

NEW MATERIAL OF *MESADACTYLUS ORNITHOSPHYOS*, A PRIMITIVE PTERODACTYLOID PTEROSAUR FROM THE UPPER JURASSIC OF COLORADO

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ABSTRACT—The Dry Mesa Dinosaur Quarry in western Colorado is characterized by a high diversity of vertebrate fossils, including pterosaur remains. Most of the pterosaur material has been referred to the species *Mesadactylus ornithosphyos*. Since its original description, additional material of this pterosaur has been uncovered. The new material includes the first described well-preserved basicranium of a Jurassic pterodactyloid pterosaur from North America and several appendicular elements. The cervical vertebra described previously was CT-scanned to reveal a complicated internal pneumatic system that can be compared to the avian system.

INTRODUCTION

In 1989, James Jensen and Kevin Padian described elements of a pterodactyloid pterosaur from the Dry Mesa Dinosaur Quarry in the Upper Jurassic Basin Member of the Morrison Formation of Colorado. The bones included many of the appendicular elements, a cervical vertebra, and a synsacrum. One bone, a wing phalanx, was previously described by Jensen and Ostrom (1977) as pterosaurian, but a tibiotarsus was regarded as potentially avian and given the name *Palaeopteryx* (Jensen, 1981). All of these bones, including the tibiotarsus, and others, were later referred to a single distinct pterosaurian species, *Mesadactylus ornithosphyos* (Jensen and Padian, 1989). The type specimen is the synsacrum (BYU 2024).

Since 1985, field crews headed by Ken Stadtman from the Earth Science Museum, Brigham Young University have recovered and prepared considerably more pterosaur material from the appendicular skeleton and basicranium. All of it is probably from the same species (Padian, pers. comm.), but the possibility remains that there are multiple taxa. This paper presents a description of the new material as it increases our knowledge of the osteology of *Mesadactylus* and, by implication, basal pterodactyloid pterosaurs.

The basicranium is nearly complete and undistorted. It represents one of the few Jurassic North American pterodactyloid basicrania. Another pterodactyloid braincase, *Laopteryx priscus* was found at Como Bluff. *Laopteryx* consists of a poorly preserved braincase that was originally regarded as possibly avian (Marsh, 1881). It was redescribed by Ostrom (1986), who concluded that this specimen was pterosaurian. The *Mesadactylus*, specimen, however, is considerably better preserved.

The taphonomy of the *Mesadactylus* site is notable in that it is from continental sediments rather than a near-shore deposit where pterosaur remains are more common (Wellnhofer, 1991). Dry Mesa beds reflect a fluvial setting (Richmond and Morris, 1999) characterized by a high diversity of dinosaurs, crocodylians, turtles, and lungfish. The quality of the preservation is variable. Some of the elements are well-preserved, but are usually disassociated. The pterosaur bones are rare and scattered throughout the quarry. Typically, they are found in fine-grained sand and siltstones closely associated with the dinosaur material, rather than the coarse grained sandstones to conglomerates. Most of the pterosaur material is uncrushed, but not associated.

The cervical vertebra (BYU 9126) was CT-scanned with a Marconi MX 8000 CT-scanner acquiring 1 mm slices at 120 kV and 250 mA exposure settings in accordance with a standard tempo-

ral bone high resolution algorithm. Coronal and sagittal planar reconstructions, as well as 3-D surface reconstruction images, were created with a Sun Microsystem computer and Advantage Windows V. 3.1 image processing software package.

Abbreviation—BYU, Brigham Young University, Provo, Utah.

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Plieninger, 1901
MESADACTYLUS Jensen and Padian, 1989
MESADACTYLUS ORNITHOSPHYOS Jensen and Padian, 1989

Holotype—BYU 2024, an isolated synsacrum from Dry Mesa Dinosaur Quarry, Mesa County, Uncompaghre Uplift, Colorado.

Horizon—Kimmeridgian, Jurassic, Brushy Basin Member, Morrison Formation.

Diagnosis—As for *Mesadactylus ornithosphyos* (Jensen and Padian, 1989).

