N. Jb. Geol. Paläont. Mh.	**1996**, H. 8	473–484	Stuttgart, August 1996

A large pterodactyloid from the Morrison Formation (Late Jurassic) of Garden Park, Colorado

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With 4 figures and 1 table in the text

HARRIS, J. D. & CARPENTER, K. (1996): A large pterodactyloid from the Morrison Formation (Late Jurassic) of Garden Park, Colorado. – N. Jb. Geol. Paläont. Mh., **1996** (8): 473–484; Stuttgart.

Abstract: A number of vertebrate fossils were recovered from the Small *Stegosaurus* Quarry during the excavation of a *Stegosaurus stenops* specimen by the Denver Museum of Natural History in 1992. Among them were bones of a large pterodactyloid pterosaur, assignable to *Kepodactylus insperatus* n. g. n. sp. These fossils represent one of the largest Jurassic pterosaurs known, comparable in size to the roughly contemporary *Pterodactylus grandis* from Germany. The pterodactyloid nature of the animal is confirmed by the length and morphology of the cervical vertebra and the absence on the wing phalanx of a longitudinal furrow.

Zusammenfassung: Aus Material der Grabungen 1992 auf *Stegosaurus stenops* stammen auch einige Flugsaurier-Knochen, die zur Aufstellung der neuen Gattung und Art *Kepodactylus insperatus* führen. Es handelt sich um einen der größten Flugsaurier aus dem Jura, vergleichbar mit *Pterodactylus grandis* aus Deutschland.

Introduction

The history of pterosaur fossil discoveries in the Upper Jurassic of the North American continent is limited to five discoveries, all from the Morrison Formation of the Western Interior. The first, made by S. W. WILLISTON, was a fragment of a right wing metacarpal found in Quarry 5 at Como Bluff, Wyoming. MARSH (1878) identified the fragment as a pterodactyloid pterosaur, and based the species *Pterodactylus montanus* on it. Later, MARSH (1881a) differentiated the metacarpal from the genus *Pterodactylus* and renamed the animal *Dermodactylus montanus*. In the brief description, MARSH (1881a) also implied an associated first wing phalanx, a scapulocoracoid, some vertebrae, and some teeth belong to *Dermodactylus;* none of these elements has been figured or described, but WELLNHOFER (1978: 65) states that they are too large to belong to the type of *Dermodactylus*. Based on this material, MARSH (1881a) estimated a 1.5–1.8 m (5–6 ft.) wingspan for *Dermodactylus;* WELLNHOFER (1991a), however, estimated only about 1 m, based on the metacarpal.

0028-3630/96/1996-0473 $ 3.00

MARSH (1881b) also described an isolated braincase from Como Bluff as belonging to a Jurassic bird, *Laopteryx priscus*. A later reanalysis of the fossil (OSTROM 1986), has shown this fossil to be pterosaurian in nature, but is too fragmentary to be assigned to a higher taxon.

JENSEN & OSTROM (1977) identified another pterodactyloid fossil, the proximal end of the proximal left wing phalanx, from the Dry Mesa Quarry, Colorado. They note only that it is of similar proportions to the metacarpal of *Dermodactylus*. WELLNHOFER (1991a: 106) places it within the genus *Mesadactylus*.

Another isolated metacarpal was discovered in the Yale Peabody collections in material originally sent to, but not described by, MARSH. GALTON (1981) identified this bone as that of a rhamphorhynchoid pterosaur, *Comodactylus ostromi*. Thus, both "rhamphorhynchoid" and pterodactyloid pterosaurs have been found in the Morrison Formation. *Comodactylus* was a large pterosaur, with an estimated wing span of 2.5 m (WELLNHOFER 1991a).

A third named pterosaur from the Morrison Formation has also been recovered from the Dry Mesa Quarry. JENSEN (1981) originally attributed many elements from this quarry to birds, including a partial right femur of *Archaeopteryx*, a tibiotarsus belonging to the new avian species *Paleopteryx thomsoni* (which was not formally described in the paper) and many "avian-like" bones, including a synsacrum and a partial left femur. JENSEN & PADIAN (1989) redescribe the right femur as that of a maniraptoran theropod, and reidentify the "tibiotarsus" as the distal radius of an indeterminate theropod. The synsacrum was made the holotype of *Mesadactylus ornithosphyos*. The left femur, and much additional postcranial material, were also attributed to this genus. It is the most complete pterosaur known from the Morrison.

