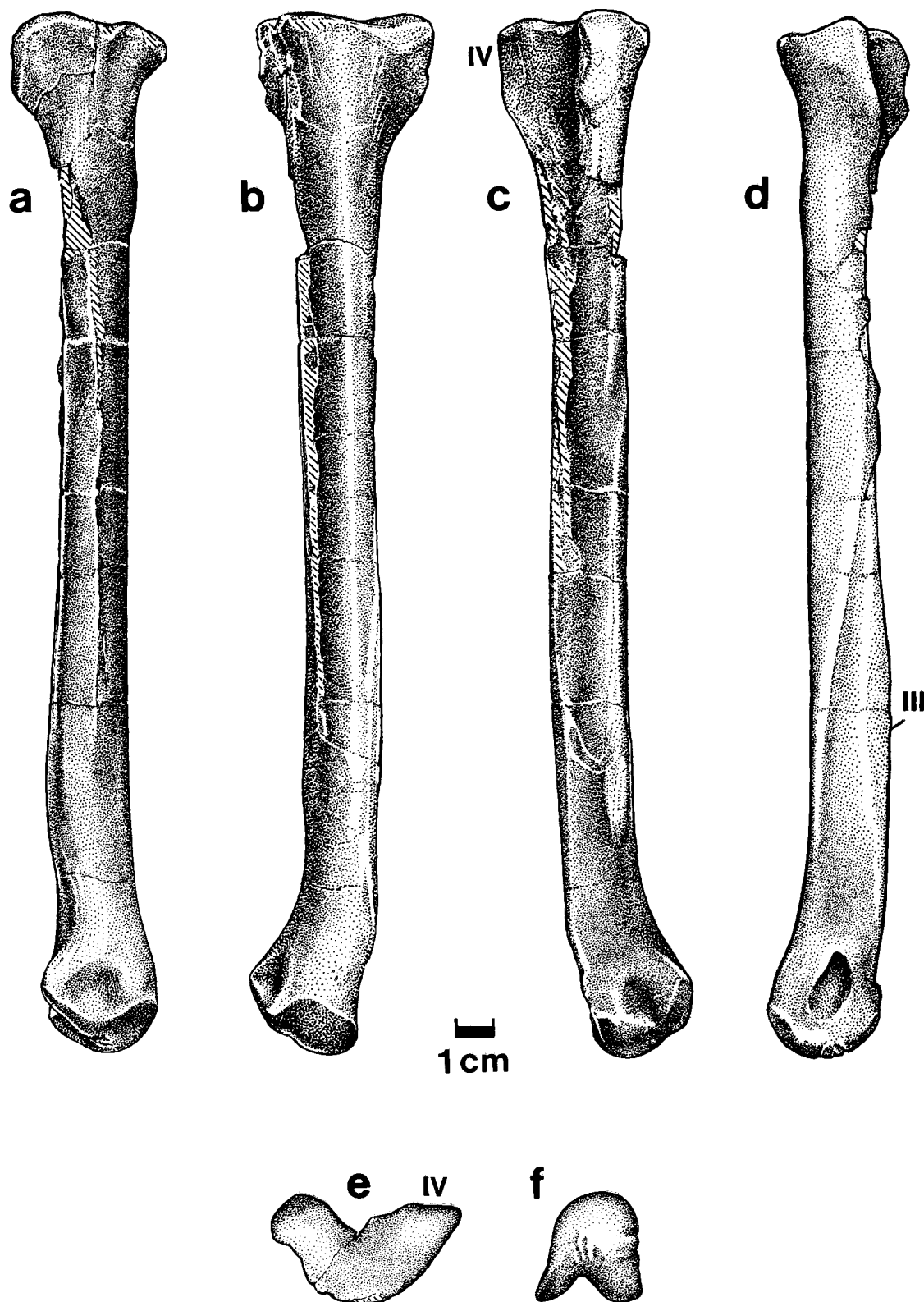
FIG. 11. *Chirostenotes* sp. Left second metatarsal (NMC 9570) in (*a*) medial, (*b*) anteromedial, (*c*) posterior, (*d*) lateral, (*e*) proximal, and (*f*) distal views. Articular surfaces for other metatarsals are identified by metatarsal numbers.

thereby excluding metatarsal III from the anterior surface of the metatarsus for at least 25 mm (Figs. 11*c*–11*e*). Articular facets for metatarsals I (Fig. 11*c*) and III (Fig. 11*d*) can easily be seen. This metatarsal is 260 mm long, about 144% the

length of that of TMP 79.20.1 and 124% that of NMC 8539.