Referred Specimens—BYU 11463, a basicranium; BYU 9126, a cervical vertebra; BYU 13033, a proximal rib; BYU 13595, a proximal humerus; BYU 17207, a fourth metacarpal; BYU 17206, and BYU 13618, two specimens of phalanx IV-1; BYU 17214, a femur. All of the referred material is from the same locality as the holotype.

DESCRIPTION

Braincase

The occipital region of the braincase of *Mesadactylus* (BYU 11463) is well-preserved and undistorted (Figs. 1, 2). It is small and although this cannot be determined from the preserved material, the occipital condyle and foramen magnum were probably oriented ventrally in life as in other pterodactyloid pterosaurs. The following description, however, uses a standard orientation. The preserved bones include the parietal, the supraoccipital, the exoccipital, the opisthotic, and the basioccipital.

The parietal is complete. It consists of very thin bones that forms a short sagittal crest anterior to the supraoccipital. The

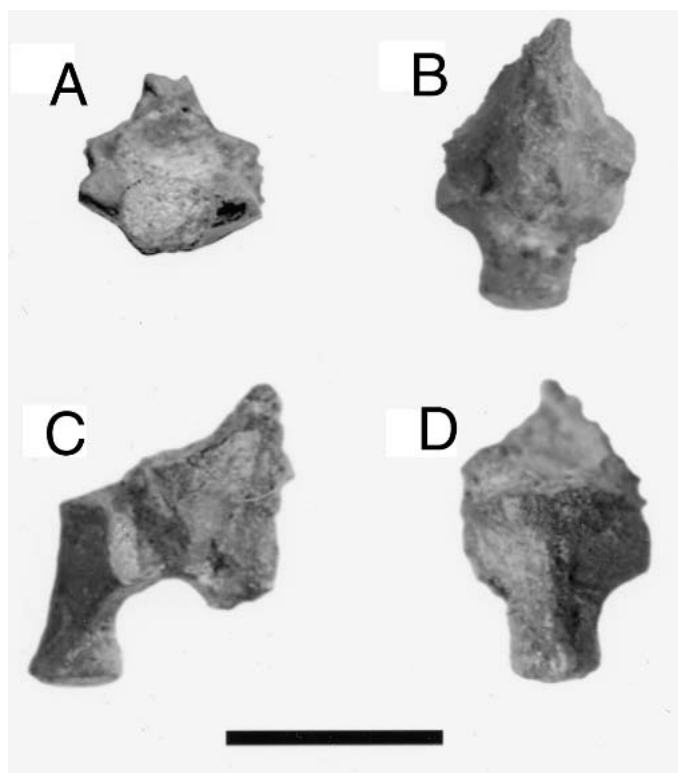


FIGURE 1. Photographs of basicranium (BYU 11463) of *Mesadactylus ornithosphyos* in A, caudal; B, dorsal; C, lateral; and D, ventral views. Scale equals 10 mm.

articulation with the supraoccipital is fused, so the sutures are not visible, but the parietal does not appear to make up any part of the occiput, as it does in the derived pterosaurs (Kellner, 1996). This arrangement may be characteristic of pterodactyloids, but it is unclear in the basal forms, such as *Pterodactylus* (Kellner, 1996). However, there is a distinct curving suture of the parietal with the opisthotic.

The supraoccipital includes the posterior part of the sagittal crest and extends down to the top of the foramen magnum. The crest is similar to that of *Tapejara*, but is shorter, with a shallow groove dorsally in *Mesadactylus*. The groove does not continue onto that part of the crest formed by the parietal. In lateral view, the supraoccipital extends beyond the foramen magnum, forming a short process posterior to it, presumably similar to *Tapejara* (Kellner, 1996). Laminae from this bone extend laterally to form the sides of the foramen magnum dorsally, meeting the exoccipitals at a linear suture between the foramen magnum and the ventromedial border of the posttemporal fenestra. The sides of the supraoccipital are very smooth, unlike the rugose condition in *Tapejara* (Kellner, 1996). Also, unlike *Tapejara*, (Kellner, 1996) and like *Pteranodon* (Bennett, 2001), and *Anhanguera* (Wellnhofer, 1985), the posttemporal fenestra of *Mesadactylus* is not enclosed by the supraoccipital and exoccipitals. However, less of the fenestra is enclosed by these two bones than in *Pteranodon*. There is no indication of pneumatic foramina in this region of *Mesadactylus*, similar to the condition in *Rhamphorhynchus* (Kellner, 1996).

