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A REEXAMINATION OF FOUR PROLACERTIFORMS WITH IMPLICATIONS FOR PTEROSAUR PHYLOGENESIS

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Riassunto. Tradizionalmente gli pterosauri venivano considerati come appartenenti agli Archosaurifomes e molti specialisti contemporanei considerano gli pterosauri quali sister groups di *Lagosuchus*, *Schleromochlus* e dei Dinosauria. La nuova analisi filogenetica qui proposta mette in discussione queste affinità in quanto tutte le presunte sinapomorfie che collegherebbero gli Pterosauria con gli Archosauriformes o con gli Ornithodira mancano in realtà negli Pterosauria, oppure sono condivise anche da alcuni taxa di prolacertiformi. Il recente riesame degli olotipi di *Cosesaurus aviceps*, *Longisquama insignis* e di *Sharovipteryx mirabilis* suggeriscono che molti caratteri potrebbero venire interpretati in maniera diversa rispetto alle precedenti descrizioni. I risultati di molteplici analisi cladistiche suggeriscono che questi tre prolacertiformi enigmatici, unitamente a *Langobardisaurus*, recentemente descritto, costituirebbero i sister taxa degli pterosauri, in base ad un insieme di sinapomorfie di nuova identificazione.

Abstract. Traditionally, pterosaurs have been included within the Archosauriformes and many contemporary workers consider the Pterosauria the sister group to *Lagosuchus*, *Scleromochlus* and the Dinosauria. New analyses cast doubts on those relationships because nearly all presumed archosauriform or ornithodire "synapomorphies" are either not present within the Pterosauria or are also present within certain prolacertiform taxa. Recent examinations of the holotypes of *Cosesaurus aviceps*, *Longisquama insignis* and *Sharovipteryx mirabilis* suggest that many characters may be interpreted differently than previously reported. Results of several subsequent cladistic analyses suggest that these three "enigmatic" prolacertiforms, along with the newly described *Langobardisaurus*, are sister taxa to the Pterosauria based on a suite of newly identified synapomorphies.

Introduction.

Pterosaurs have been known since Collini (1784) published a description of a small strange fossil he tentatively regarded as a marine amphibian preserved in Solnhofen limestone. Cuvier (1801, 1809) classified the creature among the reptiles and coined the term "Pterodactyle" from the Greek "wing finger." Workers today agree that pterosaurs are archosauromorph reptiles. The question posed by this study is: where within the Archosauromorpha cladogram do pterosaurs belong?

Traditionally the answer has been that pterosaurs are archosaurs (Romer 1956); the sister group of the Dinosauria, *Scleromochlus* and *Lagosuchus*/*Marasuchus* (Benton 1985, 1990, 1999; Padian 1984; Gauthier 1984, 1986; Sereno 1991, 1994; Kellner 1996); or perhaps archosauriformes close to proterosuchids and erythrosuchids (Bennett 1996a), chiefly because pterosaurs have a prominent antorbital fenestra and a suite of other archosaur-like characters almost entirely confined to the hind limb (Bennett 1996a). Although Benton (1982, 1984) initially indicated that the Pterosauria are archosauromorphs and the sister-group to all other archosauromorphs, later work (Benton 1985, 1990, 1999) supported the traditional view. Previous to the present work, the hypothesis that pterosaurs are archosauriformes has been challenged only by Wild (1978, 1984a) and Peters (1997).

Here a phylogenetic framework for determining the position of the Pterosauria within the Archosauromorpha is provided by analyzing a broad range of character data across an extended range of taxa including the following key prolacertiforms: *Langobardisaurus pandolfii* (Renesto 1994), *L. tonelloi* (Muscio 1996, Fig. 1C), *Cosesaurus aviceps* (Ellenberger and de Villalta 1974, Fig. 3-6), *Longisquama insignis* (Sharov 1970, Fig. 7) and *Sharovipteryx mirabilis* (Sharov 1971, Cowen 1981, Fig. 8-10). As a group these four genera have not been compared to each other or to pterosaurs in cladistic analyses, although Jalil (1997) did include *Cosesaurus* and *Langobardisaurus* in his cladistic analysis of *Jesairosaurus*. Renesto (1994) regarded *Langobardisaurus pandolfii* as a prolacertiform close to *Cosesaurus* and the Tanystropheidae but did not provide an analysis. Ellenberger and de Villalta (1974) and Ellenberger (1977, 1978, 1993) regarded *Cosesaurus* as a proto-bird, but Sanz and López-Martinez (1984) and others (Olsen 1979, Evans 1988) considered it a prolacertiform close to *Macrocnemus* (Fig. 1A) or *Tanystropheus*. Sharov

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(1971) left the affinities of *Sharovipteryx* in question. Gans, et al. (1987) tentatively identified it as a "small primitive diapsid, perhaps a lepidosaur or close to the Archosauriformes...or perhaps adjacent to the 'Protorosauria'." Tatarinov (1989) and Benton (1999) regarded it as a derived prolacertiform and analysis of the holotype confirms this placement. Sharov (1970) and Haubold and Buffetaut (1987) regarded *Longisquama* as a pseudosuchian, Benton (1999) could not assign it more precisely than within the Archosauria and Jones, et al. (2000) considered it a distant relative of birds. The present analysis of the holotype places it within the Prolacertiformes close to *Cosesaurus*.

Cosesaurus, *Longisquama* and *Sharovipteryx* are difficult taxa to study and interpret. Fortunately, all three holotypes are well articulated, but each one is represented by a single specimen. Each one has strange and/or unexpected anatomical features. All three are crushed or compressed. Often only the impressions of bone are observable. All three must be viewed under magnification from multiple angles employing a variety of illumination to gather sufficient observational data to make positive identifications. A few identifications are inferred from vague impressions of the bone in the matrix and by anatomical placement. Inference may be influenced by personal bias: whether "seeing" what one has been told to see, "seeing" what one is hoping to see, or "seeing" something altogether different. To counter the influence of bias, I had the advantage of access to the observations of previous workers and to recent finds of importance not available to earlier paleontologists. In my opinion all three taxa appear to be incompletely or improperly described and figured in the literature (Ellenberger and de Villalta 1974, Ellenberger 1977, 1978, 1993, Sharov 1970, Haubold and Buffetaut 1987, Sharov 1971, Gans, et al. 1987, Tatarinov 1989 and Benton 1999) which is one reason they have remained the "enigmatic" reptiles of the Triassic. Although each is worthy of a separate paper in which its description and classification should be given with some confidence before attempting a cladistic analysis, the key to understanding them is to consider them as a group. I do this for three reasons: 1) All three display characters also seen in higher archosaurs, which might be confusing if one were not able to readily argue that these characters are better considered synapomorphies of this small clade; 2) Many characters are difficult to observe due to preservational problems, so having more than one taxa displaying a controversial character enables one to have a higher level of confidence on duplicated interpretations and to reject unduplicated interpretations; 3) some characters are only known inside this small clade. For these reasons I would argue that sufficient evidence is currently available in each specimen to make the preliminary cladistic analyses and hypotheses advanced here. It is hoped that by proposing a phylogenetic framework at this time a new forum for discussion will emerge to enable more concentrated anatomical and phylogenetic studies in the future.

Historical background.

Bassani (1886) and Nopcsa (1922) both considered the jumbled remains of a long-necked, juvenile prolacertiform, *Tanystropheus*, to be those of a primitive Triassic pterosaur, *Tribelesodon*. Although the elongate cervicals were mistaken for wing phalanges, other aspects of the anatomy were sufficiently pterosaurian to validate the identification, especially considering the distinctive elongate fifth pedal digit. The error was not recognized until 1929 when a superior *Tanystropheus* fossil was discovered and Peyer (1931a) was able to make a positive comparison to the holotype of *Tribelesodon*. No other published research into the relationship of *Tanystropheus*, or other prolacertiforms, to pterosaurs is known.

Traditional (Pre-Cladistic) Classification

Romer (1956) expressed the generally accepted hypothesis that pterosaurs were of "thecodont" descent with no known transitional forms. Thus they were archosaurs in the traditional sense (Bennett 1996a). Wild (1978, 1984a) reviewed the various sorts of animals that had been proposed as ancestors and argued that it would be "very unlikely that the Thecodontia are the ancestors of pterosaurs" (translated from German). Instead he argued that the Pterosauria are "rooted separately in the Eosuchia or went through intermediate forms between Eosuchia and Prolacertilia." He argued that the antorbital fenestra could have arisen separately in pterosaurs and traditional archosaurs. Wild (1978) illustrated a hypothetical ancestral form based on *Heleosaurus* (Carroll 1976) provided with an elongate flight digit.

Recent Studies

The following cladistic studies focused on the interrelationships of archosauriforms. Benton (1982, 1984) indicated that the Pterosauria are archosauromorphs, but the sister-group to all other archosauromorphs. Later Benton (1985, Fig. 11A) suggested that "Pterosaurs are archosaurs and a close sister-group of the Dinosauria." Benton (1990) presented a cladogram of the Archosauromorpha (Fig. 11B) that included the Pterosauria as the sister-group of *Lagosuchus* [now *Marasuchus* (Sereno and Arcucci 1994)] and the Dinosauria. Most recently, however, Benton (1999) placed the Pterosauria, the Dinosauromorpha and a small dinosaur-like biped, *Scleromochlus*, within a new clade, Avemetatarsalia, but stated that *Scleromochlus* was not the sister group to either taxa. Padian (1984) resur-

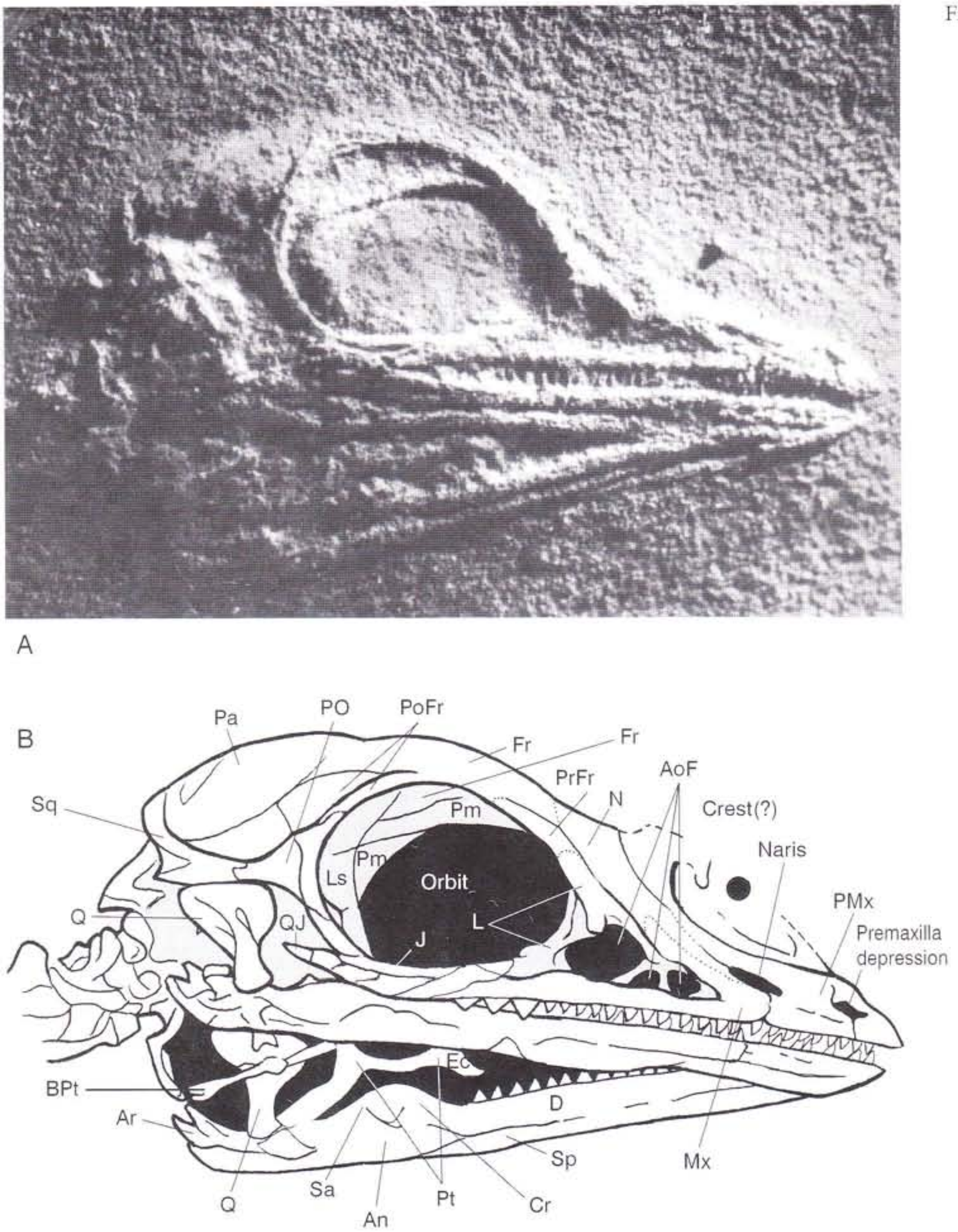


Fig. 4 - *Cosesaurus aviceps* (Ellenberger and de Villalta 1974) skull. A. Photograph of a cast of the holotype. B. Interpretation of same. Gray areas represent the internal septum and depressed portions of the antorbital area. Small black circle above snout is a fossil bubble. Three antorbital fenestrae are visible separated by slender struts. Quadratojugal spur and retroarticular apophysis as in pterosaurs.
Figure abbreviations as follows: AoF - antorbital fenestra(e). An - angular. Ar - articular. Bo - basioccipur. BPt - basipterygoid. Cb - ceratobranchial. Cr - coronoid. D - dentary. Ec - ectopterygoid. Fr - frontal. Hy - hyoid. IoS - interorbital septum. J - jugal. L - lacrimal. Ls - laterosphenoid. Mx - maxilla. N - nasal. Op - opisthotic. Pa – parietal. Pl - palatine. Pm - pseudomesethmoid. Pmx - premaxilla. PO - postorbital. PoFr - postfrontal. PrFr - prefrontal. Pt - pterygoid. Q - quadrate. QJ - quadratojugal. S - surangular. Sp - splenial. Sq - squamosal. V - vomer.

ments on Ellenberger's characters, identified by (" "), are interpreted differently than in either previous work.

The ratios of "skull to pre-sacral length," "orbit to skull length and height" and "snout to skull length" may simply point to a juvenile diapsid interpretation, as Sanz & López-Martinez (1984) note, but *Jesairosaurus* (Jalil 1997), *Langobardisaurus* (Fig. 1C), *Longisquama* (Fig. 7) and *Preondactylus* (Fig. 12 reconstructed) all have similar snout-to-skull and orbit-to-skull ratios; but note that these ratios are within the range of many diapsids, especially juveniles, and out of the range of most other prolacertiforms and pterosaurs which have longer snouts. Contra Ellenberger (1978), the naris is a narrow elongate fenestra between the extended premaxilla and maxilla (Fig. 4), as in derived prolacertiforms and *Preondactylus* (Wild 1984). Another anterior depression or fenestra appears close to the tip of the snout, but it is completely surrounded by the premaxilla, so it cannot be the naris. Three antorbital fenestrae (Fig. 4) appear to be present in *Cosesaurus*. Similar depressions often appear in the crushed and disarticulated skulls of other prolacertiforms, so one must be cautious in asserting the presence of this key character. The skull of *Cosesaurus* is not crushed but compressed and completely articulated, therefore the apparent fenestrae may be real and bordered dorsally by an inflated lacrimal, as in *Longisquama* (Sharov 1970, Haubold and Buffetaut 1987, Benton 1999, Fig. 7), and in *Sharovipteryx* (Fig. 10 reconstructed). Whether present or not, the initial appearance of the antorbital fenestra could have occurred at any point preceding the appearance of pterosaurs without affecting the cladistic results obtained in the present study. Sanz & López-Martinez (1984) reject the "structure of the temporal region" and the "morphology of the

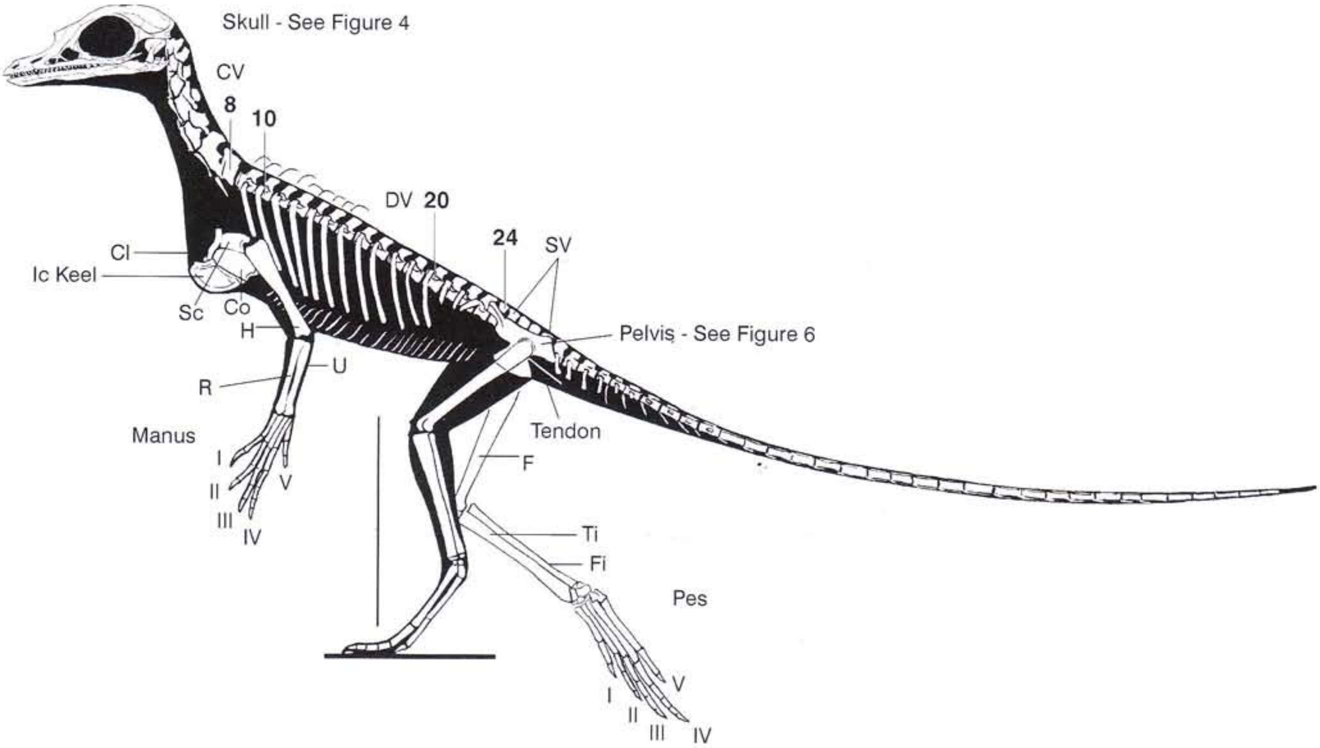


Fig. 5 - *Cosesaurus aviceps* (Ellenberger and de Villalta 1974) reconstruction in lateral view, configuration based on living lizards capable of bipedal configuration (see text, Fig. 2, Snyder 1954). Left femur foreshortened due to lateral orientation and left pes in digitigrade configuration (Peters 2000). Right pes as preserved. Note the large orbit, the short cervicals, the interclavicle keel, the comparatively large forelimb and elongate digits, the elongate ilium and fused puboischiadic plate, all as in pterosaurs. Abbreviations as in figure 3.

quadrate-jugal [sic]" without commenting on how they would reinterpret the specimen. The posterior squamosal and anterior postorbital are clearly seen, but the connecting arch is not. Rather it appears melted or compressed into the underlying braincase, so I reconstruct this portion of the temporal arch as in *Macrocnemus* (Kuhn-Schnyder 1962) and *Tanystropheus* (Wild 1973), the two closest sister taxa. Contra Ellenberger (1978), the quadratojugal is a clearly observable spur posterior to the posterior process of the jugal (Fig. 4), as in *Eudimorphodon* (Wild 1978). The "advanced position of the quadrate in relation to the occipital outline" is similar to that in *Longisquama* (Fig. 3) and *Langobardisaurus tonelloi* (Fig. 1C). The "retroarticular apophysis" is shared with *Langobardisaurus*, *Longisquama* (Fig. 7), *Sharovipteryx* (Fig. 10C) and *Preondactylus* (Fig. 12) and no other pterosaur. Sanz & López-Martinez (1984) reject the "ventral position of the foramen magnum." Judging by the emergence of the first few cervicals, the obscured occiput in *Cosesaurus* is probably angled 130° to the jaw line, approximately parallel to the posterior border of the quadrate. The "skull to neck ratio" is nearly 1.0 in *Cosesaurus*. It is less than 1.0 in other prolacertiforms and more than 1.0 in *Longisquama* and *Preondactylus* (as reconstructed here) and most pterosaurs, apparently making this ratio transitional from long-necked prolacertiforms to large-headed pterosaurs. *Cosesaurus*, *Longisquama* and basal pterosaurs have a relatively shorter neck supporting a larger head than do *Macrocnemus* and tanystropheids. Whether one considers *Cosesaurus* a juvenile or not, it appears that neoteny influenced this aspect of morphology.

The "cervical to dorsal centra length ratio" is similar to that in *Longisquama* and *Preondactylus* but shorter than in other well-known prolacertiforms except *Jesairosaurus* (Jalil 1997). The "neck to trunk length ratio" is similar to that in *Preondactylus*, but shorter than in other prolacertiforms except *Jesairosaurus* (Jalil 1997). The transverse processes of the dorsal vertebrae are long. Four sacral vertebrae are present (Fig. 6), each with broad, distal articulations suggesting capture by the anterior and posterior extensions of the ilium. Sanz & López-Martinez (1984) reject the "presence of a furcula." However, paired clavicles are present and they overlap medially, as in *Eudimorphodon* (Wild 1983). A keeled interclavicle anterior to the clavicles is present, also as in *Eudimorphodon* (Wild 1983). Other pectoral elements are similar to those of sister taxa prolacertiforms. Ellenberger (1977, 1993) noted posteriorly elongate scapulae. Here those impressions are identified as anterior dichocephalus ribs. Ellenberger noted an acrocoracoid. Here that impression is identified as the low crescentic scapula. Ellenberger (1993: figure 39) noted broad sternae. Here those impressions are identified as large coracoids.

Fig. 2 - A living lizard capable of bipedal standing and walking, *Chlamydosaurus kingii* (Shine and Lambeck 1989), 35mm transparency provided by the authors and used here as a basis for hypothetical reconstructions of prolacertiforms and pterosaurs in the bipedal configuration. Characters common to extant lizards capable of bipedal locomotion (Snyder 1954) are found in the prolacertiform and pterosaur taxa under consideration in this study.

lated and crushed adult specimen, *L. tonelloi*, 1921 MFSN (Muscio 1996, Renesto and Dalla Vecchia 2000), reveals details of the skull, cervical vertebrae and other elements (Fig 2C).

Horizon. Late Triassic (Norian), Bergamo Prealps and Friuli, Northern Italy.

Autapomorphies. Premaxilla with procumbent teeth matching a scoop-like anterior dentary; posterior teeth are elongate with multiple cusps; large coronoid process; relatively the longest neck among prolacertiforms having only eight cervical vertebrae.

. **Comments and Abbreviated Description.** Judging from photographs, the diagnosis and description of Renesto is essentially correct, although the cervical count is eight rather than nine (Fig. 1c) with the posterior cervical marked by a shorter centrum, as in other prolacertiforms. The snout is short and the cranium is high and dominated by a large orbit, rather than elongate as Renesto described it. Unusual for prolacertiforms, the presacral vertebrae are procoelous, as in pterosaurs. A small preacetabular process is present, a character common to living lizards (Fig. 2) capable of bipedal locomotion (Snyder 1954). Pedal digit V has a metapodial proximal phalanx and an elongate penultimate phalanx with a tiny ungual. In *L. tonelloi* pedal digits III and IV are subequal in length.

Cosesaurus aviceps - Ellenberger & de Villalta 1974

Materials. The holotype is a single slab containing the natural mold of an articulated and complete specimen, MGB-V1 (formerly IPB 555), in ventrolateral view, together with an adhering medusa (Fig. 3).

Horizon. Middle Triassic, upper Muschelkalk, Alcover, Spain.

Autapomorphies. Posterior teeth are broad-based triangles (Fig. 4); four sacrals are present (Fig. 6); the essentially straight clavicles overlap; the interclavicle has a pronounced keel that extends ventrally anterior to the clavicles (Fig. 5); the ilium has an anterior process on the anterior process; the puboischiadic plate appears fused and without a fenestra (Fig. 6), unlike related prolacertiforms.

Comments and Description. Based on its overall size (14 cm), the brevity of its snout, the large size of its orbit, and the disarticulation of ribs near and between the pelves, *Cosesaurus* is considered a juvenile. Note, however, that a much larger *Langobardisaurus* (Renesto and Dalla Vecchia 2000) has a relatively shorter rostrum and larger orbits while *Jesairosaurus* (Jalil 1997) has a similarly proportioned skull. Well-ossified tarsal elements suggest at least a sub-adult age in *Cosesaurus*. Poorly ossified carpal elements are typical of many prolacertiforms, such as *Macrocnemus* (Rieppel 1989) and thus are not good age indicators.

Many of Ellenberger's (1977, 1978, 1993) bird-homology interpretations were challenged by Sanz & López-Martinez (1984) who considered *Cosesaurus* close to *Macrocnemus*. Neither employed a cladistic analysis. Here many of Sanz & López-Martinez's com-

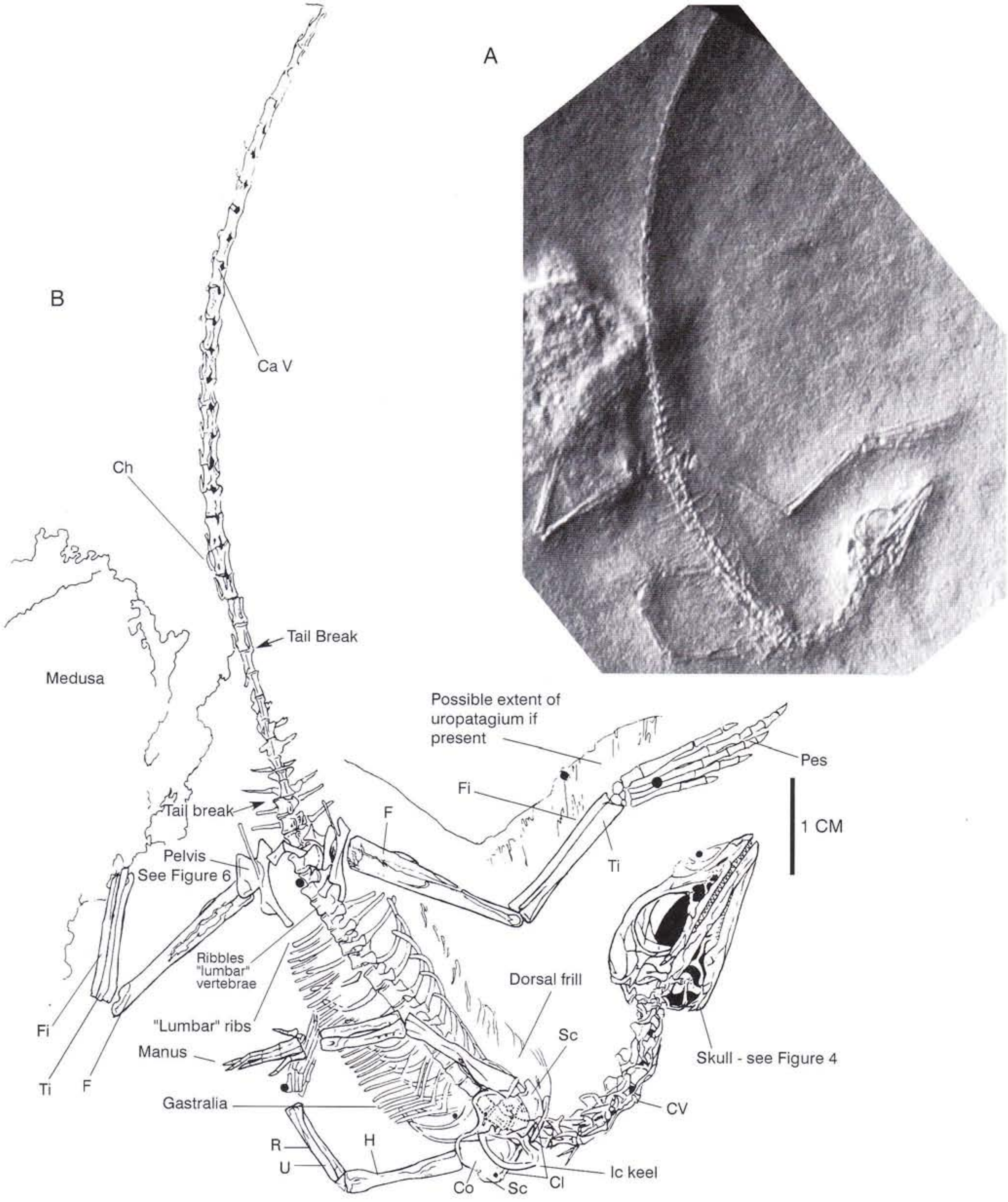


Fig. 3 - *Cosesaurus aviceps* (Ellenberger and de Villalta 1974) *in situ*. A. Latex peel of the holotype, MGB-V1, a natural cast of the articulated skeleton adhering to a medusa. B. Interpretation of the holotype, including dorsal frill and controversial uropatagium. Scale bar = 1 cm. Arrows point to disarticulations in the tail. Small black circles (e.g. on right metatarsal III) are bubbles. The right pelvis has been foreshortened during compression. Sternum and interclavicle keel impressions permit observation of underlying vertebrae impressions. Gastralia are illustrated only distally for clarity. See figures 4, 6 and 13C for skull, sacral and pedal details. Elongate manual digits, narrow fibula, overlapping clavicles, interclavicle keel, relatively short cervicals and other characters (see text) are all synapomorphies shared with pterosaurs.

Abbreviations in Figures as follows: CaV - caudal vertebrae. Ch - chevron (hemal arch). Co - coracoid. CV - cervical vertebrae. Cl - clavicle(s). DV - dorsal vertebrae. F - femur. Fi - fibula. H - humerus. Ic - interclavicle. Il - ilium. Is - ischium. Mt - metatarsal. Pp - prepubis. Pu - pubis. R - radius. Sc - scapula. St - sternum. SV - sacral vertebrae. Ti - tibia. U - ulna. Roman numerals refer to digits.

rected the view of Huene (1914) by homologizing many of the characteristics of *Scleromochlus* and the Pterosauria. Padian argued that both are sister-groups of *Lagosuchus* and the Dinosauria. Gauthier (1984) argued that the Pterosauria are the major sister-group of the Dinosauria (together termed the Ornithotarsi) with *Lagosuchus* as an outgroup. All three taxa comprise the Ornithodira. Gauthier's (1986) analysis presented *Lagosuchus*, the Dinosauria and the Pterosauria as a polytomy (Fig 11C). Sereno (1991) argued that the Dinosauria and *Lagosuchus* constituted the Dinosauromorpha with the Pterosauria as the first major sister-group (Fig. 11D). Bennett (1996a) presented a cladistic analysis that confirmed previous studies placing the Pterosauria close to the Dinosauria, but a second analysis excluding hind limb characters indicated that pterosaurs are the sister-group of the Erythrosuchidae + Proterochampsidae + *Euparkeria* + Archosauria, in that order (Fig. 11E).

