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Skeletal Morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia¹

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ABSTRACT

A detailed description of the holotype specimen of *Mononykus olecranus*, a basal flightless bird from the Late Cretaceous Nemegt Formation of Mongolia, is presented. The holotype comprises a fragmentary skull, most precaudal vertebrae, fore and hindlimbs, the thoracic girdle, and fragments of the pelvis and synsacrum. In the skull, caudal, dorsal, and rostral tympanic recesses are well developed. The maxilla is toothless, and the anterior margin of the antorbital fossa lacks accessory fenestrae. The only dental element found is a tiny isolated tooth that lacks serrations and has a constricted base. The axial skeleton is remarkable in having a biconvex posterior dorsal vertebra, and

keeled posterior synsacral vertebrae. The forelimb is short and extremely robust. The humerus bears a prominent deltopectoral crest. The olecranon process of the ulna is hypertrophied. The carpo-metacarpus is very short, subquadrangular, and massive. The alular digit is extremely robust, bearing a robust ungual phalanx. The sternum is stout and carinate. In the pelvis, the ilium bears a strong antitrochanter and the pubis is retroverted. The hindlimb is gracile. In the femur the trochanteric crest is undivided, and the popliteal fossa is bounded distally by projections from both condyles. The tibia and proximal tarsals are partially fused. Two cnemial crests are present on the tibio-

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tarsus. The metatarsals are unfused; metatarsal III is completely reduced proximally and does not reach the tarsus.

Mononykus olecranus emphasizes the complex-

ity of the transition between nonavianian theropods and modern birds, witnessing the differentiation of a totally new group of basal birds during the Cretaceous.

INTRODUCTION

The discovery of *Archaeopteryx lithographica* in the second half of the last century was a critical step in documenting the early evolution of birds. Since this discovery, and especially in the last 20 years, the description of several taxa of nonavianian theropods (Ostrom, 1969; Barsbold 1983), paralleled by developments in systematic procedure (Swoford, 1985; Farris, 1988; Maddison and Maddison, 1992), has elucidated the special relationship between birds and some groups of nonavianian theropod dinosaurs. This hypothesis, strongly supported by character evidence, suggests that birds are a clade of maniraptoran dinosaurs (Gauthier, 1986). Until recently, however, new fossil remains of basal avialians have not been forthcoming.

Over the last ten years, a series of remarkable discoveries of avialian theropods has provided important new evidence concerning the origin and diversification of this group of vertebrates (Kurochkin, 1985; Chiappe, 1991, 1992; Sanz and Bonaparte 1992; Sanz and Buscalioni, 1992; Sereno and Rao, 1992; Zhou et al., 1992; Wellnhofer, 1992; and others). Although these findings have provided significant evidence about early avialian evolution, many are incomplete, and most are preserved in essentially two dimensions, making detailed description of critical osteological features difficult or impossible.

In a shorter paper, Perle et al. (1993a, b) provided a preliminary description of a new player in this discussion: *Mononykus olecranus*, a taxon of basal avialians represented by two well-preserved skeletons. This taxon is both larger than other basal birds and radically different in morphology. Instead of a small, winged animal, *Mononykus olecranus* is turkey sized and lacks specializations for flight. Because of space limitations, the earlier paper did not allow detailed morphological description or adequate discussion of either of the two specimens. In fact, slight differences may support their allocation to two distinct taxa. Details concerning only the

holotype specimen are provided here and in a separate paper devoted to the cranium.

The importance of this specimen is twofold. First, it documents the appearance of a previously unknown group of avialians (Norell et al., 1993a). Members of this group have now been identified (on the basis of shared derived characters) in the collections of the Mongolian-American Museum Paleontological Expedition collections from the Djadokhta (Tugrugen Shireh) and Barun Goyot (Khermeen Tsav) formations, and in collections of the 1923 Central Asiatic Expedition made in the Djadokhta Formation at Bayn Dzak (the Flaming Cliffs) (Norell et al., 1993a). Because of the unusual, but characteristic, morphology of *Mononykus olecranus*, we expect that other members of this group will be discovered in collections once the morphology has been documented. Second, the remarkable preservation of this specimen allows examination of features unknown or controversial in *Archaeopteryx lithographica*, thereby allowing the primitive condition for basal avialians to be ascertained. Thus, although the skeleton of *Mononykus olecranus* is highly specialized, it has direct bearing on the problem of the origin and early diversification of birds.

GEOLOGY

The holotype specimen of *Mononykus olecranus* was discovered by Namsarai B., a preparator at the Mongolian Museum of Natural History during the 1987 Soviet-Mongolian Paleontologic expedition. The holotype locality (fig. 1), Bugin Tsav, lies in South Gobi Aimak, southwest Mongolia.

The specimen is from the Nemegt Formation. The age of the Nemegt Formation is problematic. Like most Mongolian Mesozoic formations, chrono-stratigraphic data have yet to be produced. This is compounded by the high endemicity of the Mongolian fauna and a lack of intertonging relationships with

marine sediments (Lillegraven and McKenna, 1986).

The Nemegt sediments overlie those of the Barun Goyot Formation in the Nemegt Basin and themselves are overlain by Early Paleogene rocks. The absolute or correlative age of these beds cannot be ascertained, but best estimates based on intercontinental correlation of vertebrates usually place the Nemegt Formation in the mid-Maastrichtian (Jerzykiewicz and Russell, 1991). This is based on the occurrence of dinosaur taxa (e.g., *Saurolophus*) that are similar to North American Maastrichtian taxa.

The holotype specimen of *Mononykus olecranus* was collected from variegated, predominantly red sandstones as an associated skeleton with articulated fore and hindlimbs and vertebrae. In the immediate vicinity of the holotype skeleton the remains of chelonians and the tyrannosaurid *Tarbosaurus bataar* were recovered.

MATERIALS AND METHODS

Anatomic nomenclature mostly follows Baumel and Witmer (1993), using the English equivalents of the Latin terminology. The extrapolation of modern avian nomenclature to successive sister groups and even nonavian theropods is based on acceptance of the theropodan hypothesis of avialian origins (Ostrom, 1976a; Gauthier, 1986). For most features of modern birds it is possible to trace homologous structures in more basal birds and nonavian theropods.

Concerning taxonomic nomenclature, there is disagreement as to what level the term Aves should be applied. Traditionally it is used to name a group including all taxa descended from the last common ancestor of *Archaeopteryx lithographica* and modern birds, although Hennig's (1969, 1981) concepts of total group (e.g., Ax, 1987; Patterson, 1993) and crown group (e.g., Gauthier, 1986; Perle et al., 1993) have been also applied to this clade. In this paper we apply the crown-group concept (Hennig's method 1; see Patterson, 1993 and Norell et al., 1993b) following recent theoretical suggestions restricting the use of commonly used names to crown groups based on ancestry of extant taxa (Rowe and

Gauthier, 1992; De Queiroz and Gauthier, 1992; see also a different viewpoint in Lucas, 1992). Applied to birds this requires that Aves be restricted to the crown group (Gauthier, 1986), which is composed of all taxa descended from the last common ancestor of extant bird species. Gauthier (1986) further recognized the term Avialae for the traditional taxon Aves. The casual collective term "modern birds" corresponds to Gauthier's Aves, and "birds" refers to all avialians.

In our original report of *Mononykus olecranus* (Perle et al., 1993a) we used the spelling "*Mononychus*." After the publication of this report we learned that this name is preoccupied by a coleoptera, and therefore the spelling was modified to *Mononykus* (Perle et al., 1993b).

Although this study was based on the original specimen, most of the specimen photos in this paper (figs. 4A, 5, 6, 8, 10–18) were prepared from a cast of the holotype specimen prepared in polyurethane in the Department of Vertebrate Paleontology of the American Museum of Natural History. A list of anatomical abbreviations is given in Appendix 1.

SYSTEMATIC PALEONTOLOGY

THEROPODA
AVIALAE
METORNITHES

Mononykus olecranus
Perle et al., 1993

HOLOTYPE: GI N107/6 (Geological Institute, Mongolian Academy of Sciences). Includes a fragmentary skull preserving the braincase, a portion of the right maxilla, and a tooth; eight cervical and eight dorsal vertebrae; the first, part of the second, and the last synsacral vertebrae; and one proximal caudal vertebra; both forelimbs; incomplete left coracoid, both scapulae, and sternum; three proximal ends of ribs; the acetabular portion of the left ilium, and both proximal portions of the pubes; both femora, left and partial right tibiotarsi, proximal end of right fibula, proximal and distal portions of left metatarsals II–IV, phalanges of left digits II–IV, left metatarsal I and phalanges, distal por-

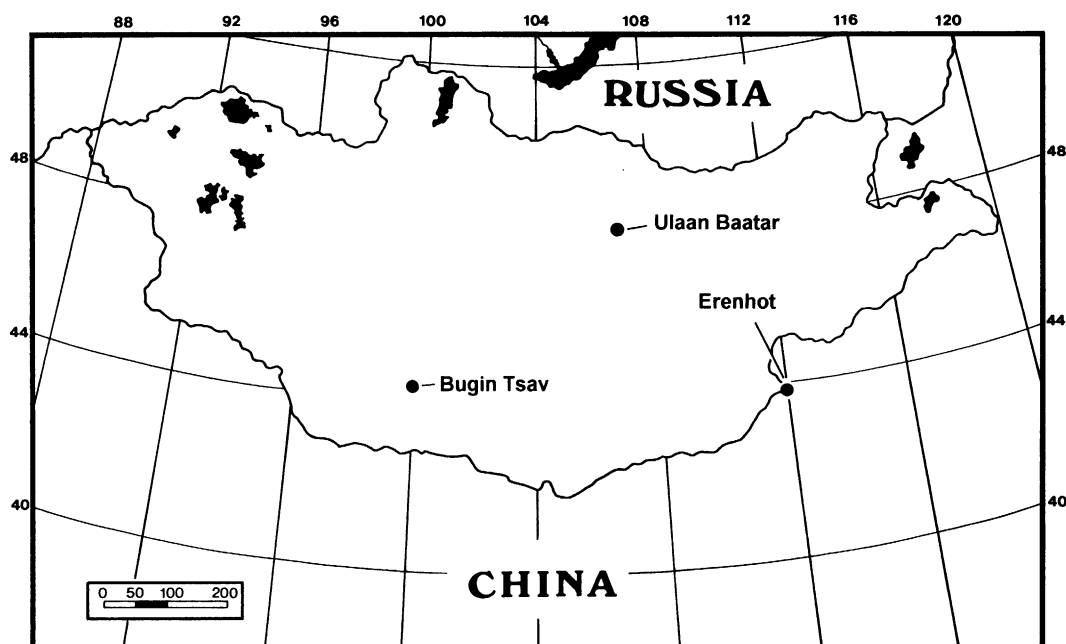


Fig. 1. Map of Mongolia indicating the locality of Bugin Tsav where the holotype specimen of *Mononykus olecranus* was found.

tion of right metatarsals II and IV, and several phalanges of the right foot.

LOCALITY AND HORIZON: Bugin Tsav, South Gobi Aimak, southwest Mongolia (fig. 1). Nemegt Formation (mid-Maastrichtian), Late Cretaceous (Jerzykiewicz and Russell, 1991).

DIAGNOSIS: *Mononykus olecranus* is diagnosed by an extremely robust and short forelimb with a pronounced deltopectoral crest of the humerus; single distal condyle of humerus; ventral tubercle of humerus pronounced; extremely short shafts of ulna and radius; very long olecranon process of ulna; carpometacarpus massive, short, quadrangular, with no intermetacarpal space; alular digit much larger than major and minor digits; claw of alular digit robust; anterior dorsal vertebrae with zygapophysial articulation surfaces in same plane as costal fossae and transverse processes; biconvex posterior dorsal vertebra; procoelic synsacral vertebrae; caudal synsacral vertebral bodies extremely compressed laterally and ventrally keeled; sternum with thick carina; robust and horizontally projected antitrochanter; two cne-mial crests on tibiotarsus; medial margin of

ascending process of astragalus excavated by deep notch.

DESCRIPTION

Skull

A detailed description of the holotype skull is presented elsewhere, which we briefly summarize here. Although only a fragmentary braincase, the rostral portion of the right maxilla, an isolated tooth, and other unidentifiable fragments are preserved, they afford significant evidence on the primitive avialian cranial morphology. Especially important is the middle ear region and its associated air sinuses. The tympanic cavity of *Mononykus olecranus* is bordered dorsally by the prootic, which forms part of the cotyla for articulation with the single-headed quadrate (fig. 2). This cavity is bordered caudally by the paroccipital process and the metotic strut, with the latter forming the posteroventral margin as well. The metotic strut forms the concave floor of the tympanic cavity. The columellar recess is large and confluent with the tympanic recesses. Inside the columellar recess,

a large subtriangular vestibular fenestra is separated from a large cup-shaped cavity by the crista interfenestralis; the latter cavity bears the cochlear fenestra rostrally, and the entrance of the caudal tympanic recess posteriorly.

