

PTEROSAUR REMAINS FROM THE KAYENTA FORMATION (?EARLY JURASSIC) OF ARIZONA

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ABSTRACT. Two records of pterosaurs, the earliest from the Western Hemisphere, are reported from the Kayenta Formation (?Early Jurassic) of north-eastern Arizona. The first specimen represents a new genus and species, *Rhamphinion jenkinsi*. It consists of three pieces of a skull, including an occipital region, most of a left jugal, and two teeth associated with a possible fragment of the dentary; it is difficult to diagnose because it is so fragmentary and because the occipital region of early pterosaurs is not well known, but may be recognized by the position and configuration of the orbital and antorbital borders of the jugal. The second specimen is the left-wing (fourth) metacarpal of a rhamphorhynchoid; it is well-preserved but cannot be classified more precisely.

OVER the past few years, field parties from the Museum of Comparative Zoology at Harvard University (MCZ), the Museum of Northern Arizona (MNA), and the Museum of Paleontology of the University of California at Berkeley (UCMP) have renewed intensive palaeontological exploration of the Kayenta Formation of northern Arizona. The Kayenta Formation was prospected sporadically since the 1930s, but its white to orange-red sandstones and grey-purple siltstones yielded few specimens. The recent finds, however, have greatly increased our knowledge of the faunal diversity of the Kayenta, which now includes large and small ornithischian and saurischian dinosaurs (Welles 1954; Colbert 1980; Attridge *et al.* MS.), several kinds of crocodylians, (Crompton and Smith 1980), testudinales, lizards, amphibians, tritylodontid mammal-like reptiles (Lewis 1958; Kermack 1982), and several kinds of mammals (Jenkins *et al.* 1983). Most remains of the smaller vertebrates have been recovered by screen-washing sediment and hand-picking the sieved residue; most of this work has been ably carried out by Mr. William R. Downs of the Museum of northern Arizona. The results of these labours, in addition to an expanded faunal list, include a better understanding of the biostratigraphical relationships among the fossiliferous horizons of the Kayenta and other early Mesozoic formations. While the exact age of the Kayenta Formation is not certain, the general faunal composition and the consistent absence of Triassic marker species now appear to argue for Early Jurassic (Olsen and Galton 1977), although difficulties with this assignment may remain (Colbert 1980). Most Kayenta vertebrates, at the taxonomic levels so far determined, do not permit of a precise stratigraphical correlation. Dinosaurs, testudinales, crocodylians, lizards, and perhaps mammals are known both from Late Triassic and Early Jurassic sediments. Until the phylogenies of the early members of these groups have been elucidated, we shall be unable to comment on the stratigraphical and geographical distribution of certain sub-groups of each, which may indeed be restricted and therefore diagnostic.

This note describes the first remains of pterosaurs (flying reptiles) from the Kayenta Formation. These are the earliest known from the Western Hemisphere, but not the oldest in the world; *Eudimorphodon ranzii* Zambelli 1973 and *Peteinosaurus zambellii* Wild 1978, from the Norian (Upper Triassic) sediments of northern Italy, are older. Pterosaurs are exceptionally light-boned animals and therefore do not preserve well. It is indeed fortunate to recover their remains from the Kayenta Formation; pterosaurs are best preserved in low energy, fine-grained marine or lacustrine sediments, and their record in any kind of terrestrial sediment is poor. Although the quality of the specimens at hand is not very good, I believe there is sufficient evidence to assign them to the Order Pterosauria, as outlined below.

SYSTEMATIC PALAEOLOGY

Class REPTILIA

Order PTEROSAURIA

Sub-order RHAMPHORHYNCHOIDEA

Family *Incertae sedis*Genus *Rhamphinion* gen. nov.*Type species. Rhamphinion jenkinsi*, sp. nov.

Etymology. *Rhampho-*, comb. form of *rhamphos*, Gr., 'beak', used in other rhamphorhynchoid names; *inion*, Gr., 'nape of the neck'; referring to the occipital region comprising much of the present specimen.

Diagnosis. The material is diagnostic of the Order Pterosauria because of the large, long, strap-like quadrate, the relatively small occipital condyle, the thin, laminar cranial bones, the large lower temporal fenestra, the shape and orientation of the ascending process of the jugal, and the form of the teeth. Without better preservation it is difficult to specify characters that diagnose the Sub-order Rhamphorhynchoidea, although the shape of the jugal is not at all similar to those of pterodactyls. The genus is characterized by nearly rounded antorbital and orbital margins next to the ascending process of the jugal. The apparent suture between the maxilla and the jugal has a long, low sloping contact and the orbit is situated at approximately the same height above the tooth row as is the antorbital opening.