The exoccipital contributes to the base of the short paroccipital processes and all of the occipital condyle. It is fused with the opisthotic. The exoccipital forms the ventral sides and the base of the foramen magnum. The occipital condyle is borne on a long (approximately 5 mm) thin neck and has a flat, slightly rugose,

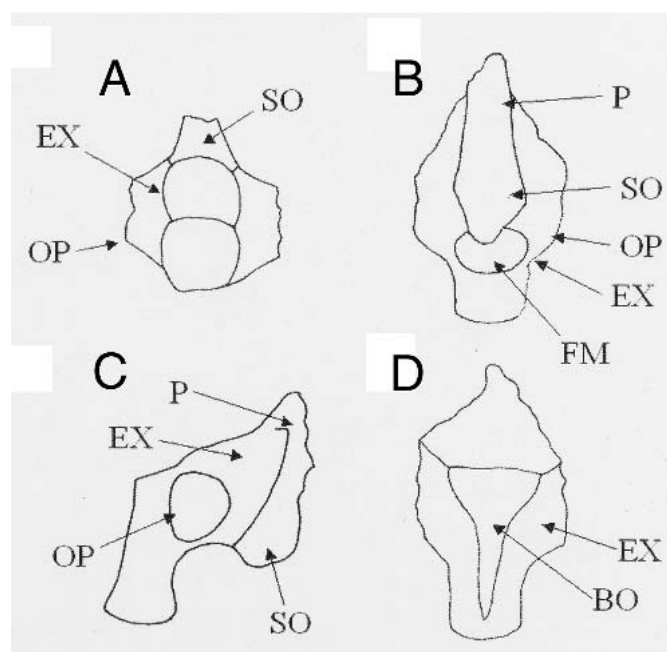


FIGURE 2. Interpretative sketch of basicranium (BYU 11463) of *Mesadactylus ornithosphyos* in A, caudal; B, dorsal; C, lateral; and D, ventral views. Abbreviations: BO, basioccipital; EX, exoccipital; fm, foramen magnum; OP opisthotic; P, parietal; PTF, posttemporal fenestra, and SO, supraoccipital. Scale equals 10 mm.

articular surface. There is no such neck in the occipital condyle of *Laopteryx* (Ostrom, 1986). The dimensions are 4.1 mm wide by 4.3 mm high. As in *Laopteryx*, the diameter of the occipital condyle is smaller than the foramen magnum, which is 4.3 mm wide by 5.4 mm high. The neck supporting the occipital condyle is excavated dorsally and straight laterally. Unlike *Laopteryx* (Ostrom, 1986), there is no sign of any foramina penetrating the exoccipital other than the foramen magnum. The exoccipital wraps around to the ventral face of the basicranium to meet the wedge formed by the basioccipital.

The opisthotic is fused with the exoccipital, so that the suture is not visible. It forms the lower part of the posttemporal fenestra and extends laterally to form a short paroccipital process that articulates with the squamosal. The paroccipital process does not flare as in *Laopteryx* (Ostrom, 1986). The squamosal articulation is socket-shaped, with raised edges and may have been kinetic. This socket is roughly the same diameter as the occipital condyle. There is an antero-posterior notch splitting the edges of the socket. The opisthotic extends anteriorly as a flat sheet of bone ventral to the parietal. The suture is clear and the bones are unfused. No foramina are preserved.

The basioccipital is a thin sheet of bone separating the exoccipitals on the ventral surface of the basicranium. The basal tubera are reduced. There is a thin process along the base of the neck of the occipital condyle that is much longer than the corresponding structure in *Anhanguera* (Wellnhofer, 1985), but this process does not contribute to the condyle itself. The relative contribution of the basioccipital to the occipital condyle varies in pterosaurs. In some pterosaurs, such as *Pteranodon* (Bennett, 2001), the process extends to the end of the condyle and forms a significant part of it. The resulting process effectively separates the adjacent exoccipitals. Anterior to the neck of the occipital condyle, the basioccipital expands laterally to form a flat sheet of bone on the ventral floor. No foramina are preserved.