The 1992 paleontological expedition by the Denver Museum of Natural History (DMNH) to the Morrison Formation exposures at Garden Park, Colorado, led to the discovery of a virtually complete specimen of *Stegosaurus stenops* (CARPENTER & SMALL 1993, CARPENTER 1993, in press). The Small *Stegosaurus* Quarry has also produced a diverse vertebrate fauna, including many microvertebrates (Table 1). Except for the *Stegosaurus* specimen, all of the elements were disarticulated. Most of the vertebrate specimens were recovered from a lenticular gray lacustrine mudstone that is capped by a sequence of progressively thin sandstones separated by very thin mudstone. The sandstone becomes progressively thicker and wider, and documents the growth of a crevasse splay complex (CARPENTER, in press). Fusian is abundant in the lacustrine mudstone, probably due to local fires accompanying a drought (CARPENTER in press). Most of the fossils from the quarry have

undergone diagenetic distortion. That some of these elements are pterosaurian is certain as they posses extremely thin walls and, in some instances, internal struts (convergent with some birds). Such struts are characteristic of later Cretaceous pterodactyloids, but are not restricted to those groups (WELLNHOFER 1991a). The pterosaur bones occur in light gray mudstones and greenish-gray fine-grained sandstones.

HOWSE (1986), UNWIN (1992, 1995), PADIAN & RAYNER (1993), and KELLNER (1995) have noted that the "Rhamphorhynchoidea" is a paraphyletic group; until the formal presentation of a new classificatory convention, we use the term "rhamphorhynchoid" in the informal, conventional sense (sensu UNWIN 1995), meaning those primitive pterosaurs retaining long tails, wing finger phalanges chevron-shaped, not ovoid, in cross-section, large fifth pedal digits, occipital condyles facing posteriorly rather than posteroventrally, and separate nasal and antorbital openings in the skull.

Systematic paleontology

Pterosauria KAUP, 1834
Pterodactyloidea PLIENINGER, 1901
Kepodactylus, n. g.

Etymology: Greek kepos meaning "garden," for Garden Park, Colorado, where the fossils were found; Greek daktylos, meaning "finger".

Type species: *Kepodactylus insperatus* n. sp.

Type locality: DMNH Loc. 611, 1992 *Stegosaurus stenops* Quarry, near the top of the lower member of the Morrison Formation, Garden Park, Colorado (CARPENTER, in press).

Diagnosis: Large pterodactyloid having an estimated wingspan of 2.5 m. Cervical centrum elongated as in *Pterodactylus* but with postzygapophyses extended beyond centrum; cervical centrum lacking diapophyses of "rhamphorhynchoids" and accessory exapophyses of azhdarchids; pneumatic foramen posteriorly located, elongated oval located on centrum rather than on neural arch as in "rhamphorhynchoids." First wing phalanx without longitudinal groove of "rhamphorhynchoids" and ovoid in cross-section. Deltopectoral crest large, rectangular, not hatchet-shaped as in "rhamphorhynchoids" and nyctosaurids, not warped as in pteranodontids.

Kepodactylus insperatus n. sp.

Etymology: Latin insperatus, meaning "unexpected."

Holotype: DMNH 21684, consisting of a cervical vertebra, a left humerus, the left proximal phalanx of the wing finger, the distal end of the right proximal wing finger phalanx, the proximal end of the left second wing finger phalanx, and a metatarsal.

Type locality: As for genus.

Diagnosis: As for genus.

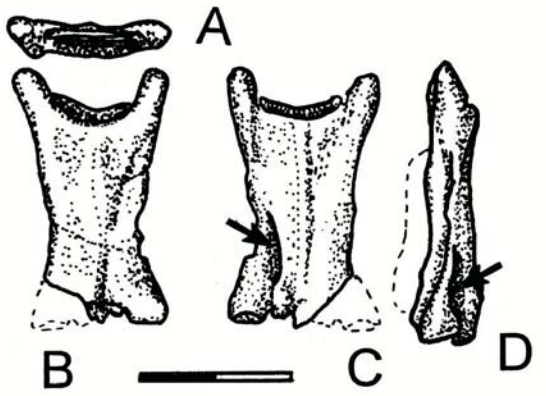

Fig. 1. Cervical vertebra of *Kepodactylus insperatus*. A: Anterior view. B: Dorsal view. C: Ventral view. D: Right lateral view. Arrow indicates pneumatic foramen. Scale = 2 cm.