The third metatarsal is complete and has not suffered as badly from crushing as the adjacent metatarsals. As in troodontids (Wilson and Currie 1985), ornithomimids (Fig. 12*f*),
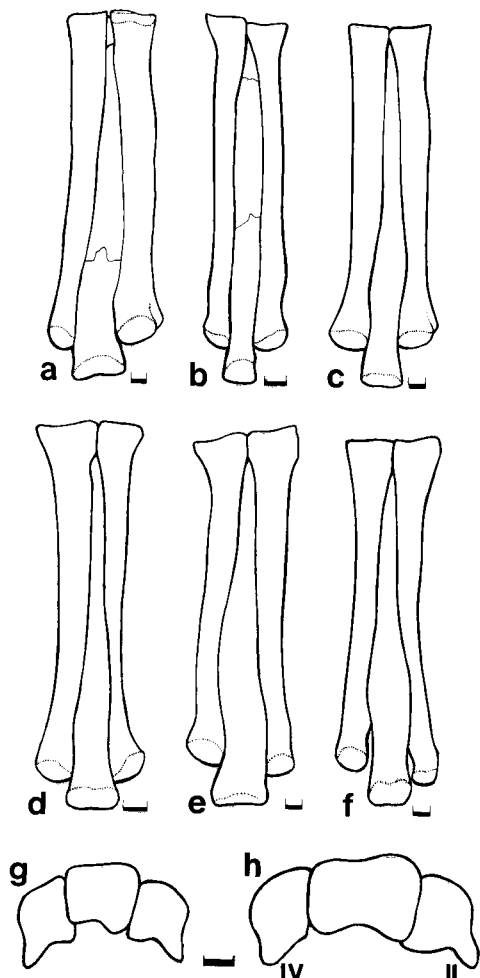
FIG. 12. Right metatarsals II, III, and IV of (a) *Chirostenotes pergracilis*, NMC 8538, (b) *Chirostenotes pergracilis*, ROM 781, (c) *Chirostenotes pergracilis*, TMP 79.20.1, (d) *Elmisaurus rarus* (after Osmolska 1981), (e) *Oviraptor* (from an unpublished photograph), and (f) *Ornithomimus velox* (after Osborn 1917). Distal view of left metatarsus of (g) TMP 79.20.1 and (h) NMC 8538. Each scale = 1 cm.

and tyrannosaurids (Russell 1970), the third metatarsal is pinched proximally. The proximal end, viewed dorsally, is diamond shaped, tapering both anteriorly (between the contact of metatarsals II and IV) and posteriorly. Its major horizontal axis, 17.5 mm long, is anteroposterior in orientation and thins backwards. Below this point, the bone twists until the medial surface is facing anteriorly and has in fact become the anterior surface of the metatarsus. Within a centimetre from the proximal surface, the anterior edge has broadened out to 7.5 mm to separate the adjacent metatarsals and is triangular in section. This may be different than in ROM 781, where the proximal end is triangular with an angle in front (Parks 1933). This is also the case in *Elmisaurus* (Currie, in preparation). There is no evidence of the foramen passing between metatarsals III and IV as in *Elmisaurus* (Osmolska 1981) and birds (Brett-Surman and Paul 1985), but this may be a result of crushing. At its widest point 49 mm from the end of the bone, the anterior surface of the third metatarsal is 19.0 mm lateromedially. In section, a shallow concave surface faces posteriorly at this level, while slightly concave surfaces face posteromedi-

ally and posterolaterally for contact with the adjacent metatarsals. The articular surfaces for the second and fourth metatarsals are well defined by ridges in the lower half of the third. The distal end of the synarthrosis with the fourth metatarsal is more distal than that with metatarsal II (Fig. 10). In contrast with *Troodon* (Russell 1969) and ornithomimids (Osborn 1917), where the distal ends of metatarsals II and IV almost touch posteriorly, these bones are well separated by III in *Chirostenotes*. The distal articulation of metatarsal III is slightly different in proportions in TMP 79.20.1 and NMC 8538 (Figs. 12g, 12h), but there is still the same basic configuration. As in ornithomimids, the distal articulation continues posteriorly on a pair of converging ridges (Fig. 10d).

Like metatarsal II, the fourth metatarsal is crushed in TMP 79.20.1. It is evident in NMC 8538 and ROM 781, however, that this bone is almost as wide as it is long anteroposteriorly. The distal articulation is a modified ovoid joint, essentially triangular in outline, with a posterolateral extension. It is almost the mirror image of the distal articulation of metatarsals I and II. These joints allow considerable range of flexion and extension and limited abduction–adduction.

A small, boomerang-shaped bone is probably the fifth metatarsal of TMP 79.20.1 (Figs. 10j, 10k). The bone is wide at one end, where it is convex on one side and concave on the other, and tapers to a point distally. This shape is typical of allosaurids (Madsen 1976), tyrannosaurids (Lambe 1917), and troodontids (Russell 1969), although it remains straight in many of the earlier theropods such as *Dilophosaurus* (Welles 1984), *Compsognathus* (Ostrom 1978), and *Deinonychus* (Ostrom 1969). C. M. Sternberg (1932) reported that metatarsal V is represented by a splint of bone on the posterior surface of the metatarsus of NMC 8538. This splint is not boomerang shaped, however, and it is 44 mm long, which is considerably larger than that of TMP 79.20.1. Because of the crushed condition of the specimen and its position on the posteromedial edge of the fourth metatarsal, it may in fact represent a splinter of the fourth.

