

David M. UNWIN

EUDIMORPHODON AND THE EARLY HISTORY OF PTEROSAURS

Eudimorphodon is certainly the most well known and arguably the most important Triassic pterosaur (Wellnhofer, 1991). Principally distinguished by its multi-cusped teeth, this long-tailed apparently piscivorous form reached at least one metre in wingspan (Wild 1978, 1994; Dalla Vecchia, 1995). Initially thought to be one of the most primitive pterosaurs (Wellnhofer, 1978), an idea consistent with its Late Triassic age, Wild (1978) allied *Eudimorphodon* with *Campylognathoides* and argued that this lineage had branched off later than others such as the Dimorphodontidae, a hypothesis that has been supported by several cladistic studies (Unwin, 1992, 1995, 2003; Kellner, 1996; Peters, 1997), but not yet substantiated in detail. Results of a new phylogenetic analysis, focused on basal taxa ('rhamphorhynchoids') and presented here, reveal considerable support for 'Wild's hypothesis' and throw new light on the early history of pterosaurs.

THE FOSSIL RECORD OF *EUDIMORPHODON*

First reported by Zambelli (1973), the principal description of the type species, *E. ranzii* (Fig. 1), was published by Wild (1978) on the basis of several specimens from the Upper Triassic (Norian) Calcare di Zorzino of Cene, near Bergamo, Italy. An isolated sternum of *E. ranzii* from the same stratigraphic unit at Endenna was noted by Renesto (1993) and another small, apparently juvenile individual of this species, with evidence of wing membranes, was recovered from the Argilliti di Riva di Solto (Norian), at Ponte Giurno, north of Bergamo (Wild, 1994). If attributable to *E. ranzii*, a large, isolated, wing phalanx 4 from the Dolomia di Forni (Norian) of Friuli, Italy (Dalla Vecchia, 2000) indicates an individual of approximately 1.75 m in wingspan and larger than any other Triassic pterosaur presently known.

A second species, *E. rosenfeldi*, so far known from a single incomplete skeleton (wingspan ~ 0.7 m), was recovered from the Dolomia di Forni of Udine province, Italy (Dalla Vecchia, 1995), and an articulated series of 24 caudal vertebrae associated with part of a wing-finger phalanx 3 and both terminal wing-finger phalanges from the same region and rock sequence (Dalla Vecchia, 2002) might also belong to *Eudimorphodon*. A third species, *E. cromptonellus*, based on a relatively small (wingspan ~ 0.24 m) and seemingly very young individual from the Fleming Fjord Formation (?Norian-Rhaetian) of Greenland was described by Jenkins *et al.* (2001). Isolated teeth attributed to *Eudimorphodon* have been reported from Europe and the USA (see Dalla Vecchia, 2003) although these identifications are uncertain (Dalla Vecchia, 1995). An incomplete skeleton of *Eudimorphodon* sp. from the Seefeld Beds (Norian) of the Tyrol, Austria will be described by Wellnhofer (2003) and *Austriadactylus cristatus*, shown below to be a close relative of *Eudimorphodon* and also known only from a single incomplete skeleton, has been reported from the same