The articular facet for the quadrate is formed by both squamosal and prootic. Caudal to the quadrate articulation lies a small foramen leading to an air-space inside the prootic, that we interpret as the dorsal tympanic recess. The caudal tympanic recess has both dorsal and ventrolateral entrances in the paroccipital process. Anteriorly, the facial foramen (CN VII) is single and at about the same level as the vestibular fenestra. Just ventral to the facial foramen is the entrance to the rostral tympanic recess, which has both dorsal and ventral outpocketings.

The only preserved rostral bone is an anterior fragment of the right maxilla (fig. 2). In lateral view, the ventral margin is sinusoidal in several small waves. It is interesting that although the dentigerous margin itself is not preserved, there is no indication of alveoli, suggesting that teeth were restricted to the unpreserved most anterior part of the maxilla or the premaxilla. Laterally, dorsal to the dentigerous margin, the maxilla is sculptured with fine striations, lacking the small nutrient foramina present in nonavian theropods such as *Velociraptor mongoliensis*. The rostroventral angle of the antorbital fenestra is preserved. Curiously, it appears that this portion of the maxilla is not perforated with an entrance to the antorbital sinus as in *Archaeopteryx lithographica* and nonavian theropods (Witmer, 1987, 1990).

A single tooth was found within the braincase close to the maxilla (see Perle et al., 1993: fig. 3). It is extremely small, laterally compressed, spatulate, and leaf shaped. The tooth surface is mostly smooth, although some fluting is present proximal to the apex. It possesses rostral and caudal carinae lacking serrations. The tooth base is constricted, just proximal to the end of the enamel covering.

Vertebral Column

The holotype specimen of *Mononykus olecranus* preserves 16 presacral vertebrae, the

cranial and caudal ends of the synsacrum, and a proximal caudal vertebra. As in many other fossils, the distinction between cervical and dorsal vertebrae is in some ways arbitrary, because the widely used criterion of identifying dorsals as those vertebrae carrying ribs articulated to the sternum (King and McLelland, 1984) cannot be applied. Hence, on the basis of general morphology, we consider that among the 16 presacral vertebrae, eight are cervicals, three cervico-dorsals, and five dorsals.

The vertebrae lack pleurocoels, and their bodies exhibit a remarkable lateral compression to an extent that varies in the different regions of the vertebral column.

CERVICAL VERTEBRAE: The exact number of cervical vertebrae of *Mononykus olecranus* is uncertain. Because none of the eight preserved elements are the atlas or the axis, however, a minimum number of 10 cervicals is estimated.

The cervical vertebrae are poorly preserved, but several remarkable features are visible. The vertebral arches are broad (especially in the anterior vertebrae) and the spinous processes are very low (fig. 3B, C). In the cranialmost vertebra, an anterior cervical, the vertebral arch is missing; however, on the basis of the morphology of the dorsal portion of the body, the vertebral arch was broad and probably low. The middle cervicals exhibit small dorsal tori on the caudal zygapophyses. In the posterior cervicals, the caudal zygapophyses become widely separated from each other, and the vertebral arches increase in height (fig. 3B, C).

The caudal articular facets of the cervical vertebrae of *Mononykus olecranus* are strongly concave (opisthocoelous), and the centra are very constricted medially (fig. 3A). The body of the first preserved vertebra is elongate and low; the cross section is nearly triangular. In the remaining anterior cervicals, the bodies are elongate and remarkably low as well. Caudally, the vertebral bodies gradually decrease in length (fig. 3B, C). Cranioventrally, the body of the anterior seven preserved vertebrae possesses a furrow bound by lateral tubercles (fig. 3A). This structure resembles the carotid process and groove through which the internal carotid artery

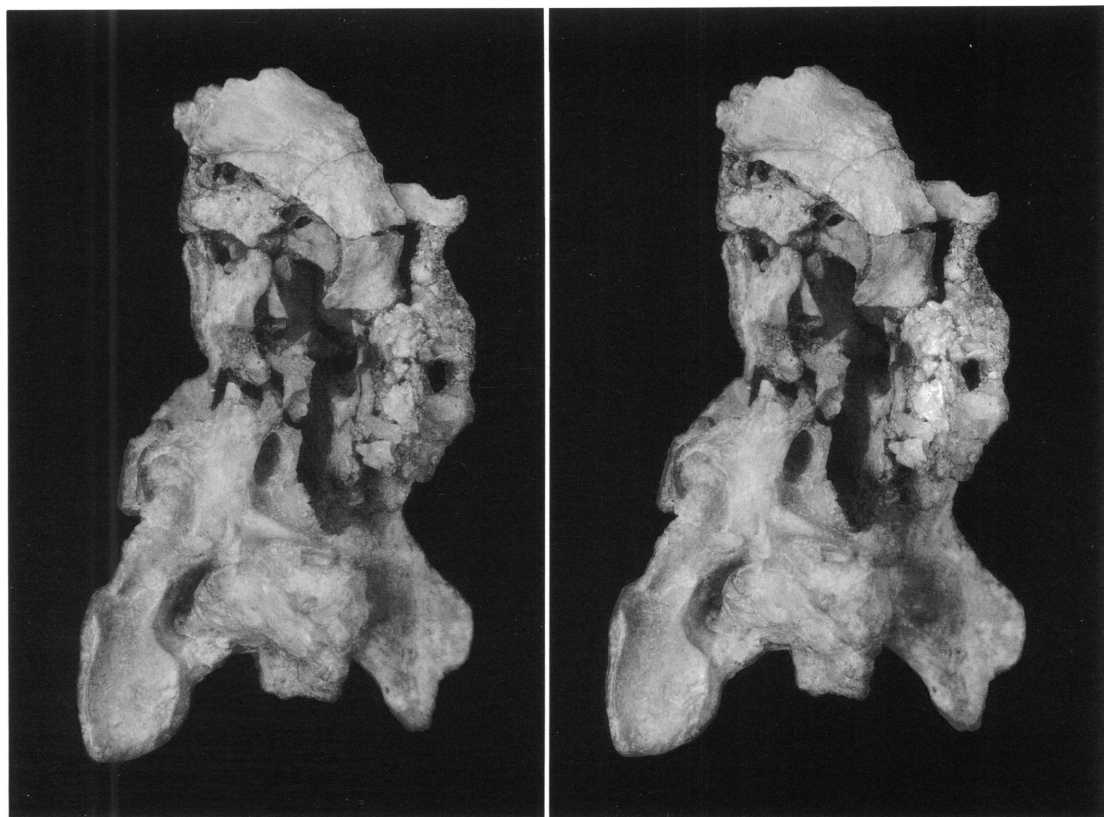


Fig. 2. Stereopair of ventrolateral view of skull, holotype specimen of *Mononykus olecranus*.

passes in modern birds. Lateral to the carotid process, and separated from it by a small groove, are robust and prominent costal foveae (fig. 3A, B). The cervical ribs of *Mononykus olecranus* were, therefore, not fused to the vertebrae.

CERVICODORSAL VERTEBRAE: Three articulated vertebrae are transitional between the typical cervicals and dorsals. These three vertebrae have a strongly concave (opisthocoealous) caudal articular facet (fig. 4A), and the cranial articular facet is distinctly ball-shaped (fig. 4B, C). The bodies of these vertebrae are very compressed, and their ventral surface forms a sharp ridge (fig. 4B). In the first vertebra no ventral process is present, while small ventral processes are developed in the second and third cervicodorsals (fig. 4C). The vertebral arch of these vertebrae is higher than in the cervical series. In the first vertebra the costal fovea is below the articular facet of the cranial zygapophyses, approximately at the

middle of the vertebral arch, while this articulation surface is located at the level of the cranial zygapophyses in the remaining two cervicodorsals (fig. 4C). An incipient infra-postzygapophysial fossa is present in the first cervicodorsal vertebra. This fossa increases in size and depth in the caudal two cervicodorsals (fig. 4A). The spinous process of the vertebral arch is preserved only in the second cervicodorsal vertebra; it is low and in lateral aspect has a dorsally convex outline (fig. 4C).

DORSAL VERTEBRAE: Only five dorsal vertebrae are preserved, and the actual number of dorsal elements is unknown. All dorsal vertebrae, with the exception of the last one preserved (see below), have concave (opisthocoealous) caudal articular facets (figs. 5C, 6A). As in the cervicodorsal vertebrae, the cranial articular facets of these vertebrae are distinctly ball-shaped (figs. 5A, B, 6B, 7A). The bodies of the dorsal vertebrae are strongly compressed laterally and, as in the remaining

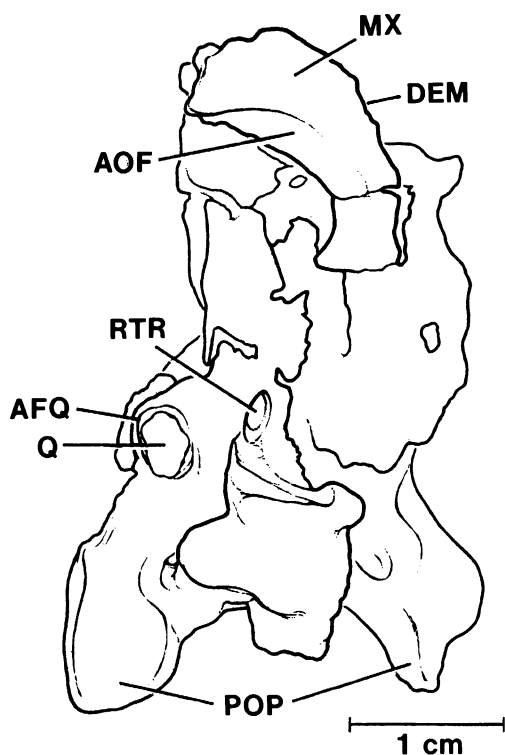


Fig. 2. Continued.

vertebrae, they lack pleurocoels (figs. 5, 6, 7). The degree of lateral compression decreases in more caudal vertebrae. The vertebral foramen is very large with respect to the body (figs. 5C, 6A, 7B, C). Dorsal vertebrae lack hyposphens and hypantra.

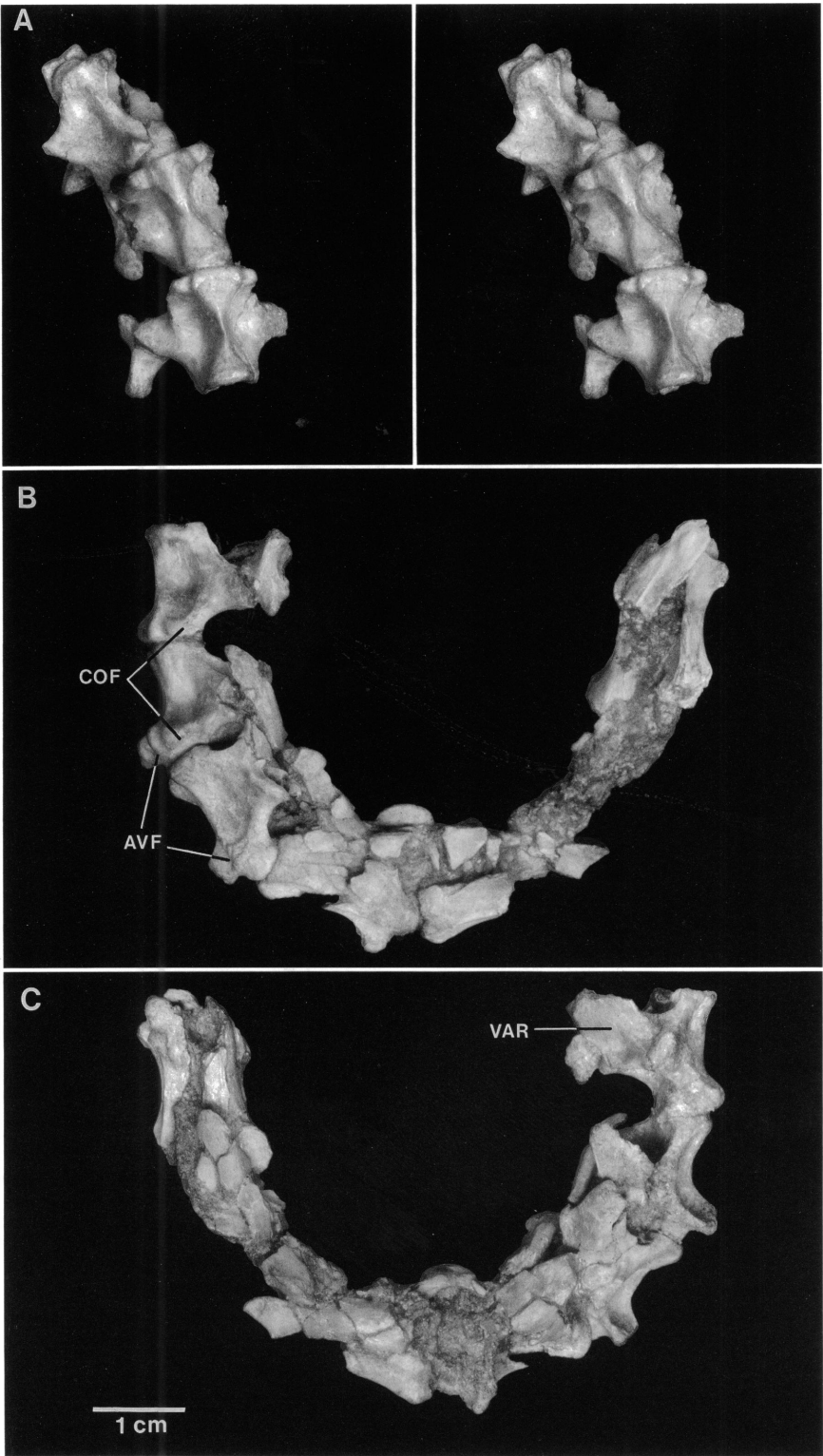
The first and second preserved dorsal vertebrae are very similar. The vertebral arches of these vertebrae are higher than the preceding ones. The costal foveae are at the same level as the transverse processes (fig. 5A). Likewise the zygapophysial articulation surfaces are in the same plane as the costal foveae and transverse processes (fig. 5B). The infrapostzygapophysial fossa is well developed (fig. 5C), becoming reduced posteriorly. The spinous process of the vertebral arch is low, and in lateral view exhibits a convex dorsal outline (fig. 5A, B). In the vertebral bodies, the caudal articular facets are vertically oval to subtriangular in caudal view (fig. 5C). The body of the first vertebra possesses

an outstanding ventral process projecting vertically from its cranial half (fig. 5A), but the ventral process of the second preserved dorsal vertebra is much less developed, similar to that in the cervicodorsal vertebrae (see above).