Two pedal phalanges (I-1, III-1) were preserved with TMP 79.20.1 (Figs. 10, 13), both of which compare well with the equivalent elements in NMC 8538 (Fig. 13). The shaft of I-1 is slightly more curved in TMP 79.20.1, suggesting that this digit was more divergent. Its relative length, 19% of the length of metatarsal III, is shorter than that of NMC 8538 (26%) and compares better with that of *Elmisaurus* (17%, Osmolska 1981). The proximal articulation is a modified ovoid with some capability for abduction and adduction, whereas the distal articulation is a typical modified sellar (ginglymoid) joint with very limited abduction–adduction. The third metatarsal–phalangial joint is a very weak, modified sellar joint, and it is wider than it is high and therefore would have been capable of only flexion and extension. The first phalanx of the third digit is approximately 30% the length of the third metatarsal in both TMP 79.20.1 and NMC 8538.

Discussion

The new specimen of *Chirostenotes* (TMP 79.20.1) shows a suite of diagnostic characters, many of which are shared with *Elmisaurus*. There are six sacral vertebrae with pleurocoels. Metacarpal I is slender and straight, and the longest phalanx is II-2. The third digit of the manus is long and slender, and the manal unguals each have a posterodorsal "lip" above the proximal articulation. The ilium has a short postacetabular
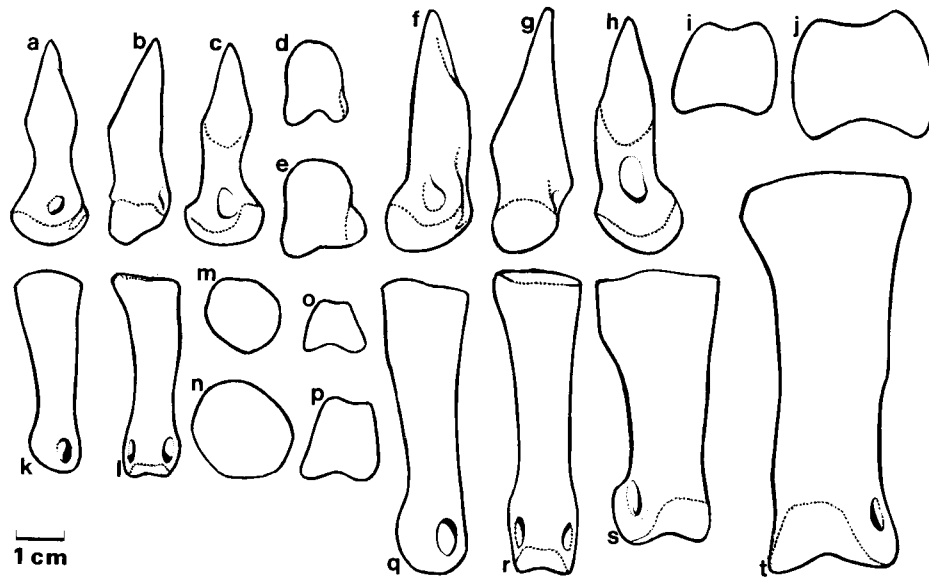
FIG. 13. *Chirostenotes pergracilis*. Comparison of (*a−h*) metatarsal I, (*k−r*) pedal phalanx I-1, and (*i, j, s, t*) pedal phalanx III-1 between TMP 79.20.1 (*a−d, i, k−m, o, s*) and NMC 8538 (*e−h, j, n, p−r, t*).

blade and has a convex dorsal margin in lateral view. The pubis inclines anteroventrally, and the ischium is relatively short. The femur is relatively long, and the tibia/femur and metatarsus/femur ratios are high. The base of the lesser trochanter is located farther down the shaft of the femur than in other theropods. The ascending process of the astragalus is high, the medial condyle is wider than the lateral, and the condyles and ascending process are not separated by a pronounced horizontal groove. The calcaneum is small but distinct. Metatarsals II and IV contact each other proximoanteriorly, and there is a tendency for tight contact or fusion of the tarsometatarsus.

The combination of manual and pedal characteristics seen in TMP 79.20.1 and *Elmisaurus* shows that these animals are closely related. The one major difference is the fusion of the tarsometatarsus in *Elmisaurus*, a feature normally associated with maturity rather than generic distinction. It would have been tempting to synonymize these genera if a fused tarsometatarsus had not been found in the same beds that produced *Chirostenotes* (Currie, in preparation). This specimen is being referred to as *Elmisaurus* and can be distinguished from *Chirostenotes* by the shape of the proximal end of the third metatarsal. The degree of fusion suggests that it is a very mature animal, but it is considerably smaller than any known specimens of *Chirostenotes*.