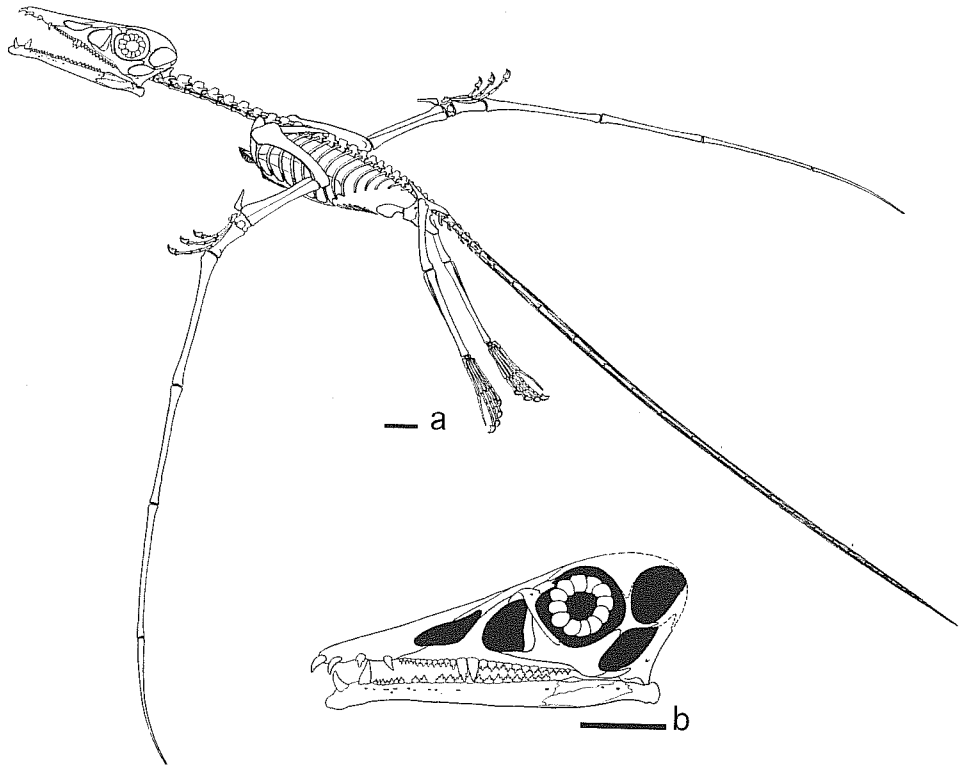


Fig. 1. The skeleton (a) and skull (b) of *Eudimorphodon* (redrawn from Wild, 1978). Scale bar = 20 mm.

region and stratigraphic sequence (Dalla Vecchia *et al.*, 2002). In summary, *Eudimorphodon* is the commonest pterosaur from Norian deposits, and may also occur in the Rhaetian. It is certainly known from Europe and Greenland and possibly also from North America.

THE PHYLOGENETIC RELATIONSHIPS OF *EUDIMORPHODON* REANALYSED

The relationships of *Eudimorphodon* to other pterosaurs were investigated using a data matrix (Table 1) consisting of 15 taxa and an outgroup, and 53 characters: 27

	5					10					15					20					25				
Outgroup	0/1	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Preondactylus</i>	0	0	?	0	0	0	0	0	0	0	?	0	?	?	?	0	0	0	0	0	0	1	0	0	0
<i>Dimorphodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
<i>Peteinosaurus</i>	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0	1	0	0	0	0
<i>Anurognathus</i>	0	1	0	0	0	0	0	0	0	0	?	1	1	0	0	?	0	?	0	1	0	1	0	1	1
<i>Batrachognathus</i>	0	1	0	0	0	0	0	0	?	?	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Dendrorhynchoides</i>	0	1	?	?	0	0	0	?	?	0	?	?	?	?	?	1	?	?	?	0	?	0	1	0	?
<i>Jeholopterus</i>	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	1	0	?
<i>Austriadactylus</i>	1	0	?	1	1	1	1	0	0	1	1	?	0	?	1	?	?	?	0	0	0	0	1	0	0
<i>Campylognathoides</i>	1	0	0	1	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0
<i>Eudimorphodon</i>	1	0	0	1	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0
<i>Scaphognathus</i>	1	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1	1
<i>Sordes</i>	1	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1	1
<i>Dorygnathus</i>	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0
<i>Rhamphorhynchus</i>	1	0	1	1	1	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	0	1	0
Pterodactyloidea	1	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1	0

	30					35					40					45					50						
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0/1	0	0	0
<i>Preondactylus</i>	0	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?	0	1	0
<i>Dimorphodon</i>	0	0	0	1	0	?	1	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Peteinosaurus</i>	0	0	?	0	1	0	0	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Anurognathus</i>	0	1	1	0	1	?	1	1	1	1	1	2	0	1	0	0	0	1	1	?	1	0	1	?	?	0	1
<i>Batrachognathus</i>	0	1	?	?	0	1	0	1	1	1	1	2	?	1	0	?	1	1	?	?	?	?	1	?	?	?	1
<i>Dendrorhynchoides</i>	?	?	1	1	0	1	?	1	1	1	1	2	0	1	0	0	?	1	0	1	0	1	?	?	?	?	1
<i>Jeholopterus</i>	?	?	1	1	0	1	?	1	1	1	1	2	0	1	?	0	1	1	0	1	0	1	?	0	0	1	0
<i>Austriadactylus</i>	0	0	0	?	0	0	?	?	?	?	?	1	?	?	0	1	?	?	?	1	1	0	1	?	?	?	?
<i>Campylognathoides</i>	0	0	0	0	1	0	1	1	1	1	0	3	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0
<i>Eudimorphodon</i>	0	0	0	0	0	0	1	1	1	0/1	0	3	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0/1
<i>Scaphognathus</i>	1	1	0	0	1	0	0	1	1	0/1	0	4	1	1	1	1	0	1	0	0	0	1	1	1	0	1	1
<i>Sordes</i>	1	1	0	0	1	0	0	1	1	1	0	4	1	1	1	1	0	1	0	0	0	1	1	1	0	1	1
<i>Dorygnathus</i>	0	1	0	0	1	0	0	1	1	1	0	4	1	1	0	1	0	1	0	1	0	0	1	1	1	0	1
<i>Rhamphorhynchus</i>	0	1	0	0	1	0	0	1	1	1	0	4	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1
Pterodactyloidea	0	1	1	0	0	1	0	1	0	1	0/1	0	5	0/1	0/1	1	1	0	0/1	0	0	0/1	1	1	1	1	0/1