The next two preserved vertebrae are in articulation (fig. 6). In these elements the spinous process of the vertebral arch is much more developed than in the preceding dorsals (cf. figs. 5A, 6B), and has a bifurcated caudal tip (fig. 6A). In the first of these two vertebrae the spinous process is caudodorsally directed. In the more caudal vertebra, the spinous process is dorsally (vertically) directed, and also higher than in the more cranial vertebra (fig. 6B). In contrast to the condition in the preceding dorsal vertebrae, the costal foveae of these two vertebrae are located below the level of the zygapophyses (fig. 6B). The infrapostzygapophysial fossa of these two vertebrae is less developed than in the preceding dorsals (cf. figs. 5C, 6A). The vertebral bodies of these two elements differ from that of the preceding dorsals in that they have no ventral processes and the caudal articular facets are round instead of oval-subtriangular in caudal view (cf. figs. 5, 6).

The ultimate preserved dorsal vertebra differs from all other vertebrae of *Mononykus olecranus* in that the body has biconvex articular facets (fig. 7). In this vertebra costal foveae are absent from the centrum (fig. 7A). Because the transverse processes are broken, the relationship between the rib articulations is unclear. No infrapostzygapophysial fossa is present (fig. 7C). The body of this vertebra is less laterally compressed than in the preceding dorsals.

SYNSACRUM: Only the cranial and caudal ends of the synsacrum are present on the holotype specimen, basically preserving the vertebral bodies. The cranial extremity of the synsacrum (fig. 8A) is concave (procoelic) suggesting that if the biconvex dorsal is not the last dorsal, then the last element of the dorsal series was procoelic. The centrum of the first synsacral vertebra also exhibits the lateral compression of the presacral vertebrae, although (as in the biconvex dorsal) to a lesser degree than the anterior dorsals. The costal process of this vertebra is broad, and it was probably incorporated with the second



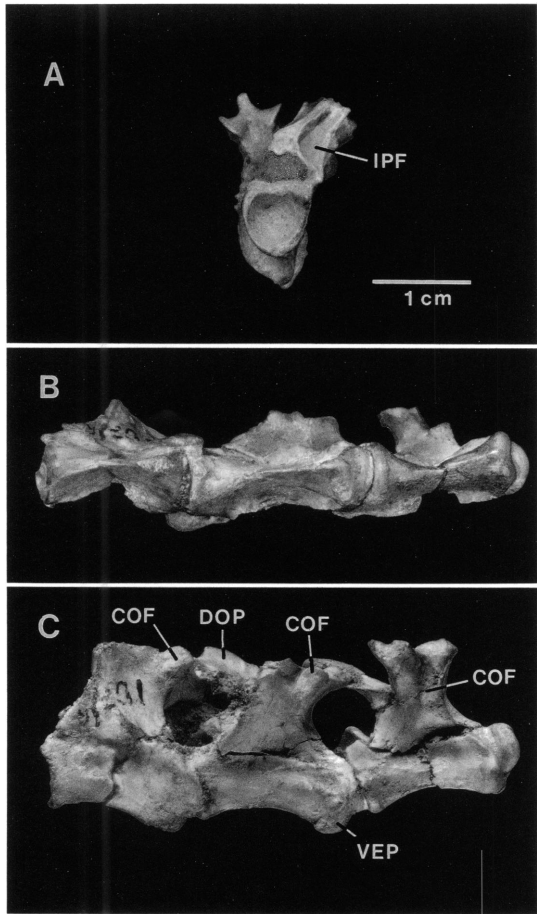


Fig. 4. Cervicodorsal vertebrae of holotype specimen of *Mononykus olecranus*. A, Caudal view of last cervicodorsal; B, ventral view; C, right lateral view.

sacral vertebra to form a continuous shelf. The caudal end of the synsacrum is laterally compressed and ventrally the centrum forms a well-developed keel (fig. 8B). The caudal articular surface is convex, indicating that the anteriormost caudal vertebra was procoelic. Caudal vertebrae: A single proximal caudal is preserved in the holotype specimen. The cranial articular facet of this vertebra is suboval and concave. The caudal articular facet

TABLE 1
Measurements (mm), Vertebral Column, Holotype Specimen of *Mononykus olecranus*

- A. Maximum length of centrum
- B. Width of centrum across parapophyses
- C. Maximum height of centrum + vertebral canal (measured caudally)

Preserved cervical vertebrae								
	C1	C2	C3	C4	C5	C6	C7	C8
A	17.5	—	—	—	16.9	14.5	13.7	13.4
B	6.4	8.2	—	—	—	9.3	11.2	10.5
C	—	—	—	—	—	15.3	—	—

Cervicodorsal vertebrae			
	CD1	CD2	CD3
A	15.1	17.2	—
B	6.2	6.5	6.7
C	—	20.1	—

Preserved dorsal (D) and sacral (S) vertebrae							
	D1	D2	D3	D4	D5	S1	S2
A	17.5	15.3	14.5	14.2	14.1	14.2	14.1
B	6.4	6.3	7.4	—	8.8	11.7	7.8
C	28.2	29.4	—	—	—	—	—

has a strong ball-shaped surface. The body is compressed laterally, and ventrally it forms a sharp edge.

Thoracic Girdle and Ribs

The holotype specimen of *Mononykus olecranus* lacks the furcula. Additional specimens must be examined before considering this either an artifact of the preservation or an apomorphic condition of this taxon. SCAPULA: Both scapulae are preserved in the holotype specimen. The scapula of *Mononykus olecranus* is firmly articulated, though not fused, to the coracoid (fig. 9). The scapular shaft is slender and lateromedially compressed, especially in the caudal half. In lat-

Fig. 3. Cervical vertebrae of holotype specimen of *Mononykus olecranus*. A, Stereopair of ventral view of last three preserved cervicals in ventral view; B, right lateral view of last seven preserved cervicals; C, left lateral view of last seven preserved cervicals.

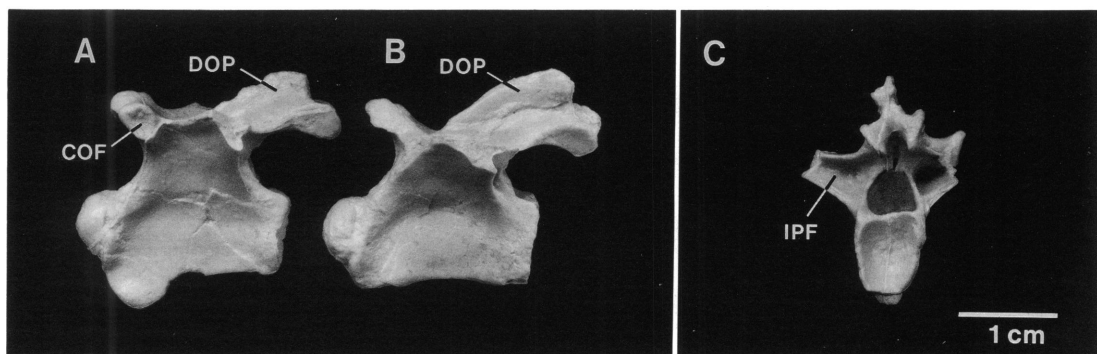


Fig. 5. Anterior first two preserved dorsal vertebrae of holotype specimen of *Mononykus olecranus*. A, B, Left lateral view; C, caudal view of the second one.

eral view the scapular shaft is straight with parallel dorsal and ventral margins. At the caudal end the scapular shaft widens and ends abruptly.

The cranial end is dorsoventrally expanded and somewhat curved medially. The acromion of the scapula is well developed. The humeral articular facet is slightly concave and faces cranioventrally. The scapula is thickest dorsal to this facet, at the level of the ventral part of the coracoid articular area. The surface for the attachment of the coracoid is subtriangular and much larger than the humeral articular facet.

CORACOID: Only the lateral part of the left coracoid is preserved in the holotype specimen. The coracoid is short, crescent-shaped, and broader than long (fig. 9). The coracoidal shaft is dorsoventrally flat, and laterally projected. No bicipital tubercle is present on the shaft of the coracoid. The lateral margin is deeply concave, and the sternal end is deeply convex. Below the scapular articulation, the shaft is perforated by a subcircular supracoracoid nerve foramen. The humeral articular facet is slightly convex and is displaced toward the ventral surface. This facet is developed in the same plane as the humeral articular facet of the scapula.

STERNUM: The sternum of *Mononykus olecranus* is a stout, elongate bone, that is subtriangular in cross section (fig. 10). It is very simple and small, with no processes or articular surfaces developed. The visceral surface is slightly concave. The sternum bears a robust carina (fig. 10A, B). Rostrally the carina possesses two ridges, the lateral crests, that

define a median groove (*sulcus carinae*) similar to the one present in some modern birds (e.g., galliforms, cathartids) (fig. 10A). The sternal body and carina taper caudally, although the most caudal end is missing.

The interpretation of this bone as a sternum is based on its general morphology (e.g., lateral crests, carina, concave visceral surface). It should be noted that no coracoidal or rib articular facets are present. This is unlike more advanced birds but similar to the condition present in nonavian theropods (Barsbold, 1983).

RIBS: Only the proximal ends of three dorsal ribs are preserved in the holotype specimen. Both the capitulum and tuberculum are well developed. The shafts of these ribs are not pneumatized and are strongly compressed craniocaudally.

Thoracic Limb

HUMERUS: The holotype specimen preserves both humeri, the left with the deltopectoral crest and the ventral tubercle missing. The humerus of *Mononykus olecranus* is short and robust (fig. 11). The proximal and distal ends are expanded in the same plane. The proximal extremity exhibits a prominent ventral tubercle, distinctly separated from the humeral head by a depression in the caudal surface (fig. 11C). This tubercle projects proximally and is ventrally directed. The humeral head is well developed, concave cranially, and convex caudally (fig. 11D). The humerus exhibits a hypertrophied, craniodorsally ori-

ented, deltopectoral crest, which rises from the dorsal margin of the humerus as a pillar like cross-sectionally oval structure.

The humeral shaft is massive and cranio-caudally compressed. Distally, it possesses only a single, large, condylar structure (fig. 11A). This condyle is subtriangular in cranial view, and is mostly developed on the cranial surface. In distal view, this structure is expanded craniocaudally and is also subtriangular (fig. 11E). The distal extremity of the humerus bears a prominent and robust dorsal epicondyle, projecting dorsodistally. The caudal surface of the distal end is concave, and no olecranon fossa is visible (fig. 11C).

ULNA: The holotype specimen preserves the right ulna and the distal part of the left one. The ulna is twice the length of the radius (fig. 12A). This is a result of the hypertrophy of the olecranon, which forms nearly half of the ulnar length. The olecranon is craniocaudally compressed and tapers proximally to form a rounded end. There is a single ulnar cotyla, subtriangular in proximal view (fig. 12B). The ulnar shaft is short and compressed dorsoventrally. The caudal border forms a stout ridge that proximally continues on the olecranon. No papillae for the insertion of secondary flight feathers are visible. The distal end bears a well-developed carpal trochlea that in distal view is subtriangular and caudocranially expanded (fig. 12C).

