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RAPID COMMUNICATION

A CRESTED RHAMPHORHYNCHOID PTEROSAUR FROM THE LATE TRIASSIC OF AUSTRIA

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The earliest pterosaurs are represented by rare, incomplete specimens from the Upper Triassic (Norian) of Italy (Wild, 1978, 1984, 1994; Dalla Vecchia et al., 1989; Dalla Vecchia, 1994, 1995, 1998) and Greenland (Jenkins et al., 1993). The almost complete skeleton of a new rhamphorhynchoid pterosaur is reported from the Upper Triassic of Austria. It comes from the Seefelder Schichten, which has also yielded marine fishes and terrestrial plants (Kner, 1867; Dobruskina, 1993). The environment of deposition of the Seefelder Schichten was a marine, anoxic and partially hypersaline basin on a very shallow carbonate platform (Hopf, 1997).The main features of the specimen are the presence of a sagittal cranial crest and a peculiar heterodont dentition with multicusped teeth. The bony sheath, consisting of very elongated caudal zygapophyses and hemal arches, so typical of the long-tailed pterosaurs, is not present in the new taxon. Cranial crests are common in Late Jurassic and Cretaceous pterodactyloids but have never been unambiguously reported in rhamphorhynchoid pterosaurs. The new specimen shows that these structures appeared very early in the history of pterosaurs and must have reappeared later in pterodactyloids. Also, *Eudimorphodon* has multicusped teeth but the denticulation and pattern of dentition are different from the new taxon. The taxonomic and morphologic diversity of Triassic rhamphorhynchoids is as high as or even higher than in the succeeding Jurassic period.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758
PTEROSAURIA Kaup, 1834
AUSTRIADACTYLUS CRISTATUS, gen. et sp. nov.
(Figs. 1–3)

Etymology—Austria, the country where the specimen was found; *dactylus* (Greek): finger; *cristatus* (Latin), crested.

Holotype—SMNS 56342, Staatliches Museum für Naturkunde Stuttgart, Germany.

Locality and Horizon—Abandoned mine near Ankerschlag, Tyrol, NW Austria; Seefelder Schichten, late Alaunian (middle Norian).

Diagnosis—Sagittal cranial crest extending from the tip of the snout back to at least the middle of the orbit and deepest anterior to the naris; heterodont dentition; tall, slender conical teeth in the premaxilla;1–2 very large, finely denticulated, blade-like teeth in the middle maxilla opposite the ascending process; triangular multicusped teeth with up to 12 denticles along each cutting edge in the posterior part of the maxilla; anterior mandibular teeth similar to the premaxillary teeth, the subsequent teeth (about 25) small, leaf-shaped with 4–6 cusps on each cutting edge; anterior multicusped teeth taller than long and bearing small side cusps, posterior multicusped teeth longer than tall and with larger cusps, tooth size decreasing slightly posteriorly; tail very long without the bony sheath formed by the enormously elongated pre- and postzygapophyses and hemal arches of the caudal vertebrae in other long-tailed pterosaurs (shared with *Eudimorphodon*).

DESCRIPTION

The specimen is a nearly complete articulated skeleton (Fig. 1) preserved on a slab of black calcareous laminites. The bones are preserved partly on the slab and partly on the counterslab (unavailable because it was destroyed). The skull and lower jaws broke along the sagittal plane and parts of these bones are missing.

The specimen is large for a Triassic pterosaur; the skull measures 110 mm long and the estimated wing span is about 120 cm. The skull is long and low, but the tip of the snout is not pointed (Fig. 2). The thin sagittal crest arises from the very tip of the snout and reaches its maximum height (about 20 mm) anterior to the narial fenestra. The height of the crest decreases posteriorly, as suggested by the curvature of its anterior margin and the distribution of the preserved fragments posteriorly. The crest seems to end on the frontal directly above the orbit. It becomes extremely thin at the distal (dorsal) margin, practically fading into the rocky matrix. Radial ridges are present in the anterior, highest portion.

The narial fenestra is elongated anteroposteriorly. The antorbital fenestra is triangular and higher than it is long. Both are large openings as in *Preondactylus*.