Kellner (1996) presented a cladistic analysis that followed those of earlier workers in placing pterosaurs close to the Dinosauria and argued that *Batrachognathus* (Rjabinin 1948) was the most primitive known pterosaur. *Batrachognathus* cannot be the most primitive pterosaur because: 1) the dentary is plesiomorphically shorter in *Preondactylus*; 2) the rostral profile of *Batrachognathus* is highly convex, whereas in *Preondactylus* it remains plesiomorphically straight; 3) the proximal phalanges on both manus and pes are reduced to disks in *Batrachognathus* and are plesiomorphically unreduced in *Preondactylus*; 4) *Batrachognathus* has only a few widely spaced teeth set in wide jaws, whereas in *Preondactylus* the dental arcade is plesiomorphically packed with teeth set in narrow jaws; 5) The metacarpals are subequal in *Batrachognathus*, but in *Preondactylus* metacarpal I is plesiomorphically short; 6) *Batrachognathus* is a Late Jurassic pterosaur and *Preondactylus* precedes it by 80 million years.

The following studies focused on prolacertiform and lower diapsid relationships. None included the Pterosauria, *Cosesaurus*, *Longisquama*, *Langobardisaurus* or *Sharovipteryx*, except as noted. Chatterjee (1986) examined *Malerisaurus langstoni* and analyzed relationships among the Prolacertiformes. Evans (1988, Fig. 11F) analyzed the lower Diapsida (employing the Archosauria as a single taxon) and proposed that *Cosesaurus* is the sister-taxa of the Tanystropheidae with *Macrocnemus*, *Boreopricea*, *Prolacerta* and *Protorosaurus* as successively more distant taxa. Jalil (1997, Fig. 11G) proposed that *Boreopricea* is a sister-taxon to *Cosesaurus* + *Tanystropheidae* while *Malerisaurus* + *Jesairosaurus* is a sister-taxon to *Macrocnemus*. Benton and Allen (1997) proposed that *Tanystropheus* is the sister group to *Cosesaurus*, *Macrocnemus*, *Langobardisaurus*, *Malerisaurus*, *Protorosaurus*, *Boreopricea* and *Prolacerta* in that order. Dilkes (1998, Fig. 11H) proposed that *Tanystropheus* is a sister taxon to *Langobardisaurus* and *Macrocnemus* and supported the monophyly of the Prolacertiformes.

Materials and methods.

Fossil archosauromorph materials were examined or reside in several collections, which are abbreviated as follows: **IPB** = Institut de Paléobiologie C.S.I. C., Barcelona; **MCSN(B)** = Museo Civico di Scienze Naturali "E. Caffi." Bergamo, Lombardy, Italy; **MFSN** = Museo Friulano di Storia Naturale, Udine, Italy; **MGB** = Museu Geologia de Barcelona; **PIN** = Paleontological Institute, Moscow. **UCB** = University of California at Berkeley; **UCMP** = University of California (at Berkeley) Museum of Paleontology. Two taxa, *Sharovipteryx* (PIN 2584/8 lower plate) and *Langobardisaurus pandolfii* (MCSN(B) 2883 and 4860) were examined using 8x10 black and white photographic enlargements. The following holotypes were examined under the microscope.

Sharovipteryx mirabilis - (upper plate) preserving most of a crushed articulated skeleton with clearly discernable soft tissues - PIN 2584/8

Cosesaurus aviceps - natural cast of the virtually complete and articulated skeleton on matrix and a latex peel of the same - MGB-V1.

Longisquama insignis - plate preserving the anterior half of a crushed articulated skeleton with elongate dorsal plumes - PIN 2584/4

Langobardisaurus tonelloi - plate preserving a virtually complete and articulated skeleton - 1921 MFSN

Preondactylus buffarinii - natural cast of an articulated skeleton with a few remaining bones and a latex peel of the same - 1770 MFSN

Each of the above fossils requires low-level lighting under a 16x microscope to observe subtle impressions in shadow and highlight. Overhead lighting was used to observe the extent of preserved bone. Drawings were created using a camera lucida and tracings were generated over a light table from scanned enlargements of 8x10 color transparencies, 8x10 black and white prints and 35 mm photographs.

Outgroup relationships and terminal taxa.

Along with traditional archosauriform/ornithodire taxa (see below) the following prolacertiforms were employed as outgroups to the Pterosauria in the present cladistic analyses: *Macrocnemus* (Rieppel 1989 and references therein, Fig. 1A), *Tanystropheus* (Wild 1973 and references therein), *Tanytrachelos* (Olsen 1979, Fig. 1B), *Langobardisaurus pandolfii* (Renesto 1994), *Langobardisaurus tonelloi* (Muscio 1996, Renesto & Dalla Vecchia 2000, Fig. 1C), *Cosesaurus* (Ellenberger & de Villalta 1974, Fig. 3-6), *Longisquama* (Sharov 1970, Fig. 7) and *Sharovipteryx* (Sharov 1971, Figs. 8-10). Synapomorphies uniting these taxa with each other, the basal pterosaur *Preondactylus* (Wild 1984b, Fig. 12), and other basal members of the Pterosauria are listed within analyses that follow.

Four separate cladistic analyses based upon previous work were performed for this study. The first analyzed a study of primitive diapsids (Evans 1988), but here adds *Langobardisaurus*, *Sharovipteryx* and basal

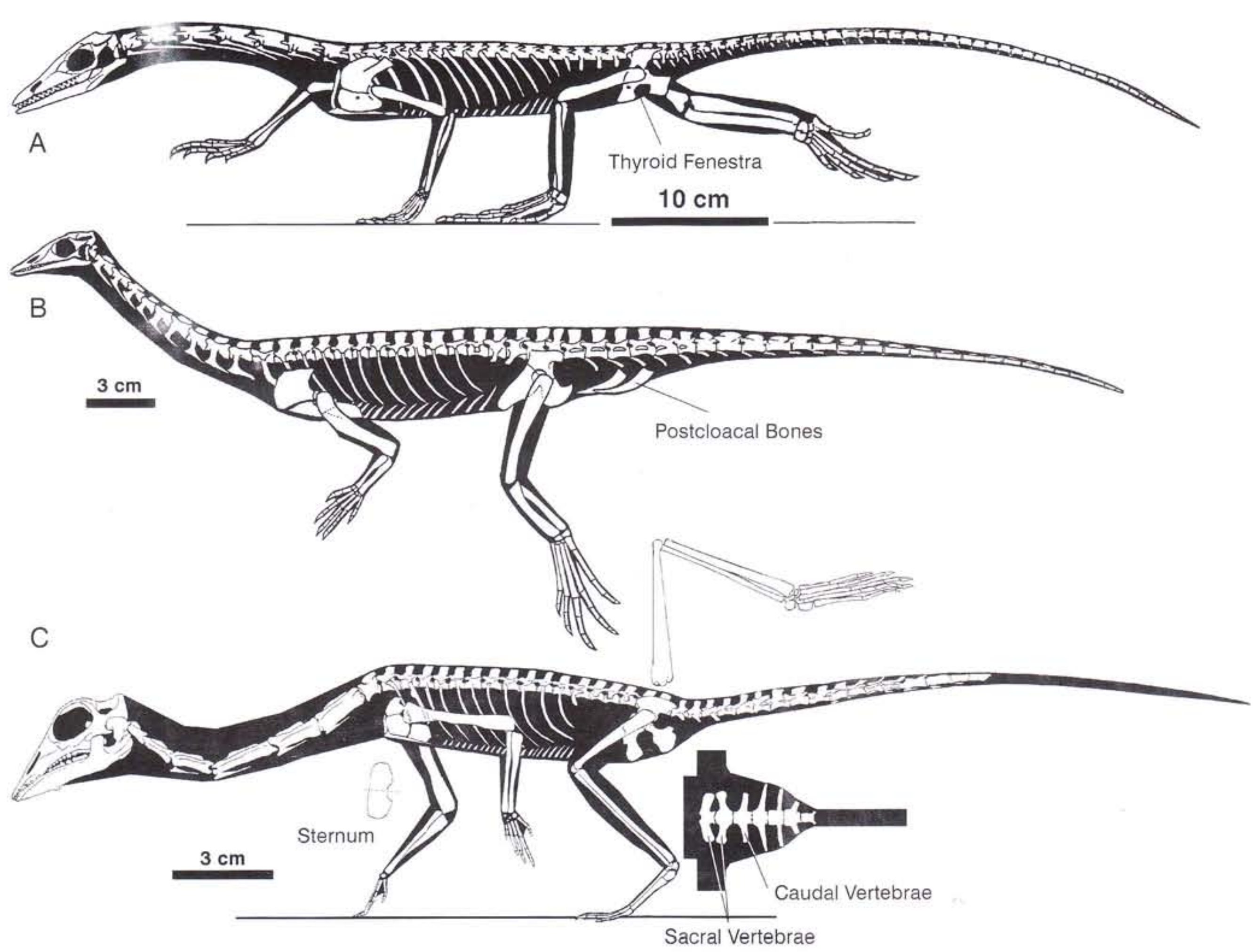


Fig. 1 - Selected Tapinoplatia (see text) in lateral view. A. *Macrocnemus bassanii*, reconstruction based on Peyer (1931), Kuhn-Schnyder (1962) and Rieppel (1989). The long, robust neck posteriorly oriented to the skull, a primitive pedal morphology and a small ilium are characters common to primitive prolacertiforms. The attenuated tail (length estimated), a low scapula; short, straight "lumbar" ribs and a thyroid fenestra between the pubis and ischium are synapomorphies of the Tapinoplatia. B. In *Tanytrachelos ahynis* (Olsen 1979) the skull is elevated on a flexible neck configured in a simple gradual curve, but here much less so than is preserved in the death pose of the type specimen (Olsen 1979 figure 2) and others. The reduction of digit IV in both manus and pes, the elongation of the proximal phalanx of pedal digit V and the presence of post-cloacal bones are derived characters also seen in pterosaurs. C. *Langobardisaurus tonelloi* (Muscio 1996, Renesto and Dalla Vecchia 2000) with left femur foreshortened. Right hind limb displayed as *in situ*. Stance and pedal configuration suggested by greatly reduced distal phalanges. Note the relatively large skull, short rostrum, large orbit, reduced scapula and the reduction of phalanges in pedal digit V as in *Cosesaurus* (Fig. 3.).

Pterosauria (= *Eudimorphodon* + *Preondactylus*). The second analyzed a smaller subset of Evans' work focusing on the Prolacertiformes and in addition to those named before, adds *Longisquama*. The third analyzed a more recent study focusing on the Prolacertiformes (Jalil 1997), but here adds *Longisquama*, *Sharovipteryx* and *Eudimorphodon*. The fourth analyzed a study of the Archosauromorpha (Bennett 1996a), but here adds *Cosesaurus*, *Longisquama*, *Sharovipteryx* and *Langobardisaurus*.

The purpose of doing four analyses, rather than one, was to simplify comparison. The inclusion of key prolacertiforms and pterosaurs into well-established cladograms allows quick comparisons of similarly numbered characters and character states in previous works. Inevitably some characters had to be rescored or otherwise modified and these are readily identified. Certain characters of *Langobardisaurus*, *Cosesaurus*, *Longisquama* and *Sharovipteryx* may have been incompletely or inaccurately described by previous workers. Here I attempt to reevaluate and redescribe these key taxa, drawing particular attention to possible pterosaur synapomorphies.

Langobardisaurus pandolfii - Renesto 1994
Langobardisaurus tonelloi - Muscio 1996

Materials. Three nearly complete and articulated specimens, crushed on slabs: the holotype, MCSN(B) 2883, and the paratype, MCSN(B) 4860, Fig. 1A), differing only in size. A third fully articu-

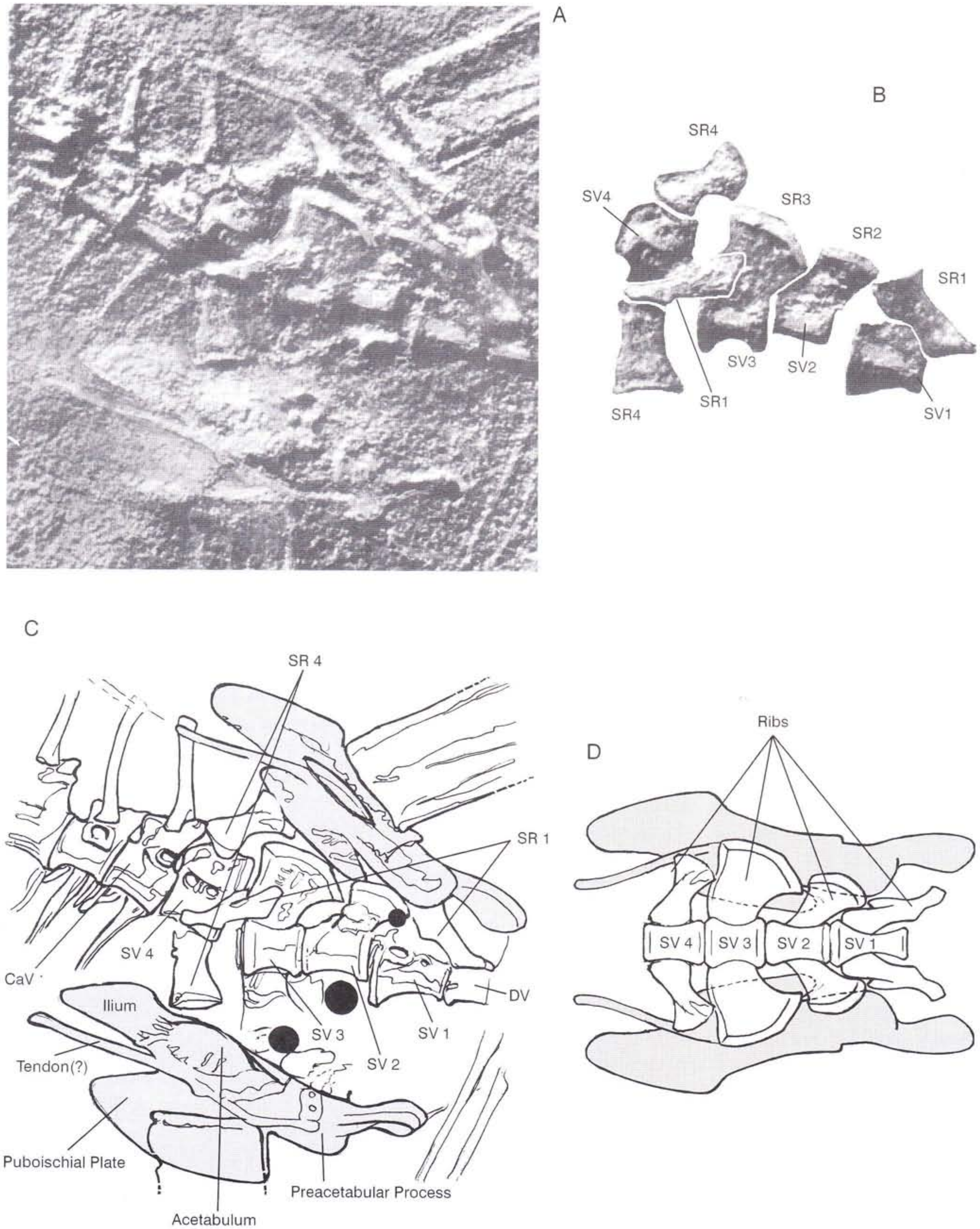


Fig. 6 - *Cosesaurus aviceps* (Ellenberger and de Villalta 1974) pelvis in ventral view. A. Photograph of the latex peel. B. Same with sacral vertebrae (SV1-4) and their associated ribs (SR1-4) isolated. C. Interpretation of the specimen. Black circles are fossil bubbles. D. Symmetrical reconstruction in ventral view. Thin rods may be tendons. Note the disarticulation of all the ribs in the area except for two pairs, the primitive central sacrals. Unlike the other caudal and dorsal ribs, the sacralized ribs have an anterolateral orientation and two points of attachment. Abbreviations as in figure 3.

The sternum is not present but the paired coracoids are embayed medially providing a site for it. The "humerus to femur length ratio" of 0.62 is greater than that of other prolacertiforms. The length ratio of the manus to the ulna is 1.3/1, or 50% greater than in *Langobardisaurus* and more than twice that in *Macrocnemus*. The length ratio of manual digit IV to the humerus is at least twice that of *Langobardisaurus* and *Macrocnemus*. Thus *Cosesaurus* has the largest manus among traditional prolacertiforms, except *Longisquama* (Fig. 7). Metacarpals II-IV are subequal in length, as in *Preondactylus* (Dalla Vecchia 1998).

The narrow, elongate impression Ellenberger (1977: figure 6) identified as the "prepubis" is the preacetabular process of the ilium. The long rod Ellenberger identified as the "postpubis" is tentatively identified here as an ossified(?) tendon connecting the caudal muscle complex to the anterior ilium. I know of no other structure like it. The "Index of Galton" (Galton 1976) is defined as the ratio of the femur + tibia + longest metatarsal length to the trunk length and is reported be related to bipedalism. *Cosesaurus* has an index ratio of 1.21, well within the range of other bipeds listed by Sanz & López-Martinez. The index number is higher still for *Langobardisaurus* (1.35), *Preondactylus* (1.41) and *Sharovipteryx* (2.1), which is one reason why they are illustrated here (Figs. 1C, 5, 8 and 12) in the bipedal configuration. Unlike *Langobardisaurus* and other similar prolacertiforms, the pubis and ischium in *Cosesaurus* (Fig. 6) is not separated by a thyroid fenestra. The two elements form a single fused plate that is smaller than the ilium. The fibula of *Cosesaurus* is much narrower than the tibia, which is unusual for prolacertiforms and typical for pterosaurs. Digit V has one less phalanx than most prolacertiforms. Sanz & López-Martinez (1984) reject the "interdigital web of the foot." The metatarsus of *Cosesaurus* (Figs. 3 and 13C) is appressed with non-radiating distal ends so the digits would not have spread for a web but were essentially parallel, as in *Rotodactylus* tracks (Peters 2000). Contra Ellenberger (1977), indisputable dermal appendages are not visible on either side of the tail, posterior to the fore limbs, or posterior to the hind limbs. Any possible indications (Fig. 3B) appear at the limit of resolution imposed by the grain of the matrix. Dorsal to the cranium are a series of short, bristle-like structures. Short rectangular frill segments appear dorsal to the anterior dorsal vertebrae, as noted by Ellenberger (1977). Ellenberger also observed a nasal crest. This was not confirmed, but tentative borders are shown in Figure 4b.

Longisquama insignis - Sharov 1970

Materials. Plate and counterplate (PIN No. 2584/4) preserving the anterior half of a crushed articulated skeleton lacking only the tip of the snout and manual digits II and III. Plume-like dermal appendages extend from the dorsal area. Disassociated plumes are also known.

Horizon. Late Triassic (Norian), Fergana Valley, Kirghizia.

Autapomorphies. The upper temporal fenestra rim is greatly expanded posteriorly; the clavicles are robust, strongly arced and coosified with a robust, anteriorly expanded, interclavicle and a deeply embayed sternum; hyper-elongate plume-like appendages extend from the dorsal area.

Comments and Description. The anterior premaxilla is missing and the posterodorsal process (if present) is indistinguishable from the dorsally expanded nasal (Fig. 7); the skull profile is low anteriorly then rises to a small premaxilla/nasal crest, then rises again to a frontal/parietal crest; the two small recurved antorbital fenestrae within the anterior maxilla are separated by slender struts; a third and larger fenestra is dorsally rimmed by an inflated lacrimal/prefrontal; the orbit is very large and a robust sclerotic ring fills it; the maxilla is narrow and extends posteriorly to mid orbit; anteriorly the maxilla bears large, sharp, anteriorly-oriented fangs, ventral to the orbit are at least six tiny sharp teeth; the jugal extends ventral to the antorbital fenestra, a dorsal process meets the lacrimal, a postorbital process meets the postorbital and a posterior spur extends to the quadrate; a quadratojugal is not distinct from this spur; the prefrontal rims the orbit dorsally; the postfrontal is a large triangular element framing the anterior rim of the upper temporal fenestra; the squamosal frames a large upper temporal fenestra expanded posterodorsally by the large parietal; the inclined quadrate is broad; the mandible is narrow anteriorly and deep posteriorly; the anterior third(?) of the dentary is missing, but bears 11 large posteriorly-oriented fangs which decrease sharply ventral to the orbit; a retroarticular apophysis is present; the eight cervicals and their associated ribs are vague, but the vertebrae are not elongate; the anterior dorsal vertebrae are barely visible, however, eight increasingly elongate and relatively straight dorsal ribs are anteriorly displaced on the right side, all provided with expanded proximal ends, probable anchors for the dorsal plumes.

The clavicles are robust, have small regular toothy decorations, form a strong **U** shape, overlap each other and the interclavicle; the robust interclavicle is segmented; it has a greatly reduced stem and a tapered anterior process; a keel may be present; the posteriorly embayed sternum fills the bowl of the clavicles to which it may be fused; concentric or layered rims are visible in low light (Fig. 7C); considering the pattern of fusion in the pectoral elements, the *in vivo* position of the clavicle/interclavicle/sternal complex is probably ventral, in many respects matching a juvenile *Eudimorphodon* (Wild 1993); the narrow scapula is nearly as long as a dorsal rib and twice as wide with a narrow waist; the dorsal end extends to the dorsal vertebrae and the ventral end

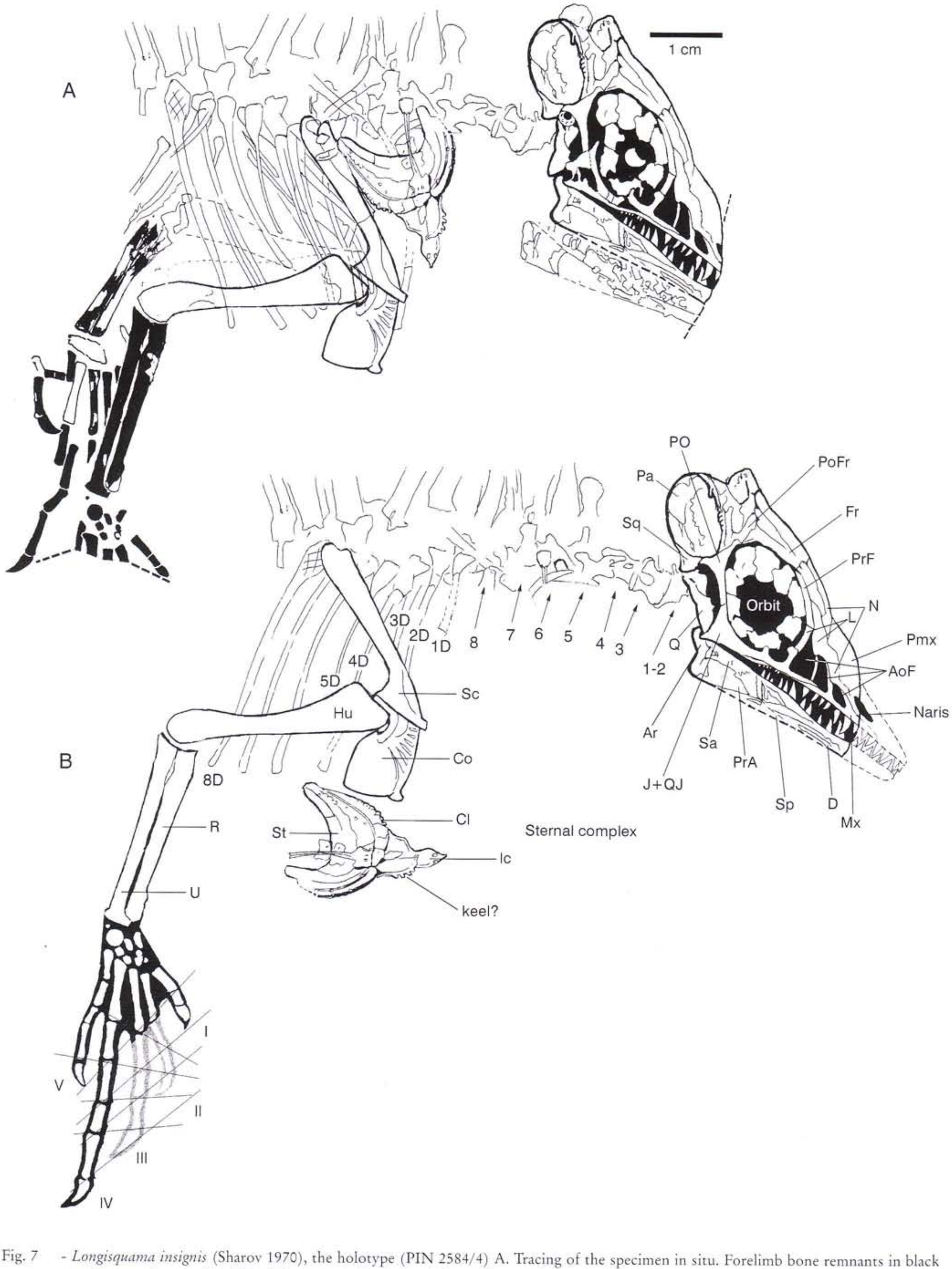


Fig. 7 - *Longisquama insignis* (Sharov 1970), the holotype (PIN 2584/4) A. Tracing of the specimen in situ. Forelimb bone remnants in black and impressions outlined. Skull fenestrae in black. The "plumes" are excluded. Scale bar = 1 cm. B. Reconstruction with the snout tip hypothetically reconstructed and displaced parts returned to their in vivo positions. Missing digits reconstructed according to Peters (2000). Jugal extends anterior to orbit, strernal complex, strap-like scapula and tall coracoid, all as in pterosaurs. Abbreviations as in Figures 3 and 4.

expands and curves to meet the coracoid; the coracoid is tall with radiating ridges anteriorly, a glenoid notch posteriorly and an articular knob at the anteroventral corner; the humerus is robust with a narrow waist; the straight radius and ulna are of equal width and display little to no spatium interosseum; the carpal elements are small, round and widely separated as in other similar prolacertiforms; manual digit I, plus the associated metacarpal, is only as long as metacarpal IV; manual digit IV is three times the length of metacarpal IV; the penultimate phalanges of IV and V are the longest in each series; the manus-to-ulna length ratio is 1.5/1, or 15% greater than in *Cosesaurus*; elongate dermal impressions appear in the throat region; the hyper-elongate plume-like dermal appendages (Haubold and Buffetaut 1987; Jones, et al. 2000) are autopomorphic characters of little use to this investigation.

Sharovipteryx mirabilis - Cowen 1981

Materials. Originally *Podopteryx* (Sharov 1971), but the name was preoccupied (Cowen 1981); part and counterpart slabs (PIN No. 2584/8) together preserving most of an articulated skeleton with clearly discernable soft tissues preserved in dorsal aspect on the plate. The present description refers chiefly to the counterplate.

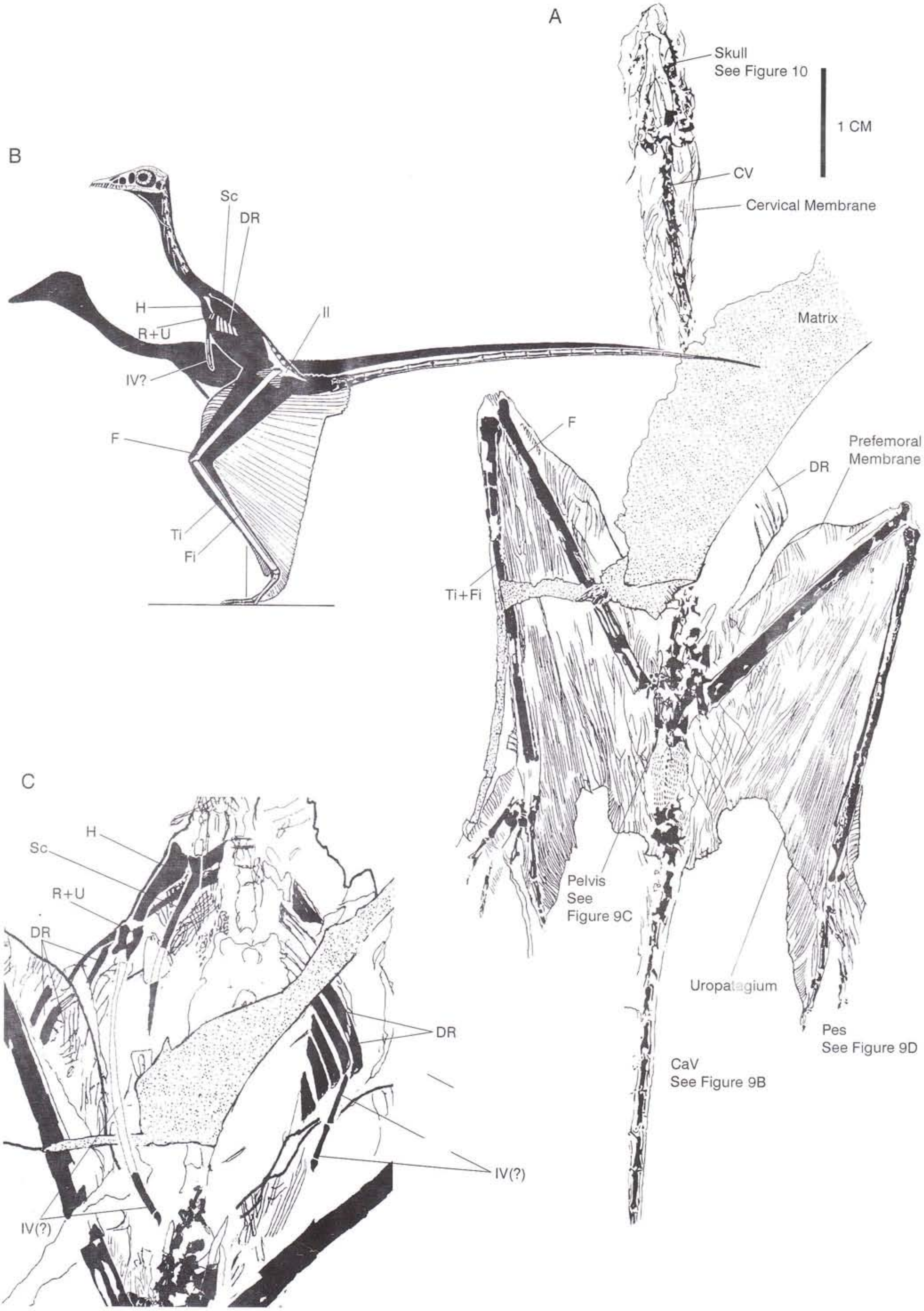
Horizon. Late Triassic (Norian), Fergana Valley, Kirghizia.

Autapomorphies (with regard to terrestrial prolacertiforms). The premaxilla comprises nearly a quarter of the skull's exposed palate (Fig. 10); the external naris is large; the maxilla has a medial process which divides the internal naris in two; long and robust hyoids extend to the third cervical vertebra; the dorsal ribs are broad and flat distally (Fig. 8C); six sacral vertebrae are present between the extended ilia (Fig. 9C) with branching at the lateral articulations; large chevrons parallel each caudal centra, equal them in length and articulate in series at expanded joints; the fore limbs are weakly developed except for digit IV(?) which is unreduced or enlarged (Fig. 8c) and nearly reaches the ilium; the tiny curved humerus has a large crescentic deltopectoral crest; the ilium is greatly extended anteriorly and posteriorly; the femur and tibia are each equivalent to the intergirdle distance; the femur has a cnemial projection; the fibula is less than 20% as wide as the tibia and is closely appressed without fusion; pedal digit V is the longest; metatarsal I is only slightly shorter than II-IV which are subequal and spreading; extensive and fiber-supported uropatagial membranes trail each hind limb and attach to the tail; other membranes appear anterior to the distal tibia and anterior to the femur; a dermal membrane, or web, between the pedal digits extends to the first interphalangeal joints.