Radius: Both radii are preserved in the holotype specimen. The radius is short and robust (fig. 12A). Its proximal end is firmly sutured to the ulna over a large surface. The humeral cotyla of the radius is continuous with that of the ulna (fig. 12B). In dorsal or ventral view, both articular facets form a crescentic articular area for the reception of the single humeral condyle (fig. 12A). The radius contributes approximately one-third to this articular area. The distal end has a large radiocarpal articular facet oriented dorsocranially (fig. 12C) and extended proximally. The caudal face has a well-developed ligamental depression ventrally limiting the radiocarpal articular facet. This depression separates the dorsal portion of the radiocarpal articular facet from a proximal ventral extension of it that may be homologous to the ventral aponeurosis tubercle of modern birds. This articular surface continues ven-

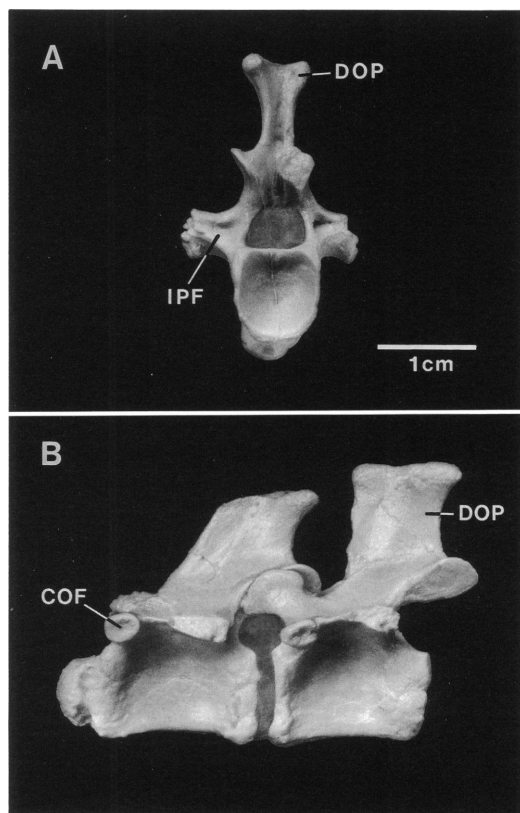


Fig. 6. Middorsal vertebrae of holotype specimen of *Mononykus olecranus*. A, Caudal view of the second one; B, left lateral view.

trally in a proximal projection nearly contacting the ulnar shaft (fig. 12A).

CARPOMETACARPUS: Both carpometacarpus are preserved in the holotype specimen. It is our contention that at least one distal carpal, presumably homologous to the "semilunate carpal" of *Archaeopteryx lithographica* and nonavianian maniraptorans (see Ostrom, 1976b), is fused with the alular metacarpal. These three metacarpus are in turn fused to each other without delimiting any intermetacarpal space (fig. 13B, C); the sutures delimiting these three bones are more distinct on the dorsal surface than on the ventral one. Dorsally, the carpometacarpus is convex, and it is concave ventrally.

The alular metacarpal of *Mononykus olecranus* is hypertrophied and is the largest bone of the carpometacarpus (fig. 13A, B, C). It is dorsoventrally compressed. Distally, the al-

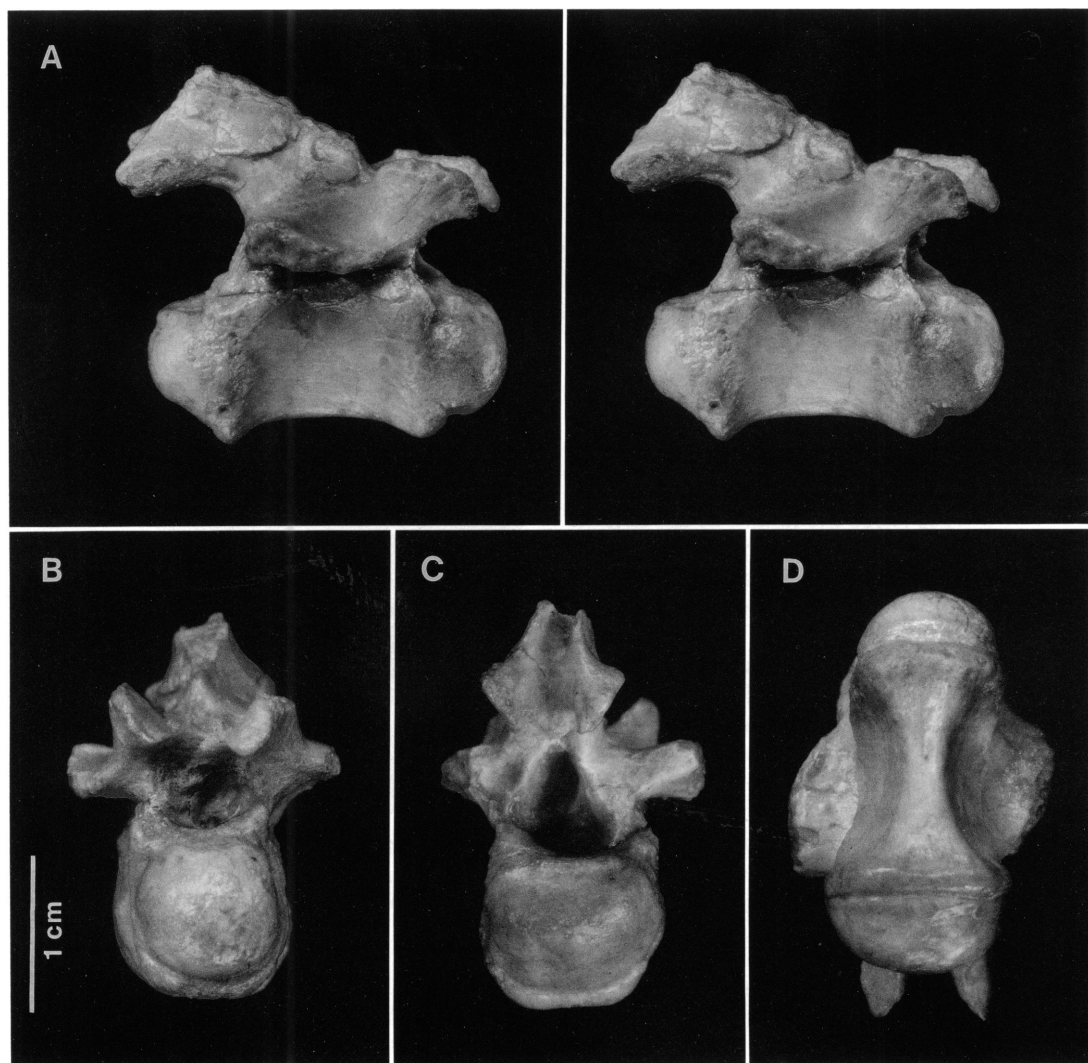


Fig. 7. Biconvex dorsal vertebra of holotype specimen of *Mononykus olecranus*. A, Stereopair of right lateral view; B, cranial view; C, caudal view; D, ventral view.

ular metacarpal possesses a well-developed articular trochlea, transversely elongated and dorsoventrally compressed (fig. 13A). The major and minor metacarpi are considerably smaller than the alular metacarpal, overhanging lateroventrally from the lateral margin of the latter. No intermetacarpal space is present between them. Distally, the major metacarpal bears a small, rounded articular surface (fig. 13A, B) suggesting the presence of a vestigial phalanx of the major digit. The minor metacarpal is even smaller than the major one (fig. 13C). As in the latter, the

distal end of the minor metacarpal possesses a small ball-shaped articulation indicating the possible presence of a vestigial minor digit.

The proximal articular surface of the carpometacarpus shows three distinct articular surfaces (fig. 13D). The medial one is pulley-like, and it is probably formed by the fused distal "semilunate" carpal. This interpretation is based on comparison with the carpus of *Archaeopteryx lithographica* and nonavian maniraptorans in which the semilunate bone also has a distal articulation in the form of a transverse trochlea, dorsoventrally com-

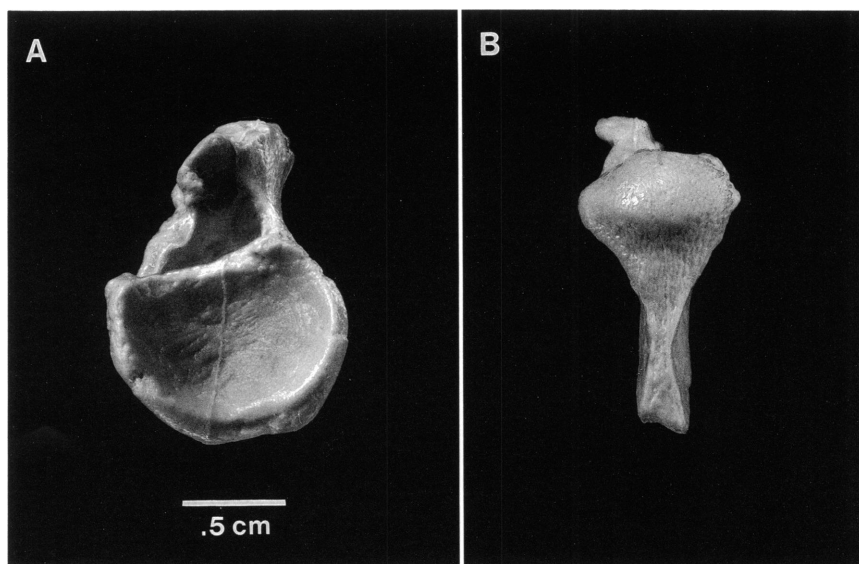


Fig. 8. Synsacrum of holotype specimen of *Mononykus olecranus* in cranial (A) and caudal (B) views.

pressed. If this were not the case, then we would expect the proximal end of the alular metacarpal to be concave rather than having a convex trochlear surface (fig. 13C, D). Lateral to this articular facet there is a subtriangular facet mostly formed by the alular metacarpal but also receiving a contribution of the major metacarpal. The third and most lateral articular facet is circular and considerably smaller than the other two. This facet, exclusively formed by the minor metacarpal, is nearly ventrally oriented, and it suggests the presence of a missing carpal. The relationships between these facets and the radius-ulna are not clear, and no free carpals have been preserved.

ALULAR DIGIT: The holotype specimen preserves both alular digits. The alular digit of *Mononykus olecranus* is large and very robust, comprising two phalanges (fig. 14A, B). The proximal phalanx is dorsoventrally compressed and highly asymmetrical (fig. 14C). The metacarpal articular facet is broad. A robust dorsal process projects from the dorsolateral corner of this facet. Ventrally, the lateral and medial borders of the phalanx form distinct ridges delimiting a broad axial furrow. The distal end of the proximal phalanx possesses a well-developed phalangeal articular facet. Proximal to this facet, on the dorsal surface, there is a subcircular depression

(fig. 14A). Fossae for the collateral ligament are present on both sides of the phalangeal articular facet (fig. 14B).

The distal phalanx of the alular digit is a robust ungual phalanx. This phalanx is arched and distally sharp (fig. 14A, B), although it is less arched than in *Archaeopteryx lithographica* and most nonavianian theropods (e.g., *Deinonychus antirrhopus*). The ventral area of the proximal end forms a flat surface; the flexor tubercle is completely absent. On both sides of this platform, small foramina are present (fig. 14D). Apparently these foramina were connected to the lateral and medial grooves of the phalanx.

Pelvic Girdle

Only a fragmentary portion of the left ilium and the proximal ends of both pubes are preserved.

ILIUM: The acetabular portion is the only available material (fig. 15A). In general, the ilium is low and the preserved postacetabular region is broader than the preacetabular one. The ilium is characterized by a robust and horizontally projected antitrochanter. The surface of the antitrochanter is convex and its main axis projects laterocaudally. The acetabular part of the ilium forms a large acetabular fossa pierced by a parabolic acetab-

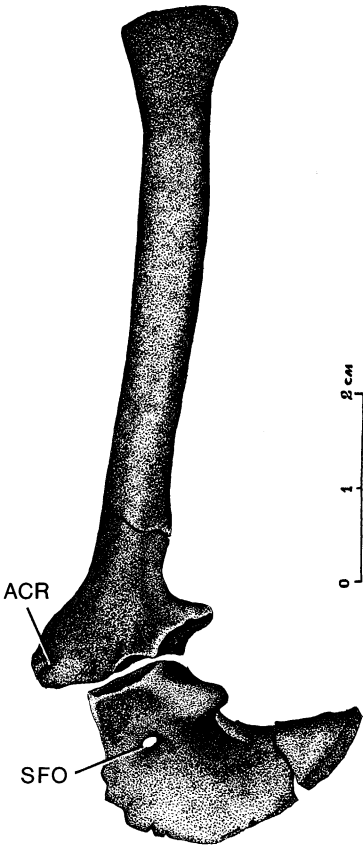


Fig. 9. Left scapula and coracoid of holotype specimen of *Mononykus olecranus* in lateral view.

ular foramen, with the main axis directed dorsocaudally. The ilium possesses a stout supracetabular crest overhanging the cranial half of the acetabular fossa (fig. 15A, B). The pubic peduncle is stout and subrectangular, with its main axis directed craniocaudally. The ischiadic peduncle is apparently either not developed or very reduced. The ischium would have abutted the ilium at the medio-ventral border of the antitrochanter. With the available material it is not possible to discern if the antitrochanter was exclusively formed by the ilium or if the latter bone and the ischium were fused, both contributing to the formation of this structure, as in modern birds.