Postcranial Axial Skeleton

A cervical vertebra in the collection (BYU 9126) was discussed in the original paper (Jensen and Padian, 1989). It is well-preserved, with little evidence of crushing (Figs. 3, 4, 5), but is missing the right prezygophysis and postzygapophysis. This specimen is very similar to the cervical vertebra described for *Kepodactylus* (Harris and Carpenter, 1996), but is much smaller. The centrum is highly pneumatized and there are no diapophyses or exapophyses. The length is about 28 mm and the width is about 12 mm, resulting in a length/width ratio of roughly 2.3, somewhat less than the 2.5 value that has been regarded as systematically significant in pterodactyloid pterosaurs (Unwin and Lü, 1997). The procoelous anterior face is crescent-shaped. The posterior end is expanded, unlike in *Kepodactylus*. Like *Pterodactylus*, the postzygapophysis does not extend beyond the centrum. There is a pronounced pneumatic foramen on the right side of the centrum, but the left side is mildly distorted, so the



FIGURE 3. Cervical vertebra (BYU 9126) of *Mesadactylus ornithosphyos* in A, dorsal; B, ventral; and C, lateral views. Scale equals 10 mm.

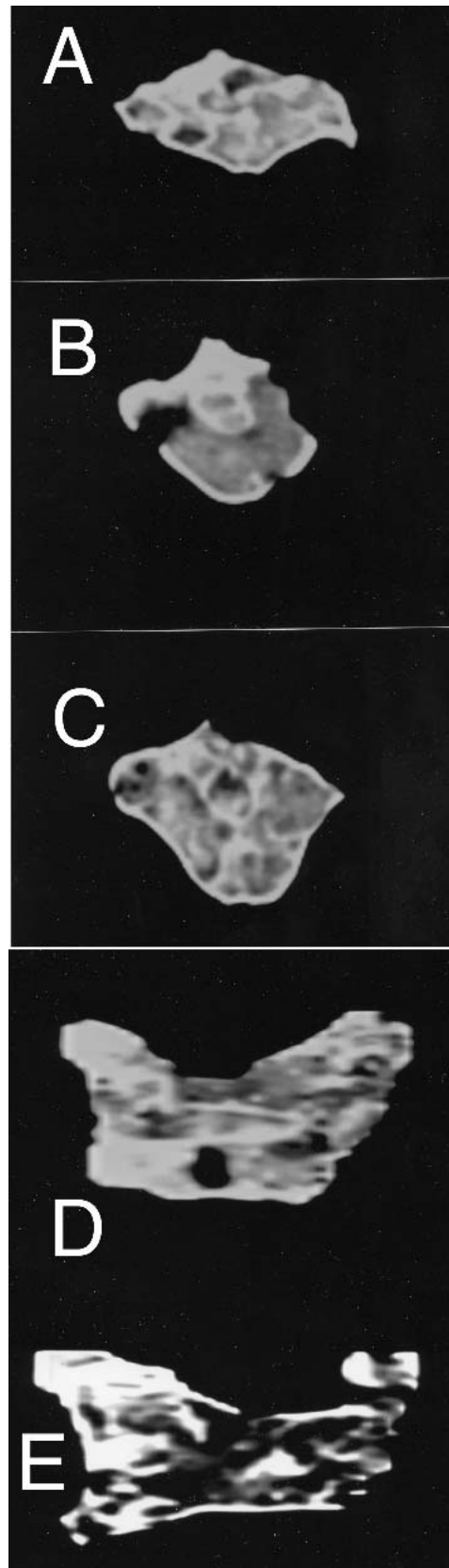


FIGURE 4. CT-scan slices of cervical vertebra (BYU 9126) of *Mesadactylus ornithosphyos*. Transverse slices through A, cranial end of centrum; B, middle of centrum; C, caudal end of centrum. Coronal sections through D, middle of spinal canal; and E, ventral margin of spinal canal.