The dentition is strongly heterodont (Fig. 3). The premaxilla probably bears five teeth (Fig. 3A). One or, possibly, two large teeth (10 mm high) (Fig. 3B) are present beneath the ascending process of the maxilla. They have about 18 denticles over a distance of 5.5 mm along the cutting edge. The posterior maxillary teeth (Fig. 3C) are triangular and reduced in height (4–6 mm) compared with the blade-like middle maxillary teeth. The anterior teeth of the lower jaw were probably conical and tall. The subsequent mandibular teeth are much smaller than those of the upper jaw. Seventeen multicusped teeth can be counted on the right ramus and the total number was probably 25. The anterior multicusped teeth (Fig. 3D) have 4 or 5 small cusps on each cutting margin. The middle mandibular teeth are slightly smaller, leaf-shaped, and bear 6 larger cusps. The posterior mandibular teeth (Fig. 3E) have 4–6 cusps on each cutting edge.

Although most of the skeleton is preserved, few useful data can be discerned from the postcrania. Wing phalanx 3 is only slightly longer than wing phalanx 2 (103.5 mm and 101 mm respectively) and the ratio of their lengths (1.02) is similar to

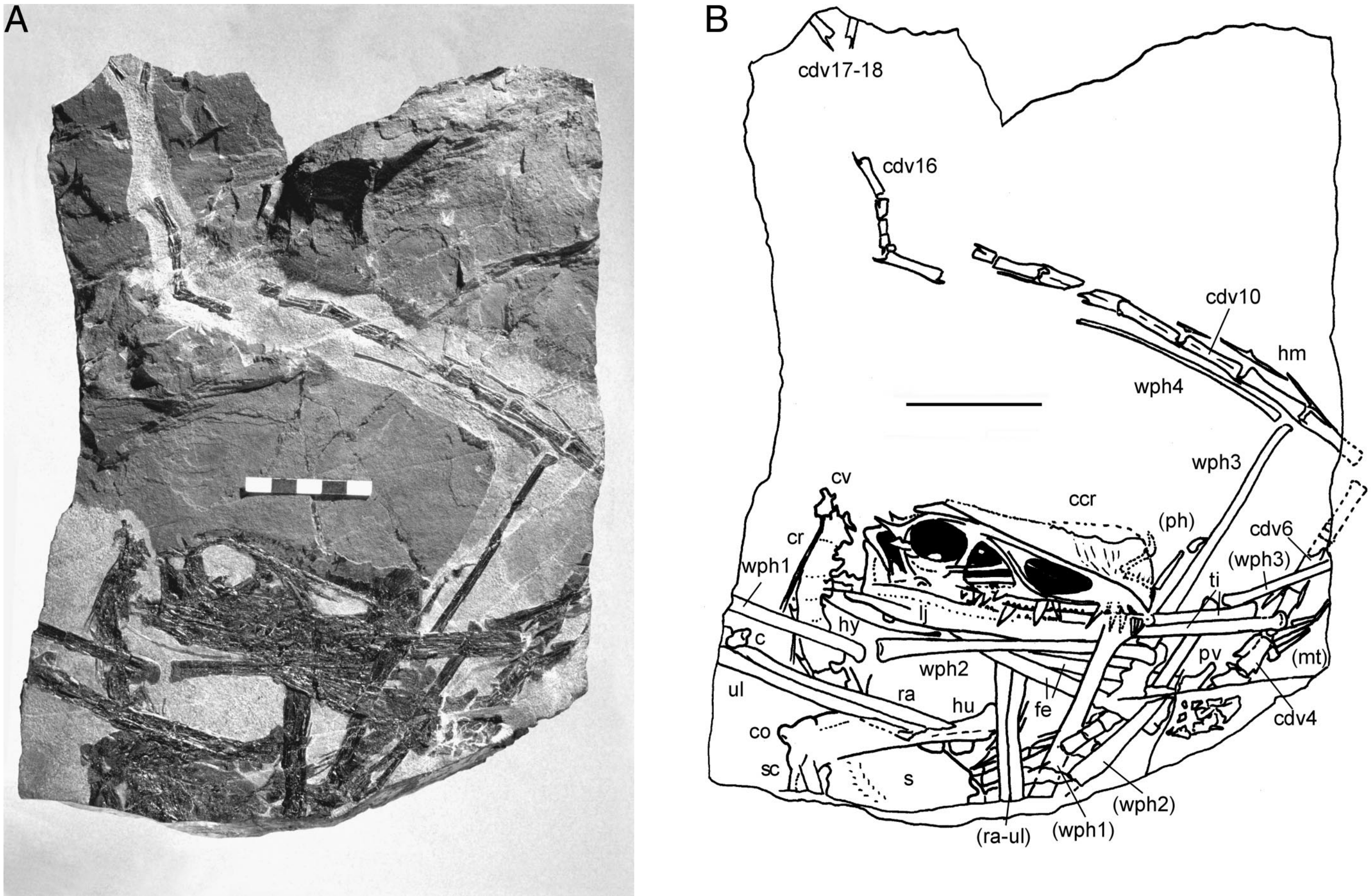

FIGURE 1. The holotype of *Austriadactylus cristatus*, gen. et sp. nov. (SMNS 56342), from the Upper Triassic (Norian) of Ankerschlag (Tyrol, Austria). **A**, photograph of the specimen, scale bar equals 5 cm. **B**, sketch of the skeleton. **Abbreviations**: **c**, carpals; **ccr**, cranial crest; **cdv**, caudal vertebrae; **co**, coracoid; **cr**, cervical ribs; **cv**, cervical vertebrae; **fe**, femur; **hu**, humerus; **hm**, hemapophyses; **hy**, ceratobranchialia of the hyoids; **lj**, lower jaw; **mt**, metatarsals; **ph**, manual phalanges; **pv**, pelvis; **ra**, radius; **s**, sternum; **sc**, scapula; **ti**, tibia; **ul**, ulna; **wph 1–3**, wing phalanx 1–3. Right-side elements are in parentheses. Scale bar = 5 cm.