Table 1. Distribution of character states among the terminal taxa used in this analysis. Uncertainty because of incomplete preservation is indicated by '?', polymorphism by '0/1'.

- 1 Rostrum: high, convex outline (0), low with straight or concave dorsal outline (1)
- 2 Skull: broad with very short preorbital region: no (0), yes (1)
- 3 Ventral margin of skull: straight (0), or curved down caudally (1)
- 4 Posterior extent of premaxilla: terminates at (0), or interfingers between frontals (1)
- 5 Nasal process of maxilla: subvertical (0), inclined backwards (1)
- 6 Maxilla-nasal contact: narrow (0), broad (1)
- 7 External nasal opening: height \geq anteroposterior length (0), low and elongate (1)
- 8 Nares: form the largest skull opening (0), smaller than orbit or nasoantorbital fenestra (1)
- 9 Antorbital fenestra: lies level with (0), or lower than the naris (1)
- 10 Antorbital fenestra: length less than (0), or more than twice the height (1)
- 11 Orbit: 1.5x higher than wide (0), similar width to depth
- 12 Orbit: smaller than (0), or larger than antorbital fenestra (1)
- 13 Supratemporal fenestra: smaller (0), or larger than other skull openings except orbit (1)
- 14 Quadrate: vertical (0), or inclined backwards (1)
- 15 Palatal elements: broad and flat (0), reduced to thin bars of bone (1)
- 16 Dentary: less (0), or more than 50 % length of lower jaw (1)
- 17 Anterior tip of the mandible: straight (0), downturned (1)
- 18 Bony mandibular symphysis: absent (0), present (1)
- 19 Mandible tips fused into a short symphysis with forward projecting prow and several large, fang-like, procumbent teeth forming a fish grab: absent (0), present (1)
- 20 Caudal end of mandible with distinct dorsal 'coronoid' eminence: present (0), absent (1)
- 21 Dimorphodontid dentition: no (0), yes (1)
- 22 Teeth small, peg-like, widely spaced: no (0), yes (1)
- 23 Multicusped teeth: no (0), yes (1)
- 24 Rostral dentition: more than (0), or less than 11 pairs of teeth (1)
- 25 Rostral dentition: more than (0), or nine or less relatively straight pairs of teeth (1)
- 26 Mandibular dentition: more (0), or ≤ 6 , widely spaced, vertically oriented tooth pairs (1)
- 27 Heterodont mandibular dentition: yes (0), no (1)
- 28 Cervical ribs: present (0), absent (1)
- 29 Dorsal+sacral vertebral series: longer than (0), or similar length to ulna (1)
- 30 Filiform processes of caudal zygapophyses: absent (0), present (1)
- 31 Caudal vertebral series: longer (0), or shorter than the dorsal series (1)
- 32 Rectangular sternum with short cristospine and short rectangular processes on each posterolateral corner: absent (0), present (1)
- 33 Coracoid: less than (0), or $\geq 66\%$ length of scapula (1)
- 34 Forelimb length: less (0) or ≥ 2.5 times the length of hind limbs (1)
- 35 Humerus: shorter (0), or longer than femur (1)
- 36 Proximal end of humerus with angular sub-symmetric profile: no (0), yes (1)
- 37 Deltopectoral crest of humerus: small (0), large and subtriangular with apex directed proximally (1), elongate and rectangular (2), hatchet-shaped (3), tongue-shaped, with necked base (4), 'pterodactyloid' (5)
- 38 Ulna length: less (0), or ≥ 1.5 times length of humerus (1)
- 39 Ulna length: \leq (0), or longer than length of tibia (1)
- 40 Metacarpals I-III: disparate lengths (0), or the same length (1)
- 41 Wing-metacarpal-humerus ratio: less than (0), or more than 35% (1)
- 42 Phalanges in manus digit three: four (0), three (1)
- 43 Manus and pes unguals: similar sized (0), manual unguals $\geq 2x$ size of pedal unguals (1)
- 44 Wing-finger: less than (0), or more than 65% total forelimb length
- 45 Wing-phalange 1: less than (0), or $\geq 35\%$ wing-finger length
- 46 Wing-phalange 2: shorter (0), or \geq length of the ulna (1)
- 47 Preacetabular iliac process: \leq length of postacetabular process (0), longer (1)
- 48 Ischiopubis: unexpanded (0), expanded (1)
- 49 Distal expansion of prepubis: length \geq width (0), transversely expanded (1)
- 50 Angle of femur caput to shaft: $\leq 145^\circ$ (0), $> 145^\circ$ (1)
- 51 Fibula: same length as tibia (0), or less than 80 % tibia (1)
- 52 Length of metatarsal 4: sub-equal (0), or shorter than metatarsals I-III (1)
- 53 Pes digit V phalanx 2: straight or curved (0), angular flexure of -45° at midlength (1)