Remarks. The shape of the quadrate is reminiscent of that of *Eudimorphodon* (see Wild 1978, fig. 1 and pl. 3), as is the general shape of the jugal and the participation of the lacrimal (prefrontal of Wild 1978) in the anterior margin of the orbit. The present specimen has single-cusped teeth that are slightly recurved and tapered at both ends. Such teeth occur in juvenile *Eudimorphodon* (Wild 1978), and are found in the maxillary region of *Dimorphodon macronyx* (Buckland) (Owen 1870; Padian, in press) and most other rhamphorhynchoids. Family division and nomenclature among the Pterosauria are greatly in need of revision, as is the generally accepted phylogeny of the group and its evolutionary position with respect to other archosaurs. Hence, no family designation is given here. The genus is generally similar to several early rhamphorhynchoids, including *Eudimorphodon*, *Dimorphodon*, and *Dorygnathus*.

Rhamphinion jenkinsi, sp. nov.

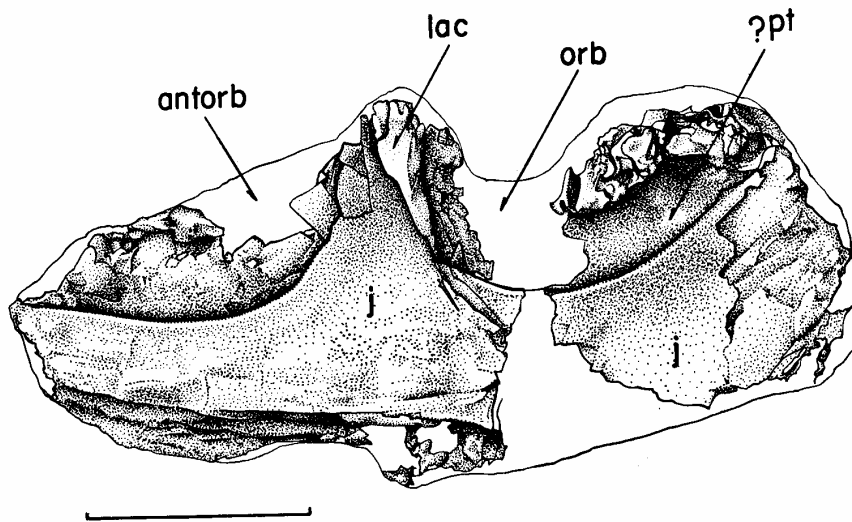
Text-figs. 1-3

Etymology. Named in honour of Dr. Farish A. Jenkins Jr., who discovered the specimen and very kindly made it available to me for description.

Material and occurrence. Holotype, MNA V 4500, consisting of four pieces: an occipital region, a left jugal fragment, a possible mandibular fragment with two associated teeth and the impression of a third, and an unidentifiable bone fragment. Middle Kayenta Formation (Lower Jurassic) of north-eastern Arizona, at the locality known as 'Foxtrot Mesa', the southern side of Sand Mesa, along the Adeii Eechii cliffs, Ward's Terrace, Little Colorado River Valley. Approximate coordinates 35°41'43" N., 111°0'25" W. The remains were found in surface float of the silty facies of the Kayenta; the horizon cannot be precisely traced. Collected by Dr. Farish A. Jenkins Jr. and his field party from the Museum of Comparative Zoology at Harvard University and the Museum of northern Arizona. With this material, which was given the field number 23/78A, were a few other scraps of as yet unidentified bone, lighter in colour and more robust in structure, and not pterosaurian.

Diagnosis. As for the genus.

Description. The preserved fragment of the left jugal (text-fig. 1) is 40 mm long and 19 mm wide at its highest point on the ascending process. The horizontal, sub-orbital portion widens posteriorly and ascends slightly. The rounded bottom of the orbit curves more gently posteriorly, whereas the base of the antorbital opening curves more gently anteriorly. The lower borders suggest that the antorbital opening may have been larger than the orbit, as in most pterosaurs. Along the posterior border of the ascending process is a splint of bone identifiable as



TEXT-FIG. 1. *Rhamphinion jenkinsi*, gen. et sp. nov. Left jugal with associated fragments. Part of holotype, MNA V 4500. Scale = 10 mm. Abbreviations: antorb = antorbital opening; j = jugal; lac = lacral; orb = orbital opening; ?pt = possible fragment of pterygoid.

the lacral (following Wellnhofer's (1978) terminology; Wild (1978) calls this the pre-frontal). This splint is about 7 mm long, and it tapers as it descends.