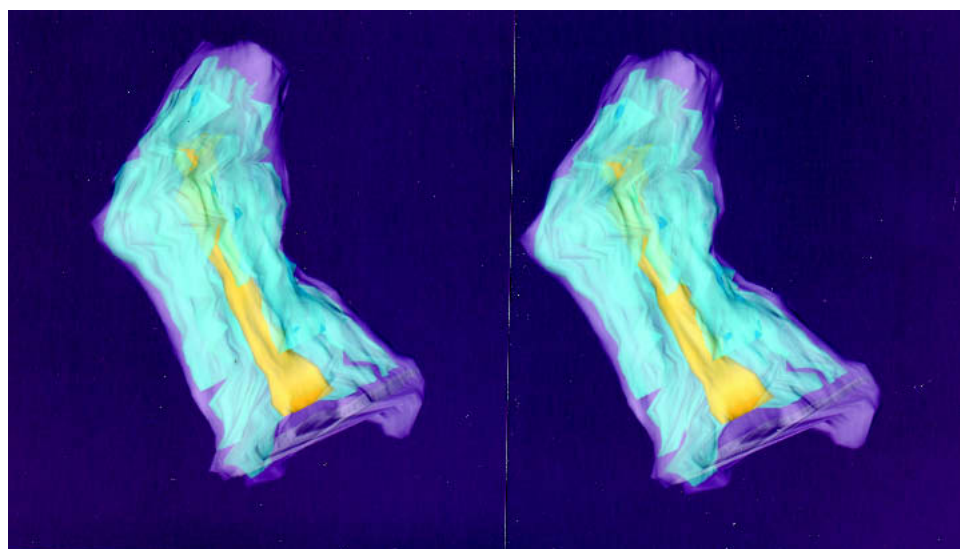


FIGURE 5. Stereophotograph of reconstructed pneumatic chambers of cervical vertebra (BYU 9126) of *Mesadactylus ornithosphyos*. Code: Grey, bone; yellow spinal column; blue, pneumatic chambers.

pneumatic foramen is not visible on that side. As in *Kepodactylus*, there is a thin neural spine with a narrow base.

The centrum of this specimen is pneumatically complex (Figs. 4, 5). The horizontally oval spinal canal has a nearly uniform diameter along its length averaging 2.5 mm in width. A minor degree of antero-posterior deformation near the cranial end of the specimen and scattered matrix infilling contribute to the loss of the otherwise smoothly contoured cross-section of the spinal canal. The cranial peduncular foramina immediately open into numerous small camellae, so that in the coronal plane, the spinal canal is the only recognizable internal tubular structure (Fig. 5). The caudal peduncular foramina are not preserved. The camellae coalesce towards the mid-centrum into progressively larger

pneumatic cavities (Fig. 5). The mid-centrum contains a single large camella that communicates ventrolaterally to the exterior of the centrum through a pair of prominent mid-centrum lateral foramina (Fig. 5). There are numerous small ostea interconnecting the camellae ranging from 0.3 to 0.6 mm in diameter (Figs. 4, 5). Similar, but less numerous openings are also present in the spinal canal. These ostea are predominantly oriented ventrolaterally and range from 0.5 to 0.6 mm in diameter.

There are at least two pneumatic diverticular tracts that communicate between the internal and external pneumatic spaces of the cervical spine. The external diverticula, or terminal air sacs, penetrate the centrum through the mid-centrum lateral pneumatic foramina. A more centrally located pair of diverticula pen-



FIGURE 6. Right rib (BYU 13033) *Mesadactylus ornithosphyos* in A, anterior and B, posterior views. Scale equals 10 mm.

trate the ends of the centrum through the peduncular foramina. There are no osteological barriers within the camellae internal to the two sets of diverticula. Because a similar intercommunication is known in birds, it is likely that the above set of diverticula also freely communicated through the camellae of the centrum.

A pterosaurian right rib with a well-preserved proximal end (Fig. 6) is present in the collection (BYU 13033). The trochlea and capitulum are distinct. The distal end is not preserved.

Appendicular Skeleton

There are several new appendicular elements. Some of them correspond with previously described material (Jensen and Padian, 1989). Only those that are new, or better preserved than the originally described material are discussed here.