Table 2. List of characters that vary within basal pterosaurs, used in this analysis. Numbers shown in bold indicate new characters, others are derived from Unwin (2003).

cranial and 26 postcranial. Twenty five characters, slightly modified in several cases, were derived from an older compilation (Unwin, 2003), 28 are new (Table 2). Rooting of the tree using an outgroup did not present a problem because although the relationship of pterosaurs to other diapsids is unclear (Brochu, 2002), pterosaur skeletal anatomy is so derived that the plesiomorphic state is usually the same irrespective of which outgroup is chosen: Ornithodira, Archosauria, or Prolacertiformes.

The taxon-character matrix (Table 1) was analysed using PAUP 3.1.1 (Swofford, 1993), with the 'branch and bound' search option, addition sequence 'furthest' and both 'Acctran' and 'Deltran' settings. Multiple-state characters were always treated as unordered. Characters that exhibited more than one state for a particular terminal taxon (shown as 0/1 in the matrix) were treated as polymorphic. Continuously variable characters were broken into discrete states on the basis of breaks between distribution peaks.

The analysis resulted in 13 most parsimonious trees, each 84 steps in length and varying only in the relationships to each other of the taxa within Anurognathidae. The strict consensus tree, together with Bootstrap values (1000 replicates) and results of a decay analysis, is shown in Fig. 2. Tree topology is congruent with the results obtained by Unwin (1995, 2003).