Description: The cervical vertebra (Fig. 1) is missing most of the neural spine and a portion of the left posterolateral corner, including the postzygopophysis. It is heavily crushed dorsoventrally, but is visibly procoelous. The centrum bears no sign of having possessed diapophyses, a pterodactyloid characteristic (Howse 1986, Unwin 1995). The centrum is somewhat elongate, more similar to that of *Pterodactylus* than that of "rhamphorhynchoids", but not nearly as long as in the later azhdarchids (Howse 1986, Wellnhofer 1991a). However, the remaining postzygopophysis appears to extend slightly beyond the posterior-most extent of the centrum, unlike the situation of *Pterodactylus* but similar to that in both "rhamphorhynchoids" and later pterodactyloids (Howse 1986).

The neural spine is missing, but the broken ridge on the dorsal edge of the centrum can be traced from the posterior edge to a point roughly 2/3 the distance to the anterior end, similar to the situation in the posterior cervicals of *Pterodactylus* and *Mesadactylus* (Jensen & Padian 1989). The base is quite narrow, and the neural spine was probably low and very thin, as in pterodactyloids but not "rhamphorhynchoids" (Wellnhofer 1991a). The vertebra lacks the accessory exapophyses found in such advanced pterodactyloids as the azhdarchids (Howse 1986). Howse (1986: 323) notes that the anterior face of the centrum of the cervicals in pterodactyloids is "crescent shaped, with the crescent directed upwards;" the specimen, despite the severe diagenetic crushing, does appear to have been slightly crescentic in this manner. Evidence of a hypapophysis, typically associated with the crescentic shape (Howse 1986) is ambiguous.

Table 1. Taxa from the Small *Stegosaurus* Quarry.

fish	amiiform indet.	*Ceratodus guntheri*
Chelonia	*Glyptops plicatus*	*Dinochelys* cf. *whitei*
Crocodylia	*Gonipholis* sp.	
Pterosauria	*Kepodactylus insperatus*	gen. indet.
Sauropoda	*Apatosaurus* sp.	
Theropoda	*Elaphrosaurus* sp.	"coelurosaur" indet.
Ornithopoda	*Dryosaurus* sp.	juvenile indet.
Stegosauria	*Stegosaurus stenops*	
Ankylosauria	? *Mymooropelta* sp.	
Mammalia	*Docodon* sp.	gen. indet

The pneumatic foramina in the sides of the cervicals of pterodactyloids have often been overlooked. Pneumatic foramina are known in virtually all described pterosaur cervicals, but in pterodactyloids they appear to be limited to small circular or ovoid openings centered in the sides of the cervical centra (e. g. Howse 1986). The new Morrison Formation specimen, however, has a somewhat more elongate ovoid foramen located immediately ventral to the right transverse process at the posterior end of the centrum; the complementary feature on the left side has been obliterated by compaction. The presence or absence of pneumatic foramina on the anterior end (e. g. Baird & Galton 1981, Wellnhofer 1991b) is indeterminate as a result of crushing.

A left humerus recovered from the same site is virtually complete, lacking only the distal prominence of the deltopectoral crest (Fig. 2). It is rather severely crushed, and the distal third is damaged. The humerus possesses the characteristic "saddle-shaped" articular head typical of pterosaurs. The deltopectoral crest is quite large and rectangular in shape as in early pterodactyloids, including *Mesadactylus* (Jensen & Padian 1989), and azhdarchids (Bennett 1989). The rectangular dimensions of the deltopectoral crest are such that it is longer than deep, as opposed to deeper than long as in early "rhamphorhynchoids" such as *Eudimorphodon* (Wild 1978) and *Campylognathoides* (Wellnhofer 1974). It is not constricted at the base, and does not widen distally into a "hatchet shape" as in "rhamphorhynchoids" (Wellnhofer 1975, Jensen & Padian 1989) and nyctosaurids (Bennett 1989), and is not "warped" as in pteranodontids (Bennett 1989, Murray et al. 1991). However, relative to the main body of the humerus, the size of the deltopectoral