Most of the bone has been worn away beneath the very front of the orbit, but the remaining bone seems to be undisturbed. The lower border of the jugal appears to slope upwards and forwards, and 22 mm of the maxillary suture is preserved. Anteriorly the bone is broken away, and posteriorly it is hidden by a support compound applied during preparation, that might be difficult to remove without damage to the specimen. Parts of internal skull bones can be seen within the openings, but these have been crushed beyond recognition.

The occipital fragment (text-fig. 2A) is about the same size as the jugal fragment. It preserves the occipital condyle with part of the adjacent basioccipital and exoccipital regions, the medial part of the left paroccipital process, an underlying fragment which may be the prootic, and two descending rami of bone that seem to be portions of the quadrates. It is difficult to estimate the size of the complete skull from these remains, but in relation to the other bones the occipital condyle is small, a characteristic of pterosaurs and birds (Seeley 1901; Wellnhofer 1978). Text-fig. 2B, based on the skull of *Rhamphorhynchus*, shows the parts of the occipital region represented in this specimen. A great deal of crushing and dislocation has taken place, and the identification of many features must be regarded as tentative.

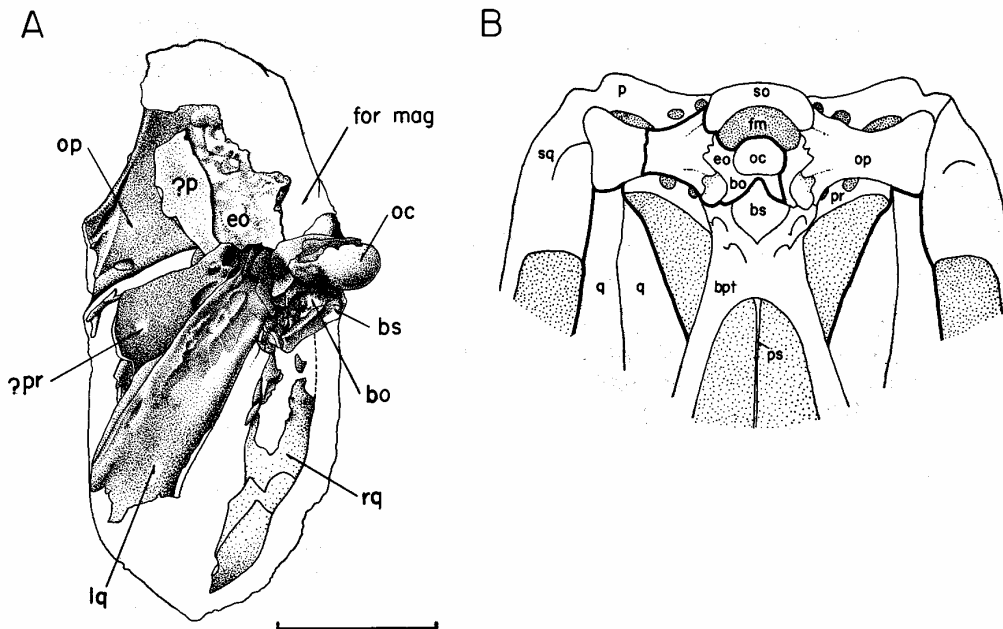
The occipital condyle is ovate in shape; it lacks some of its dorsal portion, but is otherwise fairly complete. Portions of the left exoccipital can be seen ventral and lateral to the condyle, including the basal tubera that connect the exoccipital with the basisphenoid and the basioccipital, and the lateral flange that meets the opisthotic or paroccipital process. Along its lateral border there is a recess in which the most posterior cranial foramina should be located, but no details of this region are preserved. Most of the basioccipital region is missing, and only a few bone fragments of dubious origin remain. Lateral and dorsal to this region is the medial portion of the left opisthotic or paroccipital process. Its dorsal and ventral borders are well-formed, and the positions of the post-temporal foramen and the foramen magnum can be inferred from its preserved relationship to the other bones of the occipital region. About 15 mm, or roughly half the length of the entire bone, appears to have been preserved. There is no trace of the supraoccipital. A portion of another bone, perhaps displaced from the skull roof, overlies the medial section of the opisthotic, but it has no diagnostic feature.