PUBIS: *Mononykus olecranus* is opisthopubic (fig. 15A). The proximal end of the pubis is compressed laterally, and in proximal view the articular area for the ilium is

TABLE 2
Measurements (mm), Thoracic Girdle, Holotype Specimen of *Mononykus olecranus*

- A. Maximum length of coracoid between glenoid facet and sternal margin
- B. Length of lateral projection of coracoid from level of glenoid facet
- C. Maximum width of preserved portion of sternal end of coracoid
- D. Maximum width of preserved portion of shoulder end of coracoid
- E. Maximum dorsoventral width of scapular shaft
- F. Maximum laterocostal width of scapular shaft
- G. Maximum length of scapular shaft
- H. Maximum dorsoventral width of glenoid surface of scapulocoracoid
- I. Maximum axial width of glenoid surface of scapulocoracoid

	Left	Right
A	21.1	—
B	13.3	—
C	19.7	—
D	12.3	—
E	6.8	6.8
F	4.0	4.2
G	73.1	73.2
H	8.6	—
I	7.0	—

convex medially and concave laterally (fig. 15C). The pubic shaft is subtriangular in cross section; the lateral surface is flat, the medial convex, and the caudal one is concave. The pubis clearly contributes more than the ischium to the acetabular fossa and foramen.

Pelvic Limb

FEMUR: Both femora are preserved. Proximally there is a well-developed trochanteric crest, with no indication of distinct lesser (anterior) and greater trochanters (fig. 16A, B, D, F), in contrast to nonavian theropods and *Archaeopteryx lithographica*. The medial and lateral surfaces of this crest are slightly concave and convex, respectively. The trochanteric crest is only slightly projected proximally with respect to the femoral head (fig. 16A, C). The femoral head of *Mononykus olecranus* is stout with a circular cross section; a distinct fossa for the capital ligament is absent. The femoral neck is not constricted (figs. 16A, C). The femoral head is perpendicular to the trochanteric crest; in proximal

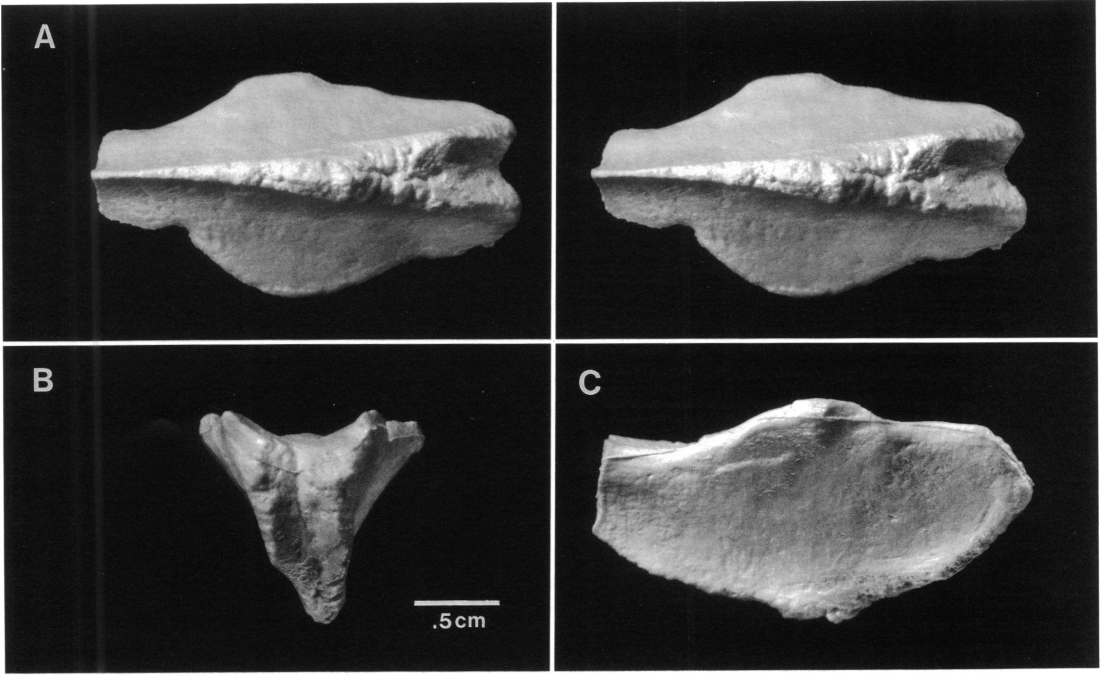


Fig. 10. Sternum of holotype specimen of *Mononykus olecranus*. A, Stereopair in ventral view; B, cranial view; C, right lateral view.

view these two structures give the proximal end of the femur an L-shaped aspect (fig. 16F). The femoral shaft of *Mononykus olecranus* is slender and craniocaudally bowed (figs. 16D). The mid-shaft area has a subtriangular cross section, with slightly convex craniola-

teral and craniomedial surfaces and a flat caudal surface. At the midpoint of the proximal half, on the medial margin of the caudal surface, there is a weak ridge that we interpret as the fourth trochanter (fig. 16C, D). Immediately distal and lateral to the fourth tro-

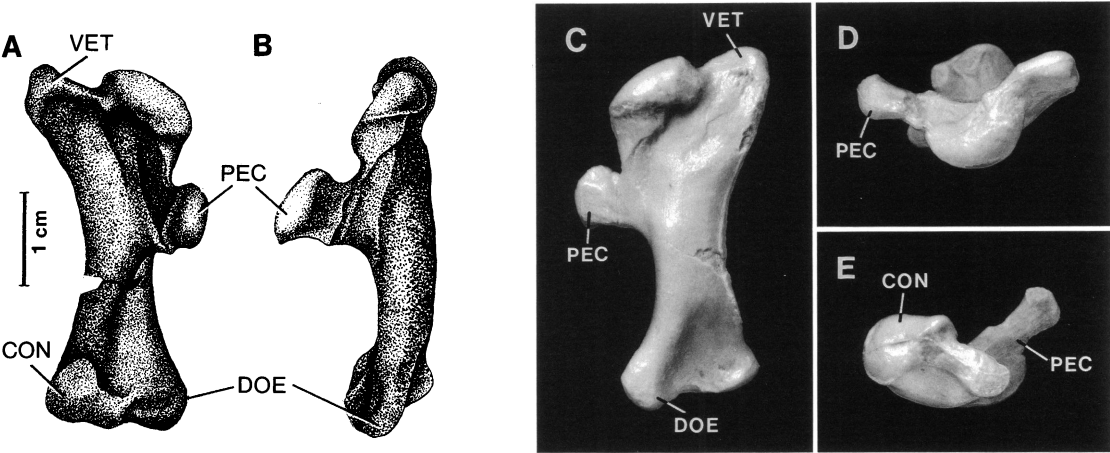


Fig. 11. Left humerus of holotype specimen of *Mononykus olecranus*. A, Cranial view; B, dorsal view; C, caudal view; D, proximal view; E, distal view.

TABLE 3
Measurements (mm), Forelimb, Holotype
Specimen of *Mononykus olecranus*

Humerus		
A.	Maximum length	
B.	Maximum transverse width of proximal end of humerus	
C.	Maximum transverse width of humeral head	
D.	Maximum caudocranial width of humeral head	
E.	Minimum transverse diameter of humeral shaft	
F.	Maximum caudocranial diameter of humeral shaft	
G.	Maximum transverse width of distal end of humerus	
H.	Maximum transverse width of humeral condyle	
I.	Maximum height of humeral deltopectoral crest from its base	
J.	Maximum proximodistal width of humeral deltopectoral crest	
	Left	Right
A	36.7	36.6
B	16.9	—
C	10.2	10.2
D	5.7	5.8
E	7.9	7.4
F	5.5	5.4
G	14.6	14.4
H	10.0	8.5
I	7.9	—
J	7.2	—
Ulna-Radius		
A.	Maximum length of ulna	
B.	Maximum length of olecranal process	
C.	Height of distal condyle	
D.	Minimum lateromedial diameter of ulnar shaft	
E.	Maximum transverse diameter of humeral articular facet of ulna	
F.	Maximum length of radius	
G.	Maximum distal extension	
H.	Minimum lateromedial diameter of radial shaft	
	Left	Right
A	34.4	33.6
B	14.0	13.7
C	8.5	8.2
D	2.9	3.2
E	6.7	6.9
F	18.2	18.1
G	8.8	8.7
H	4.1	4.0

TABLE 3—(Continued)
D. Maximum length of metacarpal I
E. Maximum length of metacarpal II
F. Maximum length of metacarpal III

	Left	Right
A	16.5	16.6
B	5.2	5.2
C	4.4	4.7
D	11.9	11.8
E	9.5	8.6
F	6.4	6.2

Manus digit I

A. Length of proximal phalanx

B. Maximum height of proximal end of proximal phalanx

C. Minimum height of proximal end of proximal phalanx

D. Maximum transverse width of proximal end of proximal phalanx

E. Maximum transverse width of distal end of proximal phalanx

F. Maximum height of distal end of proximal phalanx

G. Maximum length preserved of distal phalanx

H. Maximum height of proximal end of distal phalanx

I. Maximum transverse width of proximal end of distal phalanx

	Left	Right
A	21.3	19.2
B	12.4	12.3
C	4.6	4.2
D	16.0	13.1
E	10.5	9.7
F	7.9	7.4
G	23.9	26.7
H	9.9	9.7
I	8.6	8.6

chanter, there is a small nutrient foramen, similar to those in many birds.

The cranial face of the distal end of the femur lacks a patellar groove (fig. 16A, E), and this surface is fairly convex. Caudally, there is a well-developed, triangular popliteal fossa, limited distally by lateral and medial projections of the medial and lateral condyles, respectively, that nearly contact each other (fig. 16C, E). This condition approaches that of more advanced birds in which a horizontal shelf distally limits the popliteal fossa (Chiappe, 1992, in press). The medial con-

dyle is robust, round in distal view, and nearly flat. The lateral condyle exhibits three tubercles or prominences (fig. 16E). The distal surface of this condyle is strongly convex. Caudally, it possesses a prominent ectocondylar tuber (see Welles, 1984) which projects medially forming the distal boundary of the popliteal fossa (see above) (fig. 16E). The third prominence of the lateral condyle projects laterally from the lateral surface of the distal end, and defines caudally a triangular depressed area on the lateral face of the ectocondylar tuber (fig. 16C, D, E). The ectocondylar tuber continues proximally with the lateral border of the popliteal fossa. A tibiofibular crest (as in modern birds) is absent, and the ectocondylar tuber is separated from the convex distal articular surface of the lateral condyle by a depressed concave area (fig. 16D). The morphology of the ectocondylar tuber is consistent with the interpretation of this structure as the precursor of the modern avian tibiofibular crest (Chiappe, 1992, in press). In addition, the distal surface of the external projection of the lateral condyle probably articulated with the fibular head in the way the fibular trochlea of the femur of modern birds does.

TIBIOTARSUS: The tibia of *Mononykus olecranus* is firmly united to the fused astragalum-calcaneum, being coossified at several points (fig. 17A–D). For this reason we are describing all these ossifications as a single unit. In the holotype specimen, the left and the proximal third and distal end of the right tibiotarsi are preserved.

The cranial face of the proximal end bears a strong crest (fig. 17B, C, E). This crest defines the craniomedial border of the laterally concave tibial incision, while the medial surface of the crest is convex. Over the medial face of this crest a second smooth crest is present (fig. 17C, E). These two crests are topographically identical to the lateral and medial cnemial crests of modern birds. The medial crest of *Mononykus olecranus*, however, is not as distinct as in most modern birds, and the area separating both crests forms neither an intercrestal groove nor a patellar crest.

The proximal articular surface of the tibiotarsus is laterally inclined (fig. 17C, D). The medial border of the medial articular facet

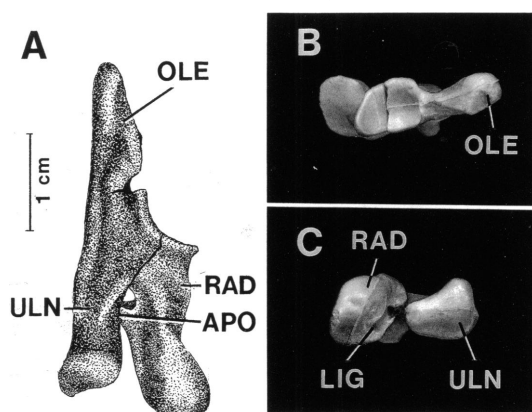


Fig. 12. Right radius and ulna of holotype specimen of *Mononykus olecranus*. A, Dorsal view; B, proximal view; C, distal view.

projects proximally. In proximal view, the medial articular facet is well delimited and suboval in shape (fig. 17E). Likewise, the lateral articular facet is well defined, rounded, and, as in modern birds, slopes laterocaudally (fig. 17B, D). The articular facets are separated by a small proximal depression and a notch caudally.

The nearly straight tibial shaft is slender. It is circular in cross section; the cortices are fairly thick, as exposed on the broken right element. On the lateral surface of the proximal third, there is a distinct fibular crest (figs. 17C, D).

On the distal end, the astragalum and calcaneum, apparently completely fused with each other, are intimately united to the tibia, being partially coossified with it (figs. 17A, B, D). Cranially there is a large triangular, laminate, ascending process. The medial margin of the ascending process, at the level of its base, is excavated by a deep notch (fig. 17C). The distal condyles are very well defined. The lateral one is transversely more narrow and craniocaudally shorter than the medial one. The tibiotarsus lacks both an extensor canal and supratendinal bridge.