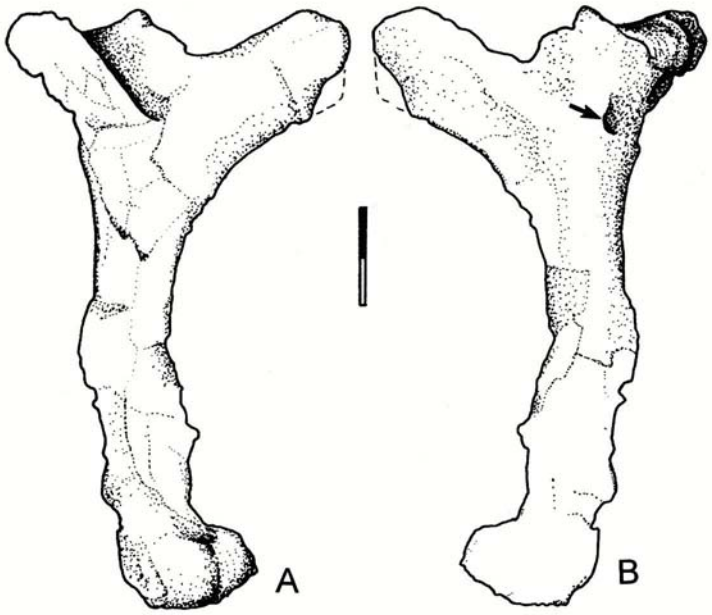

Fig. 2. Left humerus of *Kepodactylus insperatus*. A: Posterior view. B: Anterior view. Arrow indicates pneumatic foramen. Scale = 2 cm.

crest in *Kepodactylus* is more similar to that of "rhamphorhynchoids" and azhdarchids like *Quetzalcoatlus* (LAWSON 1975) than *Pterodactylus* (WELLNHOFER 1978).

There is a small pneumatic foramen on the dorsal edge of the humerus, opposite the deltopectoral crest. Foramina such as this have been reported in the "rhamphorhynchoid" *Dorygnathus bathensis* (PADIAN & WILD 1992), the pterodactyloids *Ornithocheirus* (SEELEY 1901) and *Santanadactylus araripensis* (WELLNHOFER 1983), unidentified pteranodontids from Peru and Texas (BENNETT 1989), a Lower Cretaceous azhdarchid humerus from Texas (MURRAY et al. 1991), and in the tapejarids *Tapejara* and *Tupuxuara* (KELLNER 1995, KELLNER & HASEGAWA 1993). The opening is located more laterally than in the more advanced pteranodontids and azhdarchids, however, and may be autapomorphic. A narrow groove separates the ulnar and radial condyles at the distal end of the Morrison Formation humerus. No distal (as in *Santanadactylus* sp. [WELLNHOFER 1983]) or ventral (as in *Anhanguera* [WELLNHOFER 1991b] and *Tapejara* [KELLNER 1995]) pneumatic foramina are visible – if any existed – due to crushing.