There is a well-preserved right proximal portion of a humerus (BYU13595) that is essentially complete and undistorted (Fig. 7). The deltopectoral crest, medial process and head are all represented. The pronounced deltopectoral crest is thin and lacks a terminal expansion as is the case in the more derived *Pteranodon* (Bennett, 1989). There is no sulcus between the crest and shaft, so the proximal end of the deltopectoral crest is continuous with the head of the humerus as is the case in *Pterodactylus* (Padian, pers. comm.). From there, the crest has a round outline, even-

tually meeting the shaft far from the proximal end. The head is typically saddle-shaped, but the articular surface, though present is poorly defined. The medial process is reduced and continuous with the head. As in *Pteranodon*, this process is directed posteriorly. There is, however, no pneumatic foramen present, as seen in *Pteranodon*, and *Kepodactylus*. The shaft is oval and maintains a constant diameter below the deltopectoral crest. The distal end is not preserved in any specimen (3 prepared specimens) in the collection.

The left fourth metacarpal (BYU 17207) is well-preserved (Fig. 8). It is typical for pterodactyloids. Although the shaft has undergone some mediolateral crushing, the ends are mostly undistorted. The proximal end is expanded. The notch for the wing finger extensor tendon is well-defined and bounded by two knobs. It extends onto the articular surface, but not onto the shaft as seen in *Comodactylus* (Galton, 1981). The lateral articulation with metacarpals I–III is smooth. The shaft diameter is greatest beneath the proximal end and then gradually reduced distally. On the distal end, the lateral condyle appears larger than the medial condyle, but this condition would be highly unusual for pterosaurs, so some taphonomic distortion may be present. The medial condyle angles away from the shaft axis, as in other pterosaurs. The lateral condyle is wedge-shaped and no accessory knob was observed on this specimen.