FIBULA: Only the right fibular head is preserved in the holotype specimen. It is laterally compressed and narrower cranially than caudally. The lateral surface is convex while the medial one is nearly flat. On the cranial half

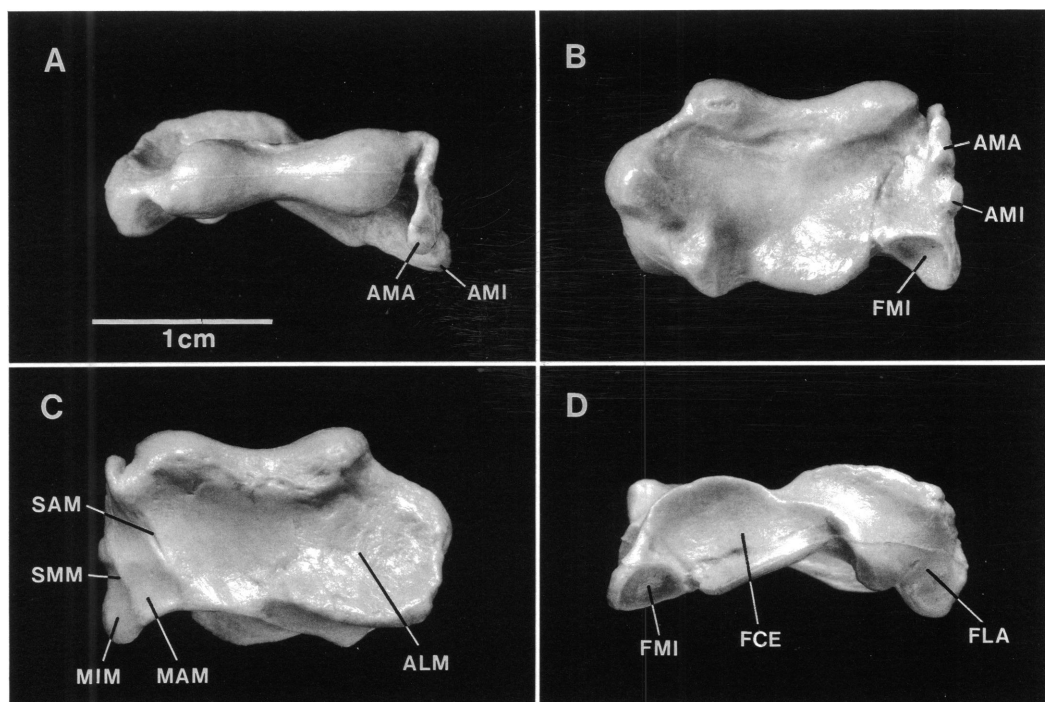


Fig. 13. Left carpometacarpus of holotype specimen of *Mononykus olecranus*. A, Distal view; B, ventral view; C, dorsal view; D, proximal view.

of the medial surface, there is a small depression that might be homologous to the much larger medial fossa of the fibula of several nonavianian theropods (e.g., ornithomimids, *Deinonychus antirrhopus*). The absence of evidence for fibular articulation on the lateral surface of the distal end of the tibiotarsus suggests that the fibula of *Mononykus olecranus* does not reach the tarsal area.

METATARSALS: The holotype specimen of *Mononykus olecranus* preserves the proximal end of left metatarsals II and IV, the distal end of left metatarsals II–IV, left metatarsal I, and the distal ends of right metatarsals II and IV. Fusion between metatarsals is absent. It is uncertain, however, whether the distal tarsals are indistinguishably fused to the metatarsals, or instead were not preserved.

Only metatarsals II and IV take part in the ankle joint of *Mononykus olecranus* (fig. 18A, D–F). The proximal end of metatarsal III is reduced and does not reach the articular surface. Both the articular surfaces and the cross section of the shaft of metatarsals II and

IV are subtriangular and subquadrangular, respectively (fig. 18F). No hypotarsus is present.

The distal end of metatarsal III projects distally more than the remaining ones. The shaft of this metatarsal tapers proximally (fig. 18B, G), and in cross section it is triangular. The dorsal surface is flat, with convex lateral and medial margins (fig. 18B, G). The plantar surface of the shaft forms a ridge separating lateral and medial surfaces for the apposition of metatarsals IV and II, respectively (fig. 18H). The trochlea of metatarsal III is symmetrical; fossae for the collateral ligaments are present on both sides of it. The trochleae of metatarsals II and IV are asymmetrical (fig. 18I). In the trochlea of metatarsal II the lateral rim is remarkably thick and projected more plantarily than the medial one; the medial rim forms a small and slender crest (fig. 18I). The lateral surface of this trochlea has a shallow fossa for the collateral ligament. On the trochlea of metatarsal IV the lateral rim is more prominent than the medial one (fig.

18H, I). Laterally, the margin of the lateral rim is separated from the cranial margin of the trochlea by a small notch (fig. 18I). This trochlea bears a lateral fossa for the collateral ligament. The cross section of the shaft of metatarsals II and IV is approximately circular.

Metatarsal I is a small, straight bone that tapers proximally (fig. 18C). Medially, there is a short vertical crest on the proximal half of the trochlea. Unfortunately, the state of disarticulation and the absence of a visible articular scar for its attachment on metatarsal II prevents determination of its position with respect to the other metatarsals (i.e., whether it was reverted).

PEDAL PHALANGES: The phalangeal formula is 2-3-4-5-0. In general terms, the articular trochleae and cotylae of all phalanges of *Mononykus olecranus* are very well developed. The hallux possesses a short and asymmetrical proximal phalanx with a well developed and dorsally extended articular trochlea (fig. 18B, C). The fossa for the collateral ligament is developed laterally but not medially. The distal phalanx of the hallux is not completely preserved. As in the remaining distal phalanges, the flexor tubercle is not developed (fig. 18C).

In the second digit, the proximal phalanx is much larger than the intermediate phalanx (fig. 18B). Like the proximal phalanges of the third and fourth digit it has a round articular cotylus. Dorsally, proximal to the articular trochlea, these phalanges exhibit a deep subtriangular fossa. Fossae for collateral ligaments are well developed on both sides of these phalanges. The distal phalanx of the second digit is the largest of the distal phalanges. As in the remaining distal phalanges, this phalanx is sharp, slightly curved, and possesses deep, L-shaped longitudinal grooves on both sides.

In the third digit, the proximal and intermediate phalanges distally decrease in length. The proximal phalanx has a well-developed fossa for the collateral ligament as well as a dorsal fossa proximal to the articular trochlea. In the two intermediate phalanges the fossa for the collateral ligament is poorly developed. The distal phalanx is similar to that of the second digit but slightly smaller.

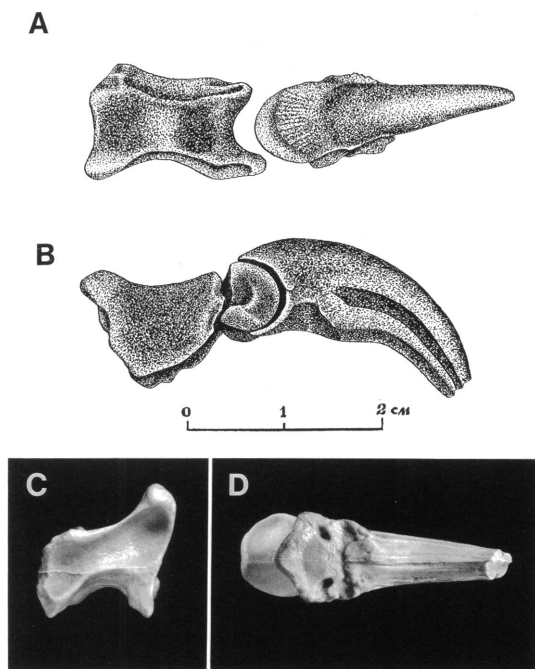


Fig. 14. Right alular digit of holotype specimen of *Mononykus olecranus*.

The proximal and intermediate phalanges of the fourth digit are short (fig. 18B). Deep dorsal fossae are developed in the proximal and first two intermediate phalanges. Likewise, well-developed fossae for the collateral ligament are present in these three phalanges, while this fossa is less developed in the last intermediate phalanx.

DISCUSSION

The phylogenetic relationships of *Mononykus olecranus* are discussed elsewhere (Perle et al., 1993a); the results of a phylogenetic analysis are portrayed in figure 19. The phylogeny depicted in figure 19 has important implications regarding the transformation pattern of many avialian characteristics (Perle et al., 1993a).

Mononykus olecranus is one of the most unusual avialians ever to be discovered (fig. 20). Its short, robust forelimb possesses features indicating that the enlarged first digit could be manipulated with great power. This forelimb evokes comparison with that of fos-

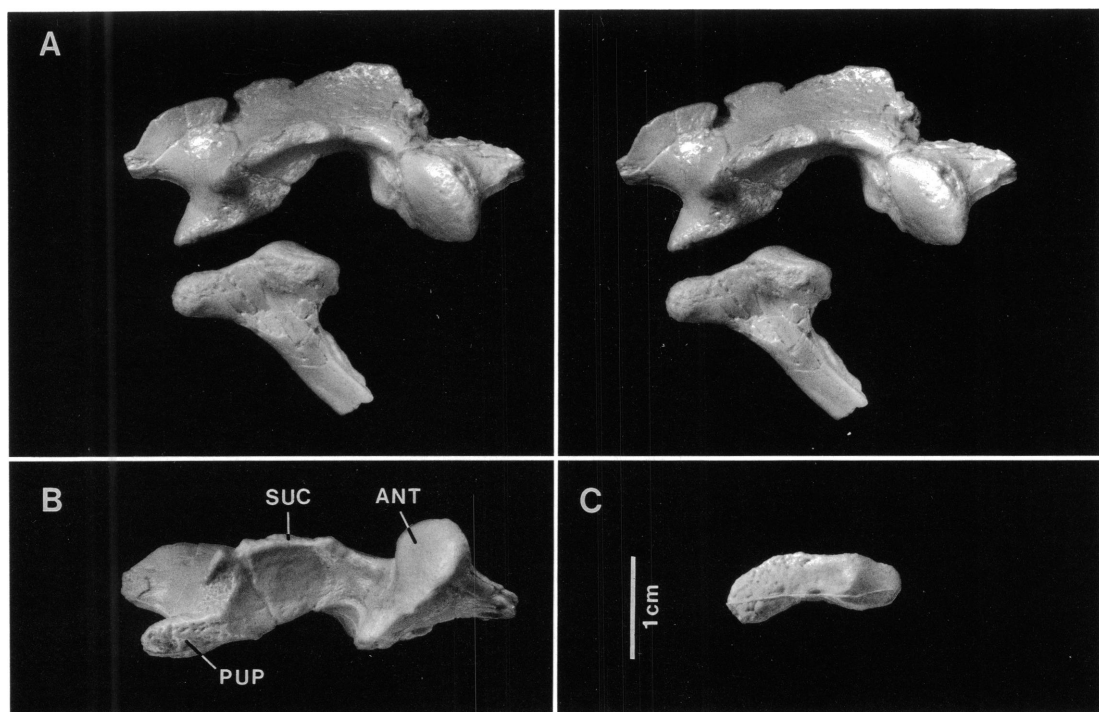


Fig. 15. Pelvis of holotype specimen of *Mononykus olecranus*. A, Stereopair of lateral view of left ilium and pubis; B, left ilium in ventral view; C, left pubis in proximal view.

sorial tetrapods, yet the remainder of the body is that of a gracile cursor. This unusual combination of features is all the more remarkable considering that our phylogenetic analysis (Perle et al., 1993a) indicates that *Mononykus olecranus* is more closely related to extant birds than is the classic "Ürvogel" *Archaeopteryx lithographica*.

Although the many unique features of *Mononykus olecranus* are readily interpretable as evolutionary specializations, other autapomorphies are apparent only within the context of a phylogenetic analysis. For example, several features that *Mononykus olecranus* shares with extant birds are most parsimoniously interpreted to be convergent because they are absent in other basal avialians (Perle et al., 1993a). These features thus evolved within the lineage leading to *Mononykus olecranus* from its common ancestor with extant birds. Below we review the evolutionary specializations of *Mononykus olecranus* as inferred from our phylogenetic analysis.