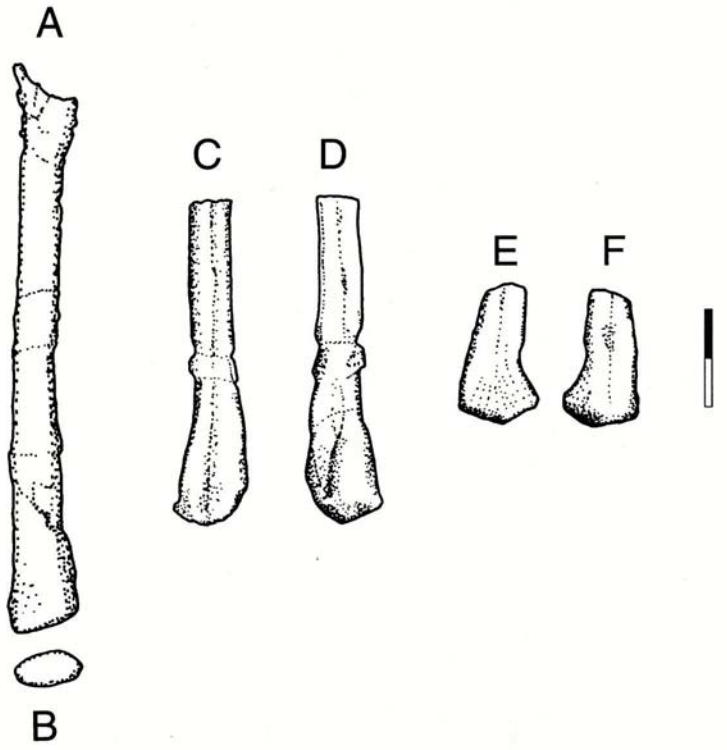

Fig. 3. Wing finger elements of *Kepodactylus insperatus*. A, B: Left proximal wing finger phalanx in (A) dorsal view and (B) distal view. C, D: ?Distal end of the right proximal wing finger phalanx in (C) ventral and (D) dorsal views. E, F: ?Distal end of the left second wing finger phalanx in (E) dorsal and (F) ventral views. Scale = 2 cm.

The proximal wing finger phalanx (Fig. 3A, B) of *Kepodactylus* is most similar in morphology to the first left wing finger of most pterosaurs, including both *Rhamphorhynchus* and several pterodactyloids (WELLNHOFER 1975, 1978). Although somewhat crushed, particularly at the proximal end, it is ovoid in cross-section and bears no trace of the longitudinal furrow into which the wing membrane attached which gives "rhamphorhynchoid" wing finger phalanges a chevron-shaped cross-section (WELLNHOFER 1978: 20, 1991a: 55). Nor is it "T-shaped" in cross-section as in *Quetzalcoatlus* (WELLNHOFER 1991a: 142).

A badly crushed fragment associated with the *Kepodactylus* material resembles the distal end of the aforementioned phalanx in shape and size, and may be the distal end of the first phalanx on the right side (Fig.

3C, D). Another, smaller fragment, matches in morphology the proximal end of the remaining wing finger phalanges (fig. 3E, F). It is similar in size to the distal end of the second phalanx, also of the left side. A small, lightly recurved, tapering fragment seems most plausibly to be a portion of the terminal wing finger phalanx. Lacking both the proximal and distal ends, it is unclear whether it belongs to the right or left side. None of these fragments bears a furrow as in "rhamphorhynchoids" (WELLNHOFER 1978, 1991a).

A complete metatarsal was also recovered (Fig. 4). It is very similar to elements figured by PADIAN (1983: figs. 14, 15) for the "rhamphorhynchoid" *Dimorphodon macronyx*, particularly metatarsal IV. The shortness of this bone supports this position. Distinct articular facets for an adjacent metatarsal occur on the medial side of both the proximal and distal ends, but not on the lateral sides.

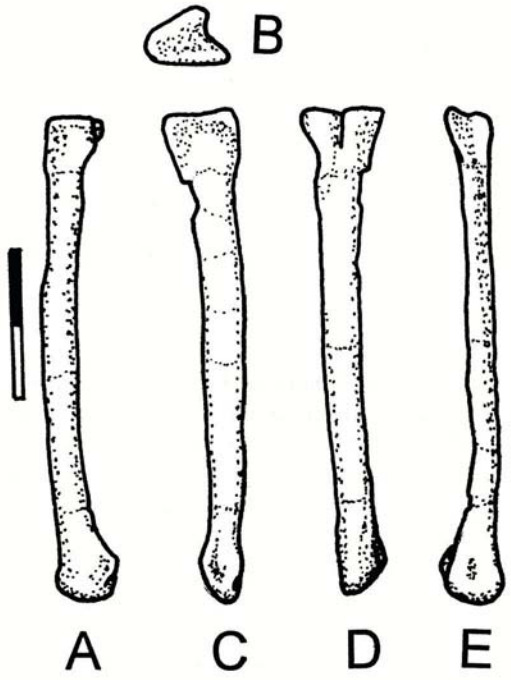

Fig. 4. Metatarsal IV of *Kepodactylus insperatus*. A: Left lateral view. B: Proximal view. C: Ventral view. D: Dorsal view. E: Right lateral view.