that of *Preondactylus* (1.00), *Sordes* (1.00), *Dorygnathus* (1.01) and a small specimen of *Eudimorphodon* (1.01, MCSNB 8950; Museo Civico di Scienze Naturali di Bergamo).

The tail is only partly preserved, lacking the distal portion (Fig. 1). The most distal caudal vertebra preserved is the 18th, whereas the total number of caudal vertebrae in rhamphorhynchoid pterosaurs is reported to be between 30 and 40 (Wild, 1978; Wellnhofer, 1991). The longest (28 mm) preserved caudal vertebral centrum is the 9th, which is 3.5 times the length of a posterior dorsal centrum. Behind this vertebra, vertebral length decreases gradually. The pre- and postzygapophyses are not as elongated and rod-like as in other rhamphorhynchoid pterosaurs, in which they surround and stiffen the tail (Wellnhofer, 1978, 1991). This ''osseous sheath'' enables the articulated preservation of the tail in most of the specimens even if the remainder of the skeleton is very disarticulated. On the contrary, the tail of SMNS 56342 is bent through an angle of 90° and partly disarticulated. The hemal arches, which also participate in the ''sheath,'' have rod-like anterior and posterior processes, but are more robust and less elongated than those of other long-tailed pterosaurs. The absence of the ''osseous sheath'' cannot be an artefact of preparation, preservation, or splitting of the rock, because the stiffening rods are very numerous in the middle portion of the tail in *Rhamphorhynchus* (up to 26 dorsal and 12 ventral (Wellnhofer, 1975a)).

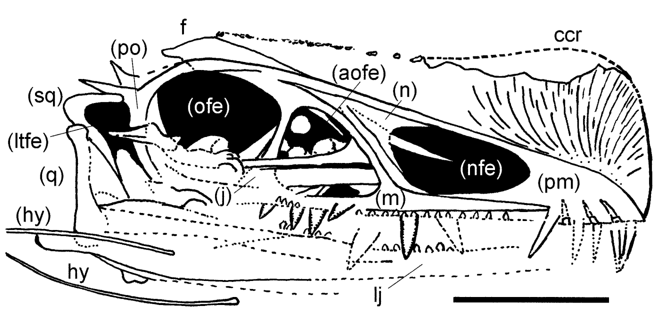

FIGURE 2. The skull of *Austriadactylus cristatus* (SMNS 56342) with the cranial crest. **Abbreviations**: **aofe**, antorbital fenestra; **ccr**, cranial crest; **f**, frontal; **hy**, ceratobranchialia of the hyoids; **j**, jugal; **lj**, lower jaw; **ltfe**, lower temporal fenestra; **m**, maxilla; **n**, nasal; **nfe**, narial fenestra; **ofe**, orbital fenestra; **pm**, premaxilla; **po**, postorbital; **q**, quadrate; **sq**, squamosal. Right-side elements are in parentheses. Scale bar equals 3 cm.