A wide, strap-like lamina of bone runs lateroventrally from just below and to the left of the occipital condyle, widening until its disappearance at the lower left edge of the specimen. Medially it tapers somewhat, but this end

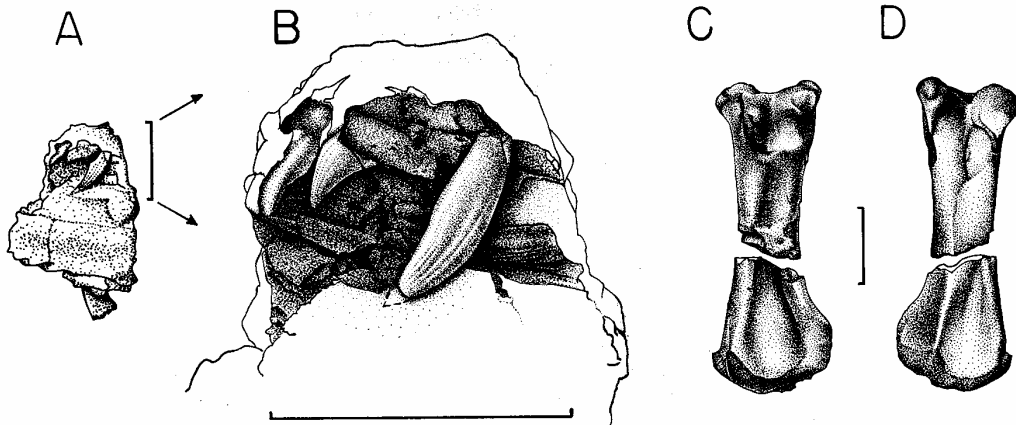
is obscured by overlying portions of the exoccipital region; it appears to be part of the left quadrate. Another similar fragment, apparently the right quadrate, is located behind the occipital region and is mostly obscured by compound applied in preparation. The quadrates in pterosaurs, though quite large, are light in structure; their apparent displacement in this specimen does not facilitate identification of their major features. They superficially resemble the basiptyergoid processes, which are unusually large in pterosaurs (Wellnhofer 1978, fig. 3). However, the structures on the specimen at hand widen as they descend from the occipital region, unlike the basiptyergoid processes, which are of fairly uniform width throughout.

In the space bounded by the paroccipital and the quadrate, and overlain by both bones, there is a small segment of bone that, from its position, I take to be part of the prootic; however, there are no identifying features of the bone, and no foramina are evident.

A third piece of matrix, encrusted with haematite, bears a sheet of bone with the remains of three teeth (text-fig. 3A, B). These teeth do not appear to be in position, and so the bone cannot be positively identified as either maxilla or dentary; its depth and general surface character, however, suggest the latter (cf. *Dimorphodon macronyx*, Owen 1870, pls. XVII and XVIII). Most of two teeth and an impression of a third are preserved. No alveoli are visible. The larger of the two preserved teeth is 6.0 mm long, missing about 0.5 mm at the tip of its crown. It shows the slightly compressed and recurved, unserrated shape of the mid-maxillary teeth of the approximately contemporaneous *Dimorphodon* (Owen 1870; Padian 1980, 1983). There are faint longitudinal striations on the tooth, and its tip is only slightly sharper than its root. A second tooth is smaller, with only 2.5 mm of the tip of the crown exposed. Next to this is a shallow impression about 5.0 mm long of most of the main body of a third tooth, preserving some detail of the longitudinal striations. Similar teeth can be found



TEXT-FIG. 2. *Rhamphinion jenkinsi*, gen. et sp. nov. Occipital region. A, part of holotype, MNA V 4500. Scale = 10 mm. Abbreviations: bo = basioccipital; bs = basisphenoid; eo = exoccipital; for mag = foramen magnum; lq = left quadrate; oc = occipital condyle; op = opisthotic; ?p = possible fragment of parietal; ?pr = possible fragment of prootic; rq = right quadrate. B, posteroventral view of occipital region of *Rhamphorhynchus* (Carnegie Museum of Natural History CM 11434; actual breadth 32 mm), schematic diagram. bpt = basiptyergoid; ps = parasphenoid; so = supraoccipital; sq = squamosal. Portions represented by the corresponding region in *Rhamphinion jenkinsi* are heavily outlined.



TEXT-FIG. 3. A, B, *Rhamphinion jenkinsi*, gen. et sp. nov. Jaw fragment with two disarticulated teeth and one tooth impression. Part of holotype MNA V 4500. B is an enlargement of indicated part of A. C, D, left fourth metacarpal of a rhamphorhynchoid pterosaur, Kayenta Formation, UCMP 128227, in medial (C) and lateral (D) view, distal end up. Scale bars = 10 mm.

in other archosaurs, but are normally serrated or keeled, whereas they never are in pterosaurs. The general shape of the teeth, particularly the relative proportions and relationships of the root and crown, is indistinguishable from that of several Jurassic pterosaurs including *Dimorphodon* and *Campylognathoides* (Wellnhofer 1974), but is not reported in any other Lower Mesozoic.