Note. Many bones in the specimen are split between the plate and counterplate with some bone shredded or impressed on both plates. The skull appears to be split chiefly at the level of the exposed palate and lower skull elements, as Sharov (1971) noted, but in dorsal aspect (Fig. 10A, D). Gans, *et al.* (1987) and Tatarinov (1989) considered the exposed bones dermal roofing elements with the orbits positioned in the anterior half of the skull. Four considerations argue against that reconstruction: 1) the proposed "roofing" elements should meet medially throughout the series, but they do not; matrix in the shape of soft tissue, here identified as the pyriform recess, separates the posterior exposed elements; 2) in all similar prolacertiforms (Figs. 1, 3, 7, Wild 1973) the orbit is not in the anterior half of the skull but an antorbital fenestra might cause confusion; 3) the observed elements correspond to elements of the palate in *Macrocnemus* (Kuhn-Schnyder 1962, Fig. 10B), *Tanystropheus* (Wild 1973 figure 6) and *Rhamphorhynchus* (Wellnhofer 1975a, Fig. 10C); 4) most exposed bones appear to be from the same horizon in the skull (Fig. 10E), a layer with break points weakened by multiple fenestrae and floored by the plate-like palate.

Comments and Description. The low premaxilla is covered by scalation; ossified portions are not visible, but the anterior extent of the vomers indicates that the premaxilla invaded, or extended, 1/5 to 1/4 the length of the palate; part of the large narrow external naris impression is seen through the internal naris, which is the largest vacuity in the palate; partial nasals are preserved on both sides, both are convex anteromedially suggesting that a dorsal extension of the premaxilla invaded them; the frontals and parietals are missing (probably embedded); a Y-shaped dorsal process of the maxilla frames the anterior antorbital fenestra and borders the external naris ventrally; the narrow maxilla rim has breaks at the base of each of three hypothetical fenestrae divider struts; posteroventrally the maxilla extends to mid orbit; a narrow medial palatal process of the maxilla divides the internal naris almost in two; at least 15 teeth per side appear in the upper jaw and each tooth is narrow, sharp and gently recurved (Unwin, et al. In press); a probable lacrimal has a long narrow ventral stem; the jugal is narrow with a triangular postorbital portion and a tiny quadratojugal spur posteriorly; the anterior halves of the broad, flat, vomers are conjoined medially forming a **Y** shape, the posterior halves diverge laterally and are sutured to the pterygoids; the anterior process of the palatine is missing but the transverse process extends anterolaterally to form a narrow contact with the maxilla; posteriorly the palatine is sutured to the pterygoid; the anterior process of the pterygoid invades the vomer; a long posterior process makes perpendicular contact with the quadrate; a medial articulation for the basipterygoid is apparent on the pterygoid, but the basipterygoid is not exposed; laterally the ptery-

Fig. 8 - *Sharovipteryx mirabilis* (Sharov 1971) A. The counterplate with bone in black and impressions outlined. Stippled area represents lost material. Scale bar = 1 cm. Scales obscure proximal caudals. See Figure 9 for details of the caudal vertebrae, pes and pelvis and Figure 10 for details of the skull. B. Two reconstructions in the bipedal configuration with femora not foreshortened. Vertical line above pes is the hypothetical center of balance. C. Lower plate, dorsal view of the dorsal area traced from photograph. Forelimb and scapula (Sc) outlined. Stippled area represents lost material. Dashed line represents hypothetical extent of carpus, metacarpus and proximal phalanges between ulna and the distal phalanges of digit IV(?). Abbreviations as in figure 3.


A
Skull
See Figure 10
1 CM
CV
Cervical Membrane
Matrix
F
Prefemoral
Membrane
DR
Ti+Fi
Pelvis
See
Figure 9C
Uropatagium
Pes
See Figure 9D
CaV
See Figure 9B
B
Sc
DR
H
R+U
II
IV?
F
Ti
Fi
C
H
Sc
R+U
DR
DR
IV(?)
IV(?)

goid makes broad contact with the ectopterygoid, the two elements are fused together and the resulting process makes broad contact with the jugal; the basioccipital and opisthotic form a half ring; the mandible is shallow (Unwin, et al. In press); a long retroarticular process is present; and a very long pair of hyoids and multiple branchial cornua project caudally.

The cervicals are narrow and elongate with low neural spines; each centra is attended by long and extremely thin parasagittal ribs with anterior heads; the torso is considerably reduced compared to other prolacertiforms; the dorsal ribs are broad and flat distally; the sacral series includes six vertebrae between the anterior and posterior processes of the ilium; the anterior short, robust caudal vertebrae are nearly covered by scalation and have robust ribs (transverse processes); many of the mid to posterior caudal vertebrae have centra five times longer than their width; Gans, et al. (1987) noted, "The [caudal] vertebral bone often seems to be expressed in two longitudinal ridges, with a deep groove between them," but the present study indicates that the dorsal "ridge" is the centra series and the ventral "ridge" is the parallel chevron series.

The pectoral girdle and forelimb are preserved in the lower plate and will be described here only briefly based on examination of photographs (Fig. 8C). The scapula is a long element distinguished from the ribs 1) by its parasagittal placement dorsal to the ribs, 2) by the glenoid articulation in conjunction with the humerus, and 3) by the posterior tip which narrows to a point. The articulated elements of the forelimb lie in a broad curved line; the proximal end of the humerus appears to have a crescentic deltopectoral crest; the radius and ulna are only half the length of the humerus; only a single long digit, probably the fourth, appears anterolateral to the ilium; mirror-image portions of these forelimb elements appear on the opposite side, as noted by Sharov (1971).

The ilium has greatly elongated pre- and postacetabular processes (Fig. 9C), each with a knife-like shape; only the anterior and posterior of the pubis and ischium are visible and together they are much smaller than the ilium; a thyroid fenestra, whether present or absent, is hidden by the femur; a femoral head is not developed; the distal femur terminates in a cnemial crest; the tibia is longer than the femur; the fibula is less than 20% the width of the tibia; the tarsus is disarticulated but includes one large oval element; the metatarsals diverge with I-IV subequal (Fig. 9D); the phalangeal formula is 2-3-4-5-4 with no penultimate phalanx the longest in a series; the metapodial bone previously identified (Gans, et al. 1987) as metatarsal V, is the proximal phalanx of digit V.

Dermal membranes are clearly preserved throughout the specimen, often as a latticework of intersecting lines; the snout is covered in small pebbly scales; ridged scales cover the anterior caudals; the unscaled, wrinkled neck skin is five times wider than the cervicals; large membranes appear posterior to the hind limbs originating at the ninth caudal vertebra and terminating at the distal end of the second phalanx; each membrane is stiffened and supported by long parallel fibers similar to those found in the wings of pterosaurs but would be homologous to less organized fibers appearing in pterosaur uropatagia (Unwin and Bakhurina 1994); other fiber-stiffened membranes appear anterior to each femur and anterior to each distal tibia.

Taxa traditionally Allied With the Pterosauria.

Scleromochlus, *Marasuchus*/*Lagosuchus*, *Lagerpeton* and the Dinosauria have traditionally been allied with the Pterosauria (Benton 1999 and references therein). Previous workers may have presumed this relationship because many characters appear to be homologous. These include: "antorbital fenestra" "procoelous vertebrae," "large head/short torso," "preacetabular ilial process," "strap-like scapula," "tibia/femur length ratio greater than one," "simple-hinge ankle joint," and "a compact metatarsus." However, these characters also appear in certain Prolacertiformes and distinct differences provide clues as to their independent acquisition. As will be shown below, the Ornithodira (sans Pterosauria) share only one character with Pterosauria not also present within Prolacertiformes: femur bowed (but it is unknown in *Longisquama*).

Cladistic analyses.

Characters used here are listed and grouped as they were in previous works (Evans 1988, Jalil 1997, Bennett 1996a), according to their presence or absence in the outgroup or ingroup. A number have been rescored due to new interpretations. A few new characters have also been added as noted.

Analysis based on Evans (1988)

Evans cladistically analyzed primitive diapsids, considered the Archosauria as a single taxon and did not include the Pterosauria, *Langobardisaurus*, *Longisquama* or *Sharovipteryx*. For this paper I duplicated Evans's data matrix (Appendix I, Table 1) relating to early diapsids and archosauromorphs (97 characters, 31 taxa, Evans's Nodes A-H). Other characters relating to lepidosauromorphs were examined but not included because pterosaurs do not exhibit any lepidosauromorph synapomorphies (Bennett 1996a). Benton (1985) noted two lepidosauromorph characters: 1) single ossified sternum and 2) specialized sternal attachments for the ribs. However, the sternum in pterosaurs is a fusion of other pectoral elements (Wild 1993), including a homologous sternum that is plesiomorphic. The "specialized

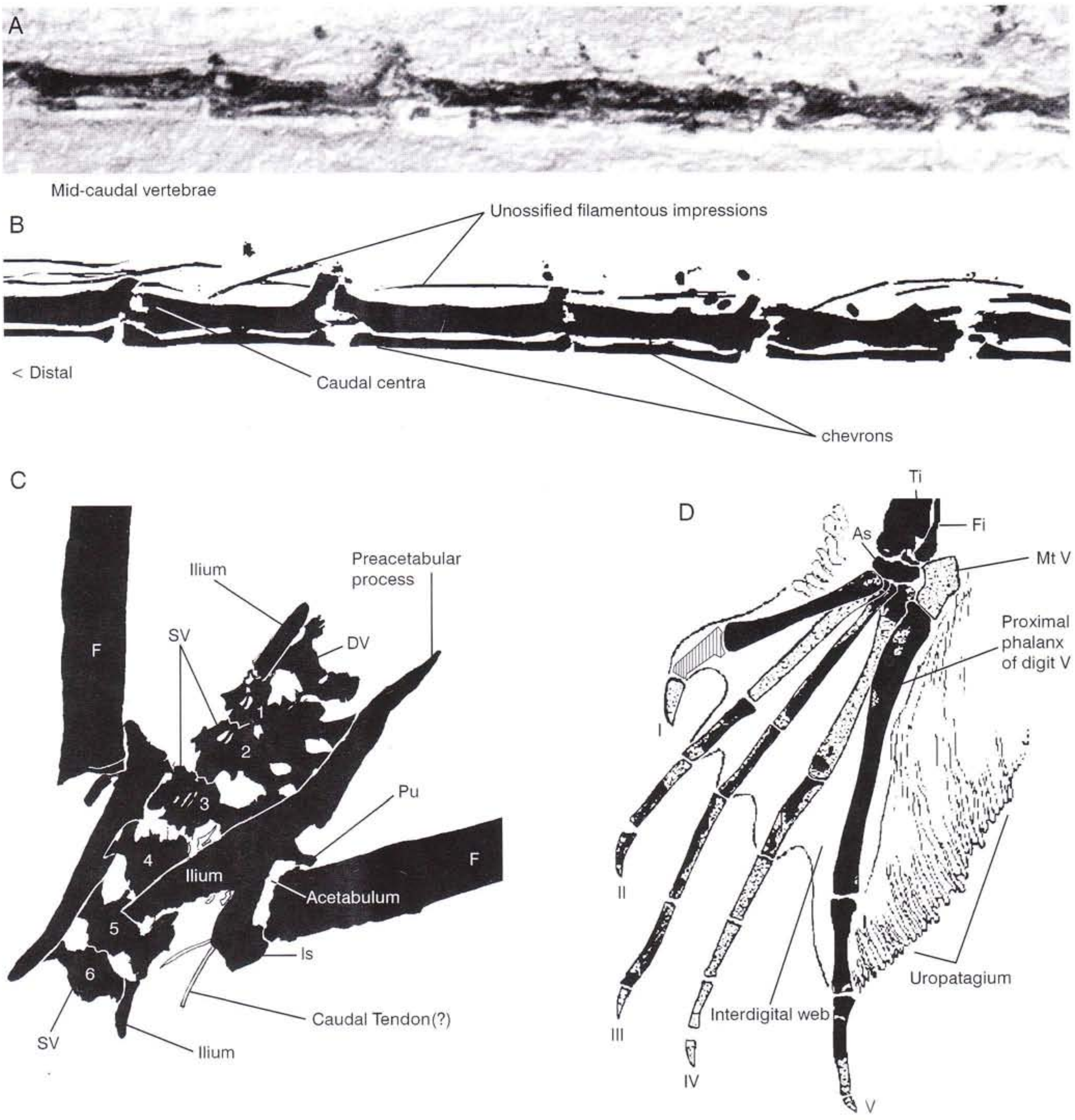


Fig. 9 - *Sharovipteryx mirabilis* (Sharov 1971) tail, pelvis and pes. A. Mid-caudal vertebrae in lateral view. Note faint strand-like impressions dorsal to vertebrae that appear similar to extended pre- and postzygopophyses in pterosaurs and similar to caudal tendons in living lizards (Hamley 1990). B. Tracing of same with tendon strands, centra and extended chevrons identified. C. Pelvic area in dorsal view. Both ossified material and impressions indicated as black. Posterior right ilium is broken but left ilium demonstrates its posterior extent. Small rod posterior to ischium, tentatively identified as a caudal tendon, may be homologous with those observed in *Cosesaurus* (Figs. 3-5). D. Left pes in dorsal view reconstructed from slightly displaced elements. Proximal phalanx of digit I is unknown and hypothetically restored. Preserved bone in black. Impressions stippled and outlined. Note uropatagium stiffened by parallel fibers and the dermal web spanning the proximal phalanges. Large disk-like tarsal element is restored edge-on here.

sternal attachments" are simply ossified sternal ribs which are plesiomorphic (Bennett 1996a). To Evans's taxon list I add *Sharovipteryx*, *Longisquama*, *Langobardisaurus*, the pterosaurs *Eudimorphodon* (Wild 1978, 1993) and *Preondactylus* (Wild 1984b, Dalla Vecchia 1998), and the ornithodires, *Scleromochlus* (Benton 1999) and *Lagosuchus/Marasuchus* (Sereno and Arcucci 1994), for a total of 38 taxa. I use two pterosaurs because certain characters in each are unclear or not preserved. I add seven characters for a total of 104. A second analysis reduced to 21 taxa, chiefly prolacertiforms, is shown here (see Appendix I - Table 2 for details).

In these analyses, as well as subsequent ones, a data matrix was generated using MacClade 3.05 (Maddison and Maddison 1992) and

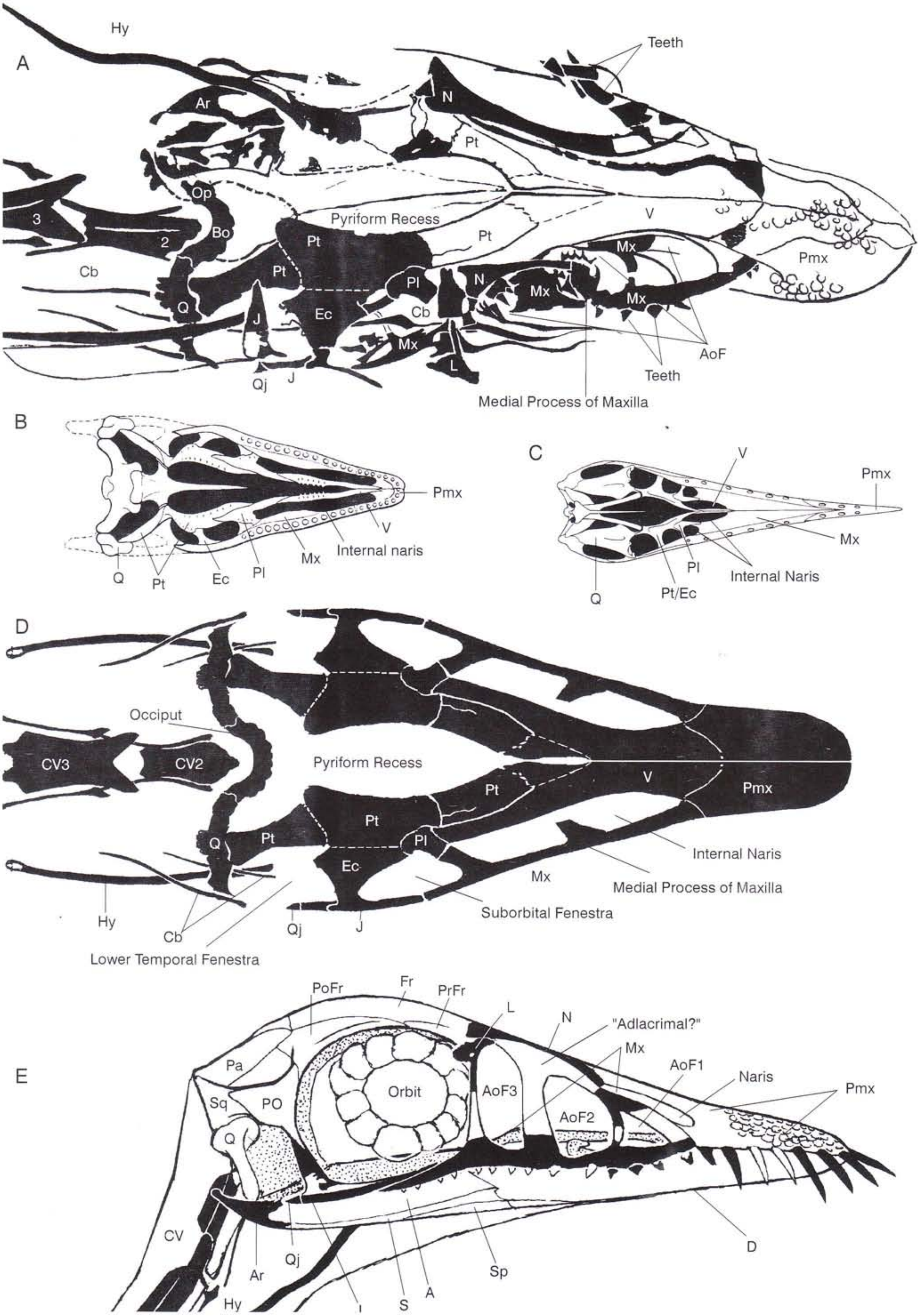
																			11111
		111	22222	33333	33333	44444	44444	5555	55555	66666	66	777	88888	8888	99999	99999	00000
Taxon/Node	4	018	13456	01234	56789	01234	56789	0124	56789	01234	67	012	01234	5689	01234	56789	01234
Petrolacosaurus	1	110	00000	00000	00000	00000	00000	0000	00000	00000	00	000	00000	0000	00000	00000	00000
Choristodera	0	001	00000	10100	10100	00100	10110	0100	1?0?0	00000	11	111	11111	0001	01011	01000	00000
Rhynchosauridae	0	000	11111	01100	10100	11001	00110	0100	01000	00000	11	111	11111	1111	10010	00000	00000
Thalattosauria	0	000	11111	00110	00110	00101	00011	00?0	01000	01000	00	100	01101	1100	01110	10000	00000
Trilophosaurus	1	001	01111	?0000	?0?00	00000	00?10	0000	00000	00000	00	?10	1111?	1011	10111	00000	00000
Megalancosaurus	1	001	011??	?01?1	10??3	000?0	00100	?10?	00000	1?020	00	11?	1100?	11?0	0122?	1?202	20?00
Drepanosaurus	?	001	0????	???01	???13	??0?0	00???	??0?	10000	1?020	?0	???	1000?	??00	0?22?	??202	20?00
Protorosaurus	1	001	11111	00001	11000	00000	00?00	?000	00000	00000	00	?1?	11011	1000	11111	11100	00000
Prolacerta	1	011	11111	00001	110?0	00000	00000	0000	00000	00000	00	100	11011	1000	11111	11100	00000
Boreopricea	1	001	11111	00101	11111	??100	?11?0	00?0	11000	000?0	?0	1?0	11011	1?11	10111	11100	??000
Macrocnemus	1	011	11111	00111	11111	0?110	011?1	1010	00000	00000	00	110	01012	1111	11111	11100	10000
Cosesaurus	1	001	11111	00111	01111	11121	111?1	0001	10110	?0?20	00	010	01013	1111	00111	?1103	1121?
Tanystropheus	1	001	11111	00101	11111	11110	11111	1111	11111	10111	00	100	01012	1111	01111	11100	10000
Tanytrachelos	1	001	111?1	001?1	111?1	1?11?	11111	1?11	11111	10111	00	1?0	01012	1111	0111?	11100	10001
Proterosuchus	1	001	11111	11010	01100	0?000	000?0	0020	00000	00000	00	111	11111	1011	11111	11100	00100
Langobardisaurus	1	001	111??	00111	?1111	10110	11111	??1?	10110	10?20	00	?10	01012	1111	0011?	?110?	10001
Longisquama	1	0??	111?1	00?11	0?1?2	?????	??1??	00?0	1???0	?0???	0?	010	????3	11??	?0?11	1110?	?12??
Sharovipteryx	1	011	111??	?01?1	01112	???21	11111	0???	?1110	20?2?	00	??0	01?13	?111	0111?	?1113	1122?
Preondactylus	1	211	111??	00111	01112	1?1?1	11111	000?	11110	20?2?	00	0?0	0101?	?111	0111?	11103	12221
Eudimorphodon	1	211	11111	00111	01112	1?121	11111	0001	11110	20120	00	0?0	01013	1111	01111	11113	12221
Scleromochlus	0	111	1111?	1?111	??110	??0??	?1??0	0?2?	11000	00010	00	011	1121?	?0?1	01??1	???01	00110
Lagosuchus	0	011	011?1	?1111	??110	??0?1	00??1	??2?	?1000	00011	00	01?	1121?	10?1	01???	?1?01	00110

Tab. 1 - Reanalysis of Evans 1988.

analyzed using Phylogenetic Analysis Using Parsimony (PAUP 4.0, Swofford, 1999). Characters were given equal weight and all multistate characters were treated as unordered. The general heuristic search option of PAUP was used to produce minimum-length trees using the accelerated (ACCTRAN) optimization option. Scoring and rescoring of characters proceeded as follows.

Evans (1988) assigned three characters (91-93, see Appendix I for character descriptions) to the clade Thalattosauria + *Trilophosaurus* + *Megalancosaurus* + Prolacertiformes + Archosauria (Node H). Basal pterosaurs and *Sharovipteryx* share all three characters unambiguously. Evans assigned one character (94) to the clade *Trilophosaurus* + *Megalancosaurus* + Prolacertiformes + Archosauria (Node H). This character is difficult to determine in Triassic pterosaurs and the key prolacertiforms due to preservational problems. Evans assigned one character (95) to the clade *Megalancosaurus* + Prolacertiformes + Archosauria (Node H). This character is also visible in the Pterosauria and *Langobardisaurus*, but difficult to ascertain in other key taxa. Evans assigned two characters (96, 97) to the clade Prolacertiformes + Archosauria (Node H). Both characters are present in the Pterosauria, *Sharovipteryx*, *Cosesaurus* and *Langobardisaurus*. Evans assigned seven characters (27-33) to the clade Archosauria (Node D). Of these only characters 27, 32 and 33 are present in the Pterosauria. Antorbital fenestrae (27) also appear in *Cosesaurus* (Fig. 4), *Sharovipteryx* (Fig. 10) and *Longisquama* (Fig. 7), but without a fossa. Trunk intercentra loss (32) is a plesiomorphic character present in the outgroup (Evans's Node E). An ectepicondylar groove or foramen (33) cannot be detected in *Cosesaurus* or *Langobardisaurus*, but the groove without the foramen is present in other prolacertiforms, so it may also be a plesiomorphic character. Evans assigned three characters (34-36) to the clade *Protorosaurus* + *Prolacerta* + *Boreopricea* + *Macrocnemus* + *Cosesaurus* + *Tanystropheus* + *Tanytrachelos* (Node E) and all are present in the Pterosauria. Characters 34 and 36 are present in *Langobardisaurus*, *Cosesaurus* and *Sharovipteryx*. Character 35 is difficult to determine in prolacertiforms. Evans assigned thirteen characters (37-49) to the clade *Boreopricea* + *Macrocnemus* + *Cosesaurus* + *Tanystropheus* + *Tanytrachelos* (Node E). Eleven of these characters are also present in the Pterosauria and *Cosesaurus*. One exception, the traditional quadratojugal (43), is

Fig. 10 - *Sharovipteryx mirabilis* (Cowen 1971), the skull. A. Tracing made from the counterplate. The palate and a few rostral elements (nasal and lacrimal) in dorsal view. Black areas are ossified materials. Outlined areas are impressions. The premaxilla is covered in simple scales. B. The palate of the primitive prolacertiform, *Macrocnemus*, in ventral view (from Kuhn-Schnyder 1962). The palatal shelf of the maxilla slightly invades the internal naris. C. The palate of the pterosaur, *Rhamphorhynchus* (Wellnhofer 1975a), with some elements relabeled from the original (see text for details). The internal naris is divided by the anterior process of the palatine and the medial process of the palatal shelf of the maxilla which conjoins its opposite medially. D. The palate of *Sharovipteryx* in dorsal view, reconstructed with symmetry. E. Hypothetical restoration of the lateral view based upon preserved bone, bone impressions and comparisons with *Cosesaurus* (Fig. 3-5), *Longisquama* (Fig. 7) and *Eudimorphodon* (Wild 1978). Three antorbital fenestrae may be reconstructed from strut bases ventral to the plane of plate separation. Certainly more work must be done and better specimens must be found to improve upon this first attempt at reconstruction. Abbreviations as in figure 3 and 4.


A
Hy
Teeth
Ar
N
Pt
Op
3
2
Bo
Cb
Pyriform Recess
Pt
V
Pt
Pt
Mx
Pmx
Q
Pl
N
Mx
Ec
Cb
Mx
J
Mx
L
Qj
J
Teeth
AoF
Medial Process of Maxilla
B
Pmx
V
Internal naris
Mx
Pl
Ec
Pt
Q
C
V
Pmx
Mx
Pl
Internal Naris
Pt/Ec
Q
D
Occiput
CV3
CV2
Pyriform Recess
Pt
V
Pmx
Pt
Pt
Q
Pl
Ec
Internal Naris
Mx
Medial Process of Maxilla
Suborbital Fenestra
Hy
Cb
Qj
J
Lower Temporal Fenestra
E
PoFr
Fr
PrFr
L
N
"Adlacrimal?"
Mx
AoF1
Naris
Pmx
Pa
Sq
PO
Orbit
AoF3
AoF2
Q
CV
Ar
Qj
I
S
A
Sp
D
Hy

			11111	11111	22222	22222	33333	33333	44444	44444	55555	55555	66666	66666	77
Taxon/Node	1234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01
Petrolacosaurus	0000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0000?	?0
Youngina	0000	00000	00000	00??1	0?000	00000	00000	00000	00000	00000	00000	000?0	00101	?0000	0?
Sphenodontida	1111	11111	11111	11111	11111	00010	00000	00000	00001	00000	00010	10011	00000	00011	10
Iguana	1111	11111	11111	11111	11111	00001	00000	00002	00011	00100	00011	10011	10000	01101	10
Choristodera	?110	0?101	11101	10000	00000	10111	10100	10100	00000	00000	00110	00010	01001	?01?0	?0
Rhynchosaurus	1111	1?111	?1111	10000	00000	10111	111?1	00001	00001	0??00	1?001	?0000	00000	01010	00
Trilophosaurus	?111	11111	?1111	?0?00	00000	10?01	11111	1110?	000?1	0000?	?0011	00100	0?000	00011	10
Proterosuchus	1111	1?111	11101	00000	00200	11111	11101	11100	00001	00?00	00000	00000	01111	111?1	10
Protorosaurus	1111	1??11	?1111	10000	0?000	??111	111?1	11110	11001	0000?	10000	00000	01111	?10??	?0
Boreopricea	?111	11?01	1111?	1000?	00?00	?1111	111?1	1??10	1?001	000?0	11101	10010	0?111	?11??	10
Prolacerta	1111	11111	11111	10000	00000	11101	111?1	11111	11101	0??00	01000	00000	01111	11111	10
Macrocnemus	1111	11?11	11111	1?0?0	00100	11001	11111	01132	11010	10011	1?101	00010	01111	?01??	?0
Tanystropheus	1111	11111	11111	10000	00100	11001	11111	01132	11110	11111	11101	11110	11?11	001??	11
Cosesaurus	1??1	1??11	11111	1000?	?0000	1100?	1111?	01132	1112?	?1110	01101	00?11	01?11	?01??	?1
Tanytrachelos	???1	1??11	1111?	??000	??100	?1001	11111	?1132	11010	11??1	11101	11110	11111	?01??	?1
Malerisaurus	????	????1	???1?	??0??	000??	?1001	111??	1??32	1?001	0??0?	11??1	?00?1	???11	?01??	??
Langobardisaurus	????	1??11	1111?	????0	00100	11001	11111	01132	11?10	0111?	?1101	00111	0?111	?01??	?1
Jesairosaurus	?111	11111	???11	??0??	00???	?1001	?11??	?1?32	1?111	0??0?	1???0	?0???	???11	?01??	??
Eudimorphodon	0111	11111	11111	10000	00000	11001	1111?	01132	11122	01?00	01101	00111	11111	?01??	?1
Sharovipteryx	????	??11?	?111?	100??	???00	??001	1111?	01132	11122	01?0?	??1??	?0111	?1?11	?01??	?1
Longisquama	1??1	1??11	1??11	1000?	?0???	?100?	1?11?	?1132	1?1?2	01??0	0???1	00???	?1?11	?01??	??
Scleromochlus	01??	???11	11101	1?000	00200	01?11	?11??	1??2?	1?0?1	01?00	0?01?	0000?	01?11	?01??	?0
Lagosuchus	?11?	1?1?1	?1101	?0??0	00200	????1	111?0	1??1?	1???1	0??0?	??11?	00011	0??11	?01??	?0

Tab. 2 - Reanalysis of Jalil 1997.

lost and replaced by a new ossification (described later) in pterosaurs and their sister taxa. "Lacrimal restricted to orbit rim" (47) is present in *Eudimorphodon* but was previously misidentified (Wild 1978) as the prefrontal. The bone in question has a small lacrimal opening. A low scapula (39) is not present in *Boreopricea*. A perforated ankle (44) is present in *Macrocnemus*, *Langobardisaurus*, and *Tanystropheus*. Evans (1988) assigned four characters (50-53) to the clade *Macrocnemus* + *Cosesaurus* + *Tanystropheus* + *Tanytrachelos* (Node E). Three of these characters are reversed in basal adult pterosaurs and *Cosesaurus*, and one is an error. A "thyroid foramen" (52) appears in a clade of Late Jurassic and Early Cretaceous pterosaurs but not in basal forms or in *Cosesaurus*. The pes centrale (53) does not disappear in any prolacertiform or pterosaur (Fig. 13D), only in archosaurs. Evans assigned five characters (54-58) to the clade *Cosesaurus* + *Tanystropheus* + *Tanytrachelos* (Node E). Four are present in pterosaurs and the exception, "fourth metacarpal shorter than third" (55) is only present in Tanystropheidae. In *Cosesaurus* and *Preondactylus* metacarpals III and IV (55) are equal in length. "Reduction in length of foot" (56) is perhaps poorly worded, but a proportional reduction in the length of pedal digit IV is apparent in *Langobardisaurus tonelloi*, *Sharovipteryx*, tanystropheids and pterosaurs. Such a reduction is frequently exhibited within the Amniota (e.g. turtles and dinosaurs) so this character should be considered homoplastic. Evans assigned six characters (59-64) to the clade *Tanystropheus* + *Tanytrachelos* (Node E). "Fused dorsal ribs" (60) are also present in *Langobardisaurus*. The last few dorsal ribs are short and unfused in *Cosesaurus*, but it may be a juvenile. The disappearance of posterior dorsal ribs in pterosaurs is probably a subsequent derivation of the same character state. "The longest cervical is at the end of the series" (61) is absent in this clade (contra Evans 1988). "Postcloacal bones" (62) are also present in *Eudimorphodon* (Wild 1978). Here characters 55, 59, 63 and 64 are considered synapomorphies of the Tanystropheidae.