DISCUSSION

Austriadactylus has a cranial crest like the derived pterodactyloids, but also a long tail that lacks elongated, stiffening zygapophyses and hemapophyses, a condition not found in the well-known Jurassic pterosaurs. A crest largely preserved as an

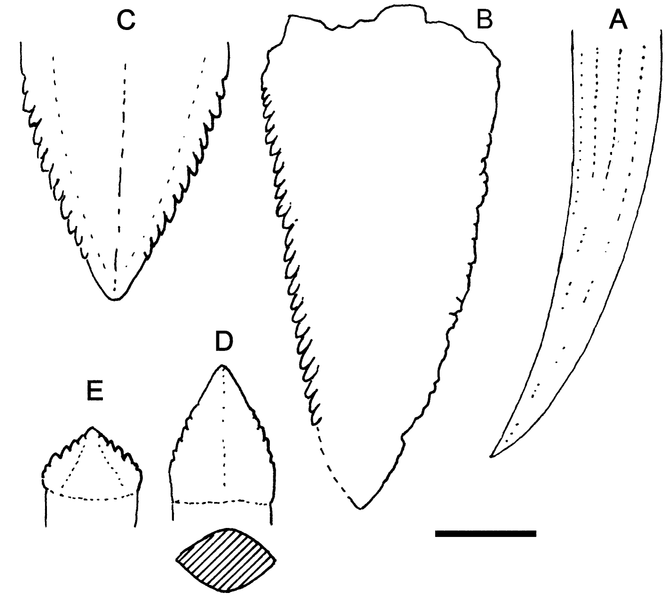

FIGURE 3. Teeth of *Austriadactylus cristatus* (SMNS 56342): **A**, Premaxillary tooth; **B**, large maxillary tooth beneath the ascending process of maxilla; **C**, posterior maxillary tooth; **D**, middle-anterior mandibular tooth, with below its cross-section near the base of the crown; **E**, posterior mandibular tooth. Scale bar equals 3 mm.

impression was described by Broili (1927) in a specimen of *Rhamphorhynchus*, but Wellnhofer (1975b) carefully reexamined the specimen without finding actual evidence of the crest. No other specimen of the several dozen *Rhamphorhynchus* studied by Wellnhofer (1975a, b) has a crest, and up to now no crested specimens have been found.

The posterior extension of the premaxillary crest is considered apomorphic for a clade of pterodactyloids including the Dsungaripteroidea and the Azhdarchoidea (Unwin and Lü, 1997), but the shape of the crest of *Austriadactylus* differs from those of all other crested pterosaurs (Wellnhofer, 1991).

Multicusped teeth could be an apomorphy uniting *Eudimorphodon* and *Austriadactylus* in the same clade. Multicusped teeth is an unusual feature for archosaurs, but it is common in the Prolacertiformes (Wild, 1973, 1978; Renesto and Dalla Vecchia, 2000). However, the common features of the dentition of Norian pterosaurs could be due to convergence caused by the particular diet in their peculiar Late Triassic habitat. The different sizes of the teeth from the upper and lower jaws of *Austriadactylus* are similar to the condition in *Preondactylus*, except that its teeth are neither serrated nor multicusped. On the other hand, the dentition of *Eudimorphodon* consists of pentacusped and tricusped teeth, and the teeth from the upper and lower jaws correspond in both size and shape.

Large caniniform teeth are also found below the ascending process of the maxilla in *Eudimorphodon* and *Preondactylus* (Wild, 1978, 1984). They appear to be a character peculiar to Triassic pterosaurs.

The tail of *Austriadactylus* is very long, as in *Peteinosaurus* (Wild, 1978), and comparatively longer than that of other rhamphorhynchoid pterosaurs (Wild, 1978). The ratio of the length of the first 15 caudal vertebrae to the skull length is about 2.8. This ratio is less in *Dimorphodon macronyx* (about 1, because of the very large skull of this pterosaur (Owen, 1870)), *Dorygnathus banthensis* (2.4), *Campylognathoides liasicus* (2.17 (Wellnhofer, 1974)) and *Rhamphorhynchus* (around 1.5–1.6 (Wellnhofer, 1975b)). The tail of *Austriadactylus* represent the primitive condition for pterosaurs as suggested by the fossil record, because all supposed relatives of pterosaurs (Wild, 1978; Gauthier, 1986; Sereno, 1991; Bennett, 1996; Peters, 2000) have a long tail without elongated zygapophyses and hemapophyses, whereas the tail in Jurassic rhamphorhynchoids (excluded the short-tailed *Anurognathus*) has elongated zygapophyses and hemapophyses and shortened during evolution; the tail reached the maximum reduction in the derived Late Jurassic–Cretaceous pterodactyloids. This primitive condition is also present in a still undescribed *Eudimorphodon* specimen (BSP 1994 I 51; Bayerische Staatssammlung für Paläontologie und historische Geologie München) from the Seefeld Schichten (Peter Wellnhofer, pers. comm., March 2001). *Peteinosaurus* has elongated zygapophyses and hemapophyses, thus their absence is not a character of all Triassic pterosaurs, but it is shared by some taxa.

Although the earliest pterosaurs are represented by only a dozen specimens, four genera have been named to date (*Austriadactylus* nov. gen., *Eudimorphodon*, *Peteinosaurus* and *Preondactylus*, but the latter two could be congeneric (Dalla Vecchia, 1998)). They all lived during the late Alaunian (an interval two million years long: Gradstein et al., 1995) in a similar carbonate platform paleoenvironment (Poleschinski, 1989; Jadoul et al., 1994; Roghi et al., 1995) along the coasts of the western Paleotethys (Marcoux et al., 1993). *Eudimorphodon* was, however, also found outside the Paleotethys in the Norian/Rhaetian continental sediments of Greenland (Jenkins et al., 1993). All the pterosaurs from the Paleotethys are preserved after deposition in small anoxic basins that developed on the platform (Dalla Vecchia, 1994).

The known taxonomic diversity of pterosaurs at their first appearance in the fossil record is higher than at the beginning of the Jurassic. In the lower Liassic only one or two genera are known (*Dimorphodon* in the Hettangian Blue Lias of England, and possibly *Rhamphinion* in the middle of the poorly dated Kayenta Formation of southwestern U.S.A.; see Owen, 1870; Padian, 1983; Unwin, 1988; Wellnhofer, 1991). *Dorygnathus*, *Campylognathoides*, and *Parapsicephalus* (Wellnhofer, 1978, 1991) are reported from the Toarcian stage (an interval 9.5 million years long; Gradstein et al., 1995) of the upper Liassic, and a fourth genus, *Dimorphodon*, from Mexico has a poorly defined late Early or early Middle Jurassic age (Clark et al., 1998). The several specimens from the Posidonienschiefer (early Toarcian) from different regions of Germany all belong to *Dorygnathus* and *Campylognathoides* (Wellnhofer, 1978, 1991). The famous Late Jurassic rhamphorhynchoids from the Solnhofen Plattenkalke (Tithonian) of Bavaria, represented by more than one hundred specimens, belong to only three genera. *Anurognathus* and *Scaphognathus* are represented by one and two individuals respectively and all the rest are *Rhamphorhynchus* (Wellnhofer, 1975b; the diversified Solnhofen pterodactyloids represent a separate adaptive radiation and are not considered in the count). It is noteworthy that Norian taxa have features that are not present in any of the successive pterosaurs (i.e., multicusped teeth in *Eudimorphodon* and *Austriadactylus*, posterior mandibular teeth with small accessory cusps in *Peteinosaurus*, very tall middle maxillary teeth in *Eudimorphodon*, *Preondactylus* and *Austriadactylus*) or were evolved by pterodactyloids 50 million years later (i.e., the cranial crest of *Austriadactylus*). This is consistent with the possible presence of an adaptive radiation of rhamphorhynchoid pterosaurs at their late Alaunian appearence in the fossil record. This is also the case for the pterodactyloids at the end of the Late Jurassic.

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