Mononykus olecranus possesses several peculiar autapomorphies. In the axial skeleton, the presence of anterior dorsal vertebrae with the zygapophysial articular surfaces located in the same plane as the costal foveae and transverse processes is a condition absent in nonavialian theropods (Ostrom, 1969; Osmolska et al., 1972; Madsen, 1976), *Iberomesornis romerali* (Sanz and Bonaparte, 1992), Enantiornithes, *Patagopteryx deferrariisi* (Chiappe, 1992), and Ornithurae. The presence of a biconvex posterior dorsal vertebra and a procoelic synsacrum are only shared between *Mononykus olecranus* and the Late Cretaceous Patagonian bird *Patagopteryx deferrariisi* (Chiappe, 1992) among Theropoda. This common condition is interpreted as independently developed in both *Mononykus olecranus* and *Patagopteryx deferrariisi* (Perle et al., 1993a). Another autapomorphic feature of the axial skeleton of *Mononykus olecranus* is the remarkable laterally compressed, keeled centra of the caudal synsacral vertebrae. Keeled synsacral verte-

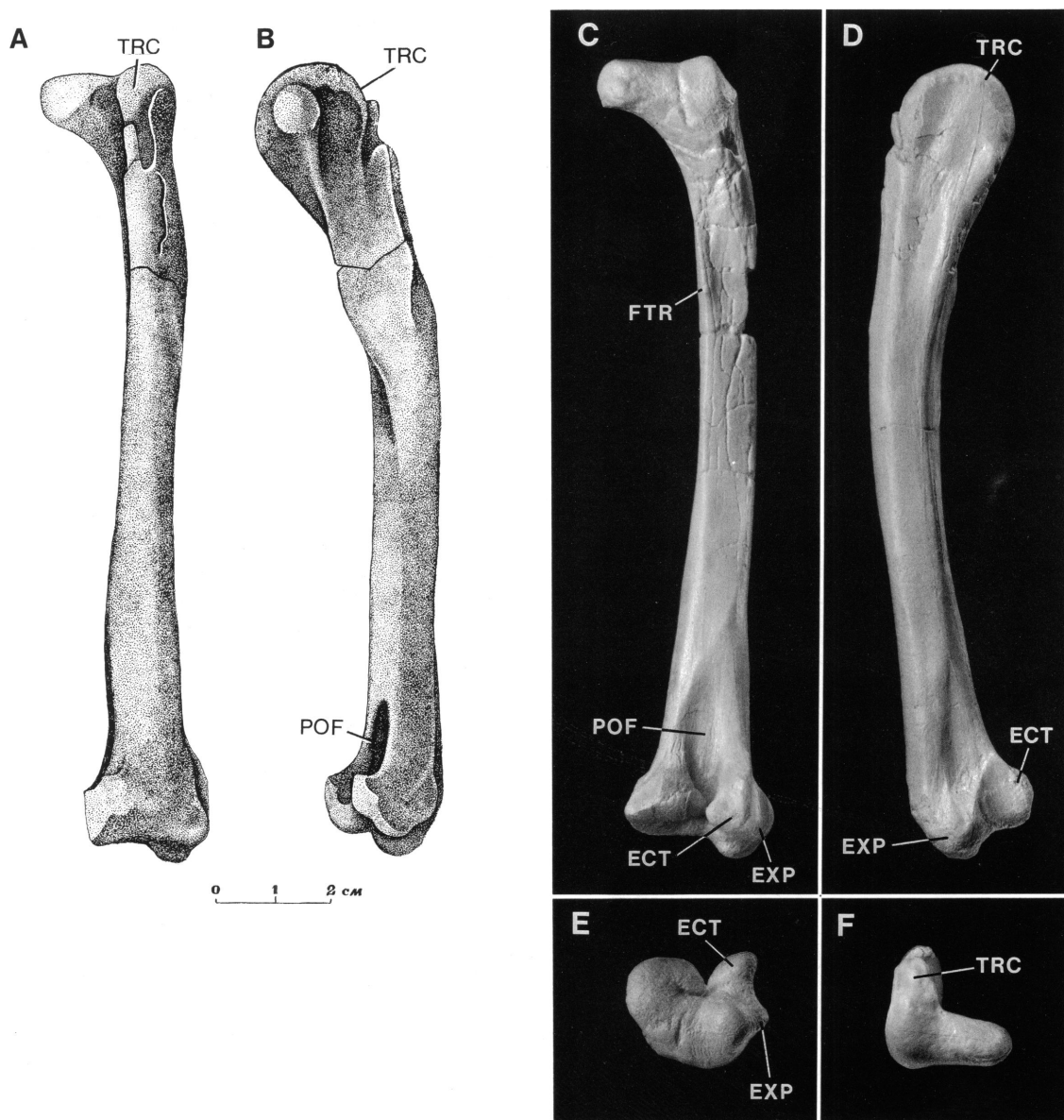


Fig. 16. Left (A, B, D, F) and right (C, E) femora of holotype specimen of *Mononykus olecranus*. A, Cranial view; B, medial view; C, caudal view; D, lateral view; E, distal view; F, proximal view.

brae were reported in *Iberomesornis romerali* (Sanz and Bonaparte, 1992) and the ornithurine Early Cretaceous British bird *Enaliornis barretti* (Seeley, 1876). Nevertheless, the synsacral vertebrae of *Iberomesornis romerali* are exposed ventrally and no indication of a keel is visible (personal observ. LMC; see also Sanz

and Bonaparte, 1992: fig. 3). Likewise, in *Enaliornis barretti* the "keel" is apparently the round ventral edge of the centra in the middle of the synsacrum (Seeley, 1876: fig. 15). In fact, the posterior part of the *Enaliornis barretti* synsacrum lacks any keel, as is shown in Seeley's figure 17. Thus, the pronounced

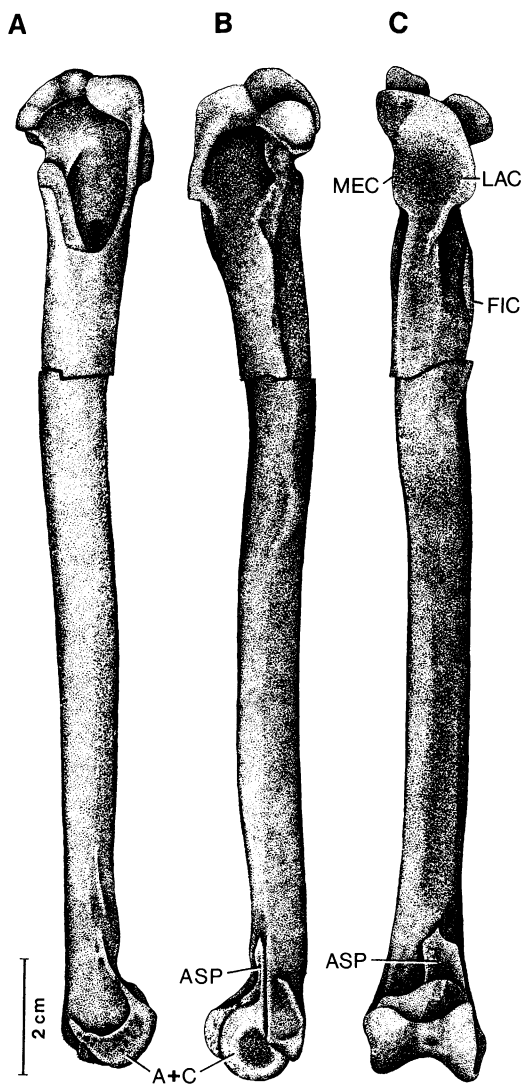


Fig. 17. Left tibiotarsus of holotype specimen of *Mononykus olecranus*. **A**, Medial view; **B**, lateral view; **C**, cranial view; **D**, caudal view; **E**, proximal view.

ventral keel of the synsacral vertebrae of *Mononykus olecranus* is clearly an autapomorphic feature of this taxon.

The thick carina on the sternum of *Mononykus olecranus* is another unique derived feature of this taxon. Although the sternal carina is considered homologous to other avialian carina (see description), its morphology differs from that of all other known avialian



TABLE 4
Measurements (mm), Hindlimb, Holotype
Specimen of *Mononykus olecranus*

Femur		
A.	Maximum length	
B.	Maximum craniocaudal width of proximal end	
C.	Maximum lateromedial width of proximal end	
D.	Craniocaudal width of mid-shaft	
E.	Maximum transverse diameter of distal end	
F.	Craniocaudal width of lateral condyle	
G.	Craniocaudal width of medial condyle	
A	138.6	138.2
B	20.9	19.8
C	23.1	23.1
D	12.1	12.6
E	22.0	25.5
F	20.9	20.3
G	18.9	17.9

Tibiotarsus		
A.	Maximum length	
B.	Maximum craniocaudal width of proximal end	
C.	Maximum lateromedial width of proximal end	
D.	Craniocaudal width of mid-shaft	
E.	Transverse width of mid-shaft	
F.	Maximum transverse diameter of distal end	
G.	Maximum craniocaudal width of lateral condyle	
H.	Maximum craniocaudal width of medial condyle	
I.	Height of astragalus with ascending process	

	Left	Right
A	175.2	—
B	22.0	22.6
C	19.5	21.4
D	9.8	—
E	11.0	—
F	20.6	19.0
G	15.1	14.2
H	16.3	16.3
I	28.1	—

Metatarsals and pedal digits		
A.	Maximum transverse width of proximal end of metatarsal II	
B.	Maximum transverse width of proximal end of metatarsal IV	
C.	Maximum dorsoplantar width of proximal end of metatarsal II	
D.	Maximum dorsoplantar width of proximal end of metatarsal IV	
E.	Maximum transverse width of distal end of metatarsal II	
F.	Maximum transverse width of distal end of metatarsal III	
G.	Maximum transverse width of distal end of metatarsal IV	

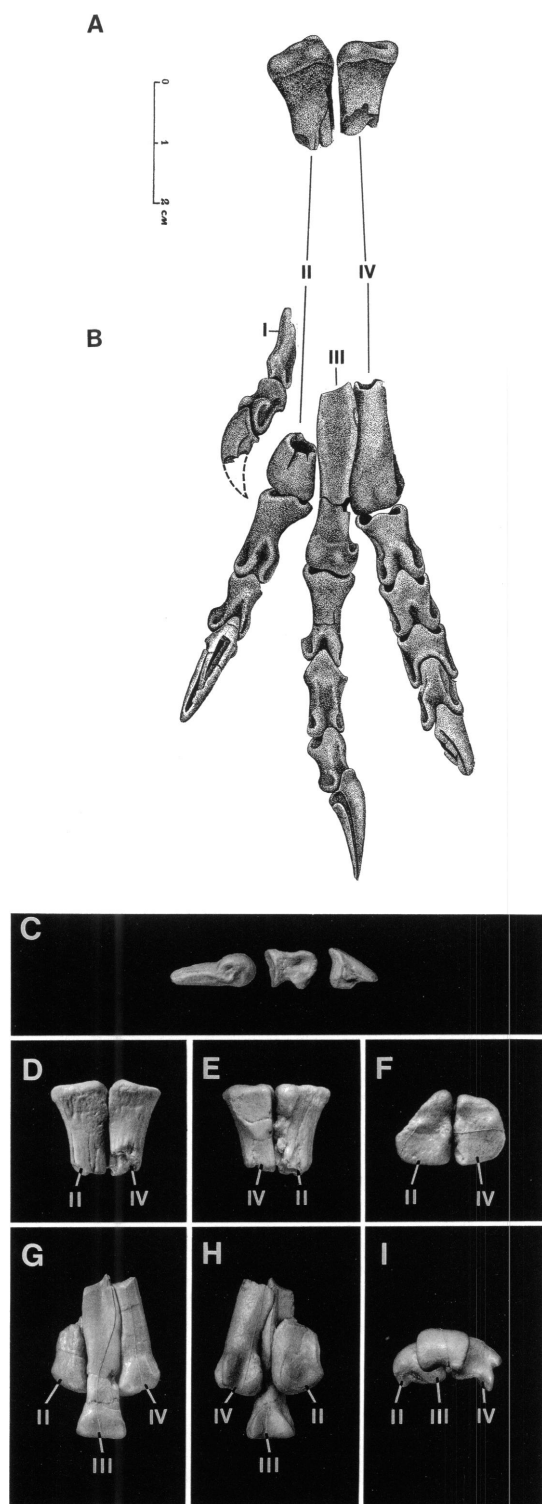
TABLE 4—(Continued)

H.	Maximum length of metatarsal I	
I.	Total length of digit I	
J.	Total length of digit II	
K.	Total length of digit III	
L.	Total length of digit IV	
	Left	Right
A	10.4	—
B	9.4	—
C	14.2	—
D	13.0	—
E	8.7	8.1
F	9.2	—
G	8.1	7.3
H	14.5	—
I	16.9	—
J	41.5	—
K	50.9	—
L	46.1	—

sterna. The sternal carina of *Avialae*, when present, forms a slender lamina in which the sides are perpendicular to the horizontal plane; in *Mononykus olecranus* the sides of the carina are not perpendicular but diagonal to this plane, giving the sternum a triangular cross section.

Another feature that *Mononykus olecranus* shares with *Patagopteryx deferrariisi* is the position of the antitrochanter. In these two taxa the main axis of the antitrochanter projects laterocaudally instead of dorsocaudally as in ornithurine birds (Chiappe, 1992). The presence of the latter condition in *Enantiornithes* plus its uncertain condition in *Iberomesornis romerali*, taxa intermediate between *Mononykus olecranus* and *Patagopteryx deferrariisi* (see Chiappe, 1992; in press), prevents definitive statement about the status of this character. Hence, with the available data this feature could be interpreted either as a primitive state with respect to the ornithurine condition or as independently acquired in both *Mononykus olecranus* and *Patagopteryx deferrariisi*.