Discussion

Kepodactylus differs from the roughly contemporaneous European pterodactyloid *Pterodactylus* in that the postzygapophysis on the cervical vertebra extends beyond the posterior end of the centrum. The morphology of the cervical vertebra and the wing phalanges demonstrates that the animal is a pterodactyloid, and thus cannot be congeneric with the "rhamphorhynchoid" *Comodactylus* (GALTON 1978). Direct comparison with *Dermodactylus* cannot be made, as the current material of *Kepodactylus* does not include a right metacarpal IV, the holotype for *Dermodactylus* (MARSH 1881b), and the remaining material attributed to *Dermodactylus* (MARSH 1881b) has not been described. Nevertheless, *Dermodactylus* appears to be the size of the European *Rhamphorhynchus,* and is smaller than *Kepodactylus.* Positive differentiation between *Kepodactylus* and *Mesadactylus* cannot be made at present, but the presence of a pneumatic foramen on the humerus and another located posteriorly on the cervical centrum of *Kepodactylus,* as well as the much greater size, suggest that *Kepodactylus* is a distinct genus.

Pterosaurian phylogenetics are currently in a state of flux, and many partial analyses, some cladistic, have been published (e. g. HOWSE 1986, BENNETT 1989, WELLNHOFER 1991a, UNWIN 1992, KELLNER 1995). Both BENNETT (1989) and UNWIN (1992) have recently proposed new classifications for pterodactyloids, although BENNETT restricted his analysis to the Cretaceous forms, using the Late Jurassic *Pterodactylus* as the most primitive outgroup.

The location of the pneumatic foramen on the humerus would place *Kepodactylus* within the unnamed Node 1 of BENNETT (1989), although other defining characteristics of this node are indeterminate in the current incomplete *Kepodactylus* material. This node includes the Nyctosauridae + Dsungaripteridae + Pteranodontidae + Azhdarchidae, but not *Pterodactylus.* However, *Kepodactylus* either lacks the autapomorphies of the Cretaceous groups or they are indeterminate in the given material (BENNETT 1989). This fact, coupled with the presence of such a foramen on *Dorygnathus* (PADIAN & WILD 1992), indicates that the presence of a pneumatic foramen on the humerus is synapomorphic at a lower taxonomic level than BENNETT's (1989) grouping.

UNWIN (1995) and KELLNER (1995) outline more all-encompassing analyses of the Pterosauria. Although most of the defining characteristics used in these analyses cannot be determined with the currently known material of *Kepodactylus,* the lack of diapophyses on the cervical vertebra indicates that *Kepodactylus* resides within the Pterodactyloidea (Node F) of UNWIN (1995). The low neural spine on the cervical further

unites it with an unnamed node (Node J), including all pterodactyloids except the Ornithocheiroidea (UNWIN 1995). KELLNER (1995) notes that tall neural spines characterize the Tapejaridae, but low spines characterize the Azhdarchidae. *Kepodactylus* also possesses a dorsal pneumatic foramen opposite of the deltopectoral crest, as in the Tapejaridae and Azhdarchidae (sensu KELLNER 1995), but lacks the ventral foramen seen in *Tapejara* (KELLNER 1995). Higher placement of *Kepodactylus* is not currently possible with the traits used by UNWIN (1995) or KELLNER (1995), again due to insufficient material.

Acknowledgements

We would like to thank Denver Museum volunteer fossil preparators GENE LINDSEY, DENNIS MCNAMEE, and JOHN SHINTON for their preparation of the *Kepodactylus* material. Thanks are also due to LIZZ CAPLAN and KEVIN FULTON for translating portions of some of the German references into English. KATHIE GULLY of the DMNH library was invaluable in finding and obtaining some references. Thanks also to Drs. ALEX KELLNER (AMNH), DAVID UNWIN (University of Bristol), and PETER WELLNHOFER (Bayerische Staatssammlung für Paläontologie und historische Geologie) for very useful conversations and suggestions. Fossils described in this paper were collected under BLM Permit C-49819c.

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Bei der Tübinger Schriftleitung eingegangen am 4. August 1995.

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