Analysis based on Jalil (1997)

I duplicated the second stage of Jalil's (1997) analysis (Appendix II, Table 2) in which *Jesairosaurus* and *Langobardisaurus* were added, the poorly known prolacertiforms were deleted, and the interrelationships of the Prolacertiformes became completely resolved. I then included *Preondactylus* + *Eudimorphodon*, *Longisquama*, *Sharovipteryx*, *Scleromochlus* and *Lagosuchus* for a total of 23 terminal taxa. Many of the characters Jalil used were duplicated from Evans (1988). About 11% of the 71 characters were rescored (see Appendix II - Table 2) due to new data on *Langobardisaurus*, *Cosesaurus* and *Boreopricea* (Benton and Allen 1997). Jalil diagnosed the Prolacertiformes using five characters – 1) Skull low and narrow with short and narrow post-orbital region; 2) Low and elongated cervical spine (Benton 1985, Chatterjee 1986, Evans 1988); 3) Long slender cervical ribs (Evans 1988); 4) Lacrimal does not meet the nasal (Evans 1988); and 5) Loss of trunk intercentrum. Pterosaurs exhibit four of these characters. The exception (4) is a reversal also found in *Cosesaurus* and *Longisquama*.

Analysis based on Bennett (1996a)

I duplicated Bennett's (1996a) analysis (Appendix III, Table 3) in which he included Prolacertiformes as a taxon. I substituted *Tanystropheus* to be specific. I also included *Langobardisaurus*, *Cosesaurus*, *Sharovipteryx* and *Longisquama*. A few characters were rescored and five new ones were added (Appendix III). Bennett (1996a) presented

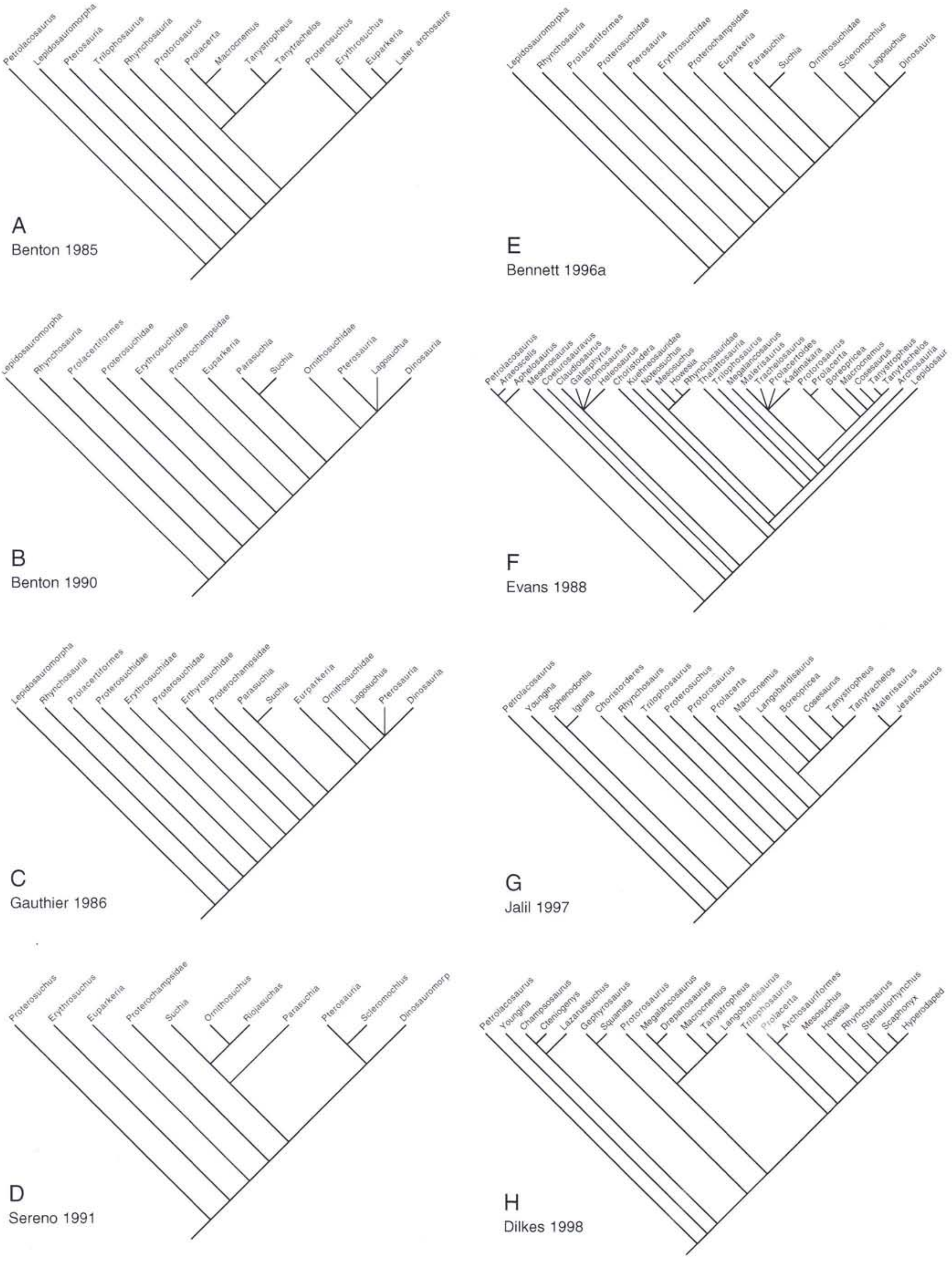


Fig. 11 - Phylogenetic trees illustrating previously proposed relationships of the Pterosauria and/or Prolacertiformes. A. From Benton (1985). B. From Benton (1990). C. From Gauthier (1986). D. From Sereno (1991). E. From Bennett (1996b). F. From Evans (1988). G. From Jalil (1997). H. From Dilkes (1998). See text for details.

			11111	11111	22222	22222	33333	33333	44444	44444	55555	55555	66666	66666	77777
Taxon/Node	1234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234
Lepidosauromorpha	0000	0000?	00000	00000	00000	00000	00000	00000	?0220	000?0	00000	00000	020?0	00000	00000
Rhynchosauria	1101	11010	10111	00001	11011	1?011	01000	2010?	00220	00000	00010	00000	020?0	00000	00000
Tanystropheus	1010	41111	02110	01101	13111	11011	11110	20100	00220	00000	00110	10000	02300	00000	10000
Pterosauria	1010	31211	01111	?1111	13111	11011	11110	?1111	11100	00010	00110	12013	02200	00110	00020
Proterosuchidae	1111	11011	11111	11111	11111	1?011	00110	10001	11001	10010	10000	00000	02000	?0010	00100
Erythrosuchidae	1111	11011	??211	?1111	11111	1??11	01110	1111?	11011	10?11	10011	00000	02100	?1110	10?10
Proterochampsida	1111	1101?	11211	11111	12111	1??11	11120	11111	?1011	10011	11010	1000?	10101	01111	11?10
Euparkeria	1111	21011	11211	11111	12111	11111	11110	11011	01011	11011	11110	00111	20101	01111	11110
Parasuchia	1011	11010	12211	11111	12111	11111	10211	11111	11011	11111	11111	10111	20101	10111	11110
Suchia	1111	11010	12211	11111	12111	11111	10211	21111	11011	11111	11111	10111	20101	10111	11111
Ornithosuchidae	1111	21011	12211	11111	12111	11112	11111	21111	11011	11111	11111	11111	20111	11111	12212
Lagosuchus	1111	21011	12211	11111	12111	11112	111?1	??111	11011	11011	10111	10?12	02211	01111	12212
Dinosauria	1111	21011	12211	11111	12111	11112	11121	21111	11011	11011	10111	10112	02211	01111	12212
Scleromochlus	111?	?1?11	12211	?11??	?2?11	?1111	101??	?????	?1011	1?011	?0?11	12???	022?1	00111	12?12
Cosesaurus	10?0	41211	?1111	?1111	13111	11011	1110?	???0?	12100	00010	0011?	12013	02??0	00210	00020
Sharovipteryx	1010	??211	0111?	?11??	131??	???11	1???0	???00	?2100	?0??0	001??	1201?	022?0	00110	0002?
Longisquama	?010	41211	???11	?11??	1??11	11???	?110?	???1?	?2100	00?10	00???	1???3	02200	00210	?00??
Langobardisaurus	1001	???11	???1?	?111?	13111	11011	11???	???0?	?0220	00000	0011?	10010	02??0	00210	00000

						11111	11111	11111	11111	11111	11111	1
	77777	88888	88888	99999	99999	00000	00000	11111	11111	22222	22222	3
Taxon/Node	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	0
Lepidosauromorpha	020-0	?0000	?00??	00??0	00000	000?0	00020	00000	000??	10-00	?0000	0
Rhynchosauria	020-0	?0000	?00??	00?00	00000	000?0	00020	00000	000??	00-00	?1000	0
Tanystropheus	020-0	00000	000??	00?00	00020	20000	00020	00000	00011	10-01	22021	0
Pterosauria	020-2	00000	0?0??	1???0	11120	22022	20000	00112	11011	10-01	02121	1
Proterosuchidae	000-0	?0000	?00??	00?00	00100	100?0	000?0	00000	0?000	00-00	01000	0
Erythrosuchidae	000-0	?1000	?00??	00?01	10100	100?0	000?0	00000	0?000	00-00	01000	0
Proterochampsida	000-1	01000	01100	00001	11100	100?0	00000	00000	0?000	00-00	01000	0
Euparkeria	100-1	01000	00100	10001	11100	10001	00031	00000	00010	00-00	01000	0
Parasuchia	120-1	01011	11121	11111	11100	10001	10020	00000	00000	00-00	01000	0
Suchia	121-1	01011	11121	11111	11110	10000	20000	01000	00000	00-00	01000	0
Ornithosuchidae	121-2	12111	1111?	11111	11110	10000	10031	00000	00010	00-00	01000	0
Lagosuchus	120-2	12100	010??	101?1	11111	111?1	11111	11111	11111	11-11	11010	0
Dinosauria	110-2	12100	010??	101?1	11111	21111	11111	11111	11111	11-11	11010	0
Scleromochlus	11?-2	?0100	0?0??	?????	1111?	000??	11131	?0011	1??1?	11-01	11010	0
Cosesaurus	020-0	00000	000??	10??0	00120	220?2	?0020	00101	00011	10-01	2212?	1
Sharovipteryx	000-0	00000	??0??	1????	1102?	2?02?	?0100	00112	??011	?0-00	02121	1
Longisquama	???-?	?????	?????	?????	?????	?0??2	20?20	?????	?????	??-??	?????	?
Langobardisaurus	020-0	00000	000??	10??0	00020	220?0	00020	00101	00011	10-01	0202?	0

Tab. 3 - Reanalysis of Bennett 1996a.

cladistic analyses of the Archosauromorpha in order to test competing theories of pterosaur relationships established previously (Benton 1982, 1984, 1985, 1990; Padian 1984; Gauthier 1984, 1986; Sereno 1991). He divided his analysis into five parts: Characters supporting: 1) the Lepidosauromorpha; 2) the Archosauromorpha; 3) the Archosauriformes; 4) the Ornithodira, *sensu* Gauthier (1986); and 5) unused characters. Bennett observed that pterosaurs do not exhibit any lepidosauromorph synapomorphies, as noted earlier. He also challenged most of the inconsistencies and errors made by earlier workers. With additional data supplied by key prolacertiform taxa, plus some rescoring, a reanalysis of Bennett (1996a) casted doubts on many of his proposed synapomorphies.

The vast majority of characters supporting Archosauromorpha (see Appendix III) are present in pterosaurs. The exceptions include the following. A prominent subnarial premaxilla process (2) is not present in *Cosesaurus* (Fig. 3) and pterosaurs, a reversal from the primitive state; the pedal centrale (27) is not laterally displaced or fused to the astragalus but persists in pterosaurs (Fig. 13D) and this appears to be an error in identification; the ectopterygoid (10) appears to be fused to the pterygoid in *Cosesaurus* and pterosaurs and this too, is a previous error in identification (details follow); the transverse processes of the trunk vertebrae (21) are extended in pterosaurs, but the middle and posterior ribs are not two-headed, as in archosauriforms.

Nearly half of the characters supporting the Archosauriformes (34, 43-47, 49-51, 54-57, 60-62, 64-66, 69, 70, 72, 74, 75, 77, 80-83, 88, 89, 92-94, 97, 98) are absent in pterosaurs; 23 others (31-33, 35-42, 48, 53, 58, 67, 68, 76, 78, 84, 87, 90, 95, 96) are also present in the outgroup, the Prolacertiformes; four other characters are treated as major

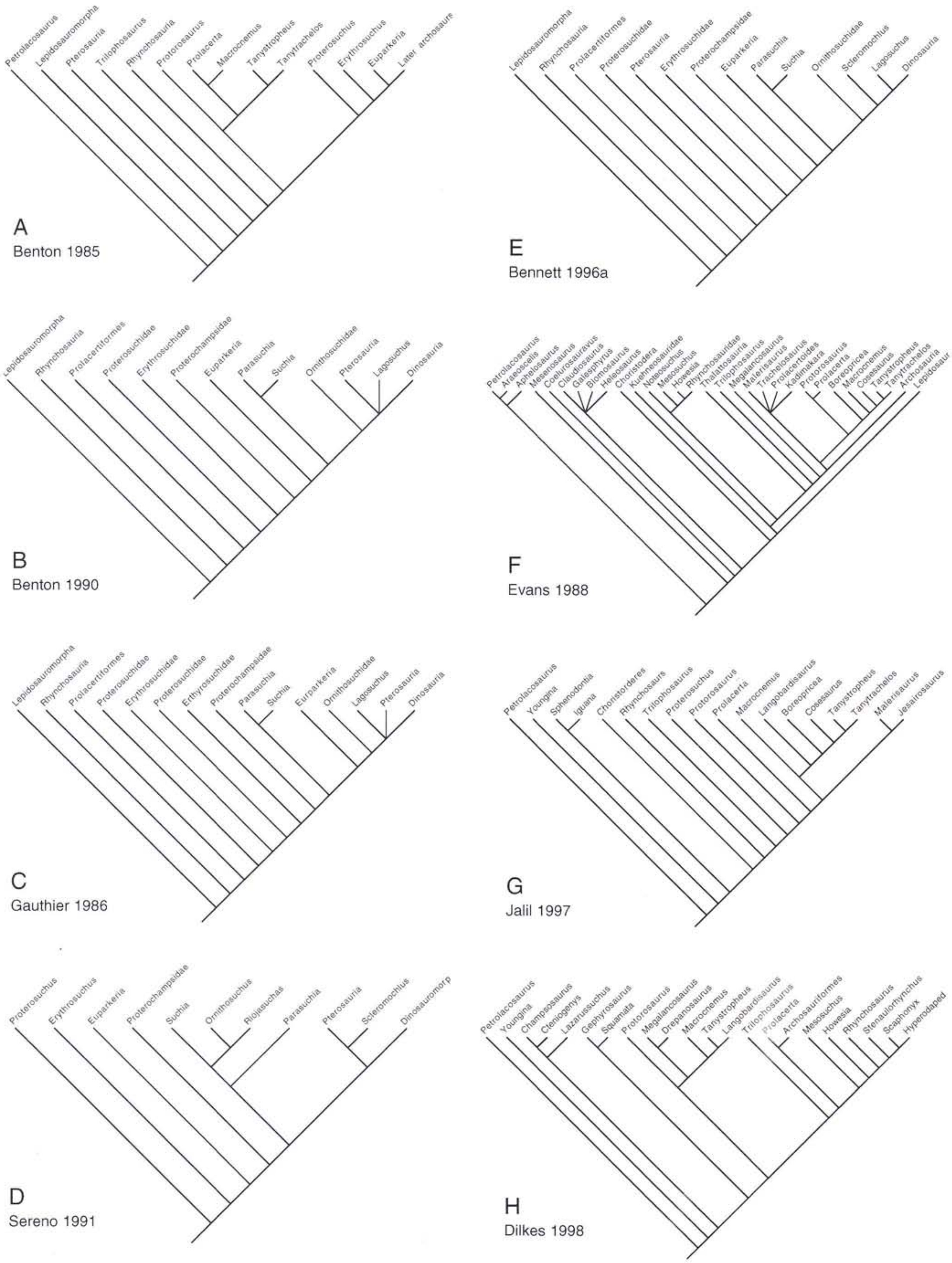


Fig. 11 - Phylogenetic trees illustrating previously proposed relationships of the Pterosauria and/or Prolacertiformes. A. From Benton (1985). B. From Benton (1990). C. From Gauthier (1986). D. From Sereno (1991). E. From Bennett (1996b). F. From Evans (1988). G. From Jalil (1997). H. From Dilkes (1998). See text for details.

Taxon/Node	1234	56789	11111 01234	11111 56789	22222 01234	22222 56789	33333 01234	33333 56789	44444 01234	44444 56789	55555 01234	55555 56789	66666 01234	66666 56789	77777 01234
Lepidosauromorpha	0000	0000?	00000	00000	00000	00000	00000	00000	?0220	000?0	00000	00000	020?0	00000	00000
Rhynchosauria	1101	11010	10111	00001	11011	1?011	01000	2010?	00220	00000	00010	00000	020?0	00000	00000
Tanystropheus	1010	41111	02110	01101	13111	11011	11110	20100	00220	00000	00110	10000	02300	00000	10000
Pterosauria	1010	31211	01111	?1111	13111	11011	11110	?1111	11100	00010	00110	12013	02200	00110	00020
Proterosuchidae	1111	11011	11111	11111	11111	1?011	00110	10001	11001	10010	10000	00000	02000	?0010	00100
Erythrosuchidae	1111	11011	??211	?1111	11111	1??11	01110	1111?	11011	10?11	10011	00000	02100	?1110	10?10
Proterochampsida	1111	1101?	11211	11111	12111	1??11	11120	11111	?1011	10011	11010	1000?	10101	01111	11?10
Euparkeria	1111	21011	11211	11111	12111	11111	11110	11011	01011	11011	11110	00111	20101	01111	11110
Parasuchia	1011	11010	12211	11111	12111	11111	10211	11111	11011	11111	11111	10111	20101	10111	11110
Suchia	1111	11010	12211	11111	12111	11111	10211	21111	11011	11111	11111	10111	20101	10111	11111
Ornithosuchidae	1111	21011	12211	11111	12111	11112	11111	21111	11011	11111	11111	11111	20111	11111	12212
Lagosuchus	1111	21011	12211	11111	12111	11112	111?1	??111	11011	11011	10111	10?12	02211	01111	12212
Dinosauria	1111	21011	12211	11111	12111	11112	11121	21111	11011	11011	10111	10112	02211	01111	12212
Scleromochlus	111?	?1?11	12211	?11??	?2?11	?1111	101??	?????	?1011	1?011	?0?11	12???	022?1	00111	12?12
Cosesaurus	10?0	41211	?1111	?1111	13111	11011	1110?	???0?	12100	00010	0011?	12013	02??0	00210	00020
Sharovipteryx	1010	??211	0111?	?11??	131??	???11	1???0	???00	?2100	?0??0	001??	1201?	022?0	00110	0002?
Longisquama	?010	41211	???11	?11??	1??11	11???	?110?	???1?	?2100	00?10	00???	1???3	02200	00210	?00??
Langobardisaurus	1001	???11	???1?	?111?	13111	11011	11???	???0?	?0220	00000	0011?	10010	02??0	00210	00000

Taxon/Node	77777 56789	88888 01234	88888 56789	99999 01234	99999 56789	11111 00000 01234	11111 00000 56789	11111 11111 01234	11111 11111 56789	11111 22222 01234	11111 22222 56789	1 3 0
Lepidosauromorpha	020-0	?0000	?00??	00??0	00000	000?0	00020	00000	000??	10-00	?0000	0
Rhynchosauria	020-0	?0000	?00??	00?00	00000	000?0	00020	00000	000??	00-00	?1000	0
Tanystropheus	020-0	00000	000??	00?00	00020	20000	00020	00000	00011	10-01	22021	0
Pterosauria	020-2	00000	0?0??	1???0	11120	22022	20000	00112	11011	10-01	02121	1
Proterosuchidae	000-0	?0000	?00??	00?00	00100	100?0	000?0	00000	0?000	00-00	01000	0
Erythrosuchidae	000-0	?1000	?00??	00?01	10100	100?0	000?0	00000	0?000	00-00	01000	0
Proterochampsida	000-1	01000	01100	00001	11100	100?0	00000	00000	0?000	00-00	01000	0
Euparkeria	100-1	01000	00100	10001	11100	10001	00031	00000	00010	00-00	01000	0
Parasuchia	120-1	01011	11121	11111	11100	10001	10020	00000	00000	00-00	01000	0
Suchia	121-1	01011	11121	11111	11110	10000	20000	01000	00000	00-00	01000	0
Ornithosuchidae	121-2	12111	1111?	11111	11110	10000	10031	00000	00010	00-00	01000	0
Lagosuchus	120-2	12100	010??	101?1	11111	111?1	11111	11111	11111	11-11	11010	0
Dinosauria	110-2	12100	010??	101?1	11111	21111	11111	11111	11111	11-11	11010	0
Scleromochlus	11?-2	?0100	0?0??	?????	1111?	000??	11131	?0011	1??1?	11-01	11010	0
Cosesaurus	020-0	00000	000??	10??0	00120	220?2	?0020	00101	00011	10-01	2212?	1
Sharovipteryx	000-0	00000	??0??	1????	1102?	2?02?	?0100	00112	??011	?0-00	02121	1
Longisquama	???-?	?????	?????	?????	?????	?0??2	20?20	?????	?????	??-??	?????	?
Langobardisaurus	020-0	00000	000??	10??0	00020	220?0	00020	00101	00011	10-01	0202?	0

Tab. 3 - Reanalysis of Bennett 1996a.

cladistic analyses of the Archosauromorpha in order to test competing theories of pterosaur relationships established previously (Benton 1982, 1984, 1985, 1990; Padian 1984; Gauthier 1984, 1986; Sereno 1991). He divided his analysis into five parts: Characters supporting: 1) the Lepidosauromorpha; 2) the Archosauromorpha; 3) the Archosauriformes; 4) the Ornithodira, *sensu* Gauthier (1986); and 5) unused characters. Bennett observed that pterosaurs do not exhibit any lepidosauromorph synapomorphies, as noted earlier. He also challenged most of the inconsistencies and errors made by earlier workers. With additional data supplied by key prolacertiform taxa, plus some rescoring, a reanalysis of Bennett (1996a) casted doubts on many of his proposed synapomorphies.

The vast majority of characters supporting Archosauromorpha (see Appendix III) are present in pterosaurs. The exceptions include the following. A prominent subnarial premaxilla process (2) is not present in *Cosesaurus* (Fig. 3) and pterosaurs, a reversal from the primitive state; the pedal centrale (27) is not laterally displaced or fused to the astragalus but persists in pterosaurs (Fig. 13D) and this appears to be an error in identification; the ectopterygoid (10) appears to be fused to the pterygoid in *Cosesaurus* and pterosaurs and this too, is a previous error in identification (details follow); the transverse processes of the trunk vertebrae (21) are extended in pterosaurs, but the middle and posterior ribs are not two-headed, as in archosauriforms.

Nearly half of the characters supporting the Archosauriformes (34, 43-47, 49-51, 54-57, 60-62, 64-66, 69, 70, 72, 74, 75, 77, 80-83, 88, 89, 92-94, 97, 98) are absent in pterosaurs; 23 others (31-33, 35-42, 48, 53, 58, 67, 68, 76, 78, 84, 87, 90, 95, 96) are also present in the outgroup, the Prolacertiformes; four other characters are treated as major

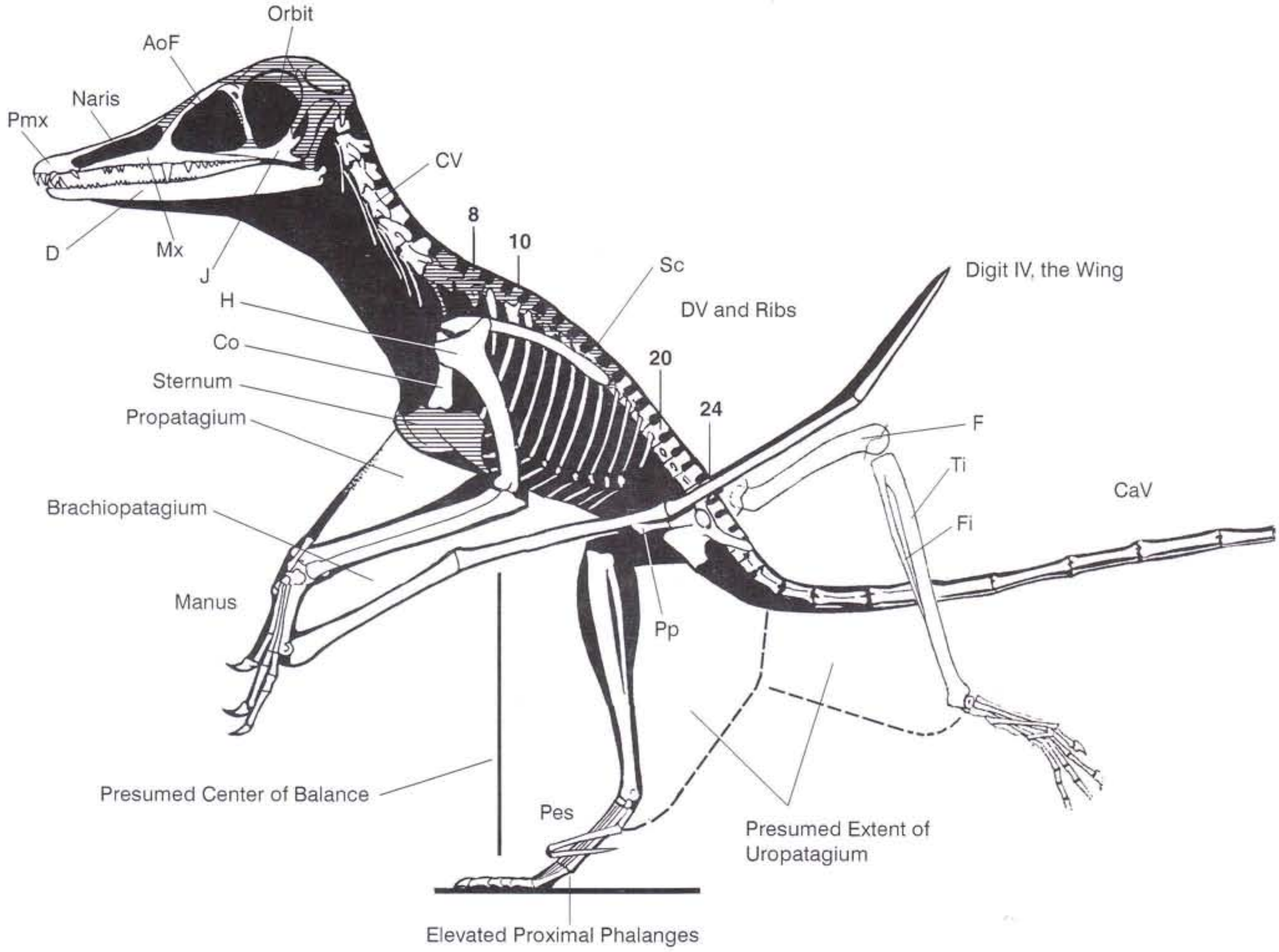


Fig. 12 - *Preondactylus buffarinii* (Wild 1984b), a basal pterosaur, reconstructed in lateral view. Restored areas are hatched. Vertical line is the hypothetical center of balance. Left femur removed to show prepubis. Full extent of tail is unknown. Sternum is unknown and reconstructed here similar to that of *Cosesaurus* (Fig. 3) and the most primitive pterosaurs that preserve sterna, *Batrachognathus volans* (Rjabinin 1948) and *Nesodactylus hesperius* (Colbert 1969). Left pedal digit V is shown retracted (fully flexed). Note proximal pedal phalanges of left pes are more or less aligned with the metatarsals, in agreement with Clark, et al. (1998) and yet contra Clark, et al., this is a digitigrade configuration. Right pes traced from the in situ specimen. Presumed extent of uropatagium is shown by dashed line. Abbreviations as in figure 3.

transformations or new character states (59, 63, 71, 73, 86); and three are difficult to determine (52, 85, 91). Only one character (79 - femoral curvature) is shared by pterosaurs and Archosauriformes to the exclusion of any known prolacertiformes. Semierect posture (78) is a functional consideration not considered in the present matrix.

Bennett (1996a) reports the following 8 characters cannot be scored due to transformation or other factors. Many are related to flight (pectoral characters) or bipedalism (tarsal characters). "Coracoid (= biceps) tubercle lies close to glenoid fossa and coracoid foramen" (63) - this is a flight muscle anchor according to Bennett (1996a) and is difficult to observe in *Longisquama*. The coracoid foramen is lost in *Cosesaurus*, *Longisquama* and pterosaurs, but not in dinosauromorphs; "Manus length less than half that of tarsus and pes" (70) - discounting the length of digit IV, the manus of *Preondactylus* (Fig. 12) is proportional to that of *Cosesaurus* (Fig. 3) and *Longisquama* (Fig. 7). In addition, the manus of *Cosesaurus* and *Sharovipteryx* is more than half that of its tarsus and pes (unknown in *Longisquama*). In characters 86, 91 and 92 the fibula does not reach the tarsus in pterosaurs so the character states cannot be determined. Character 88 pertains only to crocodyloid tarsi. In character 89 pterosaurs do not exhibit separate dorsal and ventral astragalocacaneal facets. No calcaneal tubercle (93) has been observed in pterosaurs (Bennett 1996a) or derived prolacertiforms.

In Triassic pterosaurs the laterosphenoid (40) has not been noted, but *Cosesaurus* (Fig. 4) apparently has a completely ossified interorbital septum with divisions that appear to be homologous to the laterosphenoid and pseudomesethmoid noted by Kellner (1996).

The following 3 character states offered by Bennett (1996a) may be modified: (59) - the interclavicle of *Cosesaurus* and *Longisquama* has an anterior keel or process, as in pterosaurs, meriting a third derived state: "interclavicle with anterior process or keel"; (73) - in pterosaurs and some prolacertiforms a long, narrow, knife-like iliac spine is present, unlike the short, broad, ax-like process in archosauriformes; (97) - the vestigial digit V in archosauriformes should not be homologized with the same robust elongate digit in certain prolacertiforms and basal pterosaurs.

Among the 30 characters Bennett (1996a) cites in support of the Ornithodira, 14 are absent in pterosaurs (99, 101, 102, 104, 106, 108-111, 116, 117, 121, 123, 125), 9 others are present in prolacertiforms (100, 112-114, 118-120, 122, 124), and 7 others I dispute (103, 105, 107, 115, 122, 124, 126).

I disagree that the following three characters cannot be scored due to transformation (Bennett 1996a). In this study they appear to be

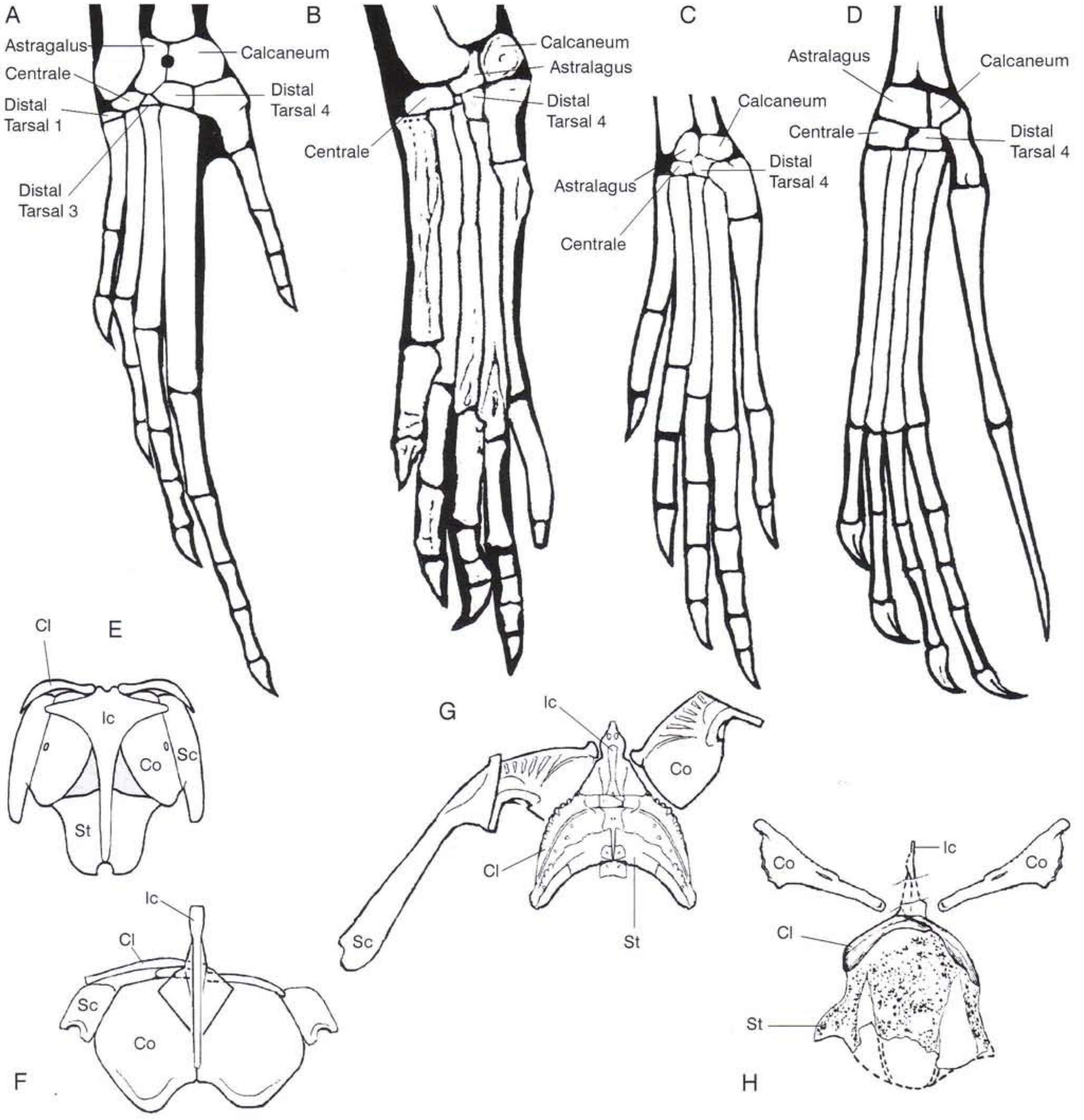


Fig. 13 - A-D. Reconstructions of pedes from three terrestrial prolacertiforms and one pterosaur demonstrating the persistence of the centrale, the diminution of the calcaneum and the disappearance of distal tarsals 1 and 3. Note the trend toward elongation of the phalanges in digit V and the reduction of metatarsal asymmetry. A. *Macrocnemus* (Peyer 1937, Rieppel 1989). B. *Langobardisaurus pandolfii* (Renesto 1994). C. *Cosesaurus* (Ellenberger and de Villalta 1978). D. *Peteinosaurus* (Wild 1978).

E-H. Reconstructions of pectoral girdles from three terrestrial prolacertiforms and one pterosaur demonstrating the radical reorganization of the elements. E. *Macrocnemus* (Peyer 1937, Rieppel 1989) in ventral view. This configuration is essentially primitive for amniotes with the exception of a short scapula, a synapomorphy of the Tapinoplatia (see text). The sternum is notched. F. *Cosesaurus* (Ellenberger and de Villalta 1978) in ventral view. The sternum is absent but would likely fill the posterior embayement of the coracoids. The coracoids are large and meet medially posteriorly. The clavicles are essentially straight and overlap medially. The interclavicle has a reduced stem and an anterior process expanded into a narrow ventral keel (Fig. 3), viewed here on edge. The scapulae are short and posteriorly notched, as in *Macrocnemus*. G. *Longisquama* (Sharov 1970), the sternal complex in ventral view, the coracoids in lateral view with right scapula omitted. The clavicles are robust, U-shaped, posteriorly oriented and their articulation to the anterior process of the interclavicle appears immobile. The sternum forms the embayed posterior edge of the sternal complex, filling the bowl and fusing to the clavicles, displacing the coracoids anteriorly. The interclavicle stem is much reduced. The anterior process is expanded to form a large spine. The coracoids are tall with knob-like ventral articulations. Positioning of the coracoids relative to the sternal complex is conjectural, but here follows the pattern in pterosaurs. H. The pterosaur, *Eudimorphodon* (Wild 1993), in dorsal view with elongate scapulae omitted. The clavicles are robust, overlap medially and are fused to the sternum and interclavicle. The sternum is expanded to fill the "bowl" of the clavicles and has pointed lateral processes. The interclavicle forms an anterior spine with a small keel. The coracoids articulate with the interclavicle anterior to the clavicles and reduce to struts ventrally.

imminently present in prolacertiforms close to pterosaurs. "Caudal zygapophyseal facets nearly vertically disposed in all but proximal part of the tail" (103) - in pterosaurs the zygapophyses are hyper-extended and intertwine. In *Sharovipteryx* the facets are not visible, but unossified, intertwined, elongate impressions following the pterosaur pattern are visible, so a third character state is warranted. "Coracoid small, with subcircular profile, and lying in nearly same plane as the scapula" (105) - in *Cosesaurus* and *Longisquama* (unknown in *Sharovipteryx*) the coracoid is large and does not lie in the same plane as the scapula. Fore limb length less than half that of hind limb" (107) - Bennett finds that the "great length and profound modifications of the fore limb are clearly adaptations to flight," however, the fore limb length of *Cosesaurus* is also greater than half the hind limb and the morphological pattern of the fore limb in *Sharovipteryx*, albeit reduced as if vestigial, is otherwise morphologically similar to that in basal pterosaurs.

The following four characters I dispute. "Advanced mesotarsal ankle" (115) - is convergent because a centrale is present in pterosaurs but not in dinosaurs and their sister taxa. "Pedal stance digitigrade" (122) - is a functional consideration that will not be addressed here (but see Peters 2000). "Metatarsus configuration compact" (124) - as in *Langobardisaurus* and *Cosesaurus* (Fig. 13) - the metatarsus remains compact in basal pterosaurs but spreads in *Sharovipteryx* and certain derived pterosaurs. "Pedal digit V reduced, does not exceed length of metatarsal IV and composed of no more than two phalanges" (126) - I disagree with Bennett's scoring of this character as reduced because digit V has no more than two phalanges. Pedal digit V is not reduced in basal pterosaurs but enlarged. Bennett also suggested that digit V is transformed in pterosaurs because it controlled a flight membrane (Unwin and Bakhurina 1994), but four terrestrial prolacertiforms share a homologous metapodial phalanx.

One character used in earlier analyses but not used by Bennett (1996a) deserves comment. Padian (1984) used "large head" and Sereno (1991) used "skull length more than 50 percent presacral column length." Both were attempts to support *Scleromochlus* + Pterosauria. Pterosaurs do have a larger head than do other prolacertiforms, except *Longisquama* (Fig. 7). However, an equally appropriate character would be "short torso." From *Cosesaurus* to *Preondactylus* a trend toward a shorter torso suggests reduced lateral undulation during the step-cycle, an important locomotory (Snyder 1954) and respiratory adaptation (Carrier 1987).

The following characters were not used by Bennett (1996a) or previous workers and have not been included in the present analyses. Nevertheless, they are probably important enough to place into future analyses. (1) Bird-like skull (nares displaced posteriorly, rostrum low and elongate, orbits large, cranium high, antorbital fenestra present; (2) Premaxilla extended to 20% of skull length; (3) Maxilla sends process medially dividing internal naris; (4) Dorsal vertebrae shorter than skull plus cervical vertebrae; (5) Hemal arches reduced cranially and elongate caudally, parallel to centra and contributing to caudal stiffening; (6) Reduced caudal transverse processes; (7) Single ossified sternal complex (conjoined overlapping posteriorly-oriented clavicles, keeled interclavicle with anterior process, enlarged sternum in contact with clavicles); (8) Manual digit IV greater than three times length of metacarpal IV; (9) Coracoid tall with sternal complex articulation; (10) Scapula elongate and posteriorly oriented; (11) Knife-like preacetabular process on ilium; (12) Fibula width less than .70 tibia width with little to no spatium interosseum; (13) Uropatagia extending from proximal caudals to pedal digit V.

Comments Regarding Benton (1999).

Benton (1999) proposed the clade "Avesuchia" for crown group archosaurs (including *Euparkeria* and the Pterosauria). The clade has three postulated synapomorphies [* = not present in basal Pterosauria. † = also present in certain prolacertiformes.]: (1) absence of palatal teeth*; (2) calcaneal tuber orientated more than 45° posterolaterally* and (3) continuous articular surfaces for fibula and distal tarsal IV on the calcaneum*. Benton also proposed the clade "Avemetatarsalia" for *Scleromochlus* + Ornithodira (including the Pterosauria). This clade has seven postulated synapomorphies: (1) fore limb/hind limb ratio less than .55†; (2) pubis longer than ischium*; (3) tibia-femur ratio more than 1.0†; (4) distal tarsal IV subequal in transverse width to distal tarsal III*; (5) compact metatarsus with metatarsals I-IV tightly appressed†; (6) metatarsals II-IV more than 50% tibial length*; (7) absence of body osteoderms†. Benton proposed five synapomorphies uniting the Ornithodira (including the Pterosauria): (1) presacral centrum #8 longer than presacral centrum #18†; (2) deltopectoral crest on humerus subrectangular*; (3) fibula tapering and calcaneum reduced in size†; (4) astragalar posterior groove present*; (5) calcaneal tuber rudimentary or absent†. In consideration of these characters, there is no reason to include pterosaurs with crown group archosaurs (including *Euparkeria*).

Phylogenetic results.

Robustness Tests

In the first analysis of Evans (1988), not including *Longisquama*, the data generated 557 trees of 244 steps with a consistency index (CI) of .434, a homoplasy index (HI) of .595 and a retention index (RI) of .694. A strict consensus of the 557 trees resulted in a large polytomy of all but the 4 most primitive taxa with *Langobardisaurus*, *Sharovipteryx*, *Eudimorphodon* and *Preondactylus* forming a stepped clade within the polytomy. A number of poorly known taxa contributed to the confusion of the polytomy.

The second analysis of Evans (1988, see Table 1) using fewer (22) but better known taxa, including *Longisquama*, generated 6 trees of 186 steps with a CI of .49, an HI of .51 and an RI of .69. The program excluded 32 characters. The strict consensus tree (Fig. 15) generated a polytomy of *Cosesaurus*, *Longisquama*, *Sharovipteryx* and the *Pterosauria* nested within the Prolacertiformes. Otherwise a stepped branch consisting of *Proterosuchus*, *Scleromochlus* and *Lagosuchus* formed a polytomy with the higher prolacertiformes and a clade consisting of *Protorosaurus* and *Prolacerta*.

In the new analysis of Jalil (1997) the data matrix of 23 taxa and 71 characters generated 120 trees with a shortest tree length of 151 steps, a CI of .51, an HI of .49, and an RI of .73. A strict consensus cladogram (Fig. 15) produced polytomies of the primitive diapsids; the primitive lepidosauromorphs; the primitive archosauromorphs together with the archosauriformes; and a stepped cladogram of the higher prolacertiforms which grouped *Macrocnemus*, *Langobardisaurus* and the Tanystropheidae separate from *Jesairosaurus* and a polytomy of *Cosesaurus*, *Sharovipteryx*, *Longisquama* and the Pterosauria.

In the new analysis of Bennett (1996a) a data matrix of 18 taxa and 130 characters generated a single minimum-length fully resolved tree of 268 steps, with a CI of .65 and HI of .35 and an RI of .79. 11 characters were parsimony-uninformative. In contrast to Bennett's

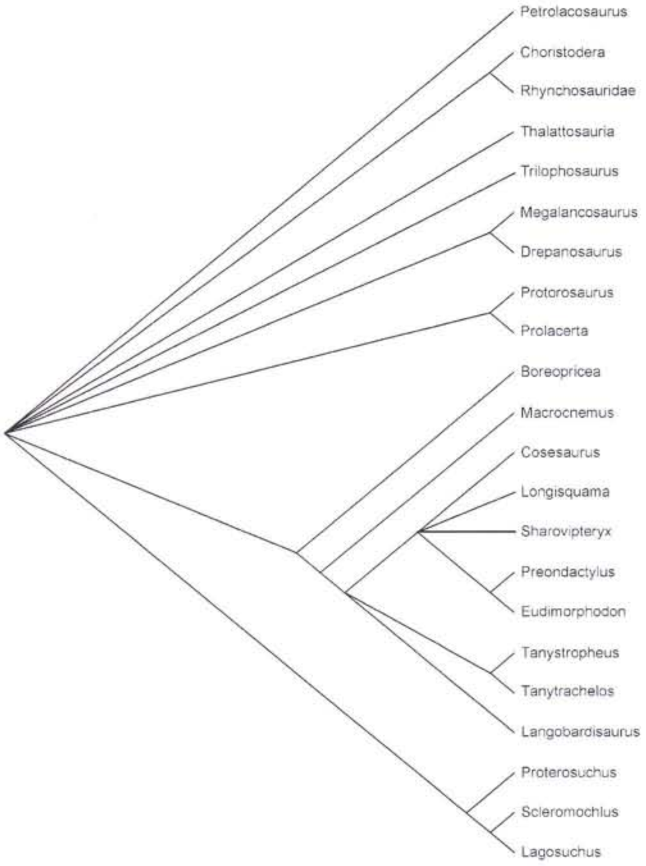


Fig. 14 - New phylogenetic tree based on reinterpretation of Evans (1988) including the taxa *Langobardisaurus*, *Cosesaurus*, *Sharovipteryx*, *Longisquama*, Preondactylus and Eudimorphodon. The Pterosauria (= *Preondactylus* + *Eudimorphodon*) is nested within the Prolacertiformes with Cosesaurus, Sharovipteryx and *Longisquama* as the closest sister-taxa.

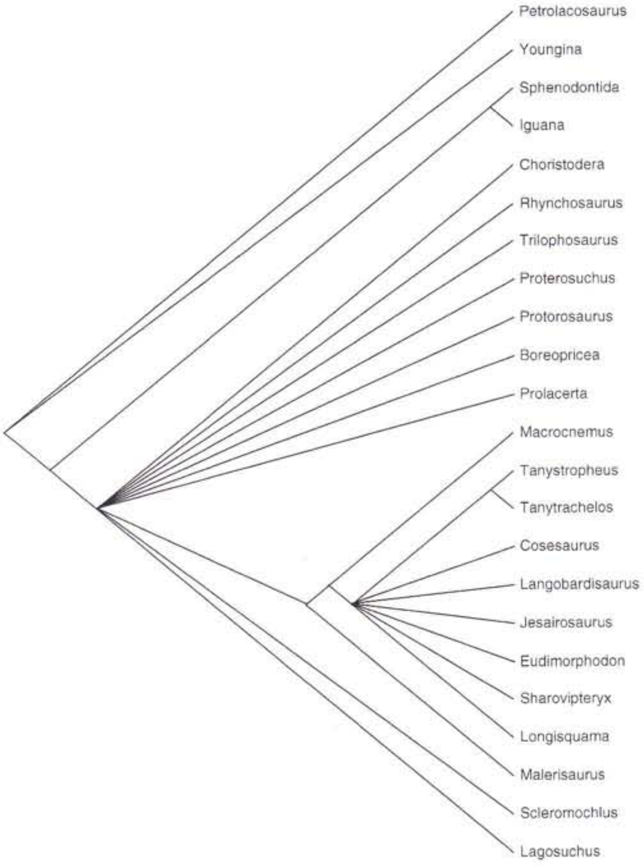


Fig. 15 - New phylogenetic tree based on reinterpretation of Jalil (1997). *Preondactylus* + *Eudimorphodon* is nested within the Prolacertiformes within an unresolved clade including *Cosesaurus*, *Sharovipteryx* and *Longisquama*.

study, pterosaurs were found to be nested within the Prolacertiformes with *Sharovipteryx*, *Longisquama*, *Cosesaurus*, *Langobardisaurus* and *Tanystropheus* as successively more distant sister-taxa (see Appendix - Table 3). Adding 5 steps generated 37 trees. A strict consensus tree produced an unresolved polytomy of *Cosesaurus*, *Sharovipteryx*, *Longisquama* and the Pterosauria within a stepped cladogram of prolacertiforms. By adding 5 more steps 320 trees were generated and a strict consensus analysis produced a stepped cladogram of the Archosauriformes and a polytomy of all other taxa. Deleting *Cosesaurus*, *Longisquama* and *Sharovipteryx* from the original analysis resulted in a single minimum-length tree of 260 steps with *Langobardisaurus* as the closest sister-taxon. Deletion of *Langobardisaurus* and *Tanystropheus* resulted in a minimum-length tree of 240 steps with the Pterosauria as the sister group to the Archosauriformes. This final result nearly duplicates Bennett (1996a), affirming his work and demonstrating the importance of using higher prolacertiforms in pterosaur phylogenetic analyses.

Diagnosis of the Pterosauria.

Romer (1956) and Wellnhofer (1978) presented diagnoses of the Pterosauria, but these were precladistic and included many plesiomorphic characters. The most recently published diagnoses (Sereno 1991, Bennett 1996a, Kellner 1996) also include many plesiomorphic characters but make good platforms from which to proceed with the present diagnosis.

The Ornithodira - Sereno (1991)

According to Sereno, the monophyly of the Ornithodira (including the Pterosauria) is supported by the following ten synapomorphies (22-32), most of which were disputed by Bennett (1996a). Here nine have problems. "Absence of dorsal body osteoderms" (22) - plesiomorphic for amniotes; "Absence of interclavicle" (23) and "Clavicle rudimentary or absent" (24) - both incorporated into the pterosaur sternal complex (Wild 1993); "Femoral shaft bowed anteriorly along over 80% of the shaft" (26) - probably convergent due

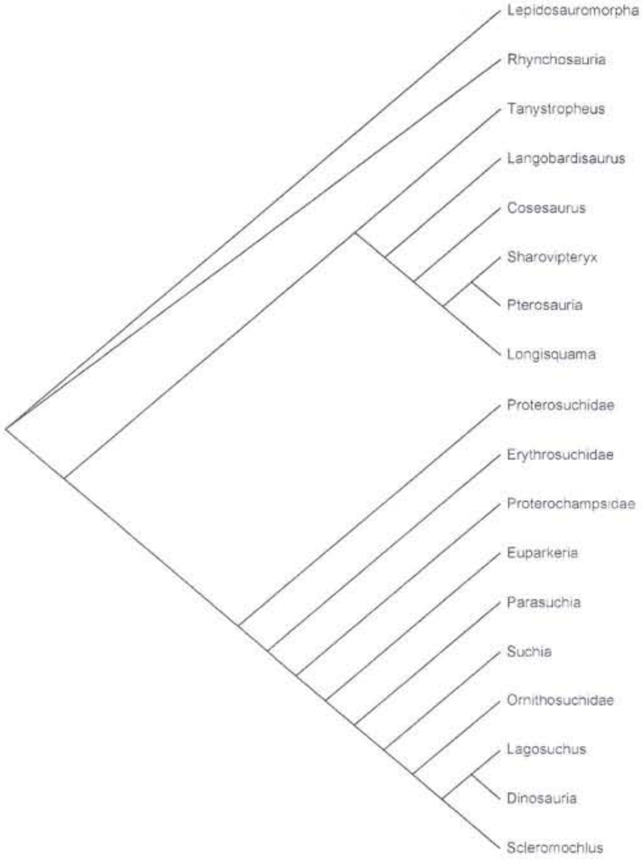


Fig. 16 - New phylogenetic tree based on a reinterpretation of Bennett (1996a). The Pterosauria (= *Preondactylus* + *Eudimorphodon*) is nested within the Prolacertiformes with *Sharovipteryx*, *Longisquama* and *Cosesaurus* as successively more distant sister taxa.

to bipedalism (Bennett 1996a); "Tibia subequal or longer than femur" (27) - as in *Sharovipteryx*; "Astragalar posterior groove absent" (28) and "Calcaneal tuber rudimentary or absent" (29) - both as in prolacertiforms; "Distal (lateral) tarsal 4 transverse width subequal to distal (medial) tarsal 3" (30) - the medial distal tarsal is the centrale and distal tarsal 3 is a tiny ossification proximal to metatarsal III primarily found in immature individuals; "Metatarsal 1-4 shaft configuration compact" (31) - as in *Langobardisaurus*; "Metatarsals 2-4 length more than 50% tibial length" (32) - as in *Cosesaurus*, but not present in most pterosaurs, except *Rhamphorhynchus*.

Scleromochlus + Pterosauria – Sereno (1991)

According to Sereno, the monophyly of *Scleromochlus* + Pterosauria is supported by the following four synapomorphies (33-36): "Skull length more than 50 percent presacral column length" (33) - despite the presence of a large skull, the proportions of the skull, neck and torso of pterosaurs and *Scleromochlus* are not similar; "Scapula length less than 75 percent of that of humerus" (34) - plesiomorphic in amniotes and in Triassic pterosaurs the scapula length can be 88 percent of the humerus (Wild 1978, 1984b, 1993); "Fourth trochanter absent" (35) - plesiomorphic for the Archosauromorpha; "Metatarsal I length 85 percent or more of metatarsal III" (36) - as in *Sharovipteryx*.

The Pterosauria – Sereno (1991)

Sereno (1991 appendix) lists two proposed synapomorphies of the Pterosauria with equivocal distribution. "Cervical 3-5 centrum length longer than mid-dorsal" (21) - plesiomorphic for the Archosauromorpha; "Deltopectoral crest subrectangular" (25) - *Preondactylus* has a crescentic crest (Bennett 1996a). Sereno (1991 text) lists 40 proposed synapomorphies of the Pterosauria. There are problems with at least 26 of these. Proposed skull synapomorphies include: "Proportionately large skull (at least half of presacral vertebral column length)" (1) - probably present in *Longisquama* (as reconstructed here and if it has only 24 presacral vertebrae as in other prolacertiforms); "Piscivorous snout" (2) - not present in Triassic pterosaurs (Bennett 1996a); "External naris displaced posterior to the premaxillary tooth row" (3) - as in *Cosesaurus* and other tanystropheids; "Elongate premaxillary posterodorsal process that extends posterior to the naris and contacts the frontal" (4) - not present in Triassic pterosaurs (Bennett 1996a); "Maxilla that forms approximately one-third of the border of the external naris" (5) - also in *Macrocnemus* and *Cosesaurus*; "Maxilla that lacks an antorbital fossa" (6) - plesiomorphic in archosauromorphs when an antorbital fenestra is not present (Bennett 1996a), otherwise as in *Longisquama* and *Cosesaurus*; "Quadratojugal-squamosal contact absent (7) - as in most prolacertiforms; "Absence of an otic notch" (8) - plesiomorphic in archosauromorphs (Bennett 1996a); "Internal naris displaced posteriorly relative to the palate bones" (9) - unknown in Triassic pterosaurs, otherwise as in *Sharovipteryx*; "Premaxilla-palatine contact that excludes the maxilla from the border of the internal naris" (10) - contra Wellnhofer (1974, 1975a) and Bennett (1991), a medial maxilla (not palatine) shelf borders the internal naris laterally and a medial process of the maxilla divides it in two; "Absence of an external mandibular fenestra" (11) - plesiomorphic in archosauromorphs (Bennett 1996a).

Sereno's proposed postcranial synapomorphies directly related to flight include the following. "Extreme hollowing and pneumatization of the skeleton" (12) - also present in *Sharovipteryx*, but Bennett (1996a) suggests this character needs clarification because no Triassic pterosaurs have been described with pneumatopores;

"Strut-shaped coracoid with coracosternal joint" (13) – imminently present in *Longisquama* (Fig. 7); "Glenoid socket facing laterally" (14) - plesiomorphic for archosauromorphs (Bennett 1996a); "Broadly arched median sternal plate with hatchet-shaped spine toward anterior end" (15) - this is a complex fusion of bones present in *Longisquama*; "Elongate fore limb" (16) - present in *Cosesaurus* and *Longisquama*; "Elongate forearm and metacarpus" (17) - the former is a valid character, but the metacarpus is not elongate in *Preondactylus*; "Pteroid bone" (18) - valid; "[Unspecified] modifications of the fourth digit associated with wing support" (19) - valid.

Other Sereno proposed postcranial synapomorphies include the following. "Procoelous cervicals" (20) - present in *Tanytrachelos* (Olsen 1979) and *Langobardisaurus* (Renesto 1994); "Elongate posterior cervicals (6th-9th) relative to mid-dorsal length" (21) - pterosaurs have only eight cervicals and all postaxial cervicals are longer than the dorsals (Bennett 1996a); "Addition of two sacral vertebrae - totaling four or more" (22) - as in *Cosesaurus* and *Sharovipteryx*; "Elongate middle and distal caudal centra that are more than five times longer than high" (23) - as in *Sharovipteryx*; "Middle and distal caudal zygopophyses and hemal arches extended as narrow intertwining rods" (24) - imminently present in *Sharovipteryx*; "Absence of the coracoid foramen" (25) - as in *Cosesaurus*; "Humerus with saddle-shaped proximal articular surface" (26) - valid; "Bowed humeral shaft" (27) and "Anteroposteriorly broad deltopectoral crest with concave dorsal margin" (28) - both as in *Sharovipteryx*; "Only two proximal carpals (often fused) with cup-shaped proximal articular surfaces for the radius and ulna" (29) - there are three distinct articular surfaces for the ulna, not a simple cup shape (Bennett 1996a); "Metacarpal 1 subequal in length to metacarpals 2 and 3" (30) - not in *Preondactylus* (Bennett 1996a); "Elongate penultimate manual and pedal phalanges" (31) - the former as in *Longisquama*, the latter as in *Sharovipteryx*; "Absence of manual digit V" (32) - probably as in *Sharovipteryx*; "Slender preacetabular process equaling or exceeding the length of the postacetabular process" (33) - as in *Cosesaurus* and *Sharovipteryx*; "Pubis and ischium fused along adjacent margins" (34) - Bennett (1996a) considered this plesiomorphic for the Pterosauria, otherwise as in *Cosesaurus* and perhaps *Sharovipteryx*; "Paired prepubic element with median symphysis" (35) - valid; "Femoral articular head hemispherical and offset by constriction of the shaft distal to the head" (36) - no Triassic pterosaur exhibits a constricted femoral neck; "Splint-like dorsal fibula coossified with tibia" (37) - as in *Sharovipteryx*, but without coossification; "Tibia and proximal tarsals usually coossified as a tibiotarsus [in subadults]" (38) - valid; "Elongate metatarsal I only slightly shorter than metatarsals 2-4" (39) - as in *Sharovipteryx*; "Elongate phalanges on pedal digit V that exceed the length of metacarpal [sic - metatarsal] 5" (40) - as in *Langobardisaurus*, *Cosesaurus* and *Sharovipteryx*.

The Pterosauria – Bennett 1996a

Bennett (1996a) referenced Sereno's (1991) diagnosis of the Pterosauria as the most recent and commented on problems with 11 of the 40 characters (see citations above). However, a revised diagnosis (Bennett 1996a: 304) with 32 characters also contains several problems, many repeated from Sereno. Only novel characters are listed here: "Elongate median dorsal process of the premaxilla that extends posterior to the external naris and laps over the nasals" (3) - as in *Cosesaurus* and perhaps *Sharovipteryx*; "Broad sternum formed of paired clavicles and sternal plates and with a cristospine formed of the interclavicle" (13) - as in *Longisquama*; "Two proximal carpals fused in adults to form a proximal syncarpal" (18) - valid; "Three of four distal carpals fused in adults to form a distal syncarpal, the other (= preaxial) carpal acting as a strut to keep an extensor tendon anterior to the axis of the limb" (19) - valid; "Manual digit IV consisting of four extremely elongate phalanges and lacking an ungual, supporting a patagium, and with interphalangeal joints permitting little movement" (22) - valid; "No pubic symphysis" (26) - valid; "Pedal digit V with two elongate phalanges and ungual absent" (32) - the former present in *Cosesaurus* while the later is an autapomorphy.

The Pterosauria - Kellner (1996)

Kellner (1996) proposed 33 synapomorphies to diagnose the Pterosauria, many repeated from Romer (1956) and Sereno (1991). Only novel characters are listed here: "Presence of a pseudomesethmoid" (6) - unknown in basal pterosaurs due to preservation problems, but appears to be present in *Cosesaurus*; "Metacarpal IV long and much stronger than metacarpals I-III" (20) - metacarpal IV is not long, but it is more robust in basal pterosaurs; "Digit IV with distal articulation of phalanges I to III expanded, boot-shaped and proximal articulation of phalanges II to IV expanded forming a concave anteroposteriorly oriented surface" (23) - valid; "Where observable, calcaneum extremely reduced compared to astragalus" (31); - the proximal tarsals are subequal according to Wild (1978) and Wellnhofer (1975).

New Taxonomic Definitions and Diagnoses

The presence of numerous characters, once thought to be synapomorphies of the Pterosauria and now shown to be shared with certain prolacertiforms, prompts the present new definitions and diagnoses of clades within the Prolacertiformes. New taxa are diagnosed and defined below.

Prolacertiformes

- *Protorosaurus* (Evans and King 1993 and references therein)
- *Prolacerta* (Gow 1975 and references therein)
- *Boreopricea* (Benton and Allen 1997 and references therein)
- *Malerisaurus* (Chatterjee 1980, 1986)
- *Jesairosaurus* (Jalil 1997)
- The poorly known forms: *Kadimakara*, *Trachelosaurus*, *Prolacertoides* and *Malutinisuchus*
- Tapinoplatia = *Macrocnemus* + Characiopoda
    - *Macrocnemus* (Rieppel 1989 and references therein)
    - Characiopoda = Tanystropheidae + *Langobardisaurus* + Fenestrasauria
        - Tanystropheidae = *Tanystropheus* (Wild 1973 and references therein) + *Tanytrachelos* (Olsen 1979)
        - *Langobardisaurus* (Renesto and Dalla Vecchia 2000 and references therein)
        - Fenestrasauria = *Cosesaurus* + *Longisquama* + *Sharovipteryx* + Pterosauria
            - *Cosesaurus* (Sanz and Lopez 1984 and references therein)
            - *Longisquama* (Unwin, et al. In press and references therein)
            - *Sharovipteryx* (Unwin, et al. In press and references therein)
            - Pterosauria (Wellnhofer 1991 and references therein)

Tapinoplatia (new taxon)

Macrocnemus + Characiopoda

Definition. *Macrocnemus*, *Preondactylus*, their common ancestor, and all its descendants, including by definition, Macrocnemidae and Characiopoda (see below).

Etymology. "Low-bladed ones" alludes to the low to elongate scapula shared by members of this clade.

Recorded Temporal Range. Middle Triassic (Anisian) to Late Cretaceous (Maastrichtian).

Diagnosis. Prolacertiformes (sensu Evans 1988) without a primitive quadratojugal; maxilla with marginal palate shelf; median palatal elements primitively gracile and toothy; scapula low grading to parasagittally elongate; chevrons short and ventrally-oriented proximally, grading to long and parasagittally-oriented distally, producing an attenuated tail; bump-like anterior process on ilium grading to elongate; radius and ulna straight and closely appressed; tibia and fibula straight and closely appressed; metatarsals appressed.

Comments. The low scapula is "paper-thin" anteriorly (Rieppel 1989) with a robust posterior portion. Apparently in derived taxa the anterior portion disappears and the posterior portion extends resulting in a narrow, posteriorly-oriented, strap-like scapula. The straightening of the distal limb elements probably reflected a change in locomotion (Rieppel 1989).

Characiopoda (new taxon)

Tanystropheidae + *Langobardisaurus* + Fenestrasauria

Definition. *Tanystropheus*, *Preondactylus*, their common ancestor, and all its descendants, including by definition, Tanystropheidae and Fenestrasauria (see below).

Etymology. "prop-footed ones" alludes to the elongation of the proximal phalanx of pedal digit V.

Recorded Temporal Range. Middle Triassic (Ladinien) to Late Cretaceous (Maastrichtian).

Diagnosis. Tapinoplatia (see above) with posterior teeth differentiated from anterior teeth (reduced, elongated or multi-cusped), at least in juveniles; occiput at obtuse angle to jaw line; pterygoids contact vomers; palatines reduced; cervical vertebrae descend from back of skull in simple curve; procoelous presacral vertebrae (except *Tanystropheus*); posterior dorsal ribs straight and fused to transverse processes in adults; distal tarsal I absent; distal tarsal III very small; proximal phalanx on pedal digit V metapodial; postcloacal bones present on males.

Comments. The straightening and fusion of the posterior ribs, the reduction in the number of tarsals and the lengthening of the proximal phalanx of pedal digit V suggest a change in the primitive undulatory locomotive pattern.

Fenestrasauria (new taxon)

Cosesaurus + *Sharovipteryx* + *Longisquama* + Pterosauria)

Definition. *Cosesaurus*, *Preondactylus*, their common ancestor and all its descendants, including, by definition, *Cosesaurus* and Pterosauria.

Etymology. "hole-lizards" alludes to the antorbital fenestrae shared by members of this clade.

Recorded Temporal Range. Late Triassic (Norian) to Late Cretaceous (Maastrichtian).

Diagnosis. Characiopoda (see above) with three antorbital fenestrae grading to one without a fossa; expanded lacrimal overhangs posterior fenestra; rostrum and palate extended by elongation of the premaxilla; new quadratojugal spur appears medioposterior to the posterior jugal spur; ectopterygoid and pterygoid fuse; retroarticular apophysis present; cervical vertebrae shorter than in other prolacertiforms (reversed in *Sharovipteryx*); dorsal vertebrae transverse processes enlarged; at least four sacral vertebrae present; caudal ribs (transverse processes) reduced to 7 proximal pairs; clavicles overlap and grade to posteriorly oriented; interclavicle with reduced stem and expanded anterior keel or process; sternum expands anteriorly to fuse with the clavicles (in *Longisquama* and pterosaurs only); coracoid displaced anteriorly, grading to a strut shape with a sternal complex joint; scapula narrow, elongate and posteriorly oriented (not in *Cosesaurus*); manual digit IV at least three times as long as metacarpal IV; extended pre- and postacetabular processes; pubis and ischium fused along common edges; fibula much narrower than tibia grading to splint-like.

Comments. Three small antorbital fenestrae appear in *Cosesaurus*. In *Sharovipteryx*, as reconstructed here (Fig. 10), all three enlarge. In *Longisquama* the anterior two fenestrae are reduced. In pterosaurs (Fig. 12) the fenestrae appear to telescope posteriorly as they merge into one. Members of the Fenestrasauria have characters Snyder (1954) observed in extant lizards capable of bipedal locomotion (Fig. 2d). They also exceed the Index of Galton (Galton 1976) for bipedality. The pectoral and pelvic girdles experienced radical changes in this clade probably to reflect changes in locomotory patterns.

The following characters appear to be shared by *Sharovipteryx* + Pterosauria: naris enlarged; anterior teeth enlarged to fangs, medial process from maxilla divides internal naris; reduced torso equal to or shorter than skull plus cervicals; mid and distal caudal vertebrae more than five times longer than tall; humerus with crescentic deltopectoral crest; digit IV longer than humerus + ulna; tibia longer than femur; fibula less than 20% as wide as tibia; elongate metatarsal I only slightly shorter than metatarsals II-IV; dermal membranes posterior to hind limbs, spanning pedal digit V to tail and embedded with fibers. The following characters are shared by *Longisquama* + Pterosauria: jugal extends anterodorsally along orbit rim plus a new anteroventral process extends ventrally to mid-antorbital fenestra; mid maxilla teeth enlarged below dorsal process; broad sternal complex formed of fused clavicles, keeled interclavicle and sternum, penultimate phalanges of clawed manual digits are the longest in each series.

Pterosauria - Kaup 1834

Definition. *Preondactylus*, *Quetzalcoatlus*, their common ancestor and all its descendants.

Recorded Temporal Range. Late Triassic (Norian) to Late Cretaceous (Maastrichtian)

Diagnosis. Fenestrasauria (see above) with the following derived characters (* = known only from post-Triassic forms; single antorbital fenestra (tentatively with "adlacrimal" displaced posteriorly); mid-maxilla teeth enlarged below dorsal process †; medial maxilla process contacts palatine*; vomers greatly reduced*; anterior three pairs of dorsal ribs are robust, especially second pair which articulates with anterior sternal complex; other ribs are gracile; caudal ribs and transverse processes absent; ossified zygapophyses of middle and distal caudals and chevrons extended as narrow rods overlapping adjacent vertebrae; humerus with saddle-shaped head; humerus subequal in length to femur; radius and ulna longer than humerus and incapable of pronation; two proximal carpals fused in adults to form a proximal syncarpal; three of four distal carpals fused in adults to form a distal syncarpal, the other (= lateral, medial, preaxial) carpal acting as a strut to keep an extensor tendon anterior to the axis of the limb; pteroid present along leading edge of distal radius partially framing a propatagium and oriented medially; manual unguals I-III are more than twice as deep as associated phalanges; metacarpal IV much more robust than metacarpal III and provided with a pulley joint twisted into the plane of the manus capable of flexing 180 degrees for wing folding; manual digit IV consisting of four extremely elongate and robust phalanges (ungual absent) with interphalangeal joints permitting little movement; extensor tendon process on the proximal articulation of the first phalanx of digit IV; manual digit V absent; paired prepubes articulating with pubis; no pubic symphysis; femur with rounded head offset from axis of shaft by 20° or more; femur bowed anteriorly along 80% of its length; fibula lacking a distal epiphysis, the head and distal end fused to tibial shaft in subadults; subequal proximal tarsals fused to tibia in adults to form a tibiotarsus; penultimate pedal phalanges are the longest in each series; elongate terminal phalanx of pedal digit V capable of 180 degrees of flexion and often preserved tightly flexed; pedal ungual V absent; brachiopatagium stretching between wing tip and proximal ulna or just posterior to it, and medioposteriorly continuing to the torso and/or to the distal femur (unclear which is basal) and strengthened with actinofibrils distally; uropatagia united medially with internal fibers not well organized; vertical metameric vane present at tail tip*; bristles present on neck and torso* (Bakhurina and Unwin 1995, Frey and Martill 1998).

Comments. The "adlacrimal" (Wild 1978 figure 1, Wellnhofer 1974 figure 2) may be a dorsal process of the maxilla with the connection unexposed beneath the anteroventral process of the jugal which laterally overlaps the maxilla primitively. If so, it would be homologous to the posterior pillar separating antorbital fenestrae in *Cosesaurus*, *Longisquama* and *Sharovipteryx* (as reconstructed here). Due to the strong flex in pedal digit V, the dorsal surface of the terminal phalanx was probably in contact with the substrate (Peters 2000), inverting the ungual and making it useless. Similarly the rotation of manual digit IV into the plane of the wing removed that ungual from use and allowed it disappear.

Discussion.

The present cladistic studies present strong evidence that certain Prolacertiformes are the sister taxa to the Pterosauria. In three previous cladistic analyses including pterosaurs (Gauthier 1984, Padian 1984, Sereno 1991), prolacertiforms were not included. In the analysis of Bennett (1996a), the critical taxa, *Langobardisaurus*, *Cosesaurus*, *Longisquama* and *Sharovipteryx* were not included. This may be so because none showed obvious forelimb modifications leading toward pterosaurian flight, as Wild (1978) proposed. Rather pterosaur phylogenesis appears to parallel that of birds (Altangerel, et al. 1994 and references therein) in which the development of wings came later, rather than earlier, in morphogenesis. Many characters, such as "elongation of the fifth pedal digit," "attenuation of the caudal vertebrae" and "enlargement of the forelimb" were once considered adaptations to flight (Bennett 1996a), but antecedents can be found within certain terrestrial prolacertiformes.

Evolutionary Trends

Antorbital Fenestra(e) - The controversial presence of three antorbital fenestrae in *Cosesaurus* (Fig. 4b) appears to be confirmed by their homologous presence in *Sharovipteryx* (as reconstructed here) and *Longisquama*. The posterior one is the largest and is framed dorsally by the overhanging lacrimal. The anterior one is ventral to the naris. If this skull morphology is antecedent to that observed in basal Pterosauria, the narrow anterior strut separating the anterior two fenestrae in *Sharovipteryx* may have narrowed further until it disappeared. The broad central strut appears to have migrated posteriorly to become the "adlacrimal" of *Eudimorphodon* (Wild 1978). From *Macrocnemus* to *Eudimorphodon* the lacrimal and prefrontal migrate dorsally and shrink as the jugal advances. In *Longisquama* (Fig. 7) and *Preondactylus* (Fig. 12) the jugal extends to the anterior of the orbit and sends a separate process to reinforce the narrow ventral rim of the antorbital fenestra.

Quadratojugal - In *Youngina* (Gow 1975) the quadratojugal is a dorsally arcing bone connecting the posterior process of the jugal to the descending ramus of the squamosal. In *Prolacerta* (Gow 1975) the jugal connection is lost and a posterior vestige remains adjacent to the quadrate and the dorsally retreating squamosal. In *Macrocnemus* and *Tanystropheus* the quadratojugal is absent. In *Cosesaurus* a small new ossification appears posterior to the posterior jugal spur. In *Eudimorphodon* (Wild 1978) a similar quadratojugal spur bridges the lower temporal fenestra at the jaw line. Thus the quadratojugal in pterosaurs appears to be a neomorph and is not homologous to the quadratojugal in other diapsids.

Squamosal - The squamosal of basal archosauromorphs bears a descending process anterolateral to the quadrate. In most archosauriforms it retains this shape and position. In most prolacertiforms the descending ramus of the squamosal retreats (Wild 1973, Fig. 4A). In pterosaurs the ramus once again extends ventrally, but posterior to the quadrate, probably to frame an eardrum (Bennett 1991).

Palate - The palate in prolacertiforms is well known in *Macrocnemus* (Kuhn-Schnyder 1962, Fig. 10B), *Tanystropheus* (Wild 1973), *Sharovipteryx* (Fig. 10A, C) and among early pterosaurs, *Rhamphorhynchus* (Wellnhofer 1975a, Fig. 10C). In *Campylognathoides* (1974) and *Scaphognathus* (Wellnhofer 1975a figure 2) the palate is partially revealed through the antorbital fenestra and orbit. In *Cosesaurus* (Fig. 4) the posterior elements are exposed ventrally. In *Macrocnemus* and *Tanystropheus*, the palatal extent of the premaxilla is small and the vomers extend nearly to the anterior teeth. In *Sharovipteryx* and pterosaurs the premaxilla invades one-fifth of the palate and the vomers are posteriorly displaced. The maxilla in *Macrocnemus* produces a wide medial margin that narrows the internal naris. The maxilla in *Sharovipteryx* produces a narrow medial process that appears to split the large internal naris into anterior (primary) and posterior (secondary) parts. In *Rhamphorhynchus* the medial maxilla process contacts the anterior process of the palatine and the maxillae expand medially, conjoining to form a broad palate shelf. Traditionally (eg. Wellnhofer 1975a, Bennett 1991) this shelf has been mislabeled the "palatine." Both *Macrocnemus* and *Tanystropheus* have vomer teeth. The vomers of *Macrocnemus* are narrow and separate except anteriorly. Those of *Tanystropheus* are broad and mostly conjoined, as in *Sharovipteryx*. Pterosaur vomers are extremely narrow, toothless and conjoined. The narrow, curved toothed palatine of *Macrocnemus* has an anterior vomer process, a lateral maxilla process and a pterygoid process lapping posteriorly. In *Tanystropheus* and *Sharovipteryx* the palatine is small and displaced laterally as the enlarged pterygoid contacts the vomers. In *Rhamphorhynchus* the former vomer process of the toothless palatine contacts a medial process of the maxilla shelf, dividing the internal naris in half while the lateral process contacts the maxilla posterior to the shelf. Traditionally (eg. Wellnhofer 1975, figure 3d) this bone has been mislabeled the "ectopterygoid," probably because of its small size. The actual ectopterygoid appears to be fused laterally to the pterygoid in *Cosesaurus*, *Sharovipteryx* and pterosaurs. The pterygoid in *Macrocnemus* is a broad, sinuous toothy plate with an anterior process lapping the palatine, a long posterolateral process contacting the quadrate and a lateral contact with the ectopterygoid. In *Tanystropheus* (Wild 1973) the broad pterygoids dominate the palate, conjoin medially in a long anterior suture and separate posteriorly to form a narrow pyriform recess. In *Sharovipteryx* (Fig. 10A, B) the pterygoids do not quite meet anteriorly and are separated by a broader pyriform recess. Posteriorly the pterygoid makes broad contact with the quadrate. The ectopterygoid makes broad contact with the pterygoid laterally and narrow contact with the jugal. In *Rhamphorhynchus* (Fig. 10C) and *Cosesaurus* (Fig. 4) the pterygoids are slender, sinuous and widely separated struts. In *Eudimorphodon* (Wild 1978) and *Dendrorhynchoides* (unpublished data) the pterygoids are broad and have toothy bumps. A lateral process (the fused ectopterygoid) contacts the jugal. The basispterygoid changes little from *Macrocnemus* to *Rhamphorhynchus*, but with pterosaurs the increased inclination of the occiput requires an anterior extension of the basipterygoids to maintain contact with the anteriorly migrating pterygoids.

Teeth - *Macrocnemus* has a full arcade of small, simple, conical, marginal teeth, plus tiny palate teeth (Kuhn-Schnyder 1962). Derived prolacertiforms display a wide variety of tooth shapes and a dimunition of palatal teeth. In *Cosesaurus* (Fig. 4) three posterior maxilla teeth are broad base triangles. In *Langobardisaurus* (Fig. 1C) many of the posterior teeth have multiple cusps while the anterior ones form an arcade of appressed pegs. In *Longisquama* (Fig. 7), *Sharovipteryx* (Fig. 10E) and pterosaurs (Fig. 12) the anterior teeth are large and sharp while the posterior teeth tend to be tiny and/or multi-cusped (Wild 1978).

The Curvature of the neck - In *Macrocnemus* (Peyer 1931b, 1937), as in basal amniotes, the cervicals articulate with the skull posteriorly resulting in a horizontal neck. In archosauriforms the neck maintains a slight to strong S-curve (Sereno 1991). By contrast, in derived prolacertiforms and pterosaurs the neck articulations permit a simple curve that is often preserved (Wild 1973, Olsen 1979, Bennett 1991) with the atlas/axis articulating perpendicular to the occiput which is typically oriented at an obtuse angle to the jaw line. Only the axis appears capable of ventroflexion in opposition to the other vertebrae. A braincase cast of the mid-Jurassic pterosaur *Parapsicephalus* (Newton 1888, Wellnhofer 1991) shows that the brain stem is directed posteroventrally in pterosaurs, rather than posteriorly as in archosauriforms. Note that in *Longisquama*, *Sharovipteryx*, *Preondactylus* and *Eudimorphodon* no cervical curve is preserved in the fossil.

Caudal Vertebrae - The mid and posterior caudal vertebrae of pterosaurs are highly specialized with centra five times longer than deep. Pre- and postzygopophyses are hyperextended parasagittally the lengths of one to five vertebrae, with chevrons of subequal length. Together these extensions stiffen the tail into a solid yet lightweight unit. Precursors to this condition can be found in *Sharovipteryx* in which the hemal arches equal the length of each centra and parallel them (Fig. 9a, b) and impressions of interweaving strands of unossified material are visible dorsally. In the prolacertiform sister taxa leading to pterosaurs, the caudal ribs and transverse processes display a morphological reduction sequence to a state of absence in *Preondactylus* (Wild 1984b). This reduction reflected important locomotory changes including a reduced influence of the large caudofemoralis muscle complex anchored on these processes (Snyder 1954, Hamley 1990, Russell and Baur 1992, Gatesy 1995).

Pectoral Girdle - In *Macrocnemus* (Fig. 13E) the shapes and placement of the pectoral elements are similar to those in primitive lepidosaurs (Carroll 1987 figure 11-7). The sternum has a posterior notch, the interclavicle is T-shaped, the clavicles curve dorsally to the anterior of the scapula, the coracoid is disk-like and the scapula is low with a supraglenoid notch and a robust posterodorsal process. In *Cosesaurus* (Fig. 13F) the sternum is absent; the coracoids are larger than the low scapulae; the interclavicle is deeply keeled; the clavicles are straighter, overlap medially and extend beyond the scapulae. In *Longisquama* (Fig. 13G) the embayed sternum is fused to and surrounded by the posteriorly curving clavicles; the interclavicle is robust anterior to the clavicles and may carry the coracoid articulation anterior to the clavicles; the clavicles overlap the interclavicle medially; the coracoid is tall with a deep glenoid and a ventral knob-like sternal complex articulation; the scapula is narrow, elongate and dorsoposteriorly oriented. In *Sharovipteryx* (Fig. 8C) only an elongate, parasagittal scapula is exposed. In a juvenile *Eudimorphodon* (Wild 1993, Fig. 13H) the sternal complex is composed of a conjoined sternum, large posteriorly-oriented, overlapping clavicles and a keeled, anteriorly projecting interclavicle. The coracoids are reduced to struts with a narrow ventral stem and a biceps tubercle near the glenoid. They articulate at the anterior of the clavicle/sternal complex. The strap-like scapulae extends dorsoposteriorly. This morphological sequence demonstrates the migration of the interclavicle and coracoids to a position anterior to the clavicles, the anterior expansion of the sternum to fuse with the clavicles, the anteroventral expansion of the interclavicle to form a keel; the posterior curving, overlapping and enlargement of the clavicles, and the elongation of the coracoids and scapulae - all prior to the elongation of the flight digit.

Fore limb - The fore limb of most prolacertiforms (e.g. Fig. 1) is less than one half the length of the hind limb, the carpals are poorly ossified and the digits are slightly longer than the corresponding metacarpals. In *Cosesaurus* the fore limb is larger than one half the hind limb and the digits are three times the length of the metacarpals. *Longisquama* has similarly elongate digits. In *Sharovipteryx* (Fig. 8C) the small humerus appears to have a crescentic deltopectoral crest. Otherwise the fore limb appears vestigial with the exception of a single long digit (presumably IV) extending nearly to the pelvis. Thus *Sharovipteryx* has a pterosaur-like humerus/ digit IV ratio. Only in pterosaurs are the carpals strongly ossified, a pteroid is present and digit V is absent. Pterosaurs retain the primitive pattern of laterally increasing digits (I-IV) but archosauriforms, like dinosaurs, reduce digit IV.

Pelvic Girdle - In primitive prolacertiforms, like *Macrocnemus* (Fig. 1A), only two sacral vertebrae are present, the ilium has a small preacetbular process and the ventral elements (pubis and ischium) are unfused. In *Cosesaurus* four sacral vertebrae are present (Fig. 6), the ilium has a substantial preacetabular process and the ventral elements are fused. In *Sharovipteryx* the hyperelongate pre- and post-acetabular processes incorporate six vertebrae in the sacral series (Fig. 9C) and the ventral elements may be fused. In pterosaurs at least four sacral vertebrae are present. In derived forms (eg. Williston 1903), additional dorsal and caudal vertebrae are incorporated into the sacral series and ribless dorsal vertebrae may reside between the extended ilia. The ilium has a knife-like preacetabular process, non-articulating pubes, articulating prepubes and fused puboischiadic plates.

The incorporation of additional vertebrae into the prolacertiform sacral series probably has important locomotory implications.

Hind Limb - The hind limb in most prolacertiforms remains conservative in proportion and structure. The femoral head only appears within pterosaurs. The tibia is longer than the femur in *Sharovipteryx* and pterosaurs. The fibula is reduced in *Cosesaurus* and more so in *Sharovipteryx* and pterosaurs. The morphogenesis of the tarsus in prolacertiforms leading to pterosaurs is characterized by a reduction of the distal elements to two and a reduction of the calcaneum to match the astragalus (Fig. 13A-D). Previous work (Wellnhofer 1978, 1991 and references therein) identified the distal tarsals simply as "distal tarsals 3 and 4," as in archosauriforms. However, identification of the centrale as the medial element becomes clear when comparing homologous elements in prolacertiforms (Fig. 13A-D). This configuration provides a simple-hinge type ankle, convergent with that of higher archosauriforms, culminating with the fusion of the proximal tarsals with the tibia in pterosaurs. In most prolacertiforms, metatarsals I-IV increase in length laterally, but in *Sharovipteryx* and pterosaurs all four are subequal. Primitively digits I-IV increase in length laterally. In *Sharovipteryx* and pterosaurs digits II-IV are subequal. The proximal phalanx of digit V is metapodial in derived prolacertiforms. This phalanx appears to be bound to the metatarsals in terrestrial forms, but in pterosaurs it is clearly separated and may be extended anterior to the others with the elongate terminal phalanx (ungual absent) flexed ventrally up to 180 degrees. Precursors to this condition can be found in *Cosesaurus* where the number of phalanges is reduced to three, including the ungual. *Sharovipteryx* displays a rare reversal with four phalanges present on digit V. Only in pterosaurs is digit V preserved flexed. The elongation of the tibia, the reduction of the lateral digits, the simplification of the tarsus and the specialization of digit V have important locomotory implications (Peters 2000).

Dermal Membranes - No fore limb wing membranes are preserved in terrestrial prolacertiforms. Wing membranes are rarely preserved in pterosaurs, but their presence is assumed in all. Proximal attachments appear to differ relative to genus. In *Rhamphorhynchus* (Padian and Rayner 1993 and references therein), the detached "Zittel" wing added to another complete specimen appears to stretch between the wing finger and elbow, then from the elbow medially to the ribs without connecting to the hind limb. In *Sordes* (Sharov 1971, Unwin and Bakhurina 1994) the wing is reported to extend to pedal digit V. In *Pterodactylus* (Wellnhofer 1987, Padian and Rayner 1993) the wing appears to stretch between the wing finger and elbow, then from the elbow to the femur.

Stretched between the tail and each hind limb of certain exceptionally preserved pterosaurs and *Sharovipteryx* are dermal membranes known as uropatagia (Sharov 1971, Wild 1993, Unwin and Bakhurina 1994, Frey and Martill 1998). In *Sharovipteryx* each uropatagium extends to the second phalanx of pedal digit V and is supported by long, straight, closely spaced, virtually parallel fibers (Fig. 9D). In *Eudimorphodon* (Wild 1993) and *Pterodactylus* (Frey and Martill 1998) the uropatagium extends only to metatarsal V and is sparsely embedded with unorganized fibers. In *Sordes* the uropatagia are seamed together medially and are reported (Unwin and Bakhurina 1994) to extend to the tips of digit V. Ellenberger (1993) reported uropatagia in *Cosesaurus*, but the impression may be a depositional illusion (Fig. 3). I was able to observe a short dorsal frill composed of squarish segments on *Cosesaurus*. *Longisquama* (Sharov 1970) has hyper-elongate dermal plumes. The two may be homologous dermal structures.

Conclusions.

Pterosaur fossils have been studied for over 200 years but ancestral forms have not been recognized. Traditionally pterosaurs were considered archosaurs and previous workers placed them close to the Dinosauromorpha, *Scleromochlus* or lower archosauriforms. However, no suite of synapomorphies unites these taxa with the Pterosauria exclusive of certain prolacertiforms. The present cladistic studies present strong evidence that certain Prolacertiformes are sister taxa to the Pterosauria with a suite of synapomorphies uniting them. Previously, the critical taxa, *Langobardisaurus*, *Cosesaurus*, *Longisquama* and *Sharovipteryx*, were not used as the outgroup. This may be so because none showed fore limb modifications leading toward pterosaurian flight, a traditional hypothesis presently without supporting evidence in the fossil record. By the evidence presented here, the wings came last, paralleling the development of wings in birds. Many characters formerly considered autapomorphies of the Pterosauria or adaptations to flight, such as elongation of the fifth pedal digit, attenuation of the caudal vertebrae, reorganization of the pectoral region and enlargement of the fore limb are shown to be synapomorphies of the outgroup, the higher terrestrial prolacertiforms. Phylogenetic results from four cladistic analyses support a monophyletic Pterosauria within the Prolacertiformes. The topology was shown to be robust by the addition of extra steps and the removal of sister-taxa. Removal of all five key prolacertiforms resulted in a cladogram that duplicated earlier work in which the Pterosauria were considered basal archosauriformes. This experiment demonstrates the need to include the sister-taxa prolacertiforms in any future cladistic analysis of the Pterosauria.

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REFERENCES

Altangerel P., Chiappe L. M., Rinchen B., Clark J. M. & Norell M. A. (1994) - Skeletal Morphology of *Mononykus olecranus* (Theropoda; Avialae) from the Late Cretaceous of Mongolia. *Novitates* 3105: 1-29, New York.

Bakhurina N. N. & Unwin D. M. (1995) - The evidence for "hair" in *Sordes* and other pterosaurs. *Jour. Vert. Paleont.*, 12: 18A, Lawrence.

Bassani F. (1886) - Sui fossili e sull'età degli schisti biuminosi triasici di Besamo in Lombardia. *Atti Soc. It. Sci. Nat.* 29: 1-72; Milan.

Bennett S. C. (1991) - Morphology of the Late Cretaceous pterosaur *Pteranodon* and systematics of the Pterodactyloidea. Unpublished Ph.D. dissertation, University of Kansas, 680 pp.

Bennett S. C. (1996) - The phylogenetic position of the Pterosauria within the Archosauromorpha. Zoological Journal of the Linnean Society 118: 261-308, London.

Benton M. (1982) - The Diapsida: revolution in reptile relationships. *Nature* 296: 306-307, London.

Benton M. (1984) - The relationships and early evolution of the Diapsida. *Symp. Zool. Soc. London*, 52: 575-596, London.

Benton M. J. (1985) - Classification and phylogeny of the diapsid reptiles. *Zool. Journ. Linn. Soc.*, 84: 97-164, London.

Benton M. J. (1990) - Origin and interrelationships of dinosaurs. *In*: Weishampel, D. B., Dobson, P., Osmolska, H., *eds*. The Dinosauria. University of California Press, Berkeley: 11-30.

Benton M. J. & Allen J. L. (1997) - *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles. *Palaeontology* 40: 931-953, London.

Benton M. J. (1999) - *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Phil. Trans. Roy. Soc. London*, B. 354, 1423-1446, London.

Carrier D. R. (1987) - The Evolution of Locomotor Stamina in Tetrapods: Circumventing a Mechanical Constraint. *Paleobiology*, 13: 326-341.

Carroll R. L. (1976) - Eosuchians and the origin of archosaurs. *In*: Churcher, C. S., ed. ATHLON Essays on Paleontology in Honour of Loris Shano Russell: Royal Ontario Museum Life Sciences Miscellaneous Publications, 58-79, Toronto.

Carroll R. L. (1987) - Vertebrate Paleontology and Evolution. W. H. Freeman and Company, New York: xiv. + 698 pp.

Chatterjee S. (1980) - *Malerisaurus*, a new eosuchian reptile from the Late Triassic of India. *Phil. Trans. Roy. Soc. London* B 291: 163-200, London.

Chatterjee S. (1986) - *Malerisaurus langstoni*, a new diapsid reptile from the Triassic of Texas. Journal of Vertebrate *Paleontology*, 6(4): 297-312, London.

Clark J. M., Hopson J. A., Hernández R., Fastovsky D. & Montellano M. (1998) - Foot posture in a primitive pterosaur. *Nature*, 391: 886-889, London.

Colbert E. H. (1969) - A Jurassic Pterosaur from Cuba. *Am. Mus. Novitates*, 2370, 26 pp.; New York.

Collini C. A. (1784) - Sur quelques Zoolithes du Cabinet d'Histoire naturelle de S.A.S.E. Palatine et de Bavière, à Mannheim. *Acta Acad. Theodoro-Palatinae Mannheim*, 5, pars physica: 58-103, Mannheim.

Cowen R. (1981) - Homonyms of *Podopteryx*. *Journ. Paleont.*, 55: 483.

Cuvier G. (1801) - (An 9), [Reptile volant.] *In* Extrait d'un ouvrage sur les espèces de quadrupèdes dont on a trouvé les ossemens dans l'intérieur de la terre. (Procès de la Classe Scientifique, Mathematique et Physique de l'Institute Nationale (26 Brumaire, l'an 9)): *Journal de Physique, de Chimie et d'Histoire Naturelle*, v. 52, p. 253-267. [p. 263] Also: Magazin Encyclopédique, p. 60-82, Paris.

Cuvier G. (1809) - Sur le squellette fossile d´un reptile volant des environs d´Aichstedt, qu quelques naturalistes ont pris pour un oiseau, et dont nous formons un genre de sauriens, sous le nom Ptero-Dactyle. *Ann. Mus. Hist. Natur.*, 13: 424-437, Paris.

Dalla Vecchia F. M. (1998) - New observations on the osteology and taxonomic status of *Preondactylus buffarinii* Wild, 1984 (Reptilia, Pterosauria). *Boll. Soc. Paleont. It.*, 36(3): 355-366, Modena.

Dilkes D. W. (1998) - The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Philosophical Transactions of The Royal Society, London 353: 501-541.

Ellenberger P. (1977) - Quelques precisions sur l'anatomie et la place systematique tres speciale de *Cosesaurus aviceps* (Ladinien supérior de Montral, Catalogne). *Cuad. Geol. Ibér.*, 4: 169-188, Madrid.

Ellenberger P. (1978) - L'Origine des Oiseaux. Historique et méthodes nouvelles. Les problémes des Archaeornithes. La venue au jour de *Cosesaurus aviceps* (Muschelkalk supérieur) *In:* Aspects Modernes des Recherches sur l'Evolution. Comp. Rend. coll. Montpellier 12-16 Septembre 1977. Vol. 1. Bons, J. ed. Mémoires et Travaux Ecole Pratique des Hautes Etudes, De l'Institut de Montpellier, 4: 91-117 [in French], Montpellier.

Ellenberger P. (1993) - *Cosesaurus aviceps*. Vertébré aviforme du Trias Moyen de Catalogne. Étude descriptive et comparative. Mémoire. Avec le concours de l'École Pratique des Hautes Etudes. Laboratoire de Paléontologie des Vertébrés. Université des Sciences et Techniques et Languedoc, Montpellier (France). 664 pp [in French and self-published].

Ellenberger P. & de Villalta J. F. (1974) - Sur la presence d'un ancêtre probable des oiseaux dans le Muschelkalk supérieure de Catalogne (Espagne). Note preliminaire. Acta. *Geol. Hisp.*, 9: 162-8, Barcelona.

Evans S. E. (1988) - The early history and relationships of the Diapsida. *In*: Benton, M. J., (ed). The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds. The Systematics Association Special Volume No. 35A. Clarendon Press, 221-260, Oxford.

Evans S. E. & King M. S. (1993) - A new specimen of *Protorosaurus* (Reptilia: Diapsida) from the Marl Slate (Late Permian) of Britain. *Proceed. Yorkshire Geol. Soc.*, 49: 229-234, Bath.

Frey E. & Martill D. M. (1998) - Soft tissue preservation in a specimen of *Pterodactylus kochi* (Wagner) from the Upper Jurassic of Germany. *Neu. Jahrb. Geol. Paläont. Abhan.*, 21: 421-441, Tübingen.

Galton P. M. (1976) - Prosauropod Dinosaurs (Reptilia, Saurischia) of North America. *Postilla*, 169: 1-98, New Haven.

Gans C., Darevksi I., Tatarinov L. P. (1987) - *Sharovipteryx*. A reptilian glider? *Paleobiology* 13(4): 415-426.

Gatesy S. M. (1995) - Functional evolution of the hind limb and tail from basal theropods to birds. *In*: Thomason, J. J. (ed). Functional Morphology in Vertebrate Paleontology. Cambridge University Press, 293 pp., New York.

Gauthier J. A. (1984) - A Cladistic Analysis of the Higher Systematic Categories of the Diapsida. Unpublished Ph.D. Dissertation, University of California at Berkeley.

Gauthier J. A. (1986) - Saurischian monophyly and the origin of birds. *In*: Padian K., *ed*. The origin of birds and the evolution of flight. *Mem. Cal. Acad. Sci.*, 8., 1-55, San Francisco.

Gow C. E. (1975) - The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeont. Afr.*, 18: 89-131, Cape Town.

Hamley T. (1990) - Functions of the tail in bipedal locomotion of Lizards, Dinosaurs and Pterosaurs. *Mem. Queensland Mus.*, 28(1): 153-158, Brisbane.

Haubold H. & Buffetaut E. (1987) - Un nouvelle interprétation de *Longisquama insignis*, reptile énigmatique du Trias supérieur d'Asie centrale (A new interpretation of *Longisquama insignis*, an enigmatic reptile from the Upper Triassic of central Asia) [in French, English, with French summary]. *Comp. Rend. Acad. Sci. II*, 305: 65-70, Paris.

Huene F. von. (1914) - Beiträge zur Geschichte der Archosaurier. *Geol. palaeont. Abhandl.* N.F. 13: 1-53, Stuttgart.

Jalil N.-E. (1997) - A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. *Jour. Vert Paleont*, 17(3): 506-525, Lawrence.

Jones T. D., Ruben J. A., Martin L. D., Kurochkin E. N., Feduccia A., Maderson P. F. A., Hillenius W. J., Geist N. R., Alifanov V. (2000) - Non-avian feathers in a Late Triassic archosaur. *Science*, 288: 2202-2204.

Kellner A. W. A. (1996) - Description of New Material of Tapejaridae and Anhangueridae (Pterosauria, Pterodactyloidea) and Discussion of Pterosaur Phylogeny. Ph.D. Thesis. Columbia University, New York: 347 pp.

Kuhn-Schnyder E. (1962) - Ein weiterer Schädel von *Macrocnemus basanii* Nopcsa aus der anisischen Stufe der Trias de Monte San Giorgio (Kt. Tessin, Schweiz). *Paläont. Zeitsch.*, 36 (Schmidt-Festband): 110-133, Basel.

Maddison W. P. & Maddison D. R. (1992) - MacClade version 3.05. Computer program distributed by Sinauer Associates, Inc, Sunderland, Massachusetts.

Muscio G. (1996) - Preliminary note on a specimen of prolacertiformes (Reptilia) from the Norian (Late Triassic) of Preone (Udine, North-Eastern Italy). *Gortania Atti Mus. Friulano St. Nat.*, 18: 33-40, Udine.

Newton E. T. (1888) - On the Skull, Brain and Auditory Organ of a new species of Pterosaurian (*Scaphognathus purdoni*) from the Upper Lias near Whitby, Yorkshire. *Phil. Trans. Roy. Soc.*, London 179: 503, London.

Nopcsa F. (1922) - Neubeschreibung des Trias-Pterosauriers *Tribelesodon*. *Paläont. Zeitsch.*, 5: 161-181, Berlin.

Olsen P. E. (1979) - A new aquatic eosuchian form the Newark Supergroup (Late Triassic, Early Jurassic) of North Carolina and Virginia. *Postilla* 176: 1-14.

Padian K. (1984) - The origin of pterosaurs. *In*: Reif W-E. and Westphal F., *eds*. Proceedings of the Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers, Tübingen: Attempto Verlag: 163-168, Tübingen.

Padian K. & Rayner J. M. V. (1993) - The wings of pterosaurs. *Am. Journ. Sci.*, 293A: 91-166, New Haven.

Peters D. (1997) - A new phylogeny for the Pterosauria. *Journ. Vert. Paleont.*, 17(3): 69A, Lawerence.

Peters D. (2000) - Description and Interpretation of Interphalangeal Lines in Tetrapods. *Ichnos*, 7(1): 11-41.

Peyer B. (1931a) - Die Triasfauna der Tessiner Kalkalpen. II. *Tanystropheus longobardicus* Bassani sp.. *Abh. Schweiz. Paläont. Gesell.*, 50 7-110, Basel.

Peyer B. (1931b) - *Macrocnemus* nicht *Macrochemus*. *Zentralb. Min. Geol. Paläont.*, B: 190-192.

Peyer B. (1937) - Die Triasfauna der Tessiner Kalkalpen XII. *Macrocnemus bassanii* Nopcsa. *Abhandl. Schweiz. Paläont. Gesell.*, Band LIX: 1-140, Zürich.

Reisz R. (1981) - A diapsid reptile from the Pennsylvanian of Kansas. *Univ. Kansas Mus. Nat. Hist., Spec. Publ.*, 7: 1-74, Lawrence.

Renesto S. (1994) - A new prolacertiform reptile from the Late Triassic of Northern Italy. *Riv. Paleont. Strat.*, 100(2): 285-306, Milano.

Renesto S. & Dalla Vecchia F. M. (2000) - The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, northern Italy). *Journ. Vert. Paleont.*, 20(3): 622-627, Lawrence.

Rieppel O. (1989) - The hind limb of *Macrocnemus bassanii* (Nopcsa)(Reptilia, Diapsida): development and functional anatomy. *Journ. Vert. Paleont.*, 9(4): 373-387, Lawrence.

Rjabinin A. N. (1948) - Remarks on a Flying Reptile from the Jurassic of the Kara-Tau. *Akad. Nauk, Paleont. Inst.*, Trudy, 15(1): 86-93; Moscow and Leningrad (in Russian).

Romer A. S. (1956) - Osteology of the Reptiles. University of Chicago Press, xxi + 772 pp, Chicago.

Russell A. P. & Baur A. M. (1992) - The M. caudifemoralis longus and its relationship to caudal autotomy and locomotion in lizards (Reptilia - Sauria). *Journ. Zool.* 227(1): 127-143, London.

Sanz J. L. & López-Martinez N. (1984) - The prolacertid lepidosaurian *Cosesaurus aviceps* Ellenberger & Villalta, a claimed 'protoavian' from the Middle Triassic of Spain. *Géobios* 17: 747-53.

Seeley K. (1888) - Researches on the structure, organization and classification of the fossil Reptilia. 1. On *Protorosaurus speneri* (von Meyer). *Phil. Trans. Roy. Soc. London*, B, 178: 178-213, London.

Sereno P. C. (1991) - Basal Archosaurs: phylogenetic relationships and functional implications. *Soc. Vert. Paleont., Memoir 2, Journ. Vert. Paleont.*, 11 (Supplement to #4): 1-53, Lawrence.

Sereno P. C. & Arcucci A. (1990) - The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. *Neu. Jahrb. Geol. Paläont., Abhandl.*, 180: 21-52, Stuttgart.

Sereno P. C. & Arcucci A. (1994) - Dinosaurian precursors from the middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journ. Vert. Paleont.*, 14(1): 53-73, Lawrence.

Sharov A. G. (1970) - Unusual reptile from the Lower Triassic of Fergana. *Paleont. Zhur.*, 1970: 127-131, Moscow (In Russian).

Sharov A. G. (1971) - New flying reptiles from the Mesozoic of Kazakhstan and Kirghizia. *Trudy Paleont. Inst., Akad. Nauk*, USSR 130: 104–113, Moscow.

Shine R. & Lambeck R. (1989) - Ecology of frillneck lizards, *Chlamydosaurus kingii* (Agamidae) in tropical Australia. *Austr. Wildlife Res.*, 16: 491-500.

Snyder R. (1954) - The anatomy and function of the pelvic girdle and hind limb in lizard locomotion. *The Am. Journ. Anat.*, 95: 1-45, New York.

Stokes W. L. (1957) - Pterodactyl tracks from the Morrison Formation. *Journ. Palaeont.*, 31: 952-954, Lawrence.

Swofford D. L. (1993) - PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1 Computer software and documentation distributed by Illinois Natural History Survey, Champaign, Illinois.

Tatarinov L. P. (1989) - The systematic position and way of life of the problematical upper Triassic reptile *Sharovipteryx mirabilis*. *Paleont. Journ.*, 2: 107-110, Moscow.

Unwin D. M. & Bakhurina N. N. (1994) - *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature* 371: 62-64, London.

Unwin D. M., Alifanov V. R. & Benton M. J. (In press). Enigmatic small reptiles from the Middle-Late Triassic of Kirghizia. *In*: The age of dinosaurs in Russia and Mongolia (*eds*. M. J. Benton, E. N. Kurochkin, M. A. Shishkin and D. M. Unwin). Cambridge University Press.

Wellnhofer P. (1974) - *Campylognathoides liasicus* (Quenstedt), an upper Liassic pterosaur from Holzmaden - the Pittsburgh specimen. *Ann. Carnegie Mus.*, 45: 5-34, Pittsburgh.

Wellnhofer P. (1975a) - Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. Teil I. Allgemeine Skelettmorphologie. *Palaeontographica*, A 148: 1-33, Stuttgart.

Wellnhofer P. (1975b) - Teil II: Systematische Beschreibung *Palaeontographica* A 148: 132-186, Stuttgart.

Wellnhofer P. (1975c) - Teil III. Paläokolgie und Stammesgeschichte. *Palaeontographica*, A 149: 1-30, Stuttgart.

Wellnhofer P. (1978) - Pterosauria. Handbuch der Paläoherpetologie, Teil 19. Gustav Fischer Verlag, 82 pp, Stuttgart.

Wellnhofer P. (1987) - Die Flughaut von *Pterodactylus* (Reptilia, Pterosauria) am Beispel des Wiener Exemplares von *Pterodactylus kochi* (Wagner). *Ann. Naturhist. Mus.* Wien 88 (A): 149-162, Basel

Wellnhofer P. (1991) - The Illustrated Encyclopedia of Pterosaurs. Salamander Books, Limited, 192 pp., London.

Wild R. (1973) - Die Triasfauna der Tessiner Kalkalpen XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). *Schweiz. Paläont. Abhandl.*, 95: 1-162, Basel.

Wild R. (1978) - Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. *Boll. Soc. Paleont. It.*, 17(2): 176–256, Bergamo.

Wild R. (1984a) - Flugsaurier aus der Obertrias von Italien. *Naturwissenschaften* 71: 1-11, Stuttgart.

Wild R. (1984b) - A new pterosaur (Reptilia, Pterosauria) from the Upper Triassic (Norian) of Friuli, Italy. *Gortania, Atti Mus. Friulano St. Nat.*, 5: 45-62, Modena.

Wild R. (1993) - A juvenile specimen of *Eudimorphodon ranzii* Zambelli (Reptilia, Pterosauria) from the upper Triassic (Norian) of Bergamo. *Riv. Mus. Civ. Sci. Nat. "E. Caffi" Bergamo*, 16: 95–120, Bergamo.

Williston S. W. (1903) - On the osteology of *Nyctosaurus* (*Nyctodactylus*) with notes on American pterosaurs. *Field Columbian Mus. Publ.*, Geological Series 2: 125-163, Chicago.

Appendix I

In the present analysis, based on Evans (1988), an abbreviated distribution of 104 characters is shown below for the single outgroup, *Petrolacosaurus*, and 21 diapsid taxa. Synapomorphies are listed for each ingroup as optimized under delayed character-state transformation. Abbreviations as follows: P = a character found in basal pterosaurs; ~~P~~ = a character not found in basal pterosaurs; P+ a character transformed to the next character state in pterosaurs; P? = questionable or unknown

PAUP Analysis

Unlisted nodes A-C, F, I-P as in Evans (1988)

(Node H) - Thalattosauria + *Trilophosaurus* + *Megalancosaurus* + Prolacertiformes + Archosauria

H1 - 91. Long narrow snout at least half the length of skull - P
H2 - 92. Ribs run back parallel to cervical vertebral column - P
H3 - 93. Cervical ribs with anterior processes - P

(Node H) - *Trilophosaurus* + *Megalancosaurus* + Prolacertiformes + Archosauria
H4 - 94. Nasals longer than frontals - P?

(Node H) - *Megalancosaurus* + Prolacertiformes + Archosauria
H5 - 95. Posterior dentary teeth lie anterior to posterior maxillary teeth - P

(Node H) - Prolacertiformes + Archosauria
H6 - 96. Laterally compressed, recurved teeth - P
H7 - 97. Tapering cervical ribs - P

(Node D) - Archosauria
*D1 - 27. Antorbital fenestra (with fossa) - Ᵽ
D2 - 28. Marginal teeth serrated - Ᵽ
D3 - 29. Postparietals retained but fused - Ᵽ
D4 - 30. Postfrontal reduced - Ᵽ
D5 - 31. Posterior border of lower temporal fenestra bowed - Ᵽ
D6 - 32. Loss of trunk intercentra - P (convergent with *Boreopricea* + Tapinoplatia = E5)
D7 - 33. No ectepicondylar groove or foramen - P (convergent with Fenestrasauria)
E20 - 53. Pes centrale absent - Ᵽ

(Node E) - *Protorosaurus* + *Prolacerta* + *Boreopricea* + Tapinoplatia
E1 - 34. Cervical neural spines long and low - P
E2 - 35. Lacrimal fails to meet nasal - Ᵽ (reversed in Fenestrasauria)
E3 - 36. Long slender cervical ribs - P

(Node E) - *Boreopricea* + Tapinoplatia (see below)
E4 - 37. Tall maxilla - P
E5 - 38. Loss of trunk intercentra - P (convergent with Archosauria = D6)
E7 - 40. First distal carpal lost or fused - P?
E8 - 41. Loss of intermedium in carpus - P?
E9 - 42. Reduced ilium contribution to acetabulum - P
E10 - 43. Loss of quadratojugal - P (a new QJ appears in Fenestrasauria)
E13 - 46. Fourth metatarsal longer than three times the fifth metatarsal - P
E14 - 47. Lacrimal restricted to orbit rim - P
E15 - 48. Loss of manus centralia - P?

Tapinoplatia = *Macrocnemus* + Characiopoda (see below)
E6 - 39. Low scapula - P+ (transformed in Fenestrasauria)
E17 - 50. Nasals taper anteromedially - Ᵽ (reversed in Fenestrasauria)
E18 - 51. Reduction of dorsomedial process of premaxilla - Ᵽ (reversed in Fenestrasauria)
E19 - 52. Thyroid foramen present - Ᵽ (reversed in Fenestrasauria)

Characiopoda = (*Tanystropheidae* + *Langobardisaurus* + Fenestrasauria)
E12 - 45. Loss of first distal tarsal - P
E21 - 54. Reduction of ventral ramus of squamosal, cotyle for quadrate head - P
E24 - 57. Fifth metatarsal short and geometrical - P
E25 - 58. Long ground (= proximal) phalanx on pedal digit V - P
E27 - 60. Last few dorsals with fused ribs (in adults) - P+
E29 - 62. Post-cloacal bones (males only) - P
E31 - 49. Maximum of five ossified tarsals - P
* new 100. Hemal arches reduced or parallel to mid and distal centra - P
* new 104. Procoelous vertebrae - P (except in *Tanystropheus*)

Tanystropheidae
E22 - 55. Fourth metacarpal shorter than third - Ᵽ
E23 - 56. Reduction in length of pedal digit IV - P (convergent with *Sharovipteryx* + Pterosauria)
E26 - 59. Twelve cervical vertebrae - Ᵽ
E28 - 61. Longest cervical vertebrae lies at end of series - (not present in any included taxa)
E30 - 63. Ilium short versus ischium - Ᵽ
E31 - 64. No more than four ossified tarsals - Ᵽ

Fenestrasauria = (*Cosesaurus* + *Longisquama* + *Sharovipteryx* + Pterosauria)
D7 - 33. No ectepicondylar groove or foramen - P (convergent with Fenestrasauria)
E11 - 44. Loss of perforated foramen in ankle - P
E23 - 56. Reduction in length of pedal digit IV - P (not *Cosesaurus* and convergent with Tanystropheidae)
* new 98. Uropatagia - P (confirmed only in *Sharovipteryx* and some pterosaurs)
* new 99. Prominent anterior process of ilium - P
* new 101. Reduced transverse processes on caudals - P
* new 102. Antorbital fenestra(e) (without fossa) - P
* new 103. Attenuated fibula - P

Characters ordered by anatomical region

Character states for the analysis based on Evans (1988)

Cranial Characters
27 D1. Antorbital fenestra - (0) absent (1) present (also see character 102)
28 D2. Marginal teeth serrated - (0) absent (1) present
29 D3. Postparietals retained but fused - (0) not fused (1) fused
30 D4. Postfrontal reduced - (0) unreduced (1) reduced
31 D5. Posterior border of lower temporal fenestra bowed - (0) absent (1) present
35 E2. Lacrimal fails to meet nasals - (0) contact (1) no contact
37 E4. Tall maxilla - (0) absent (1) present
43 E10. Loss of quadratojugal - (0) no loss (1) loss (2*) new appearance
17 E14. Lacrimal restricted to orbit rim - (0) absent (1) present
50 E17. Nasals taper anteromedially - (0) absent (1) present
51 E18. Reduction of dorsomedial process of premaxilla - (0) unreduced (1) reduced
54 E21. Reduction of ventral ramus of squamosal, cotyle for quadrate head - (0) unreduced (1) reduced
91 H1. Long narrow snout at least half the length of skull - (0) absent (1) present
94 H4. Nasals longer than frontals - (0) absent (1) present
95 H5. Posterior dentary teeth lie anterior to posterior maxillary teeth - (0) absent (1) present
96 H6. Laterally compressed, recurved teeth - (0) absent (1) present

Axial Characters
32 D6. Loss of trunk intercentra - (0) no loss (1) loss
34 E1. Cervical neural spines long and low - (0) absent (1) present
36 E3. Long slender cervical ribs - (0) absent (1) present
38 E5. Loss of trunk intercentra - (0) no loss (1) loss
59 E26. Twelve cervical vertebrae - (0) absent (1) present
58 E27. Last few dorsals with fused ribs - (0) absent (1) present
38 E28. Longest cervical vertebra lies at end of series - (0) absent (1) present

92 H2. Cervical ribs run back parallel to cervical vertebral column - (0) not parallel (1) parallel (2*) no ribs
93 H3. Cervical ribs with anterior processes - (0) absent (1) present
97 H7. Tapering cervical ribs - (0) absent (1) present (2*) no ribs
100 *new. Hemal arches reduced or parallel to medial and distal caudal centra - (0) absent (1) present
101 *new. Transverse processes on caudal vertebrae reduced - (0) absent (1) present
104 *new. Procoelous vertebrae - (0) absent (1) present

Appendicular Characters

33 D7. No ectepicondylar groove or foramen - (0) groove or foramen present (1) absent
39 E6. Low scapula - (0) broad and tall (1) low (2*) posteriorly oriented and strap-like (3*) tall and strap-like
40 E7. First distal carpal lost or fused - (0) not lost (1) lost or fused
41 E8. Loss of intermedium in carpus - (0) no loss (1) loss
42 E9. Reduced ilium contribution to acetabulum - (0) not reduced (1) reduced
44 E11. Loss of perforated foramen in ankle - (0) no loss (1) loss
45 E12. Loss of first distal tarsal - (0) no loss (1) loss
46 E13. Fourth metatarsal longer than three times the fifth metatarsal - (0) not longer (1) longer
48 E15. Loss of manus centralia - (0) no loss (1) loss
49 E16. Maximum of five ossified tarsals - (0) six or more (1) no more than five
52 E19. Thyroid foramen - (0) absent (1) present
E20. Loss of pes centrale - (0) no loss (1) loss
55 E22. Fourth metacarpal shorter than third - (0) fourth longer (1) fourth shorter
56 E23. Reduction in length of foot = 4th metacarpal not the longest in the series - (0) fourth metacarpal longest (1) fourth metacarpal not longest
57 E24. Fifth metatarsal short and geometrical - (0) not short (1) short
58 E25. Long ground (proximal) phalanx on pedal digit V - (0) absent (1) present
63 E30. Ilium short versus ischium - (0) absent (1) present
64 E31. Four ossified tarsals - (0) five or more (1) no more than four
99 *new. Prominent anterior process of ilium - (0) absent (1) present
103 *new. Attenuated fibula - (0) absent (1) present

Other Ossifications and Dermal Membranes

62 E29. Post-cloacal bones - (0) absent (1) present
98 *new. Uropatagia - (0) absent (1) present

Appendix II

In the present analysis, based on Jalil (1997), the distribution and coding of 71 characters is shown below for the outgroup, *Petrolacosaurus* and 22 other diapsid taxa. Software specifications remain the same as those above. Only stem-based synapomorphies are listed.

Youngina + Sauria

19. [All] dorsal ribs holocephalus - P+
53. Pedal centrale present - P
58. First distal tarsal present - ₽ (absent in Characiopoda)

Sauria

1. Prefrontal-nasal suture anterolaterally directed - P
2. Tabular absent - P
3. Postparietal small - P
4. Ventral flange of squamosal narrow or confined to dorsal half of lower temporal fenestra - P
5. Quadrate emarginated - P
6. Stapedial foramen absent - P
7. Paroccipital-process-suspensorium contact strong - P
8. Retroarticular process well-developed - P
9. Cleithrum absent - P
10. Lateral centrale of manus small or absent - P
11. 5th distal tarsal absent - P
12. Fifth metatarsal hooked - P
13. Lower temporal arcade incomplete - ₽ (reversed in Archosauriformes and Pterosauria)
14. Postparietals absent - P
15. Lacrimal small or absent - P
28. Posterior process of jugal extending posteriorly nearly to back of skull - ₽ (reversed in Prolacertiformes)
29. Vertebrae non-notochordal in adults - P
44. Scapula high and narrow - ₽ (reversed in Tapinoplatia)
68. Parasphenoid-basisphenoid in the side wall of braincase - P
70. Crista prootica present - P

Lepidosauromorpha

16. Prominent lateral conch of the quadrate - ₽
17. Lateral exposure of the angular restricted - ₽
18. Retroarticular process entirely formed by articular - ₽
20. Intervertebral articulation formed by zygosphene-zygantrum - ₽
21. Ectepicondylar foramen present - ₽
22. Thyroid fenestra on the pelvis - ₽ (convergent with Tapinoplatia and derived Pterosauria)
23. Astragalus and calcaneum fused - P (convergent with Pterosauria)
24. "Lepidosauromorph" ankle joint where fourth distal tarsal has dorsal process fitting into recess on astragalocalcaneum - ₽
55. 4th metacarpal shorter than third metacarpal - ₽ (convergent with Tanystropheidae)
59. Perforating foramen in ankle absent - P (convergent with Fenestrasauria)
69. Pila antotica present - ₽

Choristodera + Archosauromorpha

19. [All] dorsal ribs not holocephalus - P
25. Premaxilla with well-developed posterodorsal process - P (reversed in some Tapinoplatia)
27. Quadratojugal L-shaped and/or situated behind upper temporal fenestra - ₽ (reversed in Tapinoplatia)
30. Cervical ribs dichocephalous - P
32. Entepicondylar foramen absent - P
35. Lateral tuber on the calcaneum - ₽ (reversed in Prolacertiformes)
37. Cervical ribs with anterior process - P (reversed in Rhynchosauria)
61. Nasals longer than frontals - P?

Archosauromorpha = (Rhynchosauria + *Proterosuchus* + Ornithodira + Prolacertiformes)

26. External naris elongated anteroposterior and close to the midline - P
31. Transverse processes of trunk vertebrae well-developed - P
33. Medial centrale in carpus absent - P
34. Concavo-convex astragalo-calcaneal articulation - P?
36. Tapering cervical ribs oriented posteriorly parallel to neck axis - P
41. Long, slender cervical ribs - P
66. Occipital condyle anterior to craniomandibular joint - P

Proterosuchus + **Ornithodira + Prolacertiformes**

62. Posterior dentary teeth lie anterior to posterior maxillary teeth - P
63. Teeth recurved and laterally compressed - P
64. Long narrow snout - P
65. Post-temporal fenestra small or absent - P

Ornithodira (= *Scleromochlus* + *Lagosuchus*)

53. Pedal centrale absent - Ᵽ
67. Loss of trunk intercentra - P (convergent with prolacertiformes)

Prolacertiformes

38. Skull low and narrow with short and narrow postorbital region - P
39. Quadratojugal, when present, much reduced and situated behind the temporal fenestra - P+ (new quadratojugal in Fenestrasauria)
50. Lacrimal fails to meet the nasal - Ᵽ (convergent with Rhynchosauria, reversed in Fenestrasauria)
67. Loss of trunk intercentra - P (convergent with Ornithodira)

Prolacerta + *Malerisaurus* + *Boreopricea* + *Jesairosaurus* + **Tapinoplatia**

28. Posterior process of jugal does not extend nearly to back of skull - P
40. Low and elongate cervical neural spines - P
42. Posterior process of jugal much reduced and spur-like - P
49. Nasals tapering anteromedially - Ᵽ (reversed in Fenestrasauria)
51. Manual centralia absent - P?
59. Perforating foramen in ankle present - Ᵽ (reversed in Fenestrasauria)

Tapinoplatia = (*Macrocnemus* + **Characiopoda**)

22. Thyroid fenestra on the pelvis - Ᵽ (reversed in Fenestrasauria)
27. Quadratojugal not L-shaped and/or situated behind upper [sic - lower] temporal fenestra - P
43. Quadratojugal absent - Ᵽ (new quadratojugal in Fenestrasauria)
44. Scapula not high and narrow - P+ (see 45)
45. Low sublunate scapula - P+ (see 44)
48. Ilium with reduced contribution in the acetabulum - P?
67. Loss of trunk intercentra - P

Characiopoda = (Tanystropheidae + *Langobardisaurus* + Fenestrasauria)

1. Prefrontal-nasal suture oriented anteroposteriorly parallel to internasal suture - P
6. Stapedial foramen present - P?
18. Retroarticular process entirely formed by articular - P
19. Dorsal ribs holocephalus (except anterior three pairs) - P
35. Lateral tuber on the calcaneum absent - P
46. First distal carpal absent - P
47. Carpal intermedium absent - P
52. Maximum of five ossified tarsals - P
54. Reduced ventral flange of squamosal - P
57. Posterior dorsal vertebrae with fused ribs (in adults) - P+
58. First distal tarsal absent - P
59. Perforating foramen in ankle absent - P (except in *Tanystropheus*)
60. Post-cloacal bones (in males) - P
71. First phalanx of the fifth toe elongated (metapodial) - P

Tanystropheidae

55. Fourth metatarsal shorter than third - Ᵽ
56. Twelve cervical vertebrae - Ᵽ

Fenestrasauria (*Cosesaurus* + *Longisquama* + *Sharovipteryx* + **Pterosauria**)

22. No thyroid fenestra on the pelvis - P
43. Quadratojugal secondarily present - P
49. Nasals do not taper anteromedially - P
50. Lacrimal meets nasal - P

Characters ordered by anatomical region

Character states for the analysis based on Jalil 1997

Cranial Characters

1. Prefrontal-nasal suture - (0) oriented anteroposteriorly parallel to internasal suture (1) anterolaterally directed
2. Tabular - (0) present (1) absent
3. Postparietal - (0) large (1) small
4. Ventral flange of squamosal narrow or confined to dorsal half of lower temporal fenestra - (0) no (1) yes
5. Quadrate - (0) not emarginated (1) emarginated
6. Stapedial foramen - (0) present (1) absent
7. Paroccipital process-suspensorium contact - (0) weak (1) strong
8. Retroarticular process well-developed - (0) no (1) yes
13. Lower temporal arcade - (0) complete (1) incomplete
14. Postparietals absent - (0) no (1) yes
15. Lacrimal - (0) large (1) small or absent
16. Prominent lateral conch on the quadrate - (0) no (1) yes
17. Lateral exposure of the angular - (0) large (1) restricted
18. Retroarticular process entirely formed by articular - (0) no (1) yes
25. Premaxilla with well-developed posterodorsal process - (0) no (1) yes
26. External naris elongated anteroposteriorly and close to the midline - (0) no (1) yes
27. Quadratojugal L-shaped and/or situated behind upper [sic - lower] temporal fenestra - (0) no (1) yes
28. Posterior process of jugal extending posteriorly nearly to back of skull - (0) no (1) yes
38. Skull low and narrow with short and narrow postorbital region - (0) no (1) yes [here a low and narrow snout scored a (1) despite the presence of large orbits and a high cranium]
39. Quadratojugal, when present, much reduced and situated behind lower temporal fenestra - (0) no (1) yes (2) quadratojugal absent [refers to original qj only]
42. Posterior process of the jugal much reduced and spur-like – (0) no (1) yes
43. Quadratojugal - (0) present (1) absent (2) reappearance
49. Nasal tapering anteromedially - (0) no (1) yes
50. Lacrimal fails to meet the nasal - (0) no (1) yes
54. Reduced ventral flange of squamosal - (0) no (1) yes
61. Nasals longer than the frontals - (0) no (1) yes
62. Posterior dentary teeth lie anterior to posterior maxillary teeth - (0) no (1) yes
63. Teeth recurved and laterally compressed - (0) no (1) yes
64. Long and narrow snout - (0) no (1) yes
65. Post-temporal fenestra small or absent - (0) no (1) yes
66. Occipital condyle anterior to craniomandibular joint - (0) no (1) yes

Axial Characters

19. [All] dorsal ribs holocephalus - (0) no (1) yes

20. Intervertebral articulation formed by zygosphene-zygantrum - (0) no (1) yes

29. Vertebrae non-notochordal in adult - (0) no (1) yes

30. Cervical ribs dichocephalous - (0) no (1) yes

31. Transverse processes of trunk vertebrae well-developed - (0) no (1) yes

36. Tapering cervical ribs oriented posteriorly parallel to neck axis - (0) no (1) yes

37. Cervical ribs with anterior processes - (0) no (1) yes

40. Low and elongated cervical neural spines - (0) no (1) yes

41. Long slender cervical ribs - (0) no (1) yes

56. Twelve cervical vertebrae - (0) no (1) yes

57. Posterior dorsal vertebrae with fused ribs – (0) no (1) yes

67. Loss of trunk intercentrum - (0) no (1) yes

68. Parasphenoid-basisphenoid in the side wall of braincase - (0) no (1) yes

69. Pila antotica - (0) absent (1) present

70. Crista prootica - (0) absent (1) present

Appendicular Characters

9. Cleithrum - (0) present (1) absent

10. Lateral centrale of manus - (0) present (1) small or absent

11. Fifth distal tarsal - (0) present (1) absent

12. Fifth metatarsal hooked - (0) no (1) yes

21. Ectepicondylar foramen - (0) absent (1) present

22. Thyroid fenestra on the pelvis - (0) absent (1) present

23. Astragalus and calcaneum - (0) unfused (1) fused

24. "Lepidosauromorph" ankle joint where fourth distal tarsal has dorsal process fitting into recess on astragalocalcaneum - (0) no (1) yes

32. Entepicondylar foramen - (0) present (1) absent

33. Medial centrale in carpus - (0) present (1) absent

34. Concavo-convex astragalo-calcaneal articulation - (0) no (1) yes

35. Lateral tuber on the calcaneum - (0) no (1) yes

44. Scapula high and narrow - (0) no (1) yes

45. Low sublunate scapula - (0) no (1) yes

46. First distal carpal - (0) present (1) absent

47. Carpal intermedium - (0) present (1) absent

48. Ilium with reduced contribution in the acetabulum - (0) no (1) yes

51. Manual centralia - (0) present (1) absent

52. Maximum of five ossified tarsals - (0) no (1) yes

53. Pedal centrale - (0) present (1) absent

55. Fourth metacarpal shorter than third metacarpal - (0) no (1) yes

58. First distal tarsal - (0) present (1) absent

59. Perforating foramen in ankle - (0) present (1) absent

71. First phalanx of the fifth toe elongated (as long as the metacarpals [sic - metatarsals] of digits I-IV) - (0) no (1) yes

Other Ossifications and Dermal Membranes

60. Post-cloacal bones - (0) absent (1) present [absence is suspect - does not appear in females]

Appendix III

In the present analysis, based on Bennett (1996a), the distribution and coding of 126 previously established characters plus 4 new ones is shown below for the outgroup, Lepidosauromorpha, and the 17 diapsid taxa considered in this analysis.

Archosauromorpha = (*Trilophosaurus* + Rhynchosauria + Prolacertiformes + Archosauriformes)

1. Premaxilla enlarged and forming most of the tip of the snout - P

2. Prominent subnarial process of premaxilla present so that the maxilla is excluded from the external nares - Ᵽ (reversed in Fenestrasauria)

4. Postorbital ramus of jugal extends to the middle of the lower temporal fenestra - P

5. Squamosal reduced to one-half or less of height of lower temporal fenestra - P

6. Tabular absent - P

7. Tall dorsal process of the maxilla present - P

10. Ectopterygoid more or less broadly contacts jugal behind the posterior limit of the maxilla - P+ (fused to the pterygoid in Fenestrasauria)

12. Paroccipital process of the opisthotic contact the suspensorial region of the skull with tapered distal ends - P

13. External nares elongate and close to midline (except *Trilophosaurus*) - P

14. Parietal foramen absent - P (reversed in *Tanystropheus*)

19. Stapes slender without foramen - P

20. Vertebrae not notochordal in adults - P

21. Transverse processes of the trunk vertebra, moderate - P+ (elongate but most not two-headed)

22. Cervical rib heads plowshare-shaped and elongate shafts extend posteriorly parallel to centra and broadly overlap one another - P

23. Cleithrum absent - P

24. Entepicondylar foramen in humerus absent - P

25. Foramen between ulnare and intermedium absent - P

27. Pedal centrale not displaced laterally - P

28. Distal tarsal V absent - P

29. Metatarsal V hooked medially to contact distal tarsal IV but not gracile - P

35. Postparietals absent - P

37. Exoccipital and opisthotic fuse early in post-hatching ontogeny - P

44. Upper temporal fenestra large and facing dorsolaterally - P

53. Teeth on transverse process of pterygoids absent - P

55. Intercentra of postaxial presacral vertebrae present - Ᵽ (reversed in Tapinoplatia)

71. Manual asymmetry with digit IV the stoutest and longest; more medial digits progressively diminishing in length and robustness - P+ (plesiomorphic in amniotes; transformed in *Sharovipteryx* and pterosaurs)

95. Metatarsals II, III and IV unequal in length with metatarsal IV longest - Ᵽ (reversed in *Sharovipteryx* and pterosaurs)

96. Pedal digit III shorter than IV - Ᵽ (reversed in *Sharovipteryx* and pterosaurs)

100. Length of centra of cervical vertebral 3-5 greater than those of mid-dorsal vertebrae - P

120. Calcaneal tubercle present - Ᵽ (reversed in Prolacertiformes)

126. Pedal digit V unreduced - P+

Prolacertiformes + Archosauriformes

3. Preorbital region elongate - P

8. Ventral extent of quadrate further below braincase so that the adductor chamber is enlarged - P

9. Metakinetic skull - P

11. Pyriform recess narrow and extends forward to separate pterygoids and posterior end of vomers - Ᵽ (reversed in *Cosesaurus* + pterosaurs)

15. Posttemporal fenestra small or absent - P

16. Marginal tooth shape recurved - P

17. Marginal tooth cross-section laterally compressed with sharply pointed crowns - P
18. Maxillary tooth row extends further posteriorly than mandibular row - P
26. Medial centrale in carpus absent - P
31. Skull height greater than one-third skull length - P
32. Skull shape subtrapezoidal in cross-section from just anterior to orbits to posterior end of skull and snout high, narrow, and subtriangular in cross-section - P
33. Postfrontals reduced - P
67. Distal end of humerus subequal to proximal end - ₽ (reversed in *Sharovipteryx* + Pterosauria)
68. Ectepicondylar foramen or groove of humerus absent - P
90. Astragalocalcaneal canal present - ₽ (reversed in Fenestrasauria)
100. Length of centra of cervical vertebra greater than mid-dorsal - P

Prolacertiformes (sensu Bennett 1996a)

5. Squamosal descending ramus posterior to quadrate - P
46. Otic notch not deeply arched in profile - P
52. Tooth implantation thecodont - P? (convergent with *Euparkeria* + Archosauria)
55. Intercentra absent from postaxial/presacral vertebrae - P (convergent with Proterochampsidae + *Euparkeria* +Archosauria)
58. Parapophysis transfers to neural arch in anterior dorsal vertebrae; diapophysis and parapophysis fuse in posterior dorsal vertebrae and ribs become single-headed - P (convergent with *Euparkeria* + Archosauria)
70. Manus length, less than half that of tarsus and pes - ₽ (convergent with Erythrosuchidae + Proterochampsidae + *Euparkeria* + Archosauria; reversed in Fenestrasauria)
85. Astragalar tibial facet concave - P
86. Astragalar tibial and fibular facets adjacent - P+ (no fibula contact)
89. Ventral astragalocalcaneal facet much larger than the dorsal - P? (convergent with Archosauria)
98. Pedal digit V length extended - P (only in Characiopoda)
107. Fore limb length less than half that of hind limb - ₽ (reversed in Fenestrasauria)
112. Bird-like distal end of femur (prominent anterior and posterior intercondylar grooves with latter constricted by prominent external tibial condyle) - P (only in Characiopoda)
118. Ventral flange of astragalus absent - P
119. Astragalus posterior groove absent - P
120. Calcaneal tubercle absent - P (convergent with Ornithodira)
122. Pedal stance-not considered
124. Metatarsus configuration compact - P (reversed in *Sharovipteryx* and derived pterosaurs)
125. Metatarsal 3 length more than one half tibial length - ₽ (reversed in *Sharovipteryx* + Pterosauria)
126. Pedal digit V extended - P (only in Characiopoda)
**128. Proximal phalanx of pedal digit V elongate - P (only in Characiopoda)
**129. Postcloacal bones (in male Characiopoda only) - P

Fenestrasauria = (*Cosesaurus* + *Longisquama* + *Sharovipteryx* + Pterosauria)

11. Pyriform recess broad but confined to posterior margins of pterygoids - P
30. Anteroposterior hook of metatarsal V absent - P
36. Supratemporals absent - P (convergent with Archosauriformes)
40. Ossified laterosphenoid present - P (convergent with Archosauriformes)
41. Antorbital fenestra(e) present - P (convergent with Archosauriformes)
42. Antorbital fenestra position close to nares - P
48. Coronoid reduced or absent - P (convergent with Archosauriformes)
56. Number of sacral vertebrae four or more - P
59. Interclavicle keeled or anterior process well developed and lateral processes reduced - P
62. Anteroposterior width of scapula narrow and posteriorly directed - P
73. Iliac spine long and knife-like - P
78. Hind limb posture semi-erect - not considered
90. Astragalocalcaneal canal absent - P (convergent with *Euparkeria* + Archosauria)
97. [No more than] four phalanges on pedal digit V - P (convergent with Archosauriformes)
101. Configuration of cervicals 3-6, simple curve to vertical - P
104. Clavicles overlapping - P
107. Fore limb length not less than half that of hind limb - P
*114. Fibula 90-30% as thin as tibia - P (convergent with Archosauriformes)
122. Pedal stance not considered
125. Metatarsal 3 length not more than one half tibial length - P

Pterosauria (* = unknown in *Longisquama*)

38. Suborbital ramus of jugal extends anterior to orbit (as in *Longisquama*, convergent with Archosauriformes)
39. Vomers reduced* (convergent with Archosauriformes)
52. Tooth implantation thecodont* (convergent with *Euparkeria* + Archosauria)
67. Distal humerus narrower than proximal end (as in *Sharovipteryx*)
79. Femoral shaft curvature bowed anteriorly* (convergent with Ornithosuchidae + Ornithodira)
95. Metatarsals II, III and IV subequal in length* (as in *Sharovipteryx*)
96. Pedal digit III not shorter than IV* (as in *Sharovipteryx*)
103. Caudal zygapophyseal facets intertwined* (as in *Sharovipteryx*)
105. Coracoid strut-like (imminent in *Longisquama*, unknown in *Sharovipteryx*)
114. Fibula less than 30% as wide as tibia (as in *Sharovipteryx*)
113. Tibial length greater than or equal to femur* (as in *Sharovipteryx*)
116. Astragalus transversely widened* (as in *Sharovipteryx*?)
**130. Uropatagia present* (as in *Sharovipteryx*)

Archosauriformes

27. Pedal centrale displaced laterally - ₽
38. Suborbital ramus of jugal extends anterior to orbit - P (convergent with *Longisquama* and Pterosauria)
39. Vomers reduced - P (convergent with Jurassic Pterosauria)
40. Ossified laterosphenoid present - P (convergent with *Cosesaurus* and Pterosauria)
41. Antorbital fenestra present - P (convergent with Fenestrasauria)
42. Antorbital fenestra position separated from naris by a long stretch of premaxilla and maxilla - ₽
44. Upper temporal fenestra reduced in size, directed dorsally and barely visible in lateral view - ₽
45. Posterior margin of the lower temporal fenestra bowed anteriorly - ₽
48. Coronoid reduced or absent - P (convergent with Fenestrasauria)
50. Marginal teeth serrated - ₽

72. Distal condyles of metacarpal I slightly offset such that the pollex is directly medial - ₽
97. Four phalanges of pedal digit V - ₽
126. Pedal digit V reduced in size - ₽

Erythrosuchidae + Proterochampsidae + *Euparkeria* + Archosauria

11. Pyriform recess reduced; pterygoids meet medially in palate - ₽ (convergent with *Tanystropheus*)
12. Paroccipital process of the opisthotic contacts the suspensorial region of the skull with expanded distal ends - ₽
27. Pedal centrale displaced laterally [or absent] - ₽
30. Anteroposterior hook of metatarsal V present - ₽
36. Supratemporals absent - P (convergent with Fenestrasauria)
43. Prominent antorbital fossa surrounding antorbital fenestra - ₽
49. External mandibular fenestra present - ₽
51. Enlarged anterior dentary teeth project upward between upper tooth rows in more or less prominent diastema and often accompanied by more or less prominent notch between premaxilla and maxilla - ₽
62. Anteroposterior width of scapula tall and narrow - P (convergent with *Longisquama*)
66. Deltopectoral crest extends at least one-quarter of way down shaft of humerus - ₽
70. Manus length less than half that of tarsus and pes - ₽ (convergent with basal Tapinoplatia)
*73. Iliac spine broad and ax-like - ₽
81. Fourth trochanter of femur mound-like - ₽
94. Lateral centrale of pes fused to astragalus - ₽
105. Coracoid small and subcircular - ₽

Proterochampsidae + *Euparkeria* + Archosauria

14. Parietal foramen absent - P (convergent with Prolacertiformes, except *Tanystropheus*)
21. Transverse processes of the trunk vertebrae elongate resulting in proximal bifurcation of the trunk ribs - ₽
30. Anteroposterior hook of metatarsal V absent - P (as in basal Diapsida)
55. Intercentra of postaxial presacral vertebrae absent - P (convergent with Prolacertiformes)
59. Interclavicle lateral processes reduced - P (convergent with Fenestrasauria)
60. Dorsal body osteoderms present in a single median dorsal row - ₽
64. Archosaur humerus present - ₽
69. Ulna much stouter than radius - ₽
71. Manual digit IV not the stoutest and longest - ₽
78. Hind limb posture semi-erect (not considered)
79. Femoral shaft curvature sigmoid - ₽
86. Astragalar tibial and fibular facets adjacent - ₽
87. Crocodyloid tarsus absent - P (as in basal Diapsida)
96. Pedal digit III not shorter than IV - P (convergent with *Tanystropheus* and *Sharovipteryx* + pterosaurs)

Euparkeria + Archosauria

46. Otic notch deeply arched in profile and the squamosal has a more or less prominent process that hooks down behind the head of the quadrate - ₽ (convergent only with derived pterosaurs)
52. Tooth implantation thecodont - P? (convergent with Prolacertiformes)
57. Spine tables present - ₽
58. Parapophysis transfers to neural arch in anterior dorsal vertebrae; diapophysis and parapophysis fuse in posterior dorsal vertebrae and ribs become single-headed - P (convergent with Prolacertiformes)
60. Dorsal body osteoderms present in paired parasagittal rows - ₽
75. Length of ischium relative to width of acetabulum, posteroventrally elongate - ₽
90. Astragalocalcaneal canal absent - P (convergent with Fenestrasauria)

Archosauria

9. Metakinetic skull not present - ₽
11. Pyriform recess reduced; pterygoids meet medially in palate - ₽ (convergent with *Tanystropheus*)
34. Parietals send caudal processes onto occiput which meet the supraoccipital - ₽
40. Ossified laterosphenoid present - P (convergent with Fenestrasauria)
47. Dentary-splenial mandibular symphysis present along one-third of lower jaw - ₽
54. Palatal teeth absent - ₽
61. One-to-one alignment between dorsal body osteoderms and vertebrae - ₽
65. Medial margin of proximal humerus strongly arched - ₽
83. Fibular anterior trochanter knob-shaped and robust - ₽
84. Fibular distal end width greater than proximal end - ₽
88. Astragalar ventral articular facet for calcaneum cupped - ₽
89. Astragalocalcaneal ventral facet much larger than the dorsal - ₽
91. Hemicylindrical calcaneal condyle present - P?
92. Calcaneal facets for fibular and distal tarsal 4 contiguous - ₽
93. Calcaneal tubercle orientation more than 45° posteriorly, shaft broader than tall, and distal end rounded - ₽

Suchia + Ornithosuchidae

74. Puboischiadic plate absent but bones relatively short and broad - ₽
76. Pubis length equal to ischium - ₽ (convergent with *Cosesaurus* + pterosaurs)
77. Pubic acetabular margin recess present - ₽
85. Astragalar tibial facet saddle-shaped - ₽
98. Pedal digit V reduced (shorter than I) - ₽
111. Acetabulum perforate - ₽ (Suchia and Dinosauromorpha converge)

Ornithosuchidae + Ornithodira (sans Pterosauria)

5. Squamosal reduced and descending ramus gracile - ₽ (convergent with derived pterosaurs)
9. Metakinetic skull - P (convergent with Fenestrasauria)
29. Metatarsal V hooked medially to contact distal tarsal IV and gracile - ₽
56. Number of sacral vertebrae, three - ₽ (Ornithosuchidae only, convergent with derived dinosaurs)
63. Coracoid (= biceps) tubercle lies close to glenoid fossa and coracoid foramen - ₽
71. Manual asymmetry marked with digits IV and V very reduced - ₽
72. Distal condyles of metacarpal I conspicuously offset such that the pollex is directly medially and ungual enlarged - ₽
74. Pubis and ischium contact, puboischiadic plate absent and bones elongate - ₽
79. Femoral shaft curvature bowed anteriorly - P (convergent with Pterosauria)
80. Lesser trochanter of femur, present early in post-hatching ontogeny - ₽
81. Fourth trochanter of femur sharp (= aliform) flange - ₽
82. Prominent cnemial crest on tibia present - ₽

88. Astragalar ventral articular facet for calcaneum pegged - Ᵽ
118. Ventral flange of astragalus absent - P (convergent with Diapsida)

Ornithodira (sans Pterosauria)

33. Postfrontal absent - Ᵽ
47. Dentary-splenial mandibular symphysis distally positioned - P (as in basal Diapsida)
59. Interclavicle absent - Ᵽ
60. Dorsal body osteoderms absent - P (as in basal Diapsida)
65. Median margin of proximal humerus weakly arched - P (as in *Sharovipteryx*)
77. Pubic acetabular margin recess absent - P (as in basal Diapsida)
83. Fibula anterior trochlea crest-shaped and low - Ᵽ
84. Fibular distal end width subequal or less than proximal end width - P (as in basal Diapsida)
91. Hemicylindrical calcaneal condyle absent - P? (difficult to determine)
99. Atlantal intercentrum enlarged and surrounding odontoid process - Ᵽ
103. Caudal zygapophyseal facets nearly vertically disposed in all but proximal part of the tail - Ᵽ
104. Clavicle present, because it is present in theropods - P (as in basal Diapsida)
106. Glenoid fossa of scapulocoracoid faces ventroposteriorly - Ᵽ
107. Fore limb length less than half that of hind limb - Ᵽ (otherwise convergent with Prolacertiformes)
109. Apex of deltopectoral crest more distally placed on humerus - Ᵽ
110. Prominent supraacetabular crest on ilium present - Ᵽ
113. Tibial length greater than or equal to femur - P (convergent with *Sharovipteryx* and Pterosauria)
114. Fibula 90-30% as thin as tibia - P (convergent with Fenestrasauria)
115. Advanced mesotarsal ankle with astragalus and calcaneum tightly appressed to tibia - P (convergent with Pterosauria)
116. Astragalus transversely widened - P (convergent with *Sharovipteryx* and Pterosauria)
117. Ascending process of astragalus fitting between tibia and fibula - Ᵽ
119. Astragalar posterior groove absent - P (convergent with Prolacertiformes)
120. Calcaneal tubercle absent - P (convergent with Prolacertiformes)
121. Distal tarsal 4 transverse width subequal to distal tarsal 3 - Ᵽ
122. Pedal stance (not considered)
124. Metatarsus configuration compact - P (convergent with Prolacertiformes)
125. Metatarsal 3 more than one half tibial length - Ᵽ

Dinosauromorpha (sans **Pterosauria**)

76. Pubis length longer than ischium - Ᵽ
101. Centra of cervicals 3-6 in a sigmoid curve - Ᵽ
102. Division of presacral vertebral column into cervical, cervico-dorsal and dorsal regions - Ᵽ
108. Deltopectoral shape subrectangular - Ᵽ (convergent with derived pterosaurs)
111. Acetabulum perforate - Ᵽ
112. Bird-like distal end of femur - Ᵽ (convergent with Characiopoda)
123. Pes functionally tridactyl - P

Characters ordered by anatomical region

Character states for the analysis based on Bennett (1996a)

(*) indicates new character state

(**) indicates new characters added to Bennett's list

(~~o~~.) and (>) indicates restructured character state

Skull Characters

1. Premaxilla size - (0) small (1) enlarged, forming most of the tip of the snout
2. Prominent subnarial process of premaxilla - (0) absent, so that external naris is bounded by maxilla, lacrimal and nasal posteriorly (1) present, so that the maxilla is excluded from the external naris
3. Preorbital region (0) not elongate (1) elongate.
4. Postorbital ramus of jugal - (0) extends to the middle of lower temporal fenestra or less (1) extends well posterior to the center of lower temporal fenestra
5. Squamosal - (0) not reduced and ventral process extends to inferior margin of lower temporal fenestra (1) reduced to one-half or less of height of lower temporal fenestra (2) reduced and descending ramus gracile
4. "Ventral flange of squamosal narrow or confined to dorsal half of lower temporal fenestra - (0) no (1) yes" *restructured* as: > 4. Squamosal - (0) not reduced (1) reduced and descending ramus anterior to quadrate (2) reduced and descending ramus gracile (3) descending ramus posterior to quadrate (4) no descending ramus
6. Tabular - (0) present (1) absent
~~7~~. "Tall dorsal process of quadratojugal – (0) absent (1) present" *restructured* as: > 7. Quadratojugal - (0) contact with squamosal (1) absent (2) spur medioposterior to jugal
8. Ventral extent of quadrate - (0) not much below the level of the braincase so the adductor chamber is small (1) further below braincase so that the adductor chamber is enlarged
9. Metakinetic skull - (0) absent (1) present
10. Ectopterygoid - (0) broadly contacts the maxilla and narrowly contacts the jugal in ventral view (1) more or less broadly contacts jugal behind the posterior limit of the maxilla
11. Pyriform recess - (0) broad but confined to posterior margins of pterygoids (1) narrow and extends forward to separate pterygoids and posterior end of vomers (2) reduced, pterygoids meet medially in palate
12. Paroccipital processes of the opisthotic - (0) do not contact the suspensorial region of the skull (1) contact the suspensorial region of the skull with tapered distal ends (2) contact the suspensorial region of the skull with vertically expanded distal ends
13. External nares - (0) rounded and well separated by process of the premaxillae and nasals (1) elongate and close to midline
14. Parietal foramen - (0) present (1) absent
15. Posttemporal fenestra - (0) relatively large (1) small or absent
16. Marginal tooth shape - (0) peg-like (1) recurved
17. Marginal tooth cross-section - (0) not laterally compressed with sharply pointed crowns (1) laterally compressed with sharply pointed crowns
18. Posterior extent of mandibular and maxillary tooth rows – (0) subequal (1) unequal, with maxillary tooth row extending further posteriorly
19. Stapes - (0) with foramen for stapedial artery (1) slender without foramen
31. Skull height - (0) less than one-third skull length (1) greater than or equal to one-third skull length
32. Skull shape - (0) rounded in cross-section (1) subtrapezoidal in cross-section from just anterior to orbits to posterior

end of skull, and snout high, narrow and subtriangular in cross-section

33. Postfrontal - (0) large (1) reduced (2) absent

34. Parietals - (0) do not send caudal processes onto occiput (1) send caudal processes onto occiput which meet the supraoccipital

35. Postparietals - (0) paired (1) fused into single median element (2) absent

36. Supratemporals absent - (0) present (1) absent

37. Exoccipital and opisthotic - (0) remain separate (1) fuse early in post-hatchling ontogeny

38. Suborbital ramus of jugal - (0) does not extend anterior to the orbit (1) extends anterior to the orbit

39. Vomers reduced - (0) relatively long and broad (1) reduced

40. Ossified laterosphenoid - (0) absent (1) present

41. Antorbital fenestra - (0) absent (1) present (2*) three present

42. Antorbital fenestra position - (0) separated from naris by a long stretch of premaxilla and maxilla (1) close to nares (2*) no antorbital fenestra

43. Prominent preorbital fossa surrounding antorbital fenestra - (0) absent (1) present (2*) no AOF

44. Upper temporal fenestra - (0) large and facing dorsolaterally (1) reduced in size, directed dorsally, and barely visible in lateral view

45. Posterior margin of lower temporal fenestra - (0) vertical (1) bowed anteriorly

46. Otic notch - (0) little modified from the primitive condition found in the Archosauromorpha (1) deeply arched in profile and the squamosal has a more or less prominent process that hooks down behind the head of the quadrate

47. Dentary-splenial mandibular symphysis length - (0) distally positioned (1) present along one-third of lower jaw

48. Coronoid - (0) unreduced (1) reduced or absent

49. External mandibular fenestra - (0) absent (1) present

50. Marginal teeth - (0) not serrated (1) serrated

51. Enlarged anterior dentary teeth project upward between upper tooth rows in more or less prominent diastema, often accompanied by more or less prominent notch between premaxilla and maxilla - (0) absent (1) diastema notch present

52. Tooth implantation - (0) subthecodont (1) thecodont

53. Teeth on transverse processes of pterygoids - (0) present (1) absent

54. Palatal teeth - (0) present (1) absent.

Axial Characters

20. Vertebrae - (0) with persistent notochordal canal until quite late in ontogeny (1) not notochordal in adults, and all vestiges of the notochordal canal disappear well before the attainment of maximum adult size.

21. Transverse process of trunk vertebrae - (0) feebly developed (1) moderately developed (2) elongate, resulting in proximal bifurcation of trunk ribs

22. Cervical rib shape and orientation - (0) heads not plowshare-shaped and shafts projecting posterolaterally (1) heads plowshare-shaped and elongate shafts extend posteriorly parallel to centra and broadly overlap one another

55. Intercentra of postaxial presacral vertebrae - (0) present (1) absent

56. Number of sacral vertebrae - (0) no more than two (1*) three (2*) four or more

57. Spine tables - (0) absent (1) present

58. Diapophysis and parapophysis - (0) Parapophysis on centrum in anterior dorsal vertebrae, and diapophysis and parapophysis separate in posterior dorsal vertebrae so ribs remain double-headed (1) parapophysis transfers to neural arch in anterior dorsal vertebrae, and diapophysis and parapophysis fuse in posterior dorsal vertebrae and ribs become single-headed

99. Atlantal intercentrum - (0) not enlarged (1) enlarged, completely surrounding odontoid ventrally and laterally and fitting into prominent recessed area below odontoid on axis

100. Length of centra of cervical vertebral 3 to 5 - (0) shorter than those of mid-dorsal vertebrae (1) subequal to those of mid-dorsal vertebrae (2) greater than those of mid-dorsal vertebrae

~~101~~. "Centra of cervical vertebrae 3 to 6 – (0) no more than moderately inclined (1) steeply inclined" *restructured* as: > 101. Cervical vertebrae – (0) more or less straight alignment (1) sigmoid curve (2) simple curve

102. Division of presacral vertebral column into cervical, cervico-dorsal, and dorsal regions - (0) absent (1) present

103. Caudal zygapophyseal facets - (0) disposed at no more than 45-60° from horizontal (1) nearly vertically disposed in all but proximal part of the tail (2*) intertwined

**127. Hemal arches and transverse processes – (0) unreduced (1) reduced

Fore Limb Characters

23. Cleithrum - (0) present (1) absent

24. Entepicondylar foramen in humerus - (0) present (1) absent

25. Foramen between ulnare and intermedium in carpus - (0) present (1) absent

26. Medial centrale in carpus (0) present (1) absent

59. Interclavicle (0) roughly T-shaped with well developed lateral processes (1) lateral processes reduced (2) absent (3*) keeled

~~62~~. Anteroposterior width of scapula relatively narrow (0) relatively broad (1) relatively narrow (length e" 2 times width) *restructured* as: > 62. Scapula (0) tall and broad (1) tall and narrow (2) narrow and posteriorly directed (3) short

63. Coracoid (= biceps) tubercle (0) not displaced dorsally (1) lies close to glenoid fossa and coracoid foramen

64. Archosaur humerus - (0) absent (1) present

65. Median margin of proximal humerus - (0) weakly arched (1) strongly arched

66. Deltopectoral crest - (0) extends no more than one-quarter of way down shaft of humerus (1) extends at least one-quarter of way down shaft of humerus

67. Distal end of humerus - (0) wider than proximal end (1) narrower than proximal end (2*) subequal

68. Ectepicondylar foramen or groove of humerus - (0) foramen or groove present (1) absent

69. Ulna and radius - (0) subequal in size (1) ulna much stouter than radius

70. Manus length - (0) greater than or equal to half that of tarsus and pes (1) less than half that of tarsus and pes

71. Manual asymmetry - (0) digit IV the stoutest and longest, with the more medial digits progressively diminishing in length and robustness (1) digits I and II much stouter than digits IV and V, which are reduced and divergent and digit III is longest (2) marked with digits IV and V very reduced.

72. Distal condyles of metacarpal I - (0) perpendicular to its long axis (1) slightly offset such that the pollex is directed medially (2) conspicuously offset such that the pollex is directed medially and ungual enlarged

104. Clavicle - (0) present (1) reduced or unossified (2*) overlapping

105. Coracoid - (0) large plate that curves beneath the body to approach the interclavicle on the midline (1) small, with subcircular profile, and lying in nearly same plane as the scapula (2*) strut-like

106. Glenoid fossa of scapulocoracoid - (0) faces mostly laterally (1) faces posteroventrally

107. Forelimb length - (0) greater than or equal to half that of hind limb (1) less than half that of hind limb
108. Deltopectoral crest shape - (0) crescentic (1) subrectangular (2*) little to no crest (3*) low median rise
109. Apex of deltopectoral crest - (0) less distally placed on humerus (1) more distally placed on humerus.

Hind Limb Characters

27. Pedal centrale - (0) not displaced (1) displaced laterally
28. Distal tarsal V - (0) present (1) absent
29. Metatarsal V - (0) short and expanded proximally, but not hooked medially (1) hooked medially to contact distal tarsal IV but not gracile (2) hooked medially to contact distal tarsal IV and gracile
30. Anteroposterior hook of metatarsal V - (0) present (1) absent
73. Iliac spine - (0) absent or feebly developed (1*) broad and ax-like (2*) long and knife-like
74. Pubis and ischium - (0) puboischiadic plate and broad contact between pubis and ischium present (1) puboischiadic plate absent, but bones relatively short and broad (2) puboischiadic plate absent and bones elongate
75. Length of ischium relative to width of acetabulum - (0) short (1) posteroventrally elongate
76. Pubis length - (0) not longer than ischium (1) longer than ischium
77. Pubic acetabular margin recess - (0) absent (1) present
78. Hind limb posture - (0) sprawling (1*) semierect (2*) erect < not considered >
79. Femoral shaft curvature - (0) not markedly sigmoid (1) sigmoid (2) bowed anteriorly
80. Lesser trochanter of femur - (0) absent or appearing only in the last stage of post-hatching ontogeny (1) present early in post-hatching ontogeny
81. Fourth trochanter of femur - (0) absent (1) mound-like (2) sharp (= aliform) flange
82. Prominent cnemial crest on tibia - (0) absent (1) present
83. Fibular anterior trochanter - (0) crest-shaped and low (1) knob-shaped and robust
84. Fibular distal end width - (0) subequal or less than proximal end (1) greater than proximal end
85. Astragalar tibial facet - (0) concave (1) saddle-shaped
86. Astragalar and fibular facets - (0) separated (1) adjacent
87. Crocodyloid tarsus (foramen lost, rotation between astragalus and calcaneum possible) - (0) absent (1) present
88. Astragalar ventral articular facet for calcaneum - (0) planar (1) cupped or convex (i.e. crocodile-reversed) (2) convex (i.e. crocodile-normal)
89. Dorsal and ventral astragalocalcaneal facets - (0) subequal in size (1) ventral facet much larger than the dorsal
90. Astragalocalcaneal canal - (0) present (1) absent
91. Hemicylindrical calcaneal condyle - (0) absent (1) present
92. Calcaneal facets for fibula and distal tarsal 4 - (0) separated (1) contiguous
93. Calcaneal tubercle oriented - (0) oriented less than 45° posteriorly, shaft taller than broad, and distal end rounded (1) oriented more than 45° posteriorly, shaft broader than tall, and distal end flared
94. Lateral centrale of pes - (0) separated (1) fused to astragalus
95. Metatarsals II, III and IV - (0) unequal in length with metatarsal IV longest (1) subequal in length
96. Pedal digit III - (0) shorter than digit IV (1) not shorter than digit IV
97. Phalanges of pedal digit V - (0) four (1) fewer than four
98. Pedal digit V length - (0) unreduced (1) reduced shorter than digit I (2*) extended
110. Prominent supraacetabular crest on ilium - (0) absent (1) present
111. Acetabulum - (0) imperforate (1) perforate
112. Bird-like distal end of femur - prominent anterior and posterior intercondylar grooves with latter constricted by prominent external tibial condyle - (0) absent (1) present
113. Tibial length - (0) shorter than femur (1) greater than or equal to femur
114. "Fibula thin and strongly tapered distally - (0) absent (1) present" *restructured* as: > 114. Fibula - (0) subequal to tibia in width (1) 90–30% as thin as tibia (2) less than 30%
115. Advanced mesotarsal ankle, with astragalus and calcaneum tightly appressed to tibia - (0) absent (1) present
116. Astragalus - (0) not transversely widened (1) transversely widened
117. Ascending process of astragalus fitting between tibia and fibula - (0) absent (1) present
118. Ventral flange of astragalus - (0) present (1) absent
119. Astragalar posterior groove - (0) present (1) absent
120. Calcaneal tubercle - (0) present (1) absent
121. Distal tarsal 4 transverse width - (0) broader than distal tarsal 3 (1) subequal to distal tarsal 3
122. Pedal stance - (0) plantigrade (1) digitigrade (2*) digitigrade with digit V oriented posteriorly < not considered >
123. Pes - (0) functionally pentadactyl or tetradactyl (1) functionally tridactyl
124. Metatarsus configuration - (0) spreading (1) compact
125. Metatarsal 3 length - (0) not more than one-half tibial length (1) more than one-half tibial length
126. Pedal digit V - (0) unreduced (1) reduced, does not exceed length of metatarsal IV and composed of no more than two phalanges (2*) extended
**128. Proximal phalanx of pedal digit V - (0) unmodified (1) reduced (2*) elongated

Dermal Characters

60. Dorsal body osteoderms - (0) absent (1) present in a single median dorsal row (2) present in paired parasagittal rows
61. One-to-one alignment between dorsal body osteoderms and vertebrae - (0) absent (1) present
**129. Postcloacal bones - (0) absent (1) present
**130. Uropatagia - (0) absent (1) present