Interestingly, two cnemial crests are present on the tibia of *Mononykus olecranus*. These crests match topographically with the ornithurine lateral and medial cnemial crests. As was interpreted for ornithurines (see Chiappe, 1992), we interpret the development of a medial crest as the evolutionary



novelty, while the lateral crest is regarded as primitive and homologous to the single cnemial crest of other nonornithurine theropods (contra Ostrom, 1976a; Cracraft, 1986). The distribution of this character among different avialian taxa supports an independent origin in *Mononykus olecranus* and ornithurine birds (Chiappe, 1992). In this respect, *Mononykus olecranus* differs from other nonornithurine theropods in which the tibia bears a single cnemial crest (Chiappe, 1992; in press). The presence of a medial cnemial crest in *Mononykus olecranus* is considered an autapomorphy of this taxon.

Another autapomorphic character of the tibia of *Mononykus olecranus* is the presence of a deep notch excavating the ascending process of the astragalum. This notch is absent or slightly developed in nonavialian theropods (Osborn, 1916; Lambe, 1917; Osmolska et al., 1972; Barsbold, 1974; Madsen, 1976) and birds other than *Mononykus olecranus* (McGowan, 1985a; Sanz and Bonaparte, 1992). Relevant to the discussion of bird origins is the supposed presence of a "pretibial bone" [an ossification homologous to the ascending process (see McGowan, 1985a, b)] proximal to the calcaneum of *Archaeopteryx lithographica* and other Mesozoic birds (see Martin et al., 1980; Martin and Stewart, 1985; Martin, 1991). Our interpretation of the controversial anatomy of *Archaeopteryx lithographica*, in this case based on the Eichstätt specimen, disagrees with Martin's viewpoint. As was emphatically claimed by McGowan (1985a, b) against Martin and Stewart's (1985) arguments, the lateral location of the ascending process of *Archaeopteryx lithographica* does not necessarily require that this structure was equivalent to the neognathine "pretibial bone." Again, the anatomy of *Mono-*

←

Fig. 18. Left metatarsals and digits of holotype specimen of *Mononykus olecranus*. A, Proximal end of metatarsals II and IV in dorsal view; B, metatarsal I and digit I, distal ends of metatarsals II-IV and digits II-IV in dorsal view; C, medial view of metatarsal I and digit I; D-F, proximal ends of metatarsals II and IV in dorsal, plantar and proximal views; G-I, distal ends of metatarsals II-IV in dorsal, plantar and distal views.

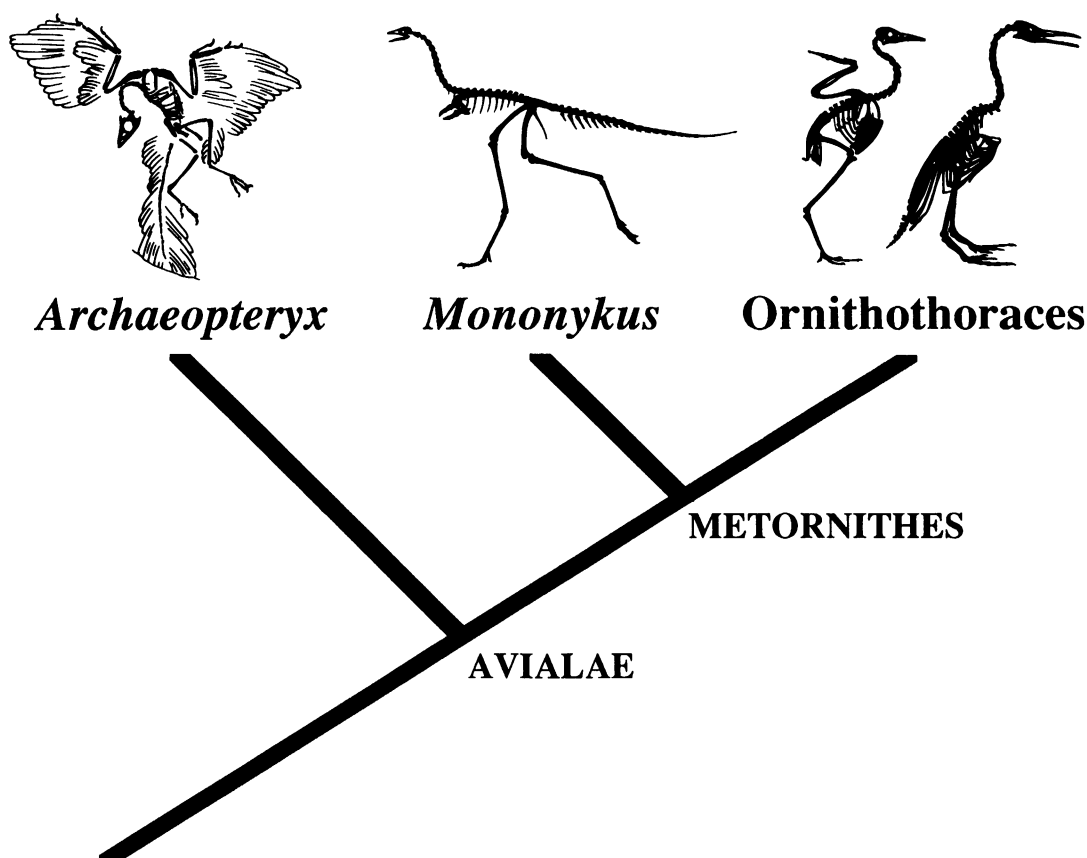


Fig. 19. Cladogram depicting the inferred relationships of *Mononykus olecranus* to other avialians (after Perle et al., 1993a).

nykus olecranus sheds light on this issue. The “pretibial bone” is absent in the superbly preserved holotype specimen of *Mononykus olecranus*, and the ascending process occupies a lateral position as it does in *Archaeopteryx lithographica* and nonavianian theropods (Osborn, 1916; Barsbold, 1974; Madsen, 1976). It is our contention that the ascending process of *Archaeopteryx lithographica* and *Mononykus olecranus* is homologous to the same structure in nonavianian theropods.

The arctometatarsalian condition of the foot of *Mononykus olecranus* is unique among Avialae. This condition has often been considered as independently developed in different nonavianian theropod groups (Gauthier, 1986; Paul, 1988; Weishampel et al., 1990), although it was recently claimed that it might have had a single origin (Holtz, 1991; Novas, 1992). Our phylogenetic interpreta-

tion of *Mononykus olecranus* indicates that regardless of whether this condition evolved only once among nonavianian theropods, it evolved at least twice in theropod history.

The forelimb of *Mononykus olecranus* possesses its most remarkable specializations. The pronounced pillarlike deltopectoral crest of the humerus, the proximal projection of the ventral tubercle, and the presence of a single condylar structure are unique to this taxon among theropods. Likewise, the hypertrophy of the olecranon of the ulna, the massive and quadrangular carpometacarpus, the robust and sturdy claw of the alular digit, and the extreme reduction of the major and minor digits, are unique derived features of this taxon.

Radical forelimb modification is a recurrent theme in theropod evolution (Novas, 1992). Generally these modifications fall into

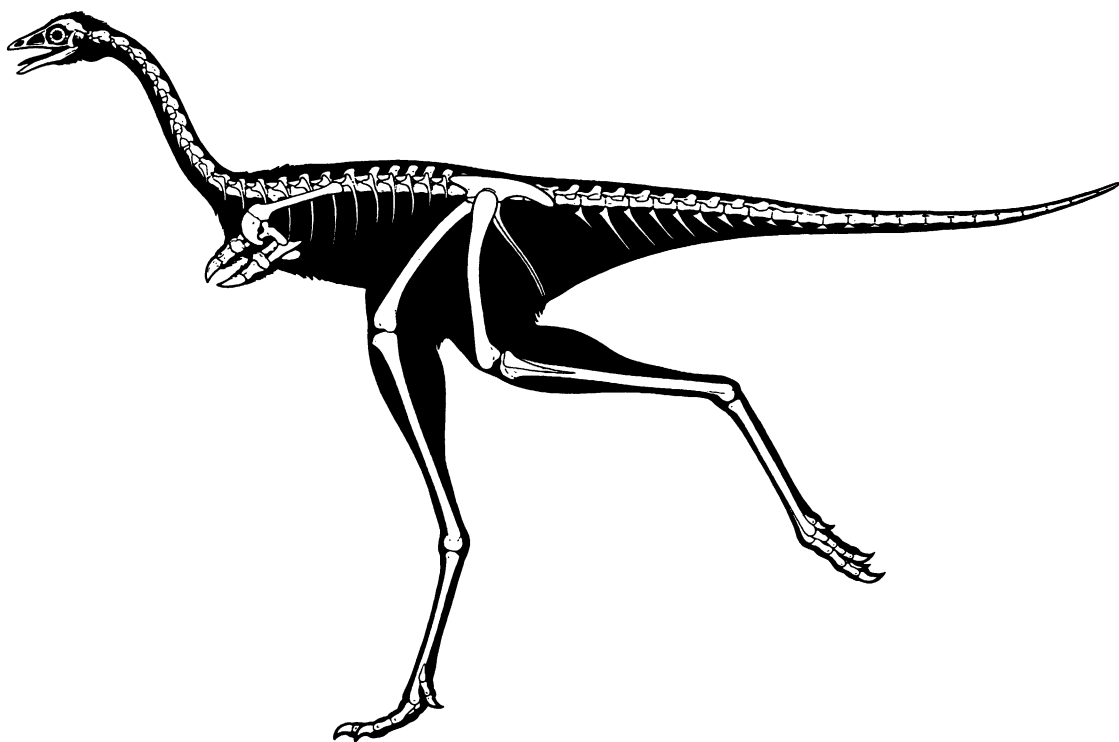


Fig. 20. Skeletal reconstruction of *Mononykus olecranus* (after Perle et al., 1993a).

two broad categories. Forelimb elongation occurs in *Therezinosaurus cheloniformis*, *Deinocheirus mirificus*, Ornithomimidae, and Maniraptora (Weishampel et al., 1990). If these taxa form a monophyletic group, this feature may represent a single evolutionary transformation. Forelimb reduction, however, has occurred independently several times during theropod history [e.g., in Neoceratosauria, Tyrannosauridae, *Torvosaurus tanneri* (see Novas, 1992), and several groups of birds (see Feduccia, 1980)]. Among birds, usually this transformation is accompanied by coincident simplification of the forelimb elements (e.g., Hesperornithiformes, Diatrymidae, Apterygidae, Dromaiidae, and others). In *Mononykus olecranus* this is obviously not the case, and in no other dinosaur example has forelimb reduction paralleled the morphological transformation seen in this taxon.

The forelimb specializations of *Mononykus olecranus* are similar to those of some

fossorial tetrapods. The large deltopectoral crest of the humerus, the huge olecranon of the ulna, the short and massive forelimb elements and carpometacarpus, and the robust claw of the alular digit all suggest extremely powerful movements of the forelimb. The relationships between the articulation surfaces of the different elements of the forelimb restrict the range of motion mainly to abduction-adduction movements, with most power during adduction. Paradoxically, the shortness of the forelimb relative to the rest of the body, and the elongate gracile hindlimb, are incongruous with a burrowing habitus, and the forelimbs were presumably used for some other function requiring powerful movement.

CONCLUSION

Mononykus olecranus demonstrates the existence of a peculiar group of primitive birds during the Cretaceous, with bizarre special-

izations that are unique among the previously known theropod diversity. The superb three-dimensional preservation of the holotype specimen provides significant new information on basal avialian anatomy and clarifies longstanding controversies on primitive conditions. The osteology of *Mononykus olecranus* emphasizes anew the complexity of the morphological transformations during the first half of avialian history, highlighting our ignorance of the transition from nonavialian theropods to modern birds.

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APPENDIX 1

Anatomical abbreviations used in figures 2–18.

ACR	acromion	LAF	lateral articular facet
AFQ	articular facet for quadrate	LIG	ligamental depression
ALM	alular metacarpal	MAF	medial articular facet
AMA	articular facet of major metacarpal	MAM	major metacarpal
AMI	articular facet of minor metacarpal	MEC	medial crest
ANT	antitrochanter	MIM	minor metacarpal
AOF	antorbital fenestra	MX	maxilla
APO	proximal extension of ventral aponeurosis tubercle	OLE	olecranon
ASP	ascending process of astragalus	PEC	deltpectoral crest
AVF	vertebral arch	POF	popliteal fossa
A+C	astragalus and calcaneum	POP	paroccipital process
COF	costal fovea	PUP	pubic peduncle
CON	condyle	Q	quadrate
DEM	dentigerous margin	RAD	radius
DOE	dorsal epicondyle	RTR	rostral tympanic recess.
DOP	spinous process of vertebral arch	SAM	suture between alular and major metacarpals
ECT	ectocondylar tuber	SFO	supracoracoid nerve foramen
EXO	external projection of lateral condyle	SMM	suture between major and minor metacarpals
FCE	central proximal articular facet	SUC	supracetabular crest
FIC	fibular crest	TRC	trochanteric crest
FLA	lateral proximal articular facet	ULN	ulna
FMI	proximal articular facet of minor metacarpal	VEP	ventral process
FTR	fourth trochanter	VET	ventral tubercle
IPF	infrapostzygapophysial fossa	I–IV	metatarsals I to IV
LAC	lateral crest		

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