ADDITIONAL PTEROSAUR REMAINS FROM THE KAYENTA FORMATION

In the Autumn of 1981 James M. Clark, a graduate student at the University of Chicago, discovered two fragments of a haematite-encrusted bone that he suspected were from a pterosaur. These proved to be the nearly complete left fourth (wing) metacarpal, about 42 mm long as reconstructed, of a rhamphorhynchoid pterosaur (UCMP 128227). It was found at the 'Airhead West' locality (V82374), not far from where the crocodylian *Eopneumatosuchus colberti* was collected by an MCZ field party in 1979 (Crompton and Smith 1980, p. 197). The horizon is near the base of the Kayenta Formation in Coconino County, Arizona, 11 miles NE of Cameron between the southern two tributaries of Five Mile Wash. The two pieces were preserved in a green siltstone with a thin sandstone stringer; no other remains were found.

The wing-metacarpal (text-fig. 3C, D) is diagnostic of rhamphorhynchoid pterosaurs because of its short, flattened shape and the topography of its articular surfaces. The pterodactyloid metacarpal is relatively longer, rounded in cross-section, and lacks the pronounced ventral flange present at the proximal end of rhamphorhynchoid metacarpals; it is often the longest, or one of the longest, segments of the pterodactyloid wing, whereas in rhamphorhynchoids it is nearly always the shortest.

Galton (1981) has recently described in detail a superbly preserved rhamphorhynchoid wing metacarpal from Como Bluff, Wyoming (Brushy Basin Member of the Upper Jurassic Morrison Formation). He named it *Comodactylus ostromi*, assigning separate generic status because of its large size and corresponding proportional differences from the metacarpals of other, smaller rhamphorhynchoids. In pterosaurs the fourth metacarpal appears to have rotated its position through 90° with respect to the other metacarpals, so that its distal condyles faced laterally instead of ventrally. As such, the wing-finger flexed and extended in a horizontal plane from its articulation with mc IV, and the first three metacarpals were also arranged in a horizontal plane (Wellnhofer 1978,

figs. 11 and 12; Wild 1978, pls. 1, 2, and 9g). This adaptation has led to some confusion in the terms used to describe orientation: the natural 'dorsal' face, for example, is properly regarded as 'medial' in orientation.

The proximal end of UCMP 128227 is badly worn and lacks most surface detail. The groove interpreted by Galton (1981) as for an extensor of the wing-finger is recognizable, but the ventral (or medial, in Galton's sense) flange near the proximal end has been mostly worn away. As in *Comodactylus* and other well-preserved metacarpals of both rhamphorhynchoid and pterodactyloid pterosaurs, the dorsal (lateral) condyle of the distal end is the larger and is skewed away from the axis of the shaft (see Wellnhofer 1978, fig. 12). There are deep ginglymal facets on both sides of the distal end.

The wing metacarpal is one of the poorest indicators of wing length in pterosaurs. In fact, no individual bone is a very good indicator because relative proportions vary among genera. However, the relative proportions of any two wing bones (except for the metacarpals and the last phalanx of the wing-finger) are almost without exception diagnostic to the generic level (Padian, unpublished). In size and proportions the present specimen resembles the larger specimens of *Dimorphodon* in the British Museum (Natural History), which have a wing span of approximately 1.5 m.

This specimen, and the cranial material of *Rhamphinion jenkinsi* described above, provide the third and fourth (and also the earliest) records of rhamphorhynchoid pterosaurs in the Western Hemisphere: the others are *Nesodactylus hesperius* Colbert 1969, from the Upper Jurassic of Cuba, and *Comodactylus ostromi*, also from the Upper Jurassic.

Acknowledgements I thank Dr. Farish A. Jenkins Jr., who presented the *Rhamphinion* material to me for study; Mr. James M. Clark, who collected the metacarpal during field work sponsored by the Museum of Paleontology, University of California; and the National Geographic Society which funded both expeditions. Mr. William Amaral prepared MNA V 4500, and Mr. Mark Goodwin prepared UCMP 128227 from its haematite crust. Ms. Augusta Lucas-Andrae illustrated text-figs. 1, 2A, and 3. I should also like to thank Mr. Charles Schaff of the Museum of Comparative Zoology for locality information on MNA V 4500, and Drs. A. J. Charig, Wann Langston Jr., and John H. Ostrom for reviewing the manuscript.

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Typescript received 9 February 1983

Revised typescript received 30 August 1983

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