There are many similarities in the postcranial skeletons of *Chirostenotes* and *Oviraptor*, including the relative proportions of manual digits I and III, the presence of a dorsoposterior "lip" on the manual unguals, the shape of the ilium, the arrangement of the metatarsus, and the six sacral vertebrae with pleurocoels. These similarities strongly suggest that the elmisaurids *Chirostenotes* and *Elmisaurus* are very closely related to *Oviraptor*. Because *Oviraptor* and *Caenagnathus* are obviously related, it can be inferred that *Caenagnathus* is also related to *Chirostenotes* and may even be conspecific. At this stage, we are confident enough of the relationship to treat the "Elmisauridae" as a junior synonym of the Caenagnathidae, but we feel that additional specimens are needed to deter-

mine whether *Caenagnathus* is synonymous with *Chirostenotes* and (or) *Elmisaurus*.

Microvenator from the Lower Cretaceous of Montana is poorly known but includes a number of characteristics that hint at caenagnathid affinities. These include the proportions of a posterior sacral centrum, the shape and proportions of the first metacarpal, the presence of a dorsoventral lip on one of the manal unguals, limb proportions, the morphology of the astragalus, and the presence of a small but distinct calcaneum. As in *Oviraptor*, the neural spines of the cervical vertebrae are very low.

A pair of small theropod jaws were referred to *Chirostenotes* by Gilmore (1924) solely on the basis of their slenderness. This is not sufficiently good evidence to establish the identification. The presence of small, serrated teeth suggests that this is a new type of dromaeosaurid (Currie *et al.*, in preparation) that is not closely related to the caenagnathids, and the assignment to *Chirostenotes* is very dubious.

Chirostenotes includes two morphs, one defined by a gracile foot (ROM 781, TMP 79.20.1) and the other by a more robust metatarsus (NMC 8538). Both morphs are known from the Judith River Formation, and as closely related species tend not to be sympatric, it seems most logical to assume that the two morphs represent sexual differences. If this is true, then all specimens can be referred to *Chirostenotes pergracilis*.

The alternative, more conservative approach would be to recognize two species. However, this introduces many problems with nomenclature and association. The third manal digit of TMP 79.20.1 is more slender than that of the type specimen and is associated with the gracile type of foot. By inference, the type specimens of *Chirostenotes pergracilis* and "*Macrophalangia canadensis*" may represent the heavier of two species, and "*Ornithomimus elegans*" and TMP 79.20.1 the lighter form. The valid names for the species would then be *Chirostenotes pergracilis* Gilmore 1924 and *Chirostenotes elegans* (Parks 1933). *Caenagnathus collinsi* is more robust than *Caenagnathus sternbergi*, and therefore these species may represent *Chirostenotes pergracilis* and *C. elegans*, respec-

tively. Both of these jaws are about the right size for *Chirostenotes* and are probably too large for the *Elmisaurus* species found in Alberta. However, it should be noted that *Elmisaurus rarus* from Mongolia is almost the same size as *Chirostenotes*, so the jaws of *Caenagnathus* cannot be associated with any degree of certainty with either species of *Chirostenotes* or with *Elmisaurus*.

Given the problems that exist in associating caenagnathid specimens, it is recommended that only three species be recognized at this time, *Chirostenotes pergracilis* from Alberta, *Elmisaurus rarus* from Mongolia, and an undiagnosed species of *Elmisaurus* from Alberta. *Microvenator celer* may turn out to be a primitive caenagnathid.

Barsbold (1977) suggested that the powerful, toothless jaws of *Oviraptor* were well adapted for crushing molluscs. The long hind limbs and large feet of *Chirostenotes* could be interpreted as adaptations for wading, whereas the hands would have been capable of collecting molluscs and other freshwater invertebrates as well as eggs. The short postacetabular iliac blade, short ischium, ventrally positioned lesser trochanter, and long sacrum suggest that the tail was relatively short.

Examination of the metacarpal–phalangial joints of *Chirostenotes* shows that the first digit was not opposable to the others. Digit III was long and very slender and is reminiscent of syndactylous digits of marsupial mammals. However, it appears to have been capable of a considerable range of adduction and abduction, which strongly suggests that it was free to move independently of the second digit. The specialized third digit may have been used for prying insects and other invertebrates from crevices in the stream or trees or possibly for "grooming."

Oviraptoroids are one of the most enigmatic and specialized groups of theropods known. The true functions of the toothless jaws, short tail, slender hands, long hind limbs, and wide feet may never be determined with certainty but would be expected in egg- and mollusc-eating waders.

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