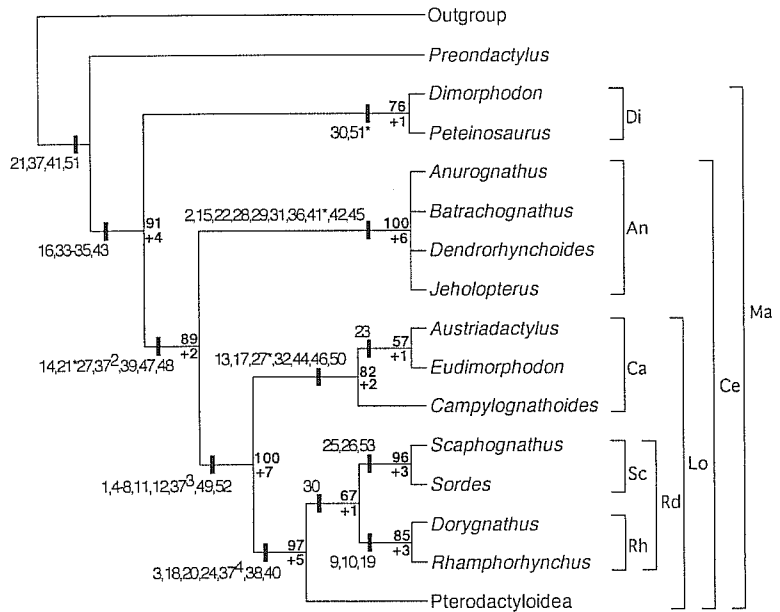


Fig. 2. Strict consensus tree resulting from a PAUP analysis of the character data matrix shown in Table 1. Distribution of derived states for each character (Acctran setting) indicated by the list of numbers opposite each vertical bar (* = reversal). Bootstrap values (above) and additional steps required to collapse a node (below) shown in bold, adjacent to each node. Consistency index = 0.824, homoplasy index = 0.329, retention index = 0.898, rescaled consistency index = 0.739. Abbreviations: An, Anurognathidae; Ca, Campylognathoididae; Ce, Caelidracones; Di, Dimorphodontidae; Lo, Lonchognatha; Ma, Macronychoptera; Rd, Rhamphorhynchidae; Rh, Rhamphorhynchinae; Sc, Scaphognathinae.

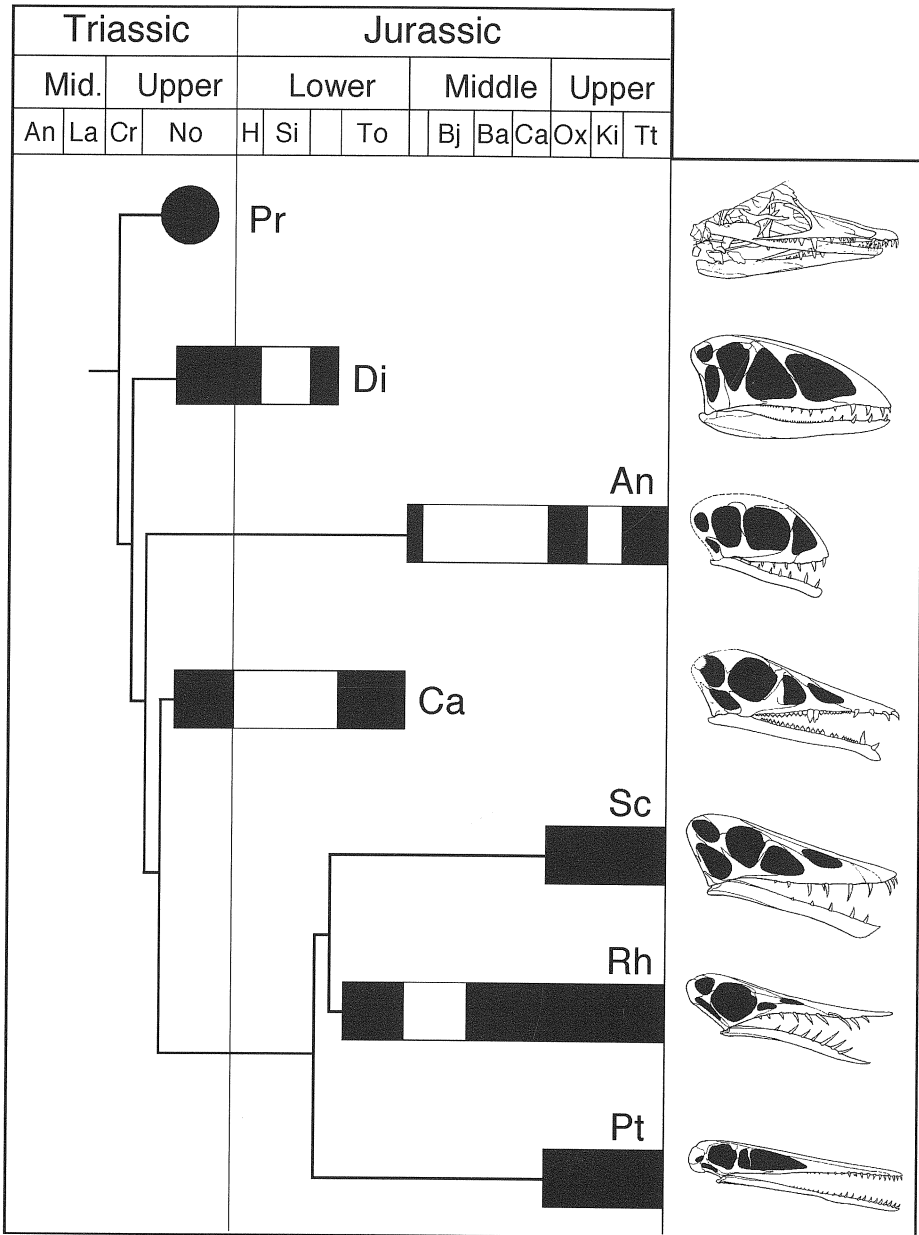


Fig. 3. Pterosaur evolutionary history for the Upper Triassic-Jurassic interval reconstructed from the tree shown in Fig. 2 and known stratigraphic occurrences, indicated by solid shading, of the principal clades. Abbreviations as for Fig. 2 except: An, Anisian; Ba, Bathonian; Bj, Bajocian; Ca, Callovian; Cr, Carnian; H, Hettangian; Ki, Kimmeridgian; La, Ladinian; No, Norian; Ox, Oxfordian; Pr, *Preondactylus*; Pt, Pterodactyloidea; Si, Sinemurian; To, Toarcian; Tt, Tithonian.

Eudimorphodon is paired with *Austriadactylus* (presence of multicusp teeth) a relationship tentatively proposed by Dalla Vecchia *et al.* (2002), and these two, together with *Campylognathoides*, form the Campylognathoididae, diagnosed by a row of cranial and postcranial apomorphies and one of the better supported clades found in this analysis. This conclusion is consistent with other cladistic studies (Unwin, 1995; Kellner, 1996) and confirms Wild's original idea (1978) of a relationship between *Eudimorphodon* and *Campylognathoides*.

Significantly, this analysis also demonstrates strong support for a derived position of *Eudimorphodon* compared to other basal pterosaurs (Fig. 2). *Eudimorphodon* is a member of the Lonchognatha (Unwin, 2003), a relatively derived clade principally distinguished by a long low skull, and also exhibits characters related to the elongation of the forelimb and modification of the pelvis that diagnose a more inclusive clade, the Caelidracones (Unwin, 2003). By contrast, *Preondactylus* and Dimorphodontidae show the plesiomorphic condition for these characters confirming their basal position within Pterosauria. A surprising discovery, that the tail of *Eudimorphodon* lacks a sheath of elongate bony rods (Dalla Vecchia, 2002), present in many other basal pterosaurs, is most parsimoniously optimised as retention of the plesiomorphic condition, but the alternative, secondary loss of this structure in the lineage leading to *Eudimorphodon* + *Austriadactylus*, is only slightly less parsimonious.

EUDIMORPHODON AND THE EARLY HISTORY OF PTEROSAURS

The early history of pterosaurs (Fig. 3) was reconstructed by combining data on the stratigraphic distribution of Triassic and Jurassic taxa (current up to July 2003) with the phylogenetic hypothesis presented above. Two significant aspects, both hinging on *Eudimorphodon*, are mentioned here. First, as noted previously (Wellnhofer, 1978; Wild, 1978; Dalla Vecchia *et al.*, 2002; Unwin, 2003), the primary radiation of pterosaurs was well underway by the early Late Triassic and almost all the principal basal clades were established by this time. *Eudimorphodon* provides critical support for this notion because, although a relatively derived form, it is practically coeval with the earliest known pterosaurs and indicates that Rhamphorhynchidae + Pterodactyloidea (the sister group to Campylognathoididae) and clades basal to the Lonchognatha (i.e. Anurognathidae, Dimorphodontidae, *Preondactylus*) must have existed at this time, even though there is, as yet, no fossil evidence of the Anurognathidae or the lineage leading to the Rhamphorhynchidae + Pterodactyloidea in the Triassic (Fig. 3).

Second, the range of taxonomic diversity evident in the Late Triassic is similar to that in the Early and Middle Jurassic (although this was greatly exceeded in later intervals following the radiation of pterodactyloids), but its composition underwent some important changes (Unwin, 2003). The Late Triassic assemblage appears to have been dominated by campylognathoidids (represented by *Austriadactylus* and the seemingly ubiquitous *Eudimorphodon*) and this lineage, together with more basal groups such as dimorphodontids, persisted into the Early Jurassic. These clades appear to have become extinct by the end of this interval, however, and later Jurassic assemblages consist entirely of rhamphorhynchids and anurognathids, joined in the Late Jurassic by pterodactyloids.

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Author address:

David M. Unwin, Institut für Paläontologie, Museum für Naturkunde,
Zentralinstitut der Humboldt-Universität zu Berlin, D-10115 Berlin,
Germany. E-mail: h0662eka@rz.hu-berlin.de