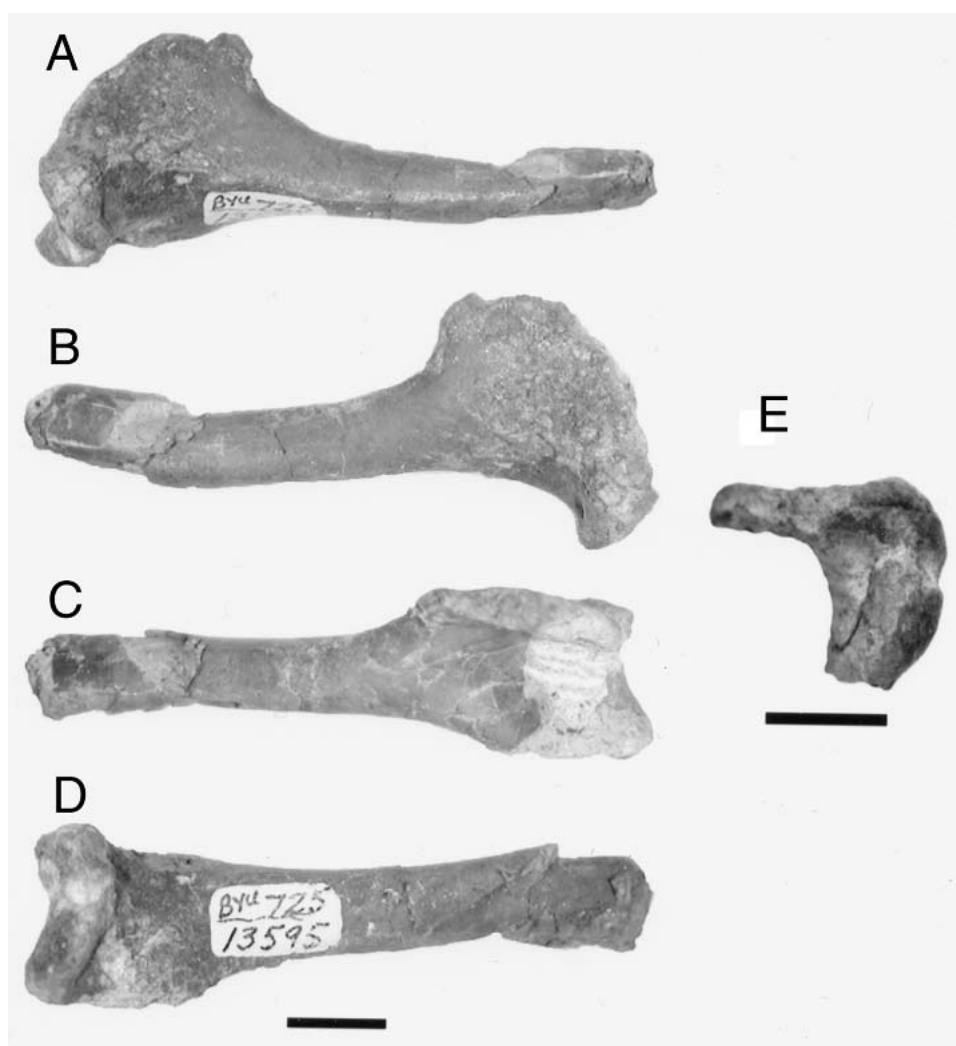


FIGURE 7. Right humerus (BYU 13595) of *Mesadactylus ornithosphyos* in A, dorsal; B, caudal; C, posterior; D, cranial; and E, proximal views. Scale equals 10 mm.



FIGURE 8. Left metacarpal IV (BYU 17207) of *Mesadactylus ornithosphyos* in A, dorsal; B, caudal; C, ventral; D, cranial; and E, distal views. Scale equals 10 mm.

There is a complete right first phalanx (BYU 17206) and proximal left first phalanx (BYU 13618) of digit IV that are very well-preserved, but typical for pterodactyloid pterosaurs (Fig. 9). Unlike the case in *Rhamphorhynchus*, there is no posterior groove running the length of the shaft in *Mesadactylus* (Wellnhofer, 1991).

A very well-preserved complete left femur (BYU 17214) of *Mesadactylus* is present (Fig. 10). Proximally, the head is rounded and the constricted neck is anteverted from the shaft at about 45°, as in primitive pterodactyloids. This characteristic also indicates that another pterosaurian femur from Dry Mesa (BYU 9509) is not *Mesadactylus*, but a more derived pterosaur, con-



FIGURE 9. Right phalanx IV-1 (BYU 13618) of *Mesadactylus ornithosphyos* in A, dorsal; B, caudal; C, ventral; and D, cranial views. Scale equals 10 mm.



FIGURE 10. Left femur (BYU 17214) of *Mesadactylus ornithosphyos* in A, anterior; B, lateral; C, posterior; and D, medial. Scale equals 10 mm.

firming the suspicions of Jensen and Padian (1989). The greater trochanter is present as a knob. The shaft is long and maintains a constant diameter. It is dorsoventrally bowed, as is typical for pterosaurs (Padian, 1986). The distal condyles are roughly the same size, forming an angle with the shaft of 90° , as in primitive pterodactyloids (Jensen and Padian, 1989).

DISCUSSION

New pterosaurian material from the Dry Mesa Dinosaur Quarry permits an enhanced description of *Mesadactylus ornithosphyos*. We follow Padian in assuming that all of the material is from the same taxon (Padian, pers. comm.). This species is a typical primitive small pterodactyloid pterosaur from the late Jurassic of Colorado. It is similar to the other Morrison pterosaurs *Comodactylus* and *Kepodactylus*, and the European *Pterodactylus*. However, several characters indicate that *Mesadactylus* is distinct from these genera. *Mesadactylus* is smaller than *Kepodactylus*. Unlike *Kepodactylus*, there is no pneumatic foramen in the humerus. Unlike *Comodactylus*, the notch for the wing finger extensor tendon does not extend onto the shaft. Due to its fragmentary nature, no phylogenetic analysis is attempted for *Mesadactylus*; however, there appears to be a mixture of primitive and derived characters (Bennett, 1989; Unwin and Lü, 1997). Characters shared with more primitive pterosaurs include the lack of a pneumatic foramen and terminal expansion of the humerus, the lack of occipital pneumatic foramina, the exclusion of the parietal from the occiput, and a 45° angle between the femoral head and shaft. Characters shared with derived pterodactyloids include the expansion of the supraoccipital to form most of the occipital region and a short cervical centrum.

The diameter of the spinal cord in relation to the size of the

vertebra appears smaller than that typically seen in bird cervicals. This configuration suggests that a supramedullary diverticulum, as seen in birds, is unlikely. However there are scattered ventrolateral ostea in the wall of the spinal canal that could provide a means for pneumatization of the dorsal elements of the vertebra from a relatively small supramedullary diverticulum. The consistency of these features in future specimens will determine if, in fact, a diminutive supramedullary diverticulum existed in pterosaurs.

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