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ANATOMY AND SYSTEMATICS OF THE PTEROSAUR *CARNIADACTYLUS* GEN. N. *ROSENFELDI* (DALLA VECCHIA, 1995)

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Key words: Triassic pterosaurs, Campylognathoididae, *Carniadactylus rosenfeldi*, *Eudimorphodon,* Late Triassic.

Abstract. The holotype specimen of the non-pterodactyloid pterosaur *Eudimorphodon rosenfeldi* from the Late Triassic (Norian) of NE Italy is described in detail and compared to the other specimens referred in literature to the genus *Eudimorphodon*. It is considered conspecific with the specimen MPUM 6009 from the Norian of NW Italy, previously attributed to *Eudimorphodon ranzii*. A new genus, *Carniadactylus*, is proposed for the two specimens based on the apomorphic shape of the 'coronoid' process, coracoid and pteroid, wing phalanx proportions and the several anatomical differences with *E. ranzii* and '*Eudimorphodon*' *cromptonellus*. No definitive evidence of a juvenile stage occurs in the two specimens. A phylogenetic analysis using parsimony shows that *Carniadactylus* is nested inside the Campylognathoididae and is the sister-group of *Caviramus schesaplanensis* + '*Raeticodactylus*' *filisurensis*. The systematics of specimens referred in the literature to *Eudimorphodon* is reviewed.

Riassunto. L'olotipo dello pterosauro non-pterodattiloideo *Eudimorphodon rosenfeldi* del Triassico superiore (Norico) del Friuli è descritto in dettaglio e confrontato agli altri esemplari riferiti in letteratura al genere *Eudimorphodon*. È considerato conspecifico all'esemplare MPUM 6009 del Norico lombardo finora attribuito ad *Eudimorphodon ranzii*. Un nuovo genere, *Carniadactylus*, è proposto per i due esemplari sulla base di apomorfie nel processo 'coronoide', nel coracoide e nello pteroide, per le proporzioni delle falangi alari e per le numerose differenze anatomiche con *E. ranzii* e '*Eudimorphodon*' *cromptonellus*. Nessuna evidenza definitiva di uno stadio ontogenetico giovanile è individuata nei due esemplari. L'analisi cladistica mostra che *Carniadactylus* è incluso nei Campylognathoididae ed è il sister-group di *Caviramus schesaplanensis* + '*Raeticodactylus*' *filisurensis*. Viene rivista la posizione sistematica degli esemplari riferiti in letteratura ad *Eudimorphodon*.

Introduction

The Triassic basal pterosaur *Eudimorphodon rosenfeldi* was named by Dalla Vecchia (1995) and preliminary described based on a nearly complete, articulated skeleton (holotype, MFSN 1797). The specimen was found in the Norian Dolomia di Forni Formation along the Forchiar brook, northern flank of Mt Lovinzola, Udine Province, north eastern Italy. Pterosaurs, although rare, are the dominant fossil tetrapods in the Dolomia di Forni of Udine Province (Dalla Vecchia 2006) and include the holotype of *Preondactylus buffarinii* Wild, 1984. Three other pterosaur specimens from the Dolomia di Forni were provisionally referred to *Eudimorphodon* Zambelli, 1973: MFSN 1922 from the Purone brook (Dalla Vecchia 2004a) and two specimens from the Seazza brook (MFSN 21545) and the Forchiar brook (MFSN 26823) mentioned in Dalla Vecchia (2004b, 2006) but still undescribed.

MFSN 1797 was attributed to the genus *Eudimorphodon* because of the presence of a quinticuspid or tetracuspid tooth, the square deltopectoral crest of humerus (shared with *Campylognathoides*) and relative lengths of the wing phalanges similar to those of a specimen, MPUM 6009, then referred to *E. ranzii* Zambelli, 1973 (Wild 1979). The referral of MFSN 1797 to *Eudimorphodon* was later questioned on a cladistic basis by Kellner (2003), who found it closer to *Peteinosaurus zambellii* Wild, 1979 than to *E. ranzii*.

Up to recent times, the multicusped dentition with tri- to quinticuspid teeth in both maxilla and dentary appeared to be the only apomorphic character of *Eudimorphodon* (Dalla Vecchia 2003). However, this kind of dentition occurs also in the recently described *Caviramus schesaplanensis* Fröbisch & Fröbisch, 2006 and *Raeticodactylus filisurensis* Stecher, 2008, both from

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the upper Norian-basal Rhaetian Kössen Formation of Switzerland.

The specimen MFSN 1797 is here described in detail, compared to the specimens referred to *Eudimorphodon* in literature and to other Triassic pterosaurs, and its phylogenetic position is assessed. The conspecificity of MPUM 6009 and MFSN 1797 is discussed as well as their inclusion in a new pterosaur genus. The systematic position of the other specimens attributed to *Eudimorphodon* is also evaluated.

Institutional abbreviations. BMNH, The Natural History Museum, London, United Kingdom; BNM, Bündner Naturmuseum, Chur, Switzerland; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburgh, USA; GPIT, Geologisch-Paläontologisch Institut, Tübingen, Germany; GSM, Geological Survey Museum, Keyworth, England; MCSNB, Museum Civico di Scienze Naturali di Bergamo, Italy; MFSN, Museo Friulano di Storia Naturale, Udine, Italy; MGUH, Geological Museum, University of Copenhagen, Denmark; MPUM, Museo di Paleontologia dell'Università di Milano, Italy; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; and SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Terminology and methods

The term 'non-pterodactyloid pterosaur' is used for all the genera included in the suborder Rhamphorhynchoidea of the Linnean systematic (Wellnhofer 1978, 1991), which is a paraphyletic group according to phylogenetic systematics (e.g., Kellner 2003; Unwin 2003; this paper). Enclosure in single quotation marks in the following part of the text indicates that the validity of the taxon is doubtful, debated or subject to change in this paper.

The orientation of the forelimb bones is that in the flight position and I follow the terminology used by Bennett (2001a) for the orientation of the bones in the space, but "cranial" and "caudal" are preferred to "anterior" and "posterior". For the identification of the tubercles and other structures of the scapulocoracoid I followed Bennett (2003). The terminology used for teeth and dentition in general is that suggested by Edmund (1969). The terms "cusps", and "cuspules" when very small, indicate topographically separate elevations on tooth crown along each cutting margin and low in number; a tooth is considered serrated when those elevations (denticles) are close to each other in a row along most of the cutting margin and have similar sizes. The terminology for the patagial structures is taken from Bennett (2000). When paired skeletal elements have different lengths, the mean was used in the calculation of the long bone length ratios. The morphology of bones covered by other skeletal elements was investigated by X-ray photography.

Besides MFSN 1922 from the Dolomia di Forni Formation, the following specimens referred in literature to *Eudimorphodon* are compared to MFSN 1797: MCSNB 2888, holotype of *E. ranzii* Zambelli, 1973, MCSNB 2887 and MPUM 6009 ("Exemplar Milano" in Wild 1979), all from the Calcare di Zorzino Formation of Lombardy and attributed to *E. ranzii* by Wild (1979); MCSNB 8950a,b from the lower Argilliti di Riva di Solto Formation of Lombardy attributed to *E. ranzii* by Wild (1994); BSP 1994 I 51 from the Seefeld Beds of Tyrol, Austria, determined as *E.* cf. *ranzii* by Wellnhofer (2003); MGUH VP 3393, holotype of *'Eudimorphodon' cromptonellus* Jenkins, Shubin, Gatesy & Padian, 2001 from the Fleming Fjord Formation of Greenland (Jenkins et al. 2001). MCSNB 3496 from the Calcare di Zorzino of Lombardy, attributed to *E. ranzii* by Wild (1979), was later referred to *Peteinosaurus zambellii*, a species occurring in the same site (Dalla Vecchia 2003). MCSNB 3359 does not share any apomorphies with the holotype of *Peteinosaurus zambellii* (MCSNB 2886) and cannot be unambiguously considered as belonging to this taxon (Dalla Vecchia 2003; contra Wild 1979; Kellner 2003, and Unwin 2003) without the support of further specimens. In my opinion, *Raeticodactylus filisurensis* is congeneric with *Caviramus schesaplanensis* (see p. 183); therefore it is mentioned in the text as *'Raeticodactylus' filisurensis*.

Systematic palaeontology

Diapsida Osborn, 1903

Pterosauria Kaup, 1834

Campylognathoididae (Campylognathoidinae) Kuhn, 1967 (sensu Unwin, 2003)

Carniadactylus gen. n.

Etymology: "*Carnia*" the name of the zone of northern Friuli where the holotype was found and "*dactylus*" Greek for "finger".

Diagnosis: Campylognathoidid pterosaur with large 'coronoid' process, triangular and pointed, and mandibular ramus very deep below it; coracoidal shaft broad, plate-like with subparallel margins and expansion only at coracosternal articulation; 'boomerang-like' pteroid, angled and slender but not tapering distally; wing phalanx 1>3>2; large sesamoid bone on ventral, proximal part of pedal phalanx V-1.

Carniadactylus differs from *Eudimorphodon* (monotypic, *E. ranzii*, here considered as represented by the sole holotype MCSNB 2888) also in: ventral margin of the skull curved down caudally (MPUM 6009); absence of a premaxillary ventral contact with the narial opening (MPUM 6009); jugal process of maxilla only tapers at its caudal termination (MPUM 6009); nasal without a premaxillary process forming the dorsal margin of the posterior part of the external naris (MPUM 6009); antorbital fenestra lies lower than the naris (MPUM 6009); dorsal (frontal) process of postorbital unexpanded (MPUM 6009); toothless pterygoid; tip of mandibular rami not bent ventrally (MPUM 6009); smooth tooth crown surface with the main cusp of multicusped teeth more labiolingually flattened than conical as in MCSNB 2008; three large teeth at the rostral end of dentary instead of two (MPUM 6009), and tooth 3 with a distal accessory cuspule (MPUM 6009); absence of large, fang-like maxillary teeth below dorsal (nasal or ascending) process of maxilla (MPUM 6009); stouter ceratobranchial I; comparatively slender humerus with more elongated humeral diaphysis; dorsal+sacral vertebral series similar length to ulna (MPUM 6009); more robust and comparatively longer tibia.

Carniadactylus differs from *'Eudimorphodon' cromptonellus* also in: shape of quadrate (the holotype MGUH VP 3393 has a large and bulbous distal quadrate condyle); shape of deltopectoral crest of humerus (triangular in *'E.' cromptonellus*); comparatively longer wing phalanx 1 (shorter than humerus, ulna, wing phalanges 2 and 3, femur and tibia in *'E.' cromptonellus*); ulna much longer than humerus (u:h = 1.31 and 1.11 respectively); comparatively shorter femur (femur longer than humerus and nearly as long as ulna and tibia in *'E.' cromptonellus*); comparatively shorter metatarsus (when compared to humerus, ulna, femur and tibia).

Type and only species: *Carniadactylus rosenfeldi* (Dalla Vecchia, 1995)

Holotype: MFSN 1797.

Referred specimens: MPUM 6009.

Type locality: Forchiar brook, Enemonzo municipality, Udine Province, Friuli Venezia Giulia Region, Italy.

Distribution: Dolomia di Forni Formation (upper Alaunian-lower Sevatian, middle-upper Norian) of Friuli Venezia Giulia and Calcare di Zorzino (upper Alaunian) of Lombardy.

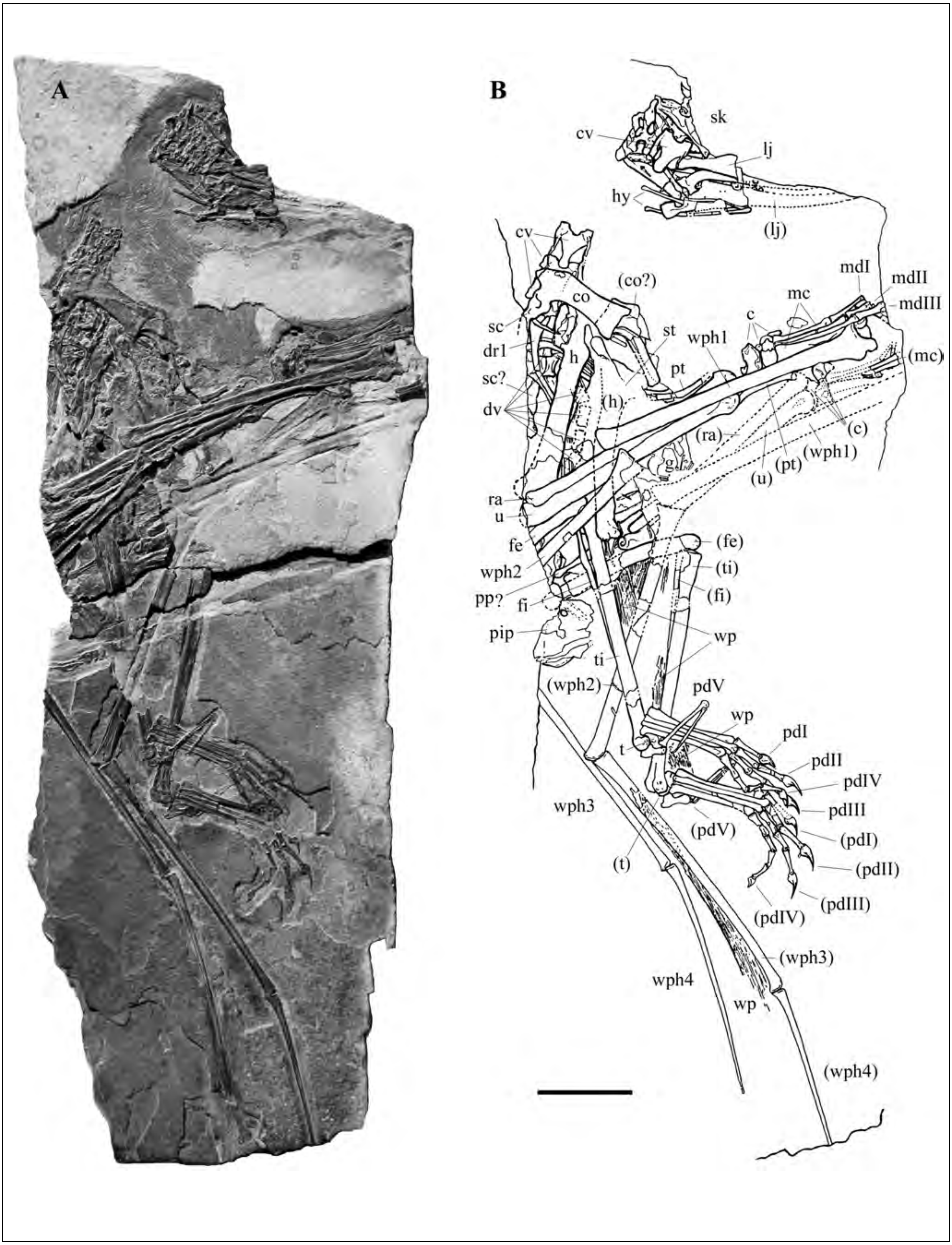

Fig. 1 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype. A) Slab A; B) composite drawing of the skeleton. Abbreviations: c = carpus, co = coracoid, cv = cervical vertebrae, dr1 = first dorsal rib, dv = dorsal vertebrae, fe = femur, fi = fibula, g = gastralia, h = humerus, hy = ceratobranchial I (hyoid apparatus), lj = mandibular ramus, mc = metacarpus, mdI-III = manual digit I-III, pdI-V = pedal digit I-V, pip = puboischiadic plate, pp = prepubic plate, pt = pteroid, ra = radius, sc = scapula, sk = skull, st = sternal plate, t = distal tarsals, ti = tibia, u = ulna, wp = wing patagium, wph 1-4 = wing phalanx 1-4. Left elements are in parentheses. Scale bar = 20 mm.

Description of MFSN 1797

The specimen is preserved on the mirroring surfaces of two thin slabs of black dolostone. The main slab (A; Fig. 1A) contains most of the bones, whereas the other slab (B) preserves mainly their impressions and some fragmentary remains. The drawing in Figure 1B is a composite of the two slabs.

The skeleton on the slab A is exposed in lateroventral view, leaning on the left flank. Only the caudal part of the skull is preserved; the rest was lost with the missing part of the slab. The caudal portions of both mandibular rami are preserved, whereas the rostral half of the left ramus is represented only by the impression of the bone and lacks the distal end. The skull is detached from the neck and is separate from the rest of the body. It rotated in a way to expose its ventral side, part of the caudal side, and probably also the right side, leaning dorsolaterally (Fig. 2A). An isolated, disarticulated cervical vertebra leans above the basicranium, showing its ventral view. The distal cervical vertebrae are articulated each other and connected to the dorsal segment of the vertebral column. Atlas, axis and at least one or two proximal cervical vertebrae were lost when the neck disarticulated. Most of the dorsal vertebrae are preserved and are only slightly disarticulated but, excluding the first two, they are covered by other bones and can be seen only in the X-ray photos. The whole sacral and caudal segments of the vertebral column are lost with the missing part of the slab. The proximal portions of the proximal dorsal ribs are exposed between the right coracoid and the right humerus. Their shafts are mostly covered by the right humerus and the sternal plate. Several fragmentary and scattered gastral ribs are preserved in the abdominal region of the body, between the proximal parts of the hind limbs. The coracoidal portion of the right scapulocoracoid is complete, but only a small portion of the scapular blade is preserved. Bones in the region of the left portion of the pectoral girdle are the most difficult to identify. The left scapulocoracoid is probably the large bone broken into several parts cropping out from beneath the distal end of the right coracoid. The sternum is a wide bony plate exposing its ventral side, covered caudally by the right radius, ulna and right wing phalanx 1. Its cristospine overlaps the proximal part of the right humerus. The right forelimb is in fair state of articulation. The humerus is detached from the glenoid, it has shifted ventrally and lies parallel to the dorsal vertebral column. Its proximal portion with the articular head is covered by the shaft of the right coracoid. Slight disarticulation occurs at the carpus, which is detached from the paired radius and ulna; the single, large proximal carpal is rotated and exposes its proximal face. The pteroid lies preaxially near the distal termination of the radius and also the left one is in the same position with respect to the left radius. The metacarpus shows its dorsal side, but the wing metacarpal has rotated because of compression and exposes its caudal side. Manual phalanges of the distal rows are partly missing; ungual phalanx I-2 is covered and III-3 is incomplete. The wing digit is exposed in dorsal view. The wing phalanx 1 is articulated with the wing metacarpal in a flexed position. Wing phalanges 1 and 2 are slightly disarticulated. Wing phalanx 3 lacks its proximal portion, but its orientation and length suggest that it was articulated with wing phalanx 2, but rotated cranially forming with it an angle of about 100°. Only the distal part of the left humerus is exposed, but X-ray photograph allows identification of its continuation beneath the right forelimb and the sternal plate. A portion of its broken deltopectoral crest pierces the sternal plate at the base of the cristospine, possibly the consequence of a trauma, as in the case of the left coracoid. The left forelimb elements from the radius-ulna to the wing phalanx 2 are mostly preserved as impressions. The carpus seems to have been well-articulated, but the impression of its distal elements is faint. The large preaxial carpal is mostly preserved as bone. Manual digits I to III were lost with the missing part of the slab. The wing digit is exposed in ventral view. Its arrangement in the space and the relative position of the single phalanges are very similar to those in the right digit. Wing phalanx 2 is still contacting wing phalanx 1, but is rotated cranially of about 55°; wing phalanx 3 is articulated with wing phalanx 2, rotated cranially of about 45°. A portion of the patagium is preserved along the caudal margin of the left phalanx 3 (slab A). As it can be seen on the slab B, the patagium crosses phalanx 3 ventrally. Traces probably belonging to the same brachiopatagium occur between the two pedes and the left tibia, and along the lateral margin of the left tibia. A patagial fragment is also visible in the zone delimited by the right tibia, left femur and left wing phalanx 2. The pelvic girdle is represented by the left puboischiadic plate exposed between the right tibia and the right phalanx 2, mainly preserved as print on slab B. Some elements in the region between the two femora may belong to other parts of the pelvis, including the left prepubic plate. A wide and thin spot of black substance caudal to the sternum in the ventral region probably represents the remains of the gastrointestinal content. Elements of both hind limbs are fairly well-articulated, although some are distorted by crushing. The hind limbs are flexed at the knees, fibula+tibiotarsus forming with the femur an angle of 58° in the left limb, 68° in the right. The right foot, exposing the dorsal side is only slightly detached from the distal tarsals; the latter are still contacting the tibiotarsus. The phalanx V-2 is flexed and nearly parallel to phalanx V-1; both cross the dorsal surface of the metatarsal block. The arrangement and orientation of the elements of the left pes are the same as in the right, but showing the plantar side. The metatarsal block forms an angle slightly greater than 90° with the tibiotarsus. A small cylindrical bone occurs on the ventroproximal part of the phalanx V-1; a similar bone can be identified in the same position also in the right foot. The articulated pedal phalanges of both pedes are preserved partly on the slab B and partly on slab A.

The measurements of the main skeletal elements are reported in Tab. 1.

Skull (Fig. 2A)

The strongly crushed skull shows the posteroventral part of the braincase, the quadrates and the caudal part of the palatal complex. Also a small portion of the caudolateral dermal skull roof is exposed (e.g., the squamosals) but, unfortunately, it is strongly crushed and no element can be outlined clearly. The single cranial elements are mostly in their natural position; the distal condyles are articulated with the mandibular cotyles in both quadrates, as well as are the proximal ones to the squamosal.

The left pterygoid exposed in ventral view is a relatively slender bone with a hatched-shaped caudal part. The long palatal ramus is strap-like and extends straight cranially but its caudal portion is bent laterally. The stocky maxillary ramus is directed laterally; alternatively it could be a fused ectopterygoid. The quadrate ramus is short and robust. It might be broken, but the close association with the distal end of the quadrate and the left basipterygoid process suggests that only a short portion can be missing and the craniopalatal joint is not very disrupted. No teeth are present on the pterygoid. The quadrate is dorsoventrally elongate and strap-like in caudomedial view. Its shaft has a straight lateral edge, thickened but narrow. The proximal condyle is small and not expanded. A broad and thin medial lamella begins just below it, gradually widens ventrally up to the middle of the bone, then it seems to narrow gradually toward the pterygoid process, but this part is not well-exposed. A deep, dorsoventrally elongated depression occurs just above the condylar region and could be the evidence of a quadrate foramen. The distal part articulating with the mandible is made of a small, triangular lateral process, and a relatively complex condyle formed by a lateral hemispherical head facing ventrally and a deep notch bordered dorsally by a thickened rim

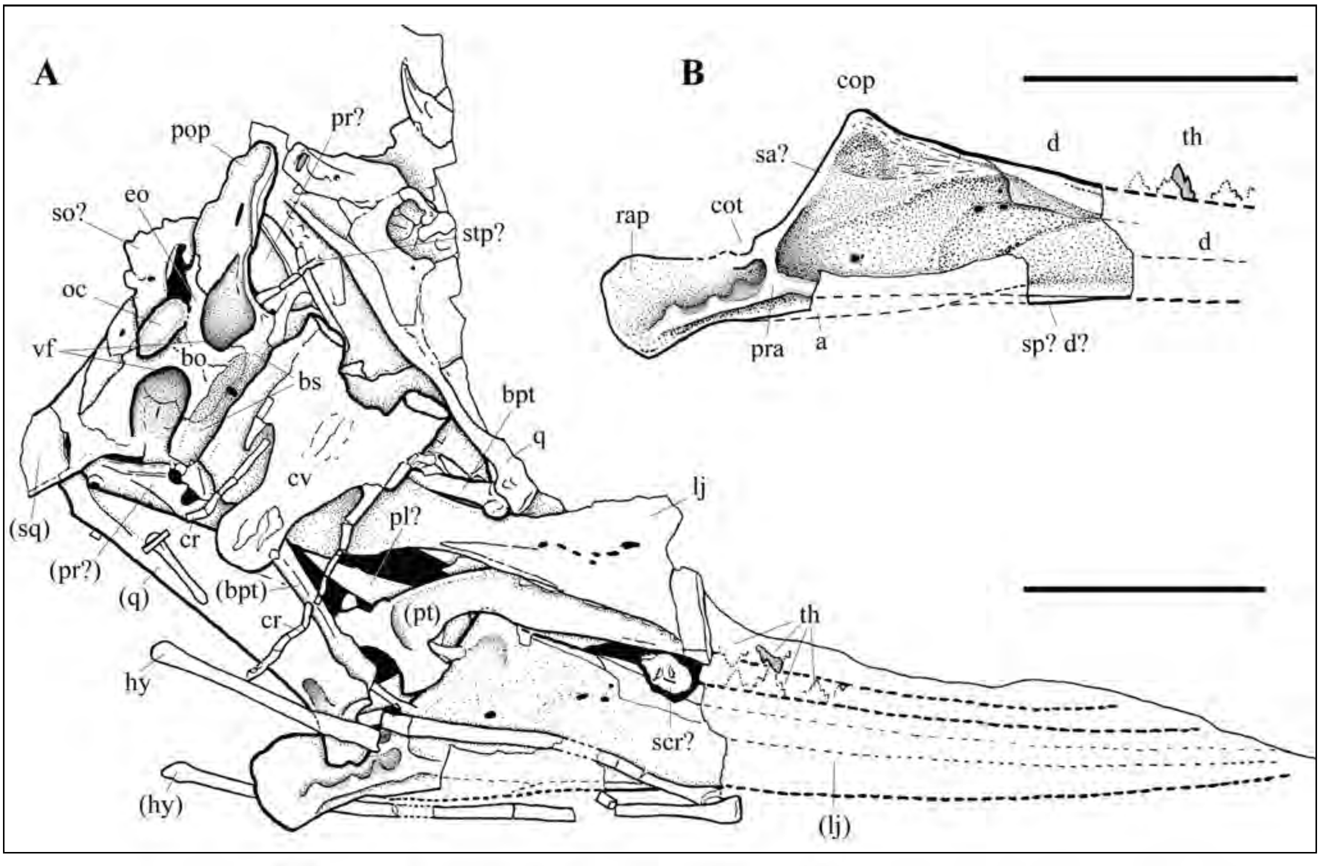

Fig. 2 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype, skull and lower jaw. A) Drawing of the preserved elements; B) particular of the caudal part of the left mandibular ramus, medial view. Abbreviations: a = angular, bo = basioccipital, bpt = basipterygoid process, bs = basisphenoid, cop = 'coronoid' process, cot = quadrate cotyle in the lower jaw, cr = cervical rib, cv = cervical vertebra, d = dentary, eo = exoccipital, hy = ceratobranchial I (hyoid apparatus), lj = mandibular ramus, oc = occipital condyle, pop = paroccipital process, pr = prootic, pra = prearticular, pt = pterygoid, q = quadrate, rap = retroarticular process, sa = surangular, scr = sclerotic ring element, so = supraoccipital, sp = splenial, sq = squamosal, stp = stape, th = tooth, vf = fossa with the vagus foramen. Left elements are in parentheses. Scale bar = 20 mm.

q	cv?5	cv?6	co	h	u	ra	pt	mcI
16.5	9.5	10	22.5	42*	56*(54)	53(52)	16	13.7
mcII	mcIII	mcIV	p1-I	p1-II	p1-III	wph1	wph2	wph3
17.2	19.2	21	8.8	6	5.7	64	58.2	63.2
wph4	fe	ti	fi	mtI	mtII	mtIII	mtIV	mtV
51.5	37*	54.2	50.7*	20.5	22	21	19.5	6.5
ppI-1	ppI-2	ppII-1	pp II-2	ppII-3	ppIII-1	ppIII-2	ppIII-3	ppIII-4
6.8(6.5)	>4.2(5.2)	6(6)	6.3(6.7)	6(6)	6.5(6)	4.3(4.5)	~5.7(5.9)	>5.2(6)
ppIV-1	ppIV-2	ppIV-3	ppIV-4	ppIV-5	ppV-1	ppV-2		
6(6)	4.2(4.3)	3.5(3.5)	~4(4.3)	4.5(2.6)	13.5	13		

Tab. 1 - Lengths of skeletal elements in the skull, pectoral girdle, forelimb and hind limb of MFSN 1797. Measurements are in millimetres; those of the left elements are in parentheses. The length referred to the cervical vertebrae is the whole vertebral length. Symbols: * length estimated partly on the base of the bone impression or on the covered or partly missing bone termination. Abbreviations: co = coracoid, cv = cervical vertebra, fe = femur, fi = fibula, h = humerus, mcI-IV = metacarpal I-IV, mtI-V = metatarsal I-V, p = manual phalanx (excluded wing phalanges), pp = pedal phalanx (included the unguals), pt = pteroid, q = quadrate, ra = radius, ti = tibia, u = ulna, wph1-4 = wing phalanx 1-4.

(Fig. 2A). The hemispherical head fits in a dorsal cotyle on the mandible, whereas the thickened rim fits in a medial cotylar depression. The broken pterygoid ramus starts medial to the notch.

Most of the identifiable skull bones belong to the braincase. The occipital condyle is ovate in shape, small (2.8 mm wide and 1.3 mm high) and convex. A partially exposed supraoccipital is tentatively identified dorsal to it and probably enters the foramen magnum, because of the crushing of the skull. Straight, long and narrow paroccipital processes extends lateral to the occipital condyle, probably made mostly by the opisthotics (cf. Padian 1984). As the skull is strongly crushed, that exposed may be only the ventral portion of the processes. Small and slender exoccipitals occurs in the proximal part of the paroccipital processes, just lateral to the basioccipital, and forming the lateral margins of the foramen magnum; however, the suture with the opisthotics is mostly obliterated and their actual shape is not clear. A very broad depression bordered medially by the basioccipital, dorsally by the exoccipital and the opisthotic, laterally by the opisthotic and ventrally by the basisphenoid is proaby a fossa containing the vagus foramen from which emerged the nerves X and XI with the nerve IX and, possibly, nerve XII and the posterior cerebral vein (e.g., Newton 1888; Romer 1976; Wellnhofer 1985; Kellner 1996; Bennett 2001a). The foramen ovalis probably occurs between the lateral rim of the fossa and the prootic; a rod-like bone located in this position may be a stapes still in situ. Remains of the prootics are exposed among the paroccipital process, the quadrates and the basisphenoid, but in both cases they are strongly deformed by crushing. The basioccipital, which probably includes the occipital condyle, is a small, dorsocaudally/ventrorostrally elongated element flared at the extremities and with concave lateral margins. The basioccipital-basisphenoid suture is not evident and it is not clear if it is lateromedially straight or if the basioccipital protrudes cranially into the basisphenoid. In the first case, the basisphenoid is a broad bony plate forming the base of the cranium, with a rectangular caudal portion which is slightly concave medially where it is pierced by a small foramen. The sutural region of basioccipital and basisphenoid in the crocodilians is pierced by the medial Eustachian foramen leading to the medial Eustachian tube, belonging to the systems of pneumatic cavities of the middle ear (Iordansky 1973). The basipterygoid processes are rod-like, straight and splayed laterally like in other non-pterodactyloid pterosaurs (e.g., *Dorygnathus*, BSP 1994 I 51 and MFSN 21545; pers. obs.), and their distal extremities are slightly expanded to articulate with the corresponding facets in the quadrate process of the pterygoids.

An isolated, small and extremely thin bone (a sclerotic ring plate?) preserves on its surface three ramified conodonts.

Lower jaw (Fig. 2)

The two mandibular rami are nearly parallel to each other, the left exposing its medial side and the right the lateral side. The rostral half of the ramus is slightly arched dorsally; the rostral termination is not preserved. The single bones composing the lower jaw cannot be identified with certainty because sutures between the elements are obliterated by complete fusion and most of the lines of discontinuity are probably fractures due to the crushing. The dentary forms most of the ramus. Following the lower jaw bones identification of MCSNB 2888 by Wild (1979), it sends a pointed mediocaudal process along the ventral edge of the jaw below the angular, reaching the level of the cotylar notch (Fig. 2B). However, this process is the caudal part of the angular according to the lower jaw bones identification of *Pteranodon* by Bennett (2001a). Dorsally, the margins of the surangular are not clear. A thin element along the medioventral edge of the ramus (Fig. 2B) corresponds to the bone identified as the splenial in MCSNB 2888 by Wild (1979), but occurs in a slightly more rostral position. Following Bennett (2001a), it could be a ventrocaudal process of the dentary. A bone along the dorsal edge of the ramus with a shelf-like dorsomedial aspect could be a dorsocaudal process of the dentary (cf. Bennett 2001a). The 'coronoid' process is triangular, pointed and large. The mandible is very deep (7 mm) at the 'coronoid' process, two times the height at mid-ramus. The caudal edge of the process toward the glenoid is steeper than the rostral edge. The medial side of the ramus below the 'coronoid' process is shallowly concave. This depression is probably a wide adductor fossa with depth reduced because of crushing. It is bordered caudally by a vertical ridge of the prearticular (according to Bennett 2001a; the angular following Wild 1979) and ventrally by a thickened edge probably of the same element. Four small foramina open inside this shallowly depressed area, but a meckelian foramen or fenestra is absent. The medial surface of the 'coronoid' process is striated longitudinally probably for the insertion of the *m. adductor mandibulae*. The glenoid is placed much ventrally with respect to the tip of the process and well below the tooth-bearing margin of the dentary. A thick ridge parallel to the ventral margin of the jaw surrounds ventrally the glenoid and is confluent with the ridges bordering the caudal end of the adductor fossa; here possibly the *m. depressor mandibulae* inserted. The retroarticular process is large, expanded and with a rounded caudal profile.

Hyoid apparatus (Fig. 2A)

Two ceratobranchials I of the hyoid apparatus occur on the caudal part of the left mandibular ramus. They are filiform (length = 23-24 mm, width at midshaft about 0.7 mm), straight or slightly curved, close to each other and nearly parallel, practically in their original position. Their proximal extremity is slightly expanded and flat; the distal extremity is fan-shaped and thicker.

Dentition (Fig. 2A)

Only a partial, distal mandibular crown is preserved. It is about 1.3 mm basoapically high, with a central cusp and two smaller accessory cusps on the preserved cutting margin (the basal one very small), showing that it was quinticuspid or tetracuspid. The crown is labiolingually flattened and its surface is smooth. The impression of another, similar tooth occurs distal to it, and both probably belong to the right mandibular ramus and are displaced from their alveoli. The faint impressions of other four teeth can be identified in the dorsocaudal edge of the left mandibular ramus; two are undoubtedly tri-to quinticuspid. Teeth apparently end much rostrally than the apex of the 'coronoid' process, at least 5.5 mm before.

Axial skeleton (Fig. 1B)

Bennett (2007b) defined the first dorsal vertebra as the first vertebra that bore a long rib that articulated with the sternum. Based on that assumption, Bennett (2007b) stated that pterosaurs have nine cervical vertebrae. Two cervicals of MFSN 1797 are fully exposed, one is partially covered by the right scapulocoracoid, one is covered nearly completely, and the most distal is covered by the proximal dorsal ribs. I consider the latter as the last cervical here because it appears morphologically similar to the preceding vertebrae, but its association with the large first dorsal ribs would suggest caution. At least four cervicals are missing, including the atlas and axis. The four distal cervicals (9-6?) are still articulated whereas the other cervical (5?) is detached and lies on the skull (Fig. 2A). They are exposed in ventral view and are strongly dorsoventrally compressed and flattened. Vertebra ?5 is 9.5 mm long measured from the cranial end of the prezygapophyses to the caudal end of the centrum and its maximum width between the prezygapophysis i s 6.75 mm; the centrum is 7.8 mm long. The vertebra ?6 is 10 mm long and 7.5 mm wide, the centrum is 7.8 mm long. Both vertebrae present a quadrangular outline in ventral view and the centrum with the prezygapophyses lying in the same plane because of crushing appear Y-shaped. The centrum tapers up to the distal third, then expands to form a rounded condyle, which projects beyond the caudal end of the postzygapophysis. The condyle fits in the deep, saddle-shaped cotyle of the preceding vertebra, which articular surface is directed forward. There is no clear evidence of a hypapophysis, although the most cranial vertebra may have two ridges in the ventral part of the condyle. The prezygapophyses are massive cylinders resembling the buffers of a train and projecting cranially beyond the centrum. The articular facets appear vertical or subvertical. The postzygapophyses are also large and massive. The vertical or subvertical articular facets of the zygapophyses probably limited the lateral mobility of the neck.

Ribs are preserved in the two exposed vertebrae, although broken by crushing. Their heads appear to be dicephalous, with the slender capitulum apparently fused to the base of the prezygapophysis and the broad tuberculum fused to the centrum in correspondence of its maximum width. After a short, tapering proximal segment, the shaft is uniformly thin (about 0.25 mm) and filiform. The preserved shaft portions are about 10 mm long, extending well beyond the caudal end of the vertebra, probably reaching and overstepping the middle of the following vertebra.

Two dorsal centra (probably belonging to the dorsal vertebrae 1 and 2) are exposed in ventral view. They are spool-shaped (like the following ones) and 4-4.5 mm long, decidedly smaller and narrower than the cervical centra. The caudal articular surface of the second centrum is shallowly concave.

At least five proximal dorsal ribs are dicephalous, with a very short tubercle and a very long capitulum. Their shafts are nearly straight and long, suggesting the presence of a deep rib cage. The most cranial are the most robust and have a deeper proximal part; the largest is the first, which is markedly more robust than the others also in MCSNB 2888 (Wild 1979) and MFSN 1922 (Dalla Vecchia 2004a).

Many small, delicate and rod-like bones are probably gastralia, disarticulated and scattered in the region delimited by the femurs and the sternum. Most of them are included in a film of dark substance possibly representing the gastrointestinal content.

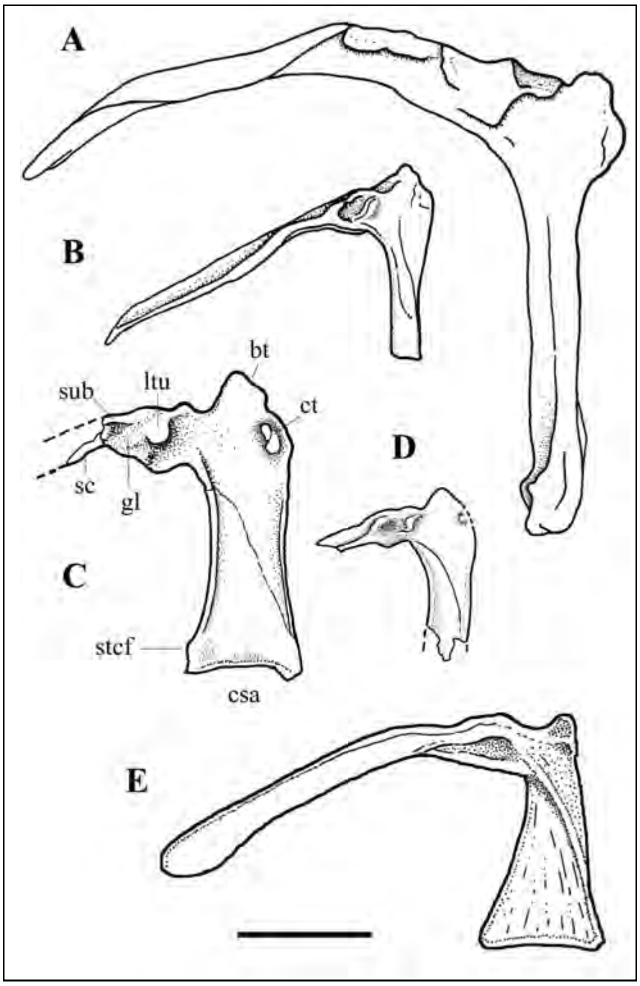

Fig. 3 - Scapulocoracoids of some Triassic pterosaur specimens, in ventrolateral or lateral view if not specified otherwise. A) *Eudimorphodon ranzii*, holotype, right element after Wild (1979), redrawn, B) MCSNB 2887, left element after Wild (1979), mirrored and redrawn, C) *Carniadactylus rosenfeldi*, holotype, right element, D) *Carniadactylus rosenfeldi*, MPUM 6009, left element mirrored, E) BSP 1994 I 51, right element in ventromedial view, from Wellnhofer (2003), mirrored and redrawn. Abbreviations: bt = biceps tubercle, csa = coracosternal articulation, ct = coracoid tubercle, gl = glenoid fossa, ltu = lower tuberosity, sc = scapula, stcf = flange for *m. sternocoracoideus*, sub = supraglenoidal buttress. Scale bar = 10 mm.

Pectoral girdle (Figs. 1A, 3C)

Only the proximal portion of the right scapula with a very small part of the blade is preserved. It is fused without suture to the coracoid to form a scapulocoracoid. The scapula is probably much longer than the coracoid, as suggested by the presence of a possible fragment of the ventral margin of the scapular blade along the edge of the slab. The coracoid in lateroventral view is a flat and thin bone, relatively broad and short (Fig. 3C). The length:width ratio (length measured from the apical part of the biceps tubercle to the coracosternal articular surface, width in the widest part of the shaft) is 2.80. The glenoid is bordered cranioventrally by a huge lower tuberosity and caudodorsally by a partially preserved supraglenoid buttress. The biceps tubercle is well-developed and separate from the glenoid process of the coracoid (supposing that this bone contributes to the glenoid) by a deep notch. A prominent coracoid tubercle occurs in the dorsal part of the laterocranial margin of the coracoid. The shaft is flat and thin, with subparallel caudal and rostral margins expanding only at the distal, coracosternal extremity. The caudal margin is slightly thickened; only the middle-distal portion of the rostral margin is thickened whereas the proximal portion is extremely thin. The ventral, coracosternal articular margin is slightly arched. There is a small but distinct flange on the caudal margin of the coracoid just above the sternocoracoid articulation, possibly for the *m. sternocoracoideus*. There is no shaft torsion; the comparison with the flat and not twisted shaft of the coracoid in BSP 1994 I 51 (Fig. 3E) and the craniocaudally straight articular processes for the coracoid on its sternum (Wellnhofer 2003) suggests that this is an original feature, not the result of crushing, although those sternal processes are not identifiable in MFSN 1797.

The sternal plate is broad and thin; its full outline cannot be detected, because it is partially covered by other bones and is strongly crushed against others. Its cranial portion is triangular in ventral view, ending with an elongated cristospine scarcely deep dorsoventrally.

Forelimb (Figs. 1, 4F, 5, 6A, 7)

The morphology of the humerus is reconstructed based on preserved portions from both slabs and from the impression in slab B. An accurate comparison between the remains of both humeri gives 42 mm as a more reliable length for this bone (it was 40.5 mm in Dalla Vecchia 1995). The deltopectoral crest is square and narrow, with a straight cranial margin nearly parallel to the axis of the humeral shaft (Fig. 4F). The crest extends for 23% of the humeral length and the ratio humeral length: maximum proximal width is about 3.4. The articular head and the external tuberosity are concealed in both humeri. The shaft is long, narrow and slightly bowed (as it can be seen in the X-ray photographs for the left humerus). The distal end bears a hemispherical *capitulum radialis* and a smaller *trochlea ulnaris* bordered by a small knob which could be the entepicondyle.

The radius and ulna are closely-bound, parallel bones with straight shafts and no *spatium interosseum* (Fig. 1B). The radius is slightly shorter than the ulna and the left elements are both slightly shorter than the right ones (Tab. 1). The ulna is proximally expanded with a prominent olecranon-like process. In dorsal view, it is expanded distally forming a rounded condyle for the articulation with the proximal syncarpal. The dorsal surface of the condyle bears a crest in the middle and a small tubercle caudally. The crest may edge caudally the groove for the flexor tendon, but this cannot be seen because of crushing. The radius is slightly more gracile than the ulna. Its proximal part probably accommodates in a cranial groove along of the ulnar shaft. The proximal head is not expanded, whereas the distal one is expanded to form the rounded condyle for the proximal syncarpal and bears a large cranial tubercle. The proximal head of the right radius is strongly convex and seems to be formed by a sutured epiphysis; the condition in the left radius is not clear.

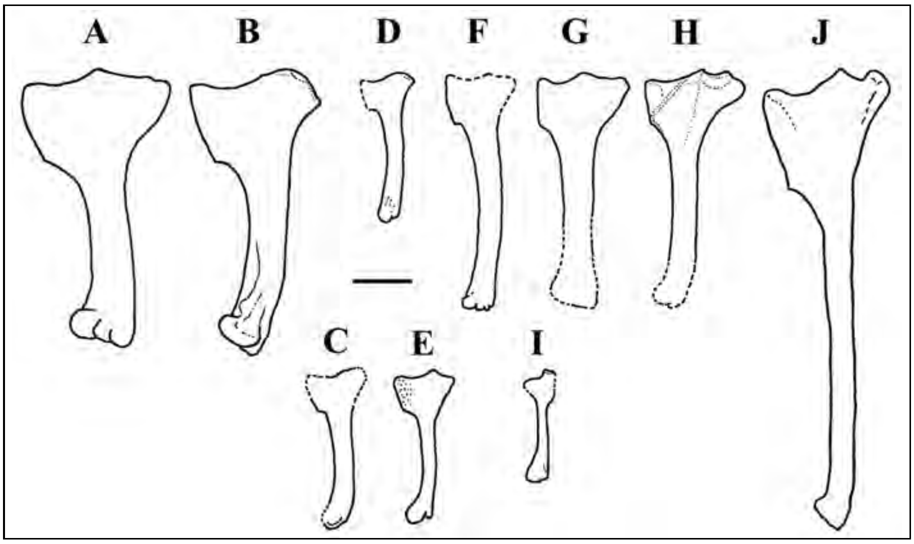

Fig. 4 - Humeri of some Triassic pterosaur specimens. A-B) *Eudimorphodon ranzii*, holotype, right and left element respectively, redrawn from Wild (1979), C) MCSNB 2887, left element mirrored and redrawn from Wild (1979), D) *Carniadactylus rosenfeldi,* MPUM 6009, right element, mirrored, E) MCSNB 8950, left element redrawn from Wild (1994), F) *Carniadactylus rosenfeldi,* holotype, right element (shaft based on the left element), G) MFSN 1922, H) BSP 1994 I 51, left element redrawn from Wellnhofer (2003), I) *'Raeticodactylus' filisurensis*, right element mirrored and redrawn from Stecher (2008), J) *'Eudimorphodon' cromptonellus*, holotype, right element mirrored and redrawn from Jenkins et al. (2001). Scale bar = 10 mm.

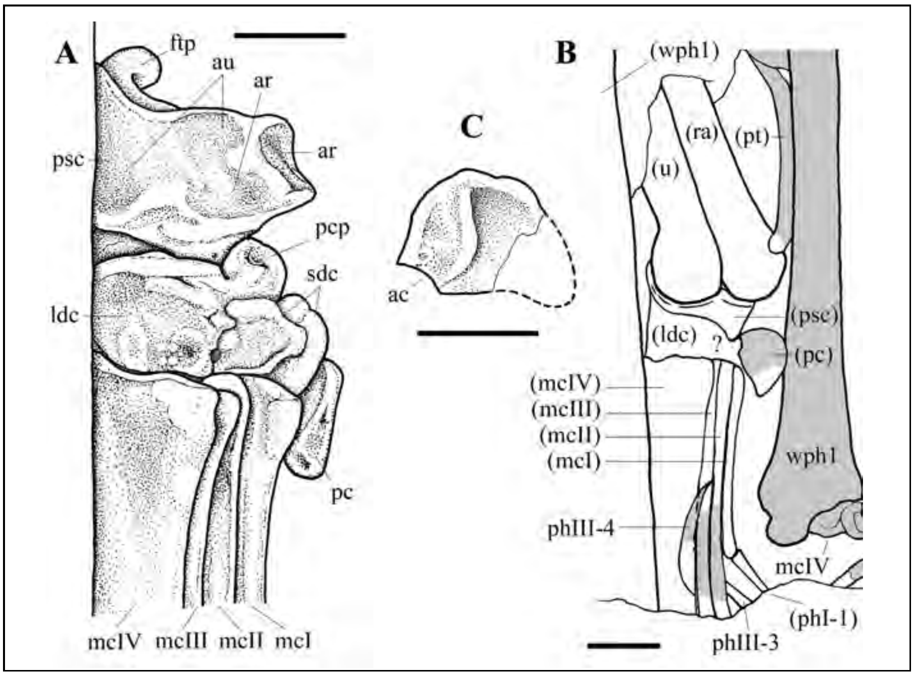

Fig. 5 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype, carpus and the proximal part of the metacarpus. A) Right carpus (for the orientation of the elements, see text), B) left carpus and neighbouring skeletal elements (elements in grey are those preserved as bone; the others are prints), C) left preaxial carpal in medial or lateral view. The drawing of the left wrist region is based mostly on the impression of the bones, consequently represents the dorsal view. Left elements are in parentheses. Abbreviations: ac = articular facet for the process of the large distal carpal or, less probably, fovea for the sesamoid, ar = articular facet for the radius, au = articular facet for the ulna, ftp = flexor tendon process, ldc = large distal carpal, mcI-IV = metacarpal I-IV, pc = preaxial carpal, pcp = process for preaxial carpal, phI-1, phIII-3, phIII-4 = manual phalanges I-1, III-3, III-4, psc = proximal syncarpal, pt = pteroid, ra = radius, sdc = small distal carpals, u = ulna, wph1 = wing phalanx 1. Scale bar = 3 mm in A and C, 5 mm in B.

There is only a single proximal element in the carpus, the proximal syncarpal. The dorsal profile of this large element (Fig. 5B) is exactly the same as in MCSNB 2888 (Wild 1979, fig. 17). The syncarpal is distoproximally narrow, mainly in the caudal half, whereas the cranial portion is wider. The proximal surface of the latter is concave to receive the radial condyle; the ulnar cotyle occurs caudally and is larger. The right proximal syncarpal has rotated in the disarticulation of the wrist and shows the rectangular, proximal articular side (Fig. 5A). The articular surfaces for the radius and ulna are shallow and barely separate, perhaps a result of crushing. The ulnar one is larger and crosses the surface dorsocaudally to ventrocranially; the radial cotyle seems to be divided into two parts, one occurring dorsocentrally and the other cranially. A curl-shaped flexor tendon process (Bennett 2001a) projects ventrally from the caudoventral corner of the syncarpal. The right distal carpal row in dorsal view may be made of three elements, tightly bound to each other. A large and massive element contacts distally the wing metacarpal, the metacarpal III and possibly partly metacarpal II. This carpal sends cranially a curl-shaped process for the preaxial carpal (Bennett 2007a). Along the distal edge, small tubercles occur, probably for ligaments to the wing metacarpal, whereas the proximal margin is uniformly thickened. A much smaller carpal with an irregular shape seems to be present cranially to the large distal carpal. The contact between the two elements is somewhat fringed and they appears strictly interlocked, with a small foramen along their border close the contact with the metacarpals. This small element contacts metacarpal II and partly metacarpal I. It sends a process cranially that overlaps a second small distal carpal, which has a rounded outline and contacts the metacarpal I. Alternatively, these small elements may be fused to the large distal carpal or be projecting parts of it. The right preaxial carpal is displaced from the original articulation on the cranial process of the larger distal carpal and moved distally, lying cranially to the distal carpals, partly covered by them and the metacarpals (Fig. 5A). Some small depressions are visible, but no wide fovea with a sesamoid bone (Bennett 2007a), thus it is only partially exposed in ventrolateral view. The left preaxial carpal is large (maximum length 4.5 mm), crescent-shaped and mediolaterally flattened, probably showing the medial or lateral face (Fig. 5C). A small notch may correspond to the fovea for the sesamoid, which is missing, or, most probably, is the facet for the articulation with the curl-shaped process of the large distal carpal. A strong ridge crossing the surface may be the place of insertion of a muscle.

The pteroid (Fig. 6A) is elongated, rod-shaped and angled at its distal third (angle ~ 150°). Its length (16 mm) is 30% of ulnar length. The proximal articular extremity is slightly expanded, has a rounded outline, and is slightly bent with respect to the proximal segment of the shaft. Excluding the proximal articular extremity, the two segments of the shaft are fundamentally straight; the resulting shape is that of an asymmetric boomerang. The shaft is 'dorsoventrally' flattened, mainly in the distal third after the bending, and grows thinner distally. The distal extremity is not tapering nor pointed. Both pteroids are preserved cranially along the distal part of the radius, with their proximal end contacting the distocranial tubercle and the distal end pointing to the humerus (Fig. 1B). Therefore, they are identically shifted from their supposed original location on the carpus; the same shifting is observed in MCSNB 2888 and MPUM 6009. This suggests that the position is not due to a chance movement after disarticulation, and it is related to post-mortem contraction of tissues; this in agreement with the involvement of the pteroid in a propatagium stretched from the carpal region to the shoulder (Bennett 2007a).

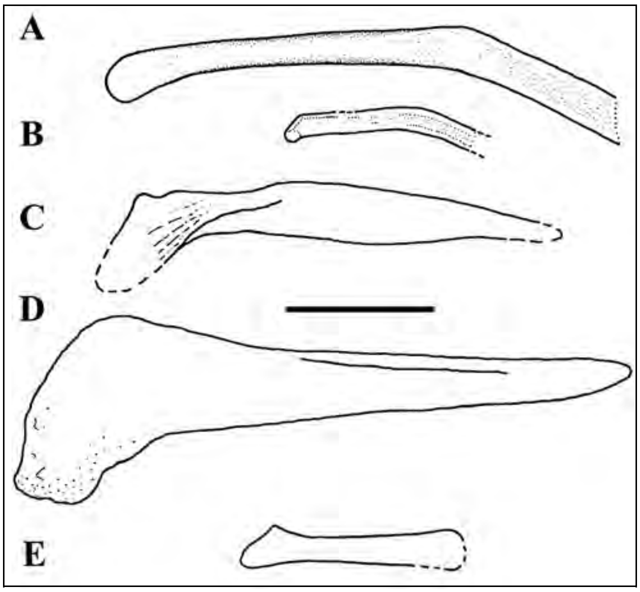

Fig. 6 - Pteroids of some Triassic pterosaur specimens. A) *Carniadactylus rosenfeldi*, holotype, composite but based mainly on the left element, B) *Carniadactylus rosenfeldi*, MPUM 6009, left element, C) MCSNB 2887, redrawn from Wild (1979), D) *Eudimorphodon ranzii*, holotype, left element redrawn from Wild (1979), E) *Preondactylus buffarinii*, holotype, left element mirrored and redrawn from Dalla Vecchia (1998). Scale bar = 5 mm.

The wing metacarpal (IV) is much more robust than the metacarpals I-III. The caudally facing distal articular trochlea is asymmetrically developed, with a much larger dorsal condyle. A large, strong crest projects from the dorsocaudal edge in the distal half of the bone as in MCSNB 2888, the *crista metacarpi* of Wild (1979), supposedly used to anchor the flexor musculature of the wing spar. Metacarpal IV is slightly longer than the metacarpal III, metacarpal II is slightly shorter than III and metacarpal I is 20% shorter than metacarpal II and 35% shorter than wing metacarpal (see Tab. 1). The proximal ends of metacarpals II and III are expanded, flattened dorsoventrally (if they are rotated 90° caudally) and overlapping. The distal condylar ends are also expanded, slightly arched cranially and asymmetrical. The proximal end of metacarpal I is also expanded and was probably overlapped cranially by the metacarpal II, but is thicker cranially.

The manual phalanges are only partly preserved. The phalanx I-1 is much more elongated and thin than the phalanx II-1 and III-1; the shortest is phalanx II-1 (Tab. 1). The distal ginglymi are well-shaped and there is a small sesamoid dorsally on that of phalanx I-1 like in *E. ranzii* and *Dimorphodon macronyx* (Wild 1979; Unwin 1988). The manual ungual phalanges are larger than those of the *pes*, as indicated by the proximal part of ungual phalanx of digit I and the distal part of that of digit III. The latter is robust, elongated, and scarcely recurved as in *Dimorphodon* (Sangster 2004).

Wing phalanx 1 is the longest; wing phalanx 3 is slightly shorter; wing phalanx 2 is shorter than 3 and wing phalanx 4 is the shortest (see Tab. 1 and Fig. 7). Wing phalanx 1 has an enlarged proximal extremity bearing a well-developed extensor tendon process, the articular concavity for the condyles of the wing metacarpal and a broad cranial crest. The extensor tendon process shows no suture with the phalanx and has a rounded apex. The phalangeal shaft is slightly curved with the concavity facing cranially; its width is minimum in the middle segment (3 mm), and then expands again in the distal part. The condylar region for wing phalanx 2 is rounded and angled, protruding obliquely caudally. A tubercle for collateral ligaments occurs dorsocranially at the distal end of the shaft. The shaft of the wing phalanx 2 is straight and its width is constant (i.e., the cranial and caudal margins are straight and parallel). The proximal cotylar part is asymmetrically expanded, with a caudal projection. The condylar extremity is slightly expanded and morphologically similar to that of the wing phalanx 1; a tubercle for the collateral ligaments occurs in the cranial corner in the ventral side of the condyle. Wing phalanx 3 is thinner than the preceding wing phalanges, faintly arched and with expanded extremities. The cotylar region is less asymmetrical than that of the phalanx 2. Wing phalanx 4 is very thin and tapering, elongated and faintly arched, with a higher curvature in the proximal segment. The cotylar region is slightly expanded and asymmetric; the distal segment is very thin and the point is blunt with no evidence of a further element.

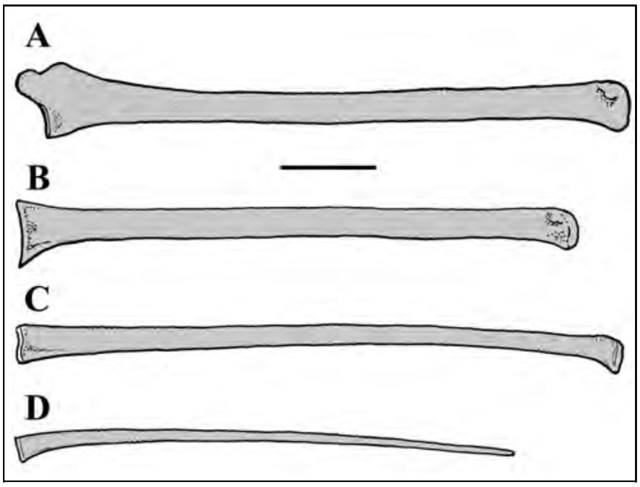

Fig. 7 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype, wing phalanges. A) right wing phalanx 1 in dorsal view, B) left wing phalanx 2 in ventral view (based also on the right one in dorsal view), C) left wing phalanx 3 in ventral view, D) right wing phalanx 4 in dorsal view. Scale bar = 10 mm.

Pelvic girdle (Fig. 1A)

Part of the probable left puboischiadic plate is preserved still articulated with the left femur. It is a broad and thin bone thickening dorsally. Its outline is partly identifiable as an impression in the slab B and resembles that of the puboischiadic plate of *Dimorphodon macronyx* (Sangster 2004). There is probably a thickening of the straight, cranial pubic edge; the broad ischium may have a large triangular caudal projection. A large circular opening visible on both slabs is probably an artefact of preparation or was caused by splitting. The slender shaft of a possible prepubic plate is exposed just cranial the left femur, slightly shifted from its original articulation with the pubis (Fig. 1B).

Hind limb (Figs. 1A, 8-9)

The femur is poorly preserved and its length (Tab. 1) is estimated considering that the *caput femoris* of the left femur is still fitting in the acetabulum, as it seems from its impression in the slab B. In mediolateral view, the shaft is slightly bowed (Fig. 1A) and the medial condyle is moderately convex. Two, possibly three small bones occur between the condyle and the corresponding cotyle of the articulated left femur and crus, apparently on the articular surface. They may be parts of the condyle and cotyle displaced by crushing, but alternatively they may be sesamoids (lunulae).

The tibiotarsus is a straight, relatively robust and long bone, longer than the humerus and nearly as long as the ulna (see Tab. 1). The proximal part of the tibia in craniocaudal view is slightly flared, then the shaft width remains constant and finally the bone expands distally in a tibiotarsal condylar part for the distal tarsus. A process on the cranial edge of the proximal articular surface divides the surface in two parts; the lateral one is much larger than the medial suggesting that the lateral condyle of the femur was much larger than the medial

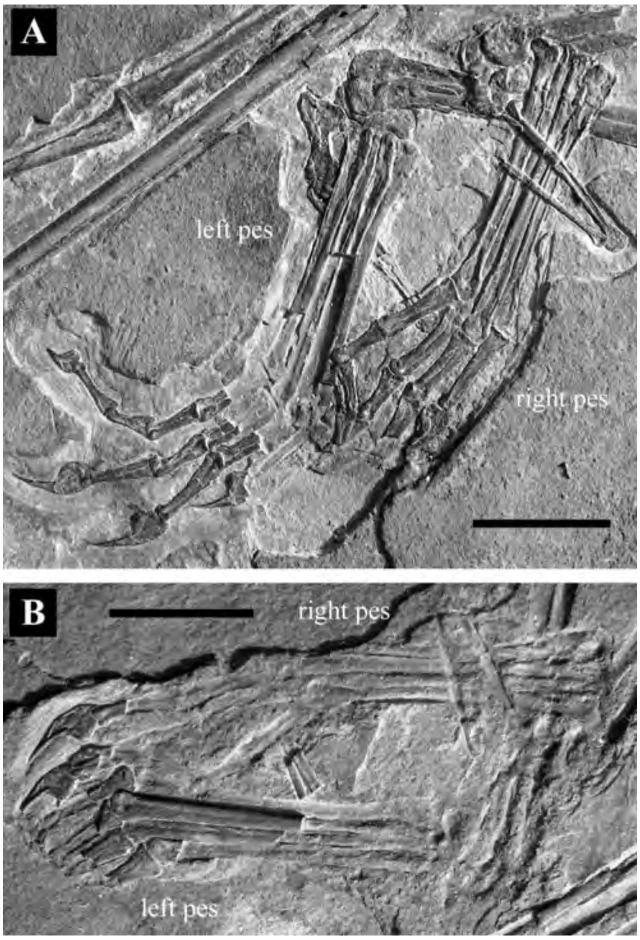

Fig. 8 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype, pedes. A) Slab A, B) Slab B. Scale bar = 10 mm.

one and that the latter articulated only on a small portion of the tibial surface; this is the opposite of the usual condition in pterosaurs. A small knob on the cranial surface just distal to the articular surface may be an incipient cnemial crest; it is displaced medially instead of being central. An elongated knob along the craniomedial margin, 5 mm from the proximal articular surface is a place of muscle or ligament insertion observed also in *Pteranodon* (Bennett 2001a). Distal to this knob, the shaft constricts and its width remains constant over the rest of its length. The tibiotarsus ends distally with two condyles formed by the fusion of the astragalus and calcaneum to the tibia (Dalla Vecchia 2003; Kellner 2004a) (Figs. 8-9). No suture is visible between the condyles and the tibial shaft, but a very narrow zone with a slightly different, grainy bone texture can be identified, which represents the sutural zone. The lateral condyle is well-shaped with a rounded outline and is twisted medially; the medial one has a more irregular profile, a feature common to other Triassic pterosaurs (Dalla Vecchia 2003). The prominent lateral and medial epicondyles are central and just distal the condyle-shaft border.

The fibula is a straight bone much thinner than the tibia and tapers distally, becoming filiform in its terminal segment with a width of only 0.2 mm. It is probably fused proximally to the tibia as no separation between the two bones is evident in the impression of the proximal part of the left crural bones. A wide *spatium interosseum* occurs between tibia and fibula in the proximal third of the bones; here the fibula shows an enlargement possibly corresponding to a biceps tubercle (Bennett 2001a; Sangster 2004). The filiform distal segment of the fibula reaches the lateral epicondyle of the tibiotarsus without a terminal expansion (Fig. 9B).

Two strictly appressed large distal tarsals occur in the left hind limb (Fig. 9A), as in *Dimorphodon macronyx* (Padian 1983). The mediolateral length of the medial and lateral distal tarsals is 3.5 mm and 3 mm respectively. They are compressed proximodistally; the medial one probably exposes its proximal surface as it is shallowly concave for the tibiotarsal articulation. As preserved, the lateral distal tarsal contacts metatarsal V, whereas the medial tarsal contacts metatarsals IV to II and only a small portion of metatarsal I; this corresponds to the actual metatarsal articulation with the distal tarsals in *Dimorphodon macronyx* (see Padian 1983).

Metatarsals I-IV of both feet are closely appressed in a single block, thin and elongated (Fig. 8). The longest is the metatarsal II; metatarsal III is slightly shorter; metatarsal I is nearly as long as the third and the shortest is metatarsal IV (see Tab. 1). Width at the mid-shaft is about 1 mm in all elements. The length of metatarsal II is about 60% the length of the femur and 40% that of the tibiotarsus. Both extremities of each metatarsal are slightly expanded; the distal ones have well-shaped condyles for the articulation of the first phalanges.

Metatarsal V is separate from the others and has a totally different shape, as in all non-pterodactyloid pterosaurs, closely resembling that of *Dimorphodon macronyx* (see Padian 1983; Sangster 2004) in overall morphology. It is short (length 6.5 mm) and stocky, with a much widened proximal part (width 3.7 mm); after a short shaft, the bone ends distally in an expanded articular head with a circular outline.

The pedal phalangeal formula is 2 3 4 5 2, as in nearly all non-pterodactyloid pterosaurs. The longest phalanx is the first in digit I, the second in digit II, and the first in digit III (but practically the same length as phalanx 3) and IV (Tab. 1). The articulation is ginglymal in all the non-ungual phalanges. The ungual phalanges are rather large with respect to the other pedal phalanges (see Tab. 1) excluding the smaller ungual phalanx of the left digit IV, but are smaller than the manual phalanges. They are elongated, pointed, slightly dorsoventrally arched and laterally flattened, with a deep longitudinal groove for the attachment of a horny sheath, and a large flexor tubercle. The ungual of digit

IV is smaller and with a shorter point possibly due to a malformation or trauma. Small antungual sesamoid ossifications like those described by Unwin (1988) in the pes of *Dimorphodon macronyx* are absent in MFSN 1797. The phalangeal portions of digits III and IV have practically the same length (Tab. 1), but digit III is slightly more projecting because metatarsal III is longer than metatarsal IV.

Like metatarsal V, also the corresponding phalanges differ from those of the other pedal digits. They are very elongated, thin and perfectly straight. Phalanx V-1 is only slightly longer than phalanx V-2 (Tab. 1). Its proximal extremity is expanded fan-shaped with a concave surface for the articulation with the condyle of the metatarsal. The distal extremity is also much expanded and with a rounded profile. The corresponding proximal extremity of phalanx 2 is expanded fan-shaped; the shaft tapers distally and the distal extremity is slightly expanded and bent caudally. In both feet, phalanx V-2 forms an obtuse angle with metatarsal V and is placed transversely on the dorsal face of the metatarsal block, while phalanx V-2 is flexed and nearly parallel to the phalanx V-1. A relatively small, cylindrical bone occurs in plantar position on the proximal part of the phalanx V-1, near the articulation with metatarsal V. This bone cannot be a displaced tarsal element, because is found in the same position on both pedes (Fig. 9). The relatively small size and shape, its absence in the general skeletal model of the diapsids (Romer 1976) and its position in correspondence of an articulation, suggest it is as sesamoid bone.

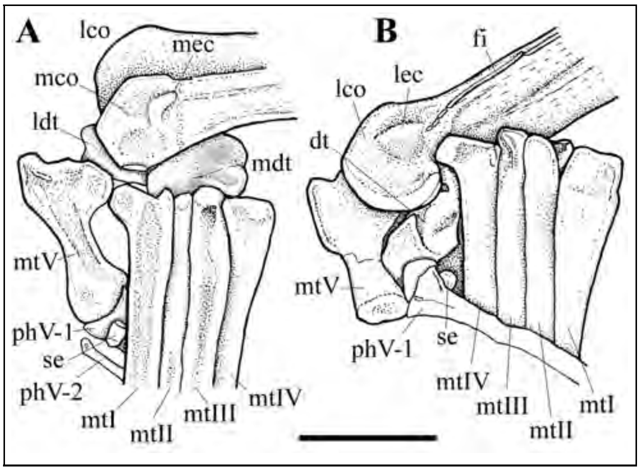

Fig. 9 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype, ankle region. A) Left ankle, with proximal metatarsus in plantar view. B) Right ankle, with proximal metatarsus in dorsal view. Abbreviations: fi = fibula, lco = lateral condyle of the tibiotarsus, ldt = lateral distal tarsal, lec = lateral epicondyle, mco = medial condyle of the tibiotarsus, mdt = medial distal tarsal, mec = medial epicondyle, mtI-V = metatarsals I-V, phV-1, phV-2 = phalanges 1 and 2 of pedal digit V, se = sesamoid. Scale bar = 5 mm.

Wing patagium (Figs. 1A, 10)

Portions of the wing patagium are preserved in four regions of the slab. These patagial portions are identified by the presence of the thin fibres (actinofibrils) characteristic of part of the pterosaurian brachiopatagium, the actinopatagium. A narrow band of the left brachiopatagium occurs along the caudal margin of left wing phalanx 3 (Fig. 10A). Here the fibers are barely identifiable and the patagium is mainly represented by a dark halo; where fibres can be recognized they are very thin (maximum width is 0.03 mm), regularly spaced, parallel and densely packed; this can be observed mainly where the patagium crosses the proximal part of the wing phalanx ventrally, in the slab B. The beginning and end of a single fibre cannot be identified and, therefore, it is not possible to accurately measure its length. They form a very low angle (8°) with the shaft of the phalanx. Obviously, the caudal margin of this tract of the brachiopatagium is not the trailing edge of the wing, but a zone where the brachiopatagium folded parallel to the length of the actinofibrils. In fact, the continuation toward the body of the patagium portion of Fig. 10A lies ventral to the left wing phalanx 3 and is directed towards the cranial margin of the left wing phalanx 2. This folding probably occurred because of the slight disarticulation of the wing spar, not forming a straight shaft anymore. Portions probably belonging to the same brachiopatagium are well evident also between the feet and along the left tibia. In the first case (Fig. 10C, D), the single fibres have a diameter of 0.010 to 0.018 mm, but where they are compressed by the phalanx V-2 they are up to 0.040 mm wide; single fibres can be followed without interruption only for 3-5 mm, but they could be much longer. The fibres are closely spaced (0.050-0.070 mm), straight and mostly parallel, although they are feebly converging approximately in the central part of the patagial fragment suggesting the presence of a fold. They lie below the right pedal phalanx V-2 and curve approaching the right metatarsus; they also lie below the left metatarsus. Three parallel dark lines, 0.085-0.170 mm wide, cross the fibres nearly perpendicularly (82°; Fig. 10D) and may be traces of blood vessels like those preserved ventral to the fibre layer in some *Rhamphorhynchus* specimens (Frey et al. 2003), although no branching can be appreciated. The fibres are wider (0.030-0.045 mm) in the brachiopatagium fragment preserved along the left tibia (Fig. 10B). They are slightly sigmoid, somewhat irregular and rather widely spaced (0.120-0.160 mm); maximum observable length of a fibre without interruption is 3.15 mm, but fibres were surely longer. As a general trend, the fibres are subparallel, but some cross other fibres. The fourth fragment of patagium is visible in a triangular area limited by the left phalanx 2, right tibia and left femur. It

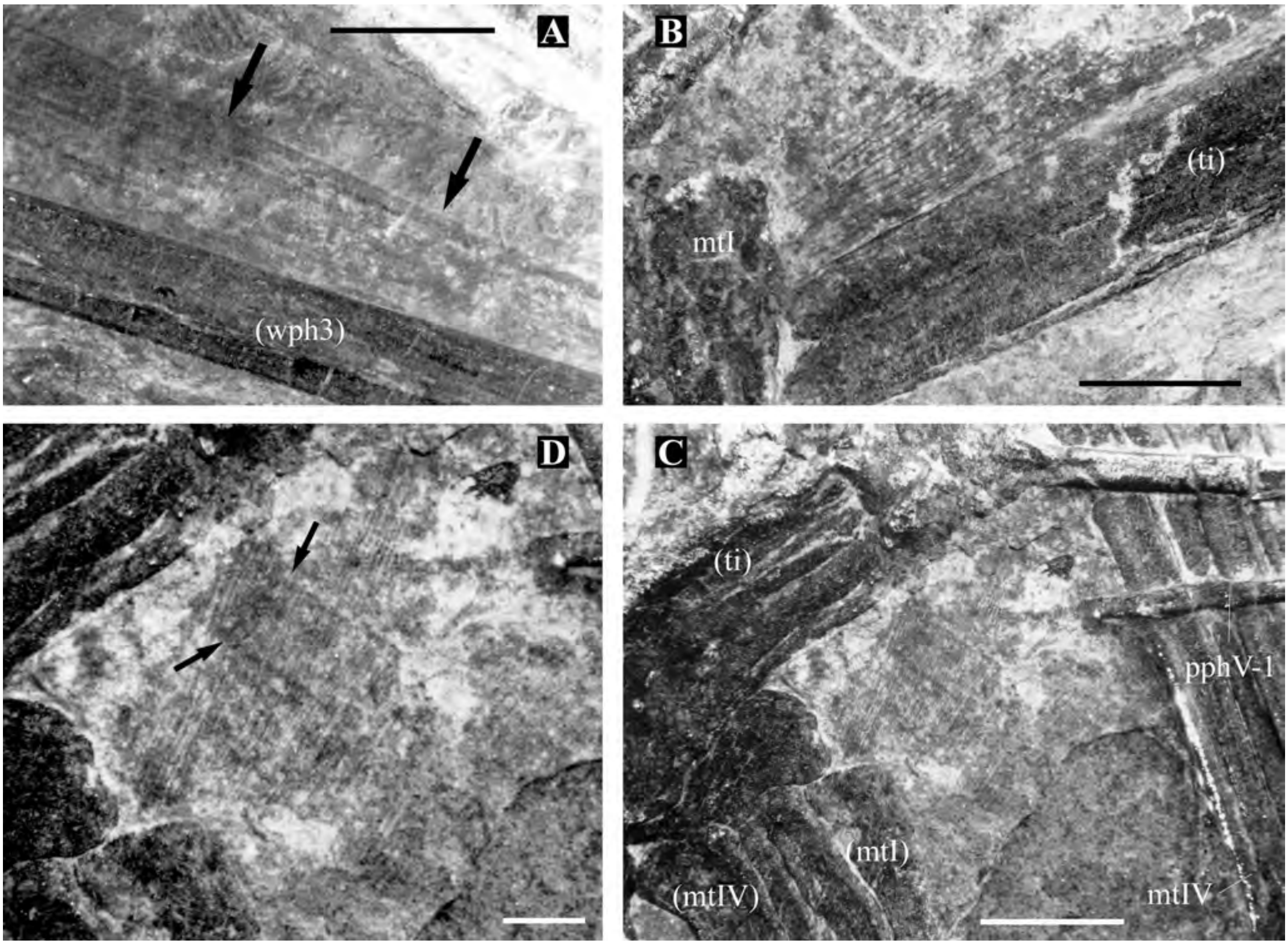

Fig. 10 - *Carniadactylus rosenfeldi*, MFSN 1797, holotype, patches of wing patagium. A) along the left wing phalanx 3 with arrows pointing to the natural edge of the patagium, B) along the left tibia, C) between the two pedes, D) close up of the fibres with the transverse lines, possibly capillaries (arrows). Abbreviations: mt I, IV = metatarsal I, IV, pphV-1 = pedal phalanx V-1, ti = tibia, wph 3 = wing phalanx 3. Left elements are in parentheses. Scale bar is 3 mm in A, B and C, 1 mm in D.

may belong to the same folded brachiopatagium, but it may have belonged to the other one. The thin (0.025-0.030 mm), closely spaced (on the order of 0.050 mm) fibres that usually cannot be followed for more than 2 mm, are generally roughly parallel to each other, but at least two bundles cross the main trend diagonally, suggesting the presence of creases or local fibre detachment.

Comparisons

Size

The wing span of MFSN 1797 estimated following the method used by Bennett (2001b) is 71.08 cm; that of MPUM 6009, MCSNB 8950, MCSNB 3359, the holotype of *Preondactylus buffarinii* and the holotype of *'Raeticodactylus' filisurensis* is 42.7, 41.2, 54.4, 45.95 and 130.6 cm, respectively. The specimen is smaller than MCSNB 2888, as the long bones are shorter, but with varying proportions of the different skeletal elements (Tab. 2). Noteworthy is the estimated length of tibia of MCSNB 2888, which is less than the tibial length in MFSN 1797 (see below). MFSN 1797 is about the same size as BSP 1994 I 51 and significantly larger than MCSNB 2887, MPUM 6009, MCSNB 8950 and MGUH VP 3393, in order of decreasing size (Tab. 2).

Skull

In the holotype of *E. ranzii*, the partially exposed pterygoids are toothed (Wild 1979), unlike MFSN 1797. As for the outline of the quadrate and maxillary (possible fused ectopterygoid) rami, the pterygoid resembles that of *Rhamphorhynchus muensteri*; however, the palatal ramus of the latter is not arched in palatal view (Wellnhofer 1975a). The palatal ramus is narrow and arched in *Scaphognathus crassirostris*, but the maxillary process is much broader (Wellnhofer 1975b). The pterygoid of *Campylognathoides liasicus* has a different morphology according to Wellnhofer's (1974) reconstruction, because it is tetraradiate but with the maxillary ramus made by a separate ectopterygoid. The quadrate is very similar to that of MCSNB 2888 and unlike that of MGUH VP 3393, which was stouter and with a huge distal condylar part (Jenkins et al. 2001).

Tab. 2 - Percentage lengths of the long bones of some Triassic pterosaur specimens with respect to the same element of MFSN 1797 (i.e., skeletal element length in MFSN 1797 = 100). The specimens are listed in order of decreasing sizes. * ratios based on estimated lengths. Abbreviations: M = mean; the others as in Tab. 1.

Specimen	h	u	mcIV	wph1	wph2	wph3	wph4	fe	ti	M
BNM 14524	195	193	-	177	187	185*	161*	151	155	175
MCSNB 2888	112	118	138	125*	-	-	-	110	92*	116
BSP1994 I 51	95	-	-	83	-	-	-	-	106	95
MCSNB 2887	67	69	-	63	63	-	-	57	52	62
MPUM 6009	63	65	50	58	57*	57	66*	50*	-	58
MCSNB 8950	62	61	43	53	61	57	62	53	46	55
MGUH VP 3393	43	36	40	28*	35	32	-	53	38*	38

Lower jaw

The lower jaws of MFSN 1797, MPUM 6009 and MCSNB 2888 have a triangular and pointed 'coronoid' process, unlike those of the other pterosaurs, which are gently curved or practically absent (cf. Owen 1870; Wiman 1925; Kuhn 1967; Wellnhofer 1974, 1975a-b, 1978, 1991; Wild 1979, 1984; Fig. 11). However, the process is significantly larger in MFSN 1797 and MPUM 6009 than in MCSNB 2888 and the mandible at the 'coronoid' process is much deeper (Fig. 11A-C). The 'coronoid' process of BSP 1994 I 51 has a distinct morphology, being gently rounded with two low peaks (Fig. 11D). The retroarticular process of MFSN 1797, MPUM 6009 (broken), MCSNB 2888 and BSP 1994 I 51 is more expanded and rounded than that of the other non-pterodactyloid pterosaurs (see Wellnhofer 1978, 1991; Wild 1979, 1984; Dalla Vecchia et al. 2002; Fröbisch & Fröbisch 2006; Stecher 2008). The space be-

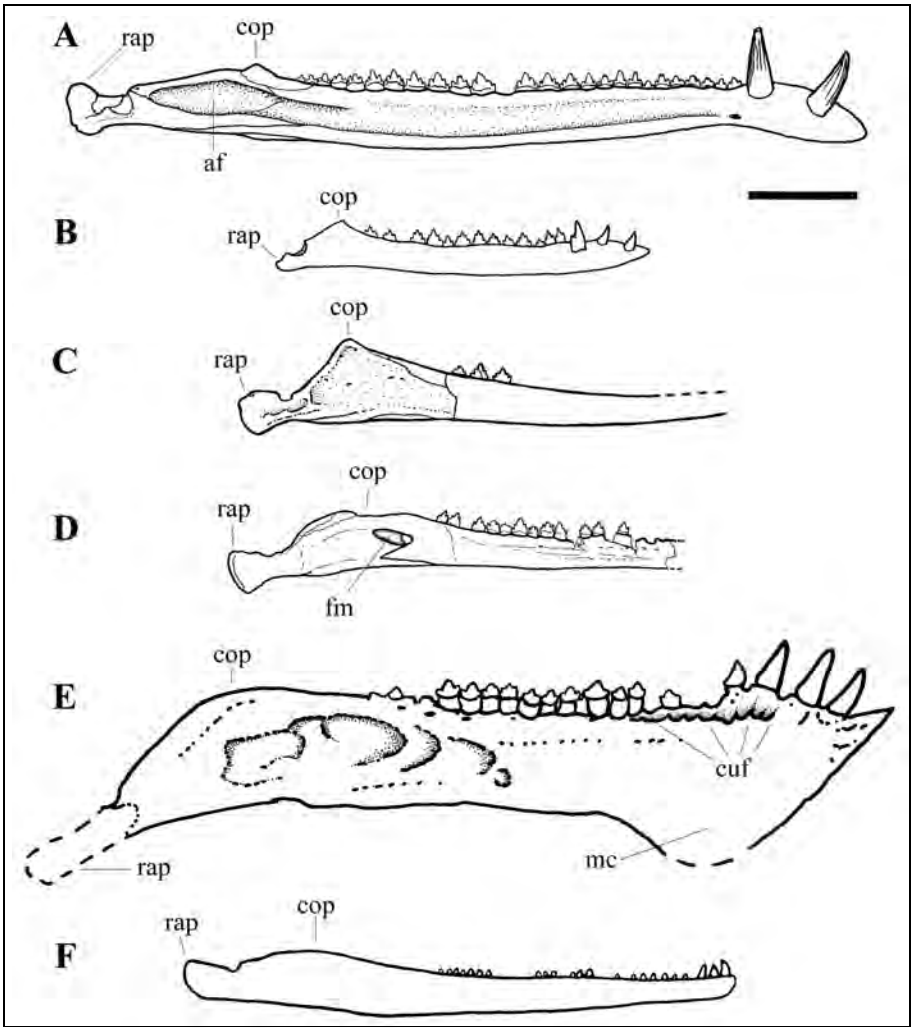

Fig. 11 - Mandibular rami of some Triassic pterosaurs. A) *Eudimorphodon ranzii*, holotype, right ramus in medial view, from Wild (1979), mirrored and redrawn, B) *Carniadactylus rosenfeldi*, MPUM 6009, left ramus in lateral view, from Wild (1979), mirrored and redrawn, C) *Carniadactylus rosenfeldi*, holotype, left ramus in medial view, D) BSP 1994 I 51, left ramus in medial view from Wellnhofer (2003), redrawn, E) *'Raeticodactylus' filisurensis*, holotype, right ramus in lateral view, from Stecher (2008), mirrored and redrawn, F) *Preondactylus buffarinii*, holotype, right ramus in lateral view, from Dalla Vecchia (1998), composite and redrawn. Abbreviations: af = adductor fossa, cop = 'coronoid' process, cuf = cup-shaped structures (large foramina) on the dorsolateral side of the rostral part of the dentary, fm = "*fenestra meckeli*", mc = mandibular crest, rap = retroarticular process. Scale bar = 10 mm.

tween the last distal tooth and the tip of the 'coronoid' process seems to be longer in MFSN 1797 than in both MCSNB 2888 and MPUM 6009 (i.e., the tooth row ends more mesially in MFSN 1797), as in MFSN 1922 (Dalla Vecchia 2004a); however, that part of the mandibular ramus is not well-exposed in MFSN 1797. The large opening that pierces the lower jaw of the BSP 1994 I 51 (the "*fenestra meckeli*" of Wellnhofer 2003; Fig. 11D) does not occur in MFSN 1797, as well as in MPUM 6009, MCSNB 2888 and all other non-pterodactyloid pterosaurs. The mandibular ramus is more slender and elongated than that of *Caviramus schesaplanensis* and '*Raeticodactylus*' *filisurensis*, where the ramus is also distinguished for the marked caudoventral angling of the caudal part and other apomorphies (Fig. 11E, see p. 183).

Hyoid apparatus

The ceratobranchial I of the holotype of *E. ranzii* is comparatively much thinner than those of MFSN 1797 and is slightly recurved all its length long (Wild 1979, fig. 3).

Dentition

Like MFSN 1797, MPUM 6009, '*Eudimorphodon*' *cromptonellus*, BSP 1994 I 51, MFSN 1922 and MFSN 21545 have non-bulbous, quinticuspid to tricuspid crowns with smooth labial and/or lingual surfaces. Instead, multicusped teeth of MCSNB 2888 have basoapical ridges in the labial and lingual surfaces. The main cusp is conical and often mesiodistally narrow in MCSNB 2888, whereas it is somewhat labiolingually flattened and mesiodistally broader in MPUM 6009. The multicusped crowns of *Caviramus schesaplanensis* and '*Raeticodactylus*' *filisurensis* are also smooth, but they appear to be slightly bulbous and with a neck at the crown-base border (Fröbisch & Fröbisch 2006; Stecher 2008).

Axial skeleton

The cervical vertebrae of MFSN 1797 do not differ sensibly from those known in other non-pterodactyloid pterosaurs (e.g., Kuhn 1967; Wellnhofer 1978). The main difference is the rounded expansion of the condyle in ventral view. The strong dorsoventral crushing of the cervical vertebrae in MFSN 1797 and MCSNB 2888 compared to the less compressed dorsal centra, suggests that the cervical vertebrae were hollow inside, possibly extremely such as those of *Rhamphorhynchus muensteri* (see Bonde & Christiansen 2003), and possibly pneumatic. The dicephalous cervical ribs of *E. ranzii* articulate with the diapophysis and the parapophysis of the vertebra (Wild 1979), whereas those of MFSN 1797 seem to be fused to them.

Pectoral girdle

The coracoid of MFSN 1797 is relatively broad, flat and short (plate-like) in comparison with the coracoids of most other non-pterodactyloid pterosaurs (e.g., Kuhn 1967; Wellnhofer 1978; Wild 1979). The length:width ratio is much lower than in the holotype of *E. ranzii* (7.75 according to Wild 1979, fig. 15) where the shaft is rod-like and unexpanded distally (Fig. 3A). It is 5.1 in MCSNB 2887 (Wild 1979, fig. 16), where the shaft is relatively narrow and thick (Fig. 3B). The coracoidal shaft of BSP 1994 I 51 is plate-like but fan-shaped and with a length:width ratio only 1.86 (Fig. 3E). The ratio cannot be calculated accurately in MPUM 6009, because the distal end of the shaft of both coracoids is incomplete. However, the better exposed left coracoid is very similar to the coracoid of MFSN 1797, with a flat, broad and thin shaft with subparallel caudal and cranial margins (Fig. 3D); also the glenoid region has a similar structure. The coracoid shafts in MCSNB 8950 are evidently broad and short (the coracoid is about half the scapular length), but they are not well preserved. In '*E.*' *cromptonellus*, the coracoid is incompletely preserved, but appears to be thicker than that of MFSN 1797. The shaft is relatively flat in MCSNB 3359, but it is fan-shaped and more slender (ratio 4.25; Wild 1979, fig. 34).

The triangular sternal plate of the BSP 1994 I 51 with two long, narrow processes for the coracoid articulation (Wellnhofer 2003) is much different from quadrangular plate of MCSNB 2888. There is no evidence of those elongated structures in MFSN 1797; they may be broken because of strong crushing or concealed among the dorsal ribs, but this is unlikely.

Forelimb

The square deltopectoral crest of the humerus is typical of all purported *Eudimorphodon* specimens (excluding '*E.*' *cromptonellus*) and *Campylognathoides*. In MFSN 1797, it is craniocaudally narrow and with a cranial edge parallel to the axis of the shaft as in BSP 1994 I 51, MFSN 1922 and possibly MPUM 6009 where it is damaged. In MFSN 1797, the shaft appears to be more elongated than that of all other specimens referred to *Eudimorphodon* and the proximal part is comparatively narrower (Fig. 4). In fact, the ratio of humeral length:maximum proximal width is 1.87-2.2 in MCSNB 2888, 2.41 in BSP 1994 I 51, 2.54 in MCSNB 8950, 2.58 in MFSN 1922, about 2.80 in MPUM 6009, and about 3 in MCSNB 2887 and MGUH VP 3393. It is higher only in the large holotype of '*Raeticodactylus*' *filisurensis* (3.60). However, the humerus in MFSN 1797 is not well-preserved and its elongation may be emphasized by crushing. The humerus is much shorter than the ulna as in all pterosaurs; it is longer than the femur as in all specimens formerly referred to *Eudimorphodon* (excluded MGUH VP 3393) and in *'Raeticodactylus' filisurensis*. The humerus is sensibly shorter than the tibia, unlike MCSNB 8950 where it is longer and unlike MCSNB 2887 and *'Raeticodactylus' filisurensis* where the two bones have nearly the same length (Tab. 3). The ratio of wing phalanx 1:humerus is closer to that of MCSNB 2887 and MPUM 6009 (Tab. 3).

The composition of the distal carpus of '*Eudimorphodon*' specimens is always ambiguous, as usual for non-pterodactyloid pterosaurs. Following Wild (1979, p. 209-210), the articulated left carpus of MCSNB 2888 in dorsal view is very similar to that of MFSN 1797. It shows a large proximal syncarpal interlocked with a large distal carpal that seems to bear a small

	1	2	3	4	5	6	7	8	9	10	11	12	13
h	18.15	26	26.3	28	47	40	42	82	75*	32	-	38.5	63-91
u/h	1.11	1.29	1.37	1.36	1.38	-	1.31	1.29	-	1.31	-	1.30	1.29
h/mcIV	2.16	2.89	2.50	--	1.62	-	1.93	-	-	2.25	-	2.29	1.95-2.36
u/mcIV	2.39	3.72	3.43	--	2.24	-	2.62	-	-	2.95	-	2.91	3.00
h/fe	0.92	1.33	1.42	1.32	1.14	-	1.13	1.46	-	0.98	-	1.05	1.04-1.09
h/ti	0.88*	1.04	-	0.98	0.94*	0.69	0.77	0.98	-	0.73	-	0.81	0.71-0.76
u/fe	1.02	1.71	1.95	1.79	1.58	-	1.49	1.89	-	1.29	-	1.34	1.34-1.40
u/ti	0.98*	1.34	-	1.33	1.30	-	1.02	1.26	-	0.95	-	1.03	0.97-0.98
ti/fe	1.04*	1.27	-	1.34	1.22*	-	1.46	1.50	-	1.35	-	1.30	1.39-1.46
fe/mcIV	2.34	2.18	1.76	-	1.41	-	1.76	-	-	2.28	-	2.18	1.87-2.23
ti/mcIV	2.44*	2.78	-	-	1.72*	-	2.58	-	-	3.09	3.12	2.82	2.74-3.15
wph1/h	0.97*	1.31	1.43	1.43*	1.70*	1.32	1.52	1.38	-	1.11	-	1.09	1.06-1.20
wph1/u	0.90*	1.01	1.04	1.05*	1.23*	-	1.16	1.07	-	0.85	-	0.86	0.82-0.90
wph1/mcIV	2.14*	3.78	3.57	--	2.75*	-	3.05	-	-	2.49	2.57	2.50	2.35-2.70
wph1/fe	0.91*	1.73	2.03	1.89*	1.95*	-	1.73	2.02	-	1.09	-	1.15	1.10-1.26
wph1/ti	0.89*	1.36	-	1.40*	1.60*	0.92	1.18	1.34	-	0.81	0.82	0.88	0.80-0.88
wph2/wph1	1.14*	1.04	0.88	0.91*	-	-	0.91	0.96	-	1.10	0.96*	1.00	1.03-1.15
wph3/wph2	1.00*	1.02	1.10*	-	-	-	1.09	1.07*	1.02	1.00	-	1.09	1.08-1.12
wph3/wph4	-	1.12	1.06	-	-	-	1.23	1.41*		1.39	-	1.33	1.25
wph3/wph1	1.14*	1.06	0.96*	-	-	-	0.99	1.03*	1.21	1.08	-	1.09	1.24-1.29

Tab. 3 - Ratios of long bone length in Triassic pterosaur specimens and *Dimorphodon macronyx*. Humerus length (in mm) is reported as general indicator of size. Legend: 1 = MGUH VP 3393 (holotype of *'Eudimorphodon' cromptonellus*, from Jenkins et al. 2001), 2 = MCSNB 8950, 3 = MPUM 6009, 4 = MCSNB 2887, 5 = MCSNB 2888 (holotype of *Eudimorphodon ranzii*), 6 = BSP 1994 I 51, 7 = MFSN 1797, holotype of *Carniadactylus rosenfeldi*, 8 = BNM 14524 (holotype of *'Raeticodactylus' filisurensis*, from Stecher 2008), 9 = SMNS 56342 (holotype of *Austriadactylus cristatus*), 10 = MFSN 1770 (holotype of *Preondactylus buffarinii*), 11 = MCSNB 2886 (holotype of *Peteinosaurus zambellii*), 12 = MCSNB 3359, 13 = *Dimorphodon macronyx* (specimens YPM350 and YPM9182 from Padian 1983, GSM1546 and BMNH R.1034 [holotype] from Unwin 1988, BMNH 41212 from Wellnhofer 1978). * = measurements estimated or approximate.

process for the preaxial carpal. A small distal carpal contacts the metacarpal I and another one, less clearly distinguishable, contacts metacarpal II-III (Wild 1979). The left preaxial carpal is slightly different morphologically because it is not crescent shaped and has a large fovea for the sesamoid. A crescentic preaxial carpal crossed by a ridge occurs instead in *Campylognathoides* (Wild 1975). MPUM 6009 has a proximal syncarpal and a large distal carpal as MCSNB 2888; the probable presence of small distal carpals corresponding to metacarpals I-III cannot be detailed because of poor preservation and the preaxial carpal is not preserved. According to Wild (1994, p. 105), MCSNB 8950 has "at least 3 larger carpals: a large proximal one and 2 distal one", although this is not evident in fig. 2 and 4; any further observation is hampered by their state of preservation.

The pteroid of MFSN 1797 differs from the characteristic handle-shaped pteroid ("hatched-shaped" for Wild 1979) of the holotype of *E. ranzii* and MCSNB 2887 (Fig. 6C-D). Instead, it is indistinguishable from the incomplete but clearly angled, rod-like pteroid of MPUM 6009 (Fig. 6B). The shape of the pteroid of the small MCSNB 8950 is undeterminable, therefore it does not resembles that of MCSNB 2887, nor it is "intermediate" between the "hatched-shaped" pteroid of MCSNB 2888 and MCSNB 2887 and the "rod-like in the Milano specimen" as reported in Wild (1994 pp. 106 and 115). The shape of the pteroid of *Dorygnathus* is the same in all the specimens despite to their size (pers. obs. at GPIT, SMNS and BSP); the same is true for *Campylognathoides* where the shape of the pteroid is considered diagnostic of the genus (Padian 2008b). All ontogenetic stages of *Rhamphorhynchus muensteri* have a, slender, rod-shaped pteroid, straight or faintly curved (pers. obs.); larger individuals (considered subadults and young adults by Bennett 1995), have just a more slender and comparatively longer pteroid than smaller specimens. Therefore, the morphology of the pteroid probably does not change with ontogeny and has a systematic importance.

Metacarpal IV is comparatively longer in MCSNB 2888 and shorter in MCSNB 8950 and MPUM 6009 than in MFSN 1797 (Tab. 2); the relative length of metacarpal IV is related to the absolute size of the individual in a sample of conspecific specimens (i.e., it has an allometric growth with respect to other long bones), but varies also among different genera, as noted by Padian & Wild (1992). Thus, ratios including metacarpal IV length can vary in both senses (Tab. 3). The dorsal condyle is much more developed than the ventral one also in MPUM 6009. The relative length of the metacarpals I-III in MFSN 1797 is like that observed in MCSNB 2888 and MPUM 6009, but unlike the holotype of *Preondactylus buffarinii* where metacarpals II-III have a same length and I is much shorter (Dalla Vecchia 1998) and the Jurassic taxa *Sordes*, *Scaphognathus*, *Rhamphorhynchus* and *Anurognathus*, where metacarpals have all the same length.

MFSN 1797 and MPUM 6009 are the only basal pterosaurs where wing phalanx 1>3>2 (cf. Tab. 3 and Dalla Vecchia 2003, tab. 2). The relative size of wing phalanges is unknown in MCSNB 2888, but in MCSNB 2887 wing phalanx 2 >1 (Wild 1979), in MCSNB 8950 wing phalanx 3>2>1, in '*Eudimorphodon*' *cromptonellus* wing phalanx 2=3>1, and in '*Raeticodactylus*' *filisurensis* wing phalanx 3>1>2. Wing phalanx 1 is longer than the tibia in MFSN 1797 (wph1:ti = 1.18), MCSNB 8950 (1.36), MCSNB 2887 (1.40) and '*Raeticodactylus*' *filisurensis* (1.34), whereas it is shorter than the tibia in BSP 1994 I 51 (0.92), '*E.*' *cromptonellus* (0.89), *Preondactylus buffarinii* (0.81), *Peteinosaurus zambellii* (0.82), MCSNB 3359 (0.88) and *Dimorphodon macronyx* (0.80-0.88).

Hind limb

The femur of MFSN 1797 is markedly shorter than the ulna and tibia as in all specimens listed in Tab. 3 excluding MGUH VP 3393; it is much shorter than wing phalanx 1 like all specimens listed in Tab. 3 excluding the taxa with short wing phalanx 1 (*Preondactylus*, MCSNB 3359 and *Dimorphodon macronyx*) and MGUH VP 3393. The tibiotarsus of MFSN 1797 is relatively long and robust with comparison to most other basal pterosaurs, as the ratios with other long bones also suggest (Tab. 2). Despite its incomplete preservation, the tibia is clearly a gracile element in MCSNB 2888 compared to the ulna and wing phalanx 1; Wild's length estimate of tibial length may be plausible (contra Wellnhofer 2003). Although Wild (1979) tried to estimate the tibial length of MPUM 6009 (estimation also used in Dalla Vecchia 2003), most of both tibiae is not preserved even as an impression, mainly in the distal half. Thus, a reliable reconstruction is not possible; however, compared to the other long bones, the tibiae are clearly less gracile than in MCSNB 2888. The tibiotarsus of MCSNB 2887 is also comparatively shorter than that of MFSN 1797 (Tabs. 2-3). Specifically, the tibia is sensibly longer than the humerus in MFSN 1797 (h:ti = 0.77), BSP 1994 I 51 (0.69) and MGUH VP 3393 (0.88), whereas it is approximately as long as the humerus in MCSNB 8950 (1.04), MCSNB 2887 (0.98) and '*Raeticodactylus*' *filisurensis* (0.98). A long tibia occurs also in *Preondactylus buffarinii* (h:ti = 0.73), MCSNB 3359 (0.81) and *Dimorphodon macronyx* (0.71-0.76).

The fibula seems not to reach the tibiotarsal lateral epicondyle in MCSNB 2887. It is not possible to check its distal end in MCSNB 8950 (contra Wild 1994 and Wellnhofer 2003) because the distal portion of the crus is not preserved. It reaches the tibiotarsal lateral epicondyle in BSP 1994 I 51, but the distal fibular portion is thicker than in MFSN 1797 and its distal end is expanded (Wellnhofer 2003).

The metatarsus of MFSN 1797 is comparatively longer than that of MCSNB 8950 (mtII:h, mtII:u, mtII:f and mtII:ti are 0.52, 0.40, 0.59, 0.41 and 0.34, 0.26, 0.45, 0.35, respectively), but shorter than that of MGUH VP 3393 (0.65, 0.60, 0.61, 0.58). Metatarsal IV is slightly shorter than metatarsal I, as in other non-pterodactyloid pterosaurs excluding *Dorygnathus*, *Sordes*, *Scaphognathus* and *Rhamphorhynchus*, where it is much shorter (Unwin 2003).

The phalanges of digit V are long and perfectly straight like those in the MCSNB 8950, MCSNB 3359, *Dimorphodon macronyx* and '*Dimorphodon*' *weintraubi*; they are unknown in all other '*Eudimorphodon*' specimens as well as in *Caviramus schesaplanensis*; the condition in '*Raeticodactylus*' *filisurensis* is not clear.

The third toe is the longest, being slightly longer than fourth, unlike MCSNB 8950, MCSNB 3359, *Dimorphodon macronyx* and '*Dimorphodon*' *weintraubi* where the fourth is slightly longer than third. The sesamoid on the proximal part of the phalanx V-1, near the articulation with the metatarsal V has never been reported from any basal pterosaurs (e.g., Wellnhofer 1978, 1991; Wild 1979, 1994; Padian 1983; Unwin 1988).

Wing ratio

The wing ratio (calculated as humerus + ulna + metacarpal IV + wing phalanges I-IV: femur + tibiotarsus + metatarsal II) is 3.78 in MCSNB 8950, 3.80 in the holotype of '*Raeticodactylus*' *filisurensis*, 4.46 in *Campylognathoides liasicus* (CM 11424, Wellnhofer 1974), 2.62 in MCSNB 3359 and 2.48 in the holotype of *Preondactylus buffarinii*. With a wing ratio of 3.13, MFNS 1797 has a relatively short wing or a long hind limb. The second option is most probable as shown by the long bone length ratios containing the tibial length. A low wing ratio was considered a primitive feature by Wild (1984), but may be also related to the wing aspect ratio (Padian & Rayner 1993) and to flight performance (Bennett 2007b).

Wing patagium

Patches of the patagium with actinofibrils were already reported in other Triassic pterosaur specimens (MCSNB 8950, Wild 1994; MFSN 1922, Dalla Vecchia 2004a), but the structures crossing the fibres nearly perpendicularly and possibly representing blood vessels are described for the first time.

Conclusions

MPUM 6009 preserves the skull, lower jaws and most of the postcranium, although the latter is partly represented by the impression of the bone. It was originally attributed to *E. ranzii* by Wild (1979) because of its stratigraphic and geographic provenance, possession of quinticuspid and tricuspid teeth, a square deltopectoral crest of humerus and a triangular and pointed 'coronoid' process of the lower jaw. The large size of the triangular 'coronoid' process united to the depth of the lower jaw in correspondence of it, the shape of the coracoid and the pteroid are apomorphic characters shared with MFSN 1797 suggesting their conspecificity. The proportions of the wing phalanges (wing phalanx 1> 3 > 2) are also unique to them, although the state in MCSNB 2888 is unknown. The smooth dentary crowns of both specimens are in agreement with this interpretation, and most long bone ratios do not show substantial differences.

Some difference exists in body size, as the long bones of MPUM 6009 are about 60% the length of those of MFSN 1797 (Tab. 2) and the last distal dentary tooth of MFSN 1797 possibly occurs more mesially than in MPUM 6009. Also, the femur and the wing metacarpal are comparatively shorter in MPUM 6009, as shown by long bone ratios (Tab. 3). However, the ratio between the wing metacarpal and other long bones may vary depending on the absolute size of the individual (Padian & Wild 1992) and the femur is poorly preserved in both specimens. The two specimens obviously belonged to different populations and the differences may be due to intraspecific variability. As an alternative, MPUM 6009 and MFSN 1797 may belong to closely related but separate species, also because they lived in different localities in an insular palaeogeographic context of a wide carbonate platform that probably favoured speciation. This could be ascertained only with new material. Waiting for an increase of the sample that could shed light on this aspect, here I consider them as conspecific.

MPUM 6009 gives information on the skull and dentition (Wild 1979) and tail (Dalla Vecchia 2002) of *Carniadactylus* that are unknown in the holotype and are utilized in the differential diagnosis of the taxon.

The ontogenetic stage of MFSN 1797 and MPUM 6009

MPUM 6009 was considered a juvenile by Wild (1979) because sensibly smaller than MCSNB 2888. As MFSN 1797 is also smaller than the holotype of *Eudimorphodon ranzii*, it could also be an immature specimen and the morphological differences with MCSNB 2888 may be ontogenetic (Wild 1979; Wellhofer 2003). However, absolute size is not by itself a sufficient parameter to discriminate between adult and immature (juveniles and 'subadults') individuals of a same species (Bennett 1993, 1995, 1996; Brochu 1996), mainly when the sample is made of specimens from different populations (i.e., sampled in different stratigraphic horizons) and even different localities. In insular settings like those where probably nearly all the Triassic pterosaurs lived (cf. Jadoul et al. 1994; Gaetani et al. 2000), body size variability may be related to island dimensions (e.g., Burness et al. 2001) and ecological factors (e.g., Wikelski 2005). Features related to the skeletal maturity are more reliable in assessing the ontogenetic stage of a fossil vertebrate (Bennett 1993, 1995, 1996; Brochu 1996). Also in this case, only a possible trend of increasing osteological maturity can be observed, whereas the categories of "juvenile", "subadult" and "adult" are established arbitrarily.

According to Bennett (1993) size-independent characters, unrelated to skeletal proportions that allow distinguishing the different ontogenetic stages in pterosaurs are: fusion of various cranial and post-cranial bones, degree of epiphyseal ossification, bone grain or degree of ossification of limb-bone shafts, change in shape of some elements. Because of the very small sample, the provenance from different horizons and often different localities too, the change in shape of bones alone cannot be utilized as ontogenetic indicators for '*Eudimorphodon*' specimens. In fact, we cannot determine whether they reflect intraspecific or interspecific rather than ontogenetic variation. Instead, skeletal maturity can be unambiguously observed also on a single specimen.

In MFSN 1797, the scapula is coossified to the coracoid without suture and the proximal tarsals are fused to tibia. Elements of the mandible are fused, mostly with barely visible sutures. The proximal carpals are fused in a single syncarpal; interphalangeal collateral ligament attachment tubercles in wing phalanges are often distinct as in mature specimens (Bennett 2000); ginglymi of pedal phalanges are well-shaped. This is suggestive of a relative skeletal maturity of the specimen, which cannot be considered a "juvenile" (cf. Bennett 1993, 1995, 1996). The scapula is unfused to coracoid and distal tarsals are not coosified to tibia in other '*Eudimorphodon*' specimens (e.g., MGUH VP 3393 and MCSNB 8950), which probably were immature individuals. It can be argued that the probable presence of three distal carpals in MFSN 1797 is related to immaturity. However, that is also the outgroup condition (whatever group is chosen among the Archosauromorpha), thus it cannot be excluded that it is a plesiomorphic trait rather than an ontogenetic one. This interpretation is supported by the similar composition of the carpus in MCSNB 2888, generally considered as an adult (Wild 1979; Jenkins et al. 2001; Wellnhofer 2003). Furthermore, the actual structure of the distal carpus is not well-known in non-pterodactyloid pterosaurs, because the single elements are small, and could be lost or scattered and misinterpreted in disarticulated specimens; in articulated specimens, they could be closely packed in a single mass or only partially exposed and difficult to detect for their small size. In mature individuals of large pterodactyloids, where a single distal syncarpal undoubtedly occurs, metacarpals I-II are much reduced and even do not reach the carpus. Therefore, the discrete distal carpals for metacarpals I and II would have no functional meaning. In pterosaurs where metacarpals I-III are comparatively well-developed and reach the carpus, the presence of small carpals proximal to metacarpals I and II would allow a slight mobility at the wrist that may have a functional significance.

The only possible evidence of osteological immaturity in MFSN 1797 may be the wrinkled surface of the distal tibia, and the striated surface of the distal wing phalanx 1 and of part of the coracoid shaft.

MPUM 6009 was a priori considered a juvenile by Wild (1979) because of its small size. At the time, the presence of multicusped teeth and the square deltopectoral crest of humerus where shared only with the much larger MCSNB 2888 from the same site, thus it was the most parsimonious option to consider MPUM 6009 as a small individual of *E. ranzii*. Consequently, the several osteological differences between the two specimens (i.e., shape of the postorbital, lower jaw morphology, extension of the dentigerous part of the lower jaw, teeth number, relative number of tri- and quinticuspid teeth, robustness of humeri and pteroid shape) were explained as ontogenetic changes by Wild (1979). However, the increased record of Triassic pterosaurs suggests that those differences have a systematic nature. They may be considered ontogenetic only if there is independent demonstration that MCSNB 2888 and MPUM 6009 are a mature and an immature specimen of the same species. The slightly different shape of the postorbital and the differences in the lower jaw morphology can be due to the belonging to different taxa. A lesser caudal extension of the teeth in MCSNB 2888 is related by Wild (1979) to the higher space needed in adult individuals to accommodate the larger adductor musculature for the lower jaw, but this is obviously related to size, not necessarily to ontogeny. Actually, the lower jaw at the level of the 'coronoid' process is much deeper in MPUM 6009 than in MCSNB 2888 to accommodate the adductor musculature. MFSN 1797 has both a wide insertion area along the dorsal margin of the mandible before the 'coronoid' process and a very deep lower jaw, thus had probably a comparatively more developed adductor musculature despite to the smaller size with respect to MCSNB 2888.

The tooth count in living diapsid can increase with the growth of the individuals (mainly in the Squamates; Edmund 1969). The tooth count in *Rhamphorhynchus muensteri* (see Bennett 1995) and *Scaphognathus* (pers. obs.) does not change during ontogeny, but it does in other pterosaurs. The tooth count increase is related to the allometric increasing size of the jaws and teeth. MPUM 6009 and MCNSB 2888 have a similar pattern of dentition, but different jaw length and it is impossible to state whether the different tooth count means that MPUM 6009 is a juvenile individual of the same species of MCSNB 2888 or an adult individual of a smaller species, without other evidences of immaturity.

The increased sample shows that the relative number and distribution of quinti-, tetra- and tricuspid teeth in '*Eudimorphodon*' specimens is irregular (Dalla Vecchia 2004a).

Wild (1979) suggested that the humerus is stockier and more robust in larger, adult specimens of *Eudimorphodon* to accommodate the increased muscular mass related to flight. This implies that a stout humerus with a low maximum length:maximum proximal width ratio is related to large size rather than late ontogenetic stage, although large size and late ontogenetic stage may coincide. The comparison of the robust humerus of MCSNB 2888 with the gracile one of the holotype of "*Raeticodactylus*" *filisurensis* (Fig. 4A-B, J) shows that a low maximum length:maximum proximal width ratio can be independent from ontogeny and size, because BNM 14524 is larger than MCSNB 2888 and nothing indicates it is not adult. Furthermore, the ratio in MFSN 1797 is higher than that of the smaller '*Eudimorphodon*' specimens like MCSNB 2887, MPUM 6009 and MCSNB 8950. The pteroid is very different in MPUM 6009 and MCSNB 2887 (that Wild 1979 considers a subadult of *E. ranzii*), which have similar body sizes (Tab. 2). The pteroid of MCSNB 2887 is handle-shaped like that of MCSNB 2888, although comparatively larger. MCSNB 2887 is smaller than both MFSN 1797 and MCSNB 2888, thus the handle versus "rod-shaped" pteroid is not dependent upon the size of the individuals or ontogenetic variation among members of a same species.

Wild (1979) added additional evidence of immaturity to support his identification of MPUM 6009 as a juvenile:

1) Orbit proportionally much larger in MPUM 6009 than in MCSNB 2888. Actually, this is not the case when the photographs of the specimens are compared, instead of skull drawings subject to graphic deformation. Anyway, an unusually large orbit could also be a specific feature not only an ontogenetic trait, as shown by the comparison with *Campylognathoides liasicus*.

2) Snout more elongated in MCSNB 2888 than in MPUM 6009. This is only due to the graphic deformation of the drawings in Wild (1979). When the photographs are compared instead of the drawings (cf. fig. 2 and 5 in Wild 1979) the snout of MPUM 6009 is not less elongated than that of MCSNB 2888.

3) In analogy with ontogenetic changes in the dentition of *Tanystropheus longobardicus* (based on Wild 1973), cusps have basoapical crests of enamel in adults, whereas they are smooth in juveniles. This is not conclusive evidence of the immaturity of the specimen with smooth teeth, because it could be simply related to a different diet, as suggested by the different shape of the lower jaw. Also, the *Tanystropheus* ontogenetic trend in the dentition is just a hypothetical interpretation. In fact, recent revisions of *Tanystropheus* suggest the presence of two species in the sample, and cast doubts about the ontogenetic significance of the differences in tooth morphology also among *Tanystropheus* specimens (Rieppel 2001; Fraser et al. 2004).

4) A poor ossification of the limbs; in particular, the porous aspect of the bone would suggest that the phalanges of the pes (only partially preserved) are to be considered incompletely ossified. However, the whole layer surface containing the bones has a grainy morphology, because it was covered by a sheet of small calcite crystals and this affected the preservation of the bones. Instead, the phalangeal ginglymi are well-shaped, suggesting complete ossification.

Actually, the fused scapula and coracoid, fibula coosified proximally to the tibia, the proximal carpals fused in a syncarpal and the well-articulated skull and lower jaw elements suggest that MPUM 6009 is not a very immature individual.

Phylogenetic analysis

According to Kellner's cladistic analysis (2003) MFSN 1797 (as holotype of '*Eudimorphodon*' *rosenfeldi*) forms a clade with *Peteinosaurus zambellii* (node 8, unnamed taxon), thus to maintain *Eudimorphodon* monophyly it should be renamed. The presence of multicusped teeth is the only synapomorphy at node 8. Kellner based his codings of *Peteinosaurus zambellii* on two specimens: the very incomplete holotype (MCSNB 2886) and MCSNB 3359. However, the latter cannot be unambiguously referred to *Peteinosaurus* (Dalla Vecchia 2003). Furthermore, only the distal mandibular teeth of *Peteinosaurus zambellii* bear very small cusps along their cutting margins (teeth are crenulated rather than multicusped). Multicusped teeth occur also in *Eudimorphodon ranzii* as Kellner himself underlines (p. 114), and in *Caviramus schesaplanensis* and '*Raeticodactylus*' *filisurensis* that where unknown when Kellner performed his analysis. *Austriadactylus cristatus*, another taxon not included in his analysis, has mandibular teeth that may be considered multicusped or serrated with few serrations (Dalla Vecchia et al. 2002). Also, the long bone length ratios of MFSN 1797 are sensibly different from those of both MCSNB 2886 and MCSNB 3359 (Tab. 3). Thus, the strict phylogenetic relationships of *Peteinosaurus zambellii* and *Carniadactylus rosenfeldi* are doubtful.

To formulate a hypothesis of phylogenetic relationships of *Carniadactylus rosenfeldi*, I performed a phylogenetic analysis by parsimony using PAUP* 4.0b10 for Microsoft Windows (Swofford 2002). I used the heuristic search option and the ACCTRAN character state optimization; characters were given equal weight and multistate characters where treated as unordered. The data matrix of 73 characters (see Appendix 1) is basically that of Unwin (2004), the only published one which was created for investigating the relationships among non-pterodactyloid pterosaurs. Some characters of Unwin's matrix were modified, eight characters were taken from Kellner (2003) and 19 are new. Unlike Unwin (2004), I used three outgroups (*Macrocnemus bassanii, Ticinosuchus ferox* and *Herrerasaurus ischigualastensis*) and I scored the characters for three pterodactyloid taxa (*Pterodactylus antiquus*, *Pteranodon longiceps* and *Anhanguera* spp.) instead of an inclusive "Pterodactyloid". Moreover, species and single specimens are chosen as systematic units, instead of genera. The 24 ingroup taxa include all the non-pterodactyloid pterosaurs scored by Unwin (2004), plus *Caviramus schesaplanensis*, *'Raeticodactylus' filisurensis* and *Carniadactylus rosenfeldi*. MCSNB 3359 is scored as a taxon separate from *Peteinosaurus zambellii*; MCSNB 8950 and BSP 1994 I 51 have been treated as unnamed, distinct taxa, because they do not share apomorphies with the holotype of *Eudimorphodon ranzii* and seem to be distinct morphologically (see below).

The analysis produced 18 equally parsimonious trees with a length of 210 steps, consistency index = 0.5714, homoplasy index = 0.4952, retention index = 0.7321, rescaled consistency index = 0.4184. The Strict and the 50% Majority Rule Consensus trees coincide (Fig. 12). The results of this analysis are quite different from those obtained in previous phylogenetic analyses (Kellner 2003, 2004b; Unwin 2003, 2004; Sangster 2004; Lü & Ji 2006; Bennett 2007b; Wang et al. 2005, 2008). They will be discussed elsewhere; here I discuss only the position of *Carniadactylus rosenfeldi*. This taxon is nested inside a clade corresponding to the Campylognathoididae as defined by Unwin (2003). The clade is pectinate, with *Campylognathoides* spp., *Eudimorphodon ranzii*, MCSNB 8950 and *Carniadactylus rosenfeldi* as consecutive sister-groups of (*Caviramus schesaplanensis*+*'Raeticodactylus' filisurensis*). The bootstrap va-

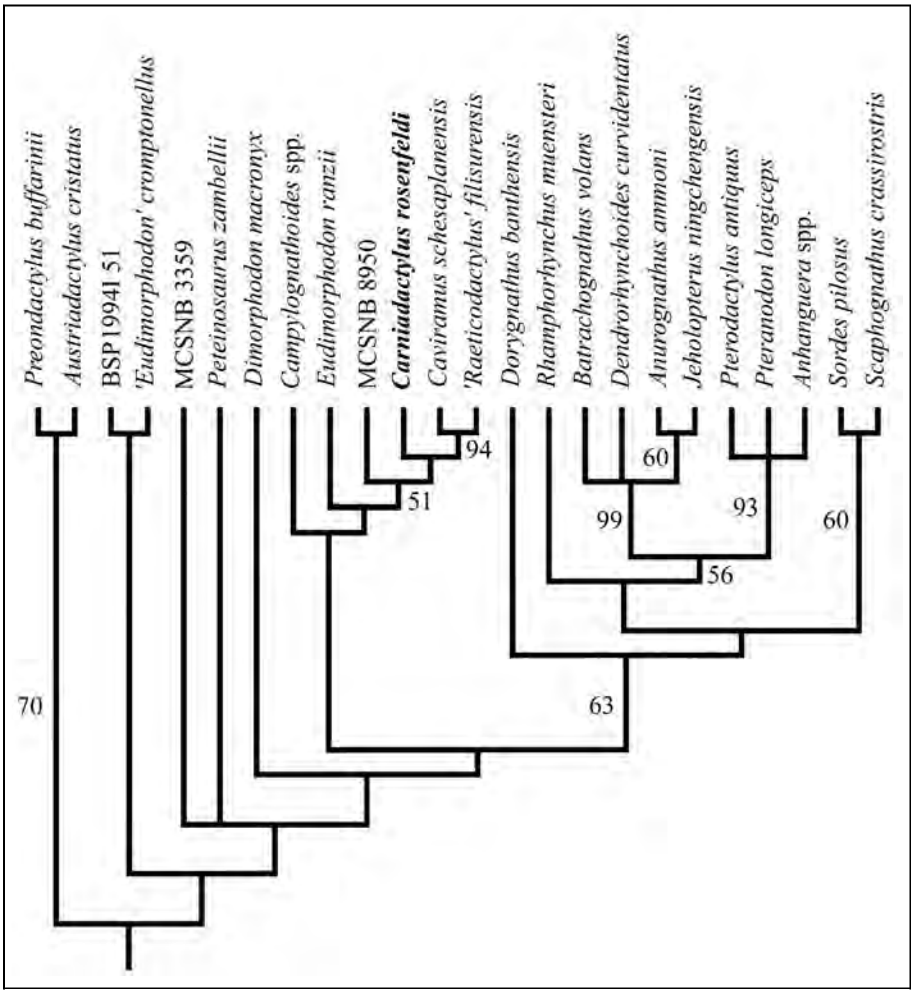

Fig. 12 - Strict Consensus Tree of 18 most parsimonious trees resulting from a maximum parsimony analysis of 24 pterosaur taxa. Numbers refer to bootstrap values. Outgroup taxa are omitted.

lues (1000 replicates) show that the tree topology is weak, i.e. strongly subject to modification with random changes in the data matrix. Few clades have a bootstrap value higher than 50 (Fig. 12). A clade *Carniadactylus rosenfeldi* (*Caviramus schesaplanensis* + *'Raeticodactylus' filisurensis*) has a slightly lower bootstrap value (49.2).

Revision of the '*Eudimorphodon*' record

Eudimorphodon is reported in the literature as the best known and the most common Triassic pterosaur genus (e.g., Dalla Vecchia 2003, 2004b; Unwin 2004, 2006). Three species have been named: the type species *E. ranzii* Zambelli, 1973 (Wild 1979, 1994), *E. rosenfeldi* and *E. cromptonellus* Jenkins, Shubin, Gatesy & Padian, 2001 (Jenkins et al. 2001). As in the case for MFSN 1797, other specimens were attributed to the genus based on the presence of tricuspid to quinticuspid maxillary and mandibular teeth and the square deltopectoral crest of the humerus (Dalla Vecchia 2003, 2004b).

Besides the holotype (MCSNB 2888), the Calcare di Zorzino Formation (Norian, upper Alaunian; Jadoul et al. 1994) of Lombardy, northwestern Italy, has yielded other specimens which were referred to *E. ranzii*: three partial skeletons (MPUM 6009; MCSNB 2887 and MCSNB 3496; Wild 1979), an isolated tooth (MCSNB 3345, Wild 1979) and an isolated sternal plate (MPUM 7039, Renesto 1993). MCSNB 2888-2887, MCSNB 3345, MCSNB 3496 and MPUM 6009 come from a stratigraphic interval only a few centimetres thick of the Cene site (Bergamo Province). MCSNB 3496 is not considered here because it is referred to *Peteinosaurus zambellii*.

MCSNB 2888

It is a relatively large individual (the skull is 90 mm long and the ulna is 65 mm long) lacking most of the wing digit, hind limbs and tail, and was considered an adult individual by Wild (1979). It is the only specimen of *E. ranzii* Zambelli, 1973. The revised diagnosis of the species, and the genus for monotypy is: campylognathoidid pterosaur with a toothed pterygoid; small 'coronoid' process, triangular and pointed; tricuspid third premaxillary tooth; two very large tri- and tetracuspid teeth (with diminutive accessory cusps) in correspondence of the dorsal (ascending) process of maxilla; basoapical crests of enamel in the labial and lingual surfaces of multicusped teeth; handle-shaped, robust pteroid with a hump at the proximal bending and a tapering shaft. The shovel-like prepubis may be apomorphic, but that element is unknown in *Carniadactylus*, *'E.' cromptonellus*, MCSNB 2887 and BSP 1994 I 51.

MCSNB 2887

It is represented by several disarticulated and sparse bones, but no skull and lower jaw elements, as well as teeth. It is slightly larger than MPUM 6009 (Tab. 2) and was considered a "subadult" by Wild (1979). However, there is no size-independent evidence of immaturity other than the possible disarticulation of the pelvis. Instead, the scapula and coracoid are fused without suture and the proximal tarsals are fused to the tibia. Its attribution to *E. ranzii* was originally based on the square deltopectoral crest of humerus and on the ratios of some long bones lengths similar to those of MPUM 6009 (Wild 1979). The handle-shaped pteroid is more similar to that of *Eudimorphodon* than to the pteroid of *Carniadactylus*, but it is comparatively larger than in MCSNB 2888 and the shaft morphology is rather different (Fig. 6C-D). The scapula is comparatively much longer than the coracoid with respect to MCSNB 2888 and the coracoid has a different shape (Fig. 3A-B). The angle of the *caput femoris* to shaft is higher in MCSNB 2887 than in MCSNB 2888 (Wild 1979). MCSNB 2887 is here prudently considered as an indeterminate campylognathoidid.

MCSNB 8950

It is a skeleton without skull, lower jaw, teeth and most of the neck and tail, belonging to a small individual with the same size as MPUM 6009. It is from the lower Argilliti di Riva di Solto Formation (upper Norian, Sevatian; Jadoul et al. 1994) of Ponte Giurino (Bergamo Province). It was originally attributed to *Eudimorphodon* because of the square deltopectoral crest of humerus, shield-like sternum, and proportions of skeletal bones (Wild 1994). Based on body size, smaller than that of the holotype, and some evidence of osteological immaturity (e.g., unfused proximal tarsals and tibia, sacrum, and possibly also scapula and coracoid), it has been considered a juvenile of *E. ranzii* (Wild 1994). However, the square deltopectoral crest of humerus is not apomorphic of *E. ranzii* and the poorly ossified sternum is unlike that of MCSNB 2888 and similar to that of *Campylognathoides*. Proportions of skeletal bones are also similar to those of *C. liasicus*, if the wing metacarpal (its ratios with other long bones vary depending on the absolute size of the individual) and wing phalanges are excluded (Tab. 3). Wing phalanx length ratios are unlike those of MPUM 6009 and MFSN 1797 (wing phalanx 3>2>1; Tab. 3). Wing phalanx 1 is as long as the ulna, whereas it is longer in *Carniadactylus* (Tab. 3). Contra Wild (1994), ratios wph2:wph1 and wph1:u do not show a clear allometric trend during ontogeny in an adequate sample of *Rham-*

phorhynchus muensteri specimens (Bennett 1995). Thus, the relative proportions of wing phalanx 1 and 2 and the ulna are significative. Missing the skull and lower jaw bones, as well as teeth, and being undoubtedly an immature individual, a reliable attribution to a known genus or the institution of a new one is impossible. It is noteworthy that MCSNB 8950 is roughly coeval with *Caviramus* (lower Argilliti di Riva di Solto = Alplihorn Member of the Kössen Formation, following Fröbisch & Fröbisch 2006). According to the phylogenetic hypothesis here presented, it is the sister taxon of *Carniadactylus rosenfeldi* + (*Caviramus schesaplanensis* + *'Raeticodactylus' filisurensis*). Further material, mainly cranial, from the same horizon and locality is needed to give support to this hypothesis.

BSP 1994 I 51

It is a partial, disarticulated skeleton from the Seefeld Formation (Sevatian; Moix et al. 2007, but see Donofrio et al. 2003) of Tyrol, Austria. It was considered an immature individual ('subadult') mainly because of body size 15% smaller than MCSNB 2888 and the resemblance of the coracoid, humerus, and dentition to MPUM 6009, considered as a juvenile of *E. ranzii* (Wellnhofer 2003). Further evidences of immaturity would be the large orbit, the shape and poor ossification of the sternum, and the nonfusion of tibia and fibula (Wellnhofer 2003). Actually, the presence of a large orbit is suggested only by the shape of the jugal, but this is also the case of *Campylognathoides*. The sternal plate is not less ossified than in MCSNB 2888 and has a similar shape also in adult specimens of *Dorygnathus* (Padian 2008a). The fibula is probably coosified with the tibia although a groove separates them proximally, as in MCSNB 2888. BSP 1994 I 51 shows actual evidences of osteological immaturity: the pelvis not fused to the sacrum and a suture still visible between the proximal tarsals and the tibia (however, this latter feature is present also in *Dimorphodon macronyx* BMNH 43051 considered an adult; Sangster 2004). The synostosis of scapula and coracoid, the pelvic girdle coosified without sutures, and the fusion of the proximal tarsals to the tibia suggest it is not a juvenile. This specimen was identified as *E.* cf. *ranzii* by Wellnhofer (2003) based on the tricuspid to quinticuspid teeth and the squared deltopectoral crest of humerus. However, several apomorphic features suggest it does not belong to *Eudimorphodon* and *Carniadactylus* as well and represent a new taxon (pers. obs.). These include: presence of a mandibular fenestra (Fig. 11D); a 'coronoid' process of peculiar 'two-peaked' shape, not triangular and pointed (Fig. 11D); a slender jugal of peculiar shape suggesting the presence of a large orbit and a slit-like antorbital fenestra; at least one large multicusped tooth with at least three accessory cuspules along each cutting margin, but probably up to five-six counting also the small crenulations (a rostral dentary tooth for Wellnhofer 2003, but the slight curvature, size and shape suggest it is much probably a mid-maxillary tooth); plate-like and fan-shaped coracoid (Fig. 3E); distal end of scapula expanded, spatula-like and rounded (Fig. 3E); a peculiar triangular sternal plate with narrow structures for the coracoid articulation projecting externally. Furthermore, the probable rostral tooth is ornate with apicobasal ridges, unlike MPUM 6009, whereas the lateral dentary teeth are smooth, unlike MCSNB 2888; the tibia is longer than wing phalanx 1 and comparatively more robust than in *Eudimorphodon ranzii*; the fibula is long, ending at the lateral tibiotarsal epicondyle with a rounded expansion.

According to the phylogenetic hypothesis presented here, BSP 1994 I 51 falls outside the Campylognathoididae (Fig. 12), thus it is phylogenetically distant from both *Eudimorphodon* and *Carniadactylus* and more primitive. It forms a weakly supported clade with *'Eudimorphodon' cromptonellus*.

'Eudimorphodon' cromptonellus

It is based on a single, very small (Tab. 2), disarticulated and incomplete specimen (MGUH VP 3393) from the lowermost Ørsted Dal Member of the Fleming Fjord Formation, Eastern Greenland (Jenkins et al. 2001), probably late Norian in age (Clemmensen et al. 1998). It is an immature individual, as suggested by the lacking of fusion between several skeletal elements (Jenkins et al. 2001). It was referred to *Eudimorphodon* based on the heterodont dentition with uni-, tri- and quinticuspid teeth, and a separate species mainly on the appendicular proportions unlike those of other '*Eudimorphodon*' specimens (Jenkins et al. 2001). The femur is nearly as long as the tibia (f:ti = 0.96) and the ulna (0.98) and is longer than the humerus (f:h = 1.08); ulna:humerus length ratio is low (1.11, shared with *Campylognathoides*); the metatarsals are comparatively longer (as suggested by ratios of metatarsal II with wing metacarpal, humerus, ulna, femur and tibia in MCSNB 8950 and MFSN 1797). As no apomorphy is shared with *Eudimorphodon ranzii* and *Carniadactylus rosenfeldi*, a new generic name should be attributed to this taxon. According to the phylogenetic hypothesis here presented, it falls outside the Campylognathoididae (Fig. 12), and is more primitive than both *Eudimorphodon* and *Carniadactylus*. However, this may be a result of its immaturity.

MFSN 1922

This incomplete specimen was referred to *Eudimorphodon* because of tooth and humerus morphology (Dalla Vecchia 2004a). It plausibly belongs to *Carniadactylus rosenfeldi* because of geographical and stratigraphic provenance, and because the dentary tooth row ends well before the 'coronoid' process. However, the absence of diagnostic skeletal elements suggests being cautious in this attribution.

MFSN 21545

This specimen was preliminarily attributed to *Eudimorphodon* because of tooth morphology (Dalla Vecchia 2004b, 2006). Its study is in progress, but preliminary observations suggest it may be neither *Eudimorphodon ranzii* nor *Carniadactylus rosenfeldi*.

MFSN 26823

It was attributed to *Eudimorphodon* because the ratio of wing phalanges 1 and 2 (wph2:wph1 = 0.90) is closer to that of MFSN 1797 than that of *Preondactylus buffarinii*, *Peteinosaurus zambellii* and MCSNB 3359 (Tab. 3; Dalla Vecchia 2004b, 2006). The attribution to *Carniadactylus* is plausible and may be supported by further preparation of the specimen.

Other '*Eudimorphodon*' specimens

Multicusped teeth attributed to *Eudimorphodon* have been reported from some Late Triassic localities in SW USA (Chatterjee 1986; Murry 1986; Jacobs & Murry 1980), but only one specimen from Texas can be reliably referred to a pterosaur (Andres 2006). Isolated multicusped teeth attributed to *Eudimorphodon* have been reported also from Switzerland (Clemens 1980), Luxembourg (Hahn et al. 1984; Cuny et al. 1995), and France (Godefroit 1997; Godefroit & Cuny 1997). However, isolated teeth do not allow a reliable generic assignation.

Caviramus schesaplanensis and '*Raeticodactylus*' *filisurensis*

Caviramus schesaplanensis is represented by a partial right mandibular ramus (PIMUZ A/III 1225; Fröbisch & Fröbisch 2006). Stecher (2008) based '*Raeticodactylus*' *filisurensis* on a partial skeleton (BNM 14524) preserving the skull and lower jaw. These specimens share at least four apomorphic features: cup-shaped structures (large foramina) on the dorsolateral side of the rostral part of the dentary (Fig. 11E); large oval foramina every 2-3 teeth, in a row parallel to the tooth row along the laterodorsal margin of the dentary; short and deep lower jaw ramus (ratio of mandibular length:height at mid-ramus <9) (Fig. 11E); long and narrow retroarticular process posteroventrally directed, making with the dentary axis an angle of about 35° (Fig. 11E). This is reflected in the phylogenetic hypothesis here presented where they form a well-supported clade inside the Campylognathoididae (Fig. 12). Furthermore, both come from the Alplihorn Member of the Kössen Formation of NE Switzerland (Fröbisch & Fröbisch 2006; Stecher 2008). This suggests that they belong to the same genus, which would be *Caviramus* Fröbisch & Fröbisch, 2006 because of priority. Although the differences between the two specimens may be related to ontogeny (PIMUZ A/III 1225 is much smaller than BNM 14524 and lacks a mandibular crest), sexual dimorphism (mandibular crest) and intraspecific variability, I would prudently consider them as two separate species, pending the discovery of further material.

Conclusions

The genus *Eudimorphodon* as defined by Wild (1979, 1994) is not supported by any apomorphy after the discovery of *Caviramus schesaplanensis* and '*Raeticodactylus*' *filisurensis*. *E. ranzii* is restricted to the sole holotype and the genus is monotypic. '*Eudimorphodon*' *cromptonellus* needs a new generic name, as suggested by its phylogenetic position, although it is desirable that osteologically mature individuals are found to support it. Surprisingly, also BSP 1994 I 51 falls outside the Campylognathoididae; this specimen shows several autapomorphies and belongs to a new, still unnamed genus and species. MCSNB 8950 falls inside the Campylognathoididae, but only the discovery of more mature individuals from the same horizon and with skull material will shed light on its systematic position.

MFSN 1797 and MPUM 6009 were non-juvenile individuals belonging to *Carniadactylus* n. gen. *rosenfeldi*, a relatively small non-pterodactyloid pterosaur nested inside the Campylognathoididae, characterized by a deep lower jaw below the large, triangular and pointed 'coronoid' process, a plate-like coracoidal shaft with subparallel margins, a boomerang-like pteroid, wing phalanx 1>3>2 and a large sesamoid bone on ventroproximal part of pedal phalanx V-1.

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Appendix 1

Characters and character state descriptions

1. Rostrum, outline (Unwin 2004, char. 1): (0) high, convex outline, (1) low with straight or concave dorsal outline.
2. Skull, broad with very short preorbital region and broadly arching jaws (Unwin 2004, char. 2, modif.): (0) no, (1) yes.
3. Ventral margin of skull (Unwin 2004, char. 3): (0) straight, (1) curved down caudally.
4. Premaxilla, caudoventral (maxillary) process beneath the naris: (0) present and extending for half of the narial length or more, (1) extending for less than half the narial length, (2) absent for absence of a premaxillary ventral contact with the narial opening.
5. Premaxillary bony crest: (0) absent, (1) present.
6. Dorsal process of maxilla, orientation (Unwin 2004, char. 5, modif.): (0) inclined backwards and forming the caudal margin of the external naris, (1) subvertical and forming the caudal margin of the external naris, (2) inclined backwards but forming the rostral margin of the external naris.
7. Maxilla-nasal contact (Unwin 2004, char. 6): (0) broad, (1) narrow, (2) not existent.
8. Maxilla, jugal and premaxillary processes subequal in shape and size, low, long, tapering and pointed: (0) absent, (1) present.
9. External naris, shape (Unwin 2004, char. 7): (0) low and elongate, (1) height higher or equal to anteroposterior length.
10. External naris, relative size (Unwin 2004, char. 8): (0) smaller than orbit or antorbital fenestra, (1) form the largest skull opening.
11. Position of the external naris (Kellner 2003, char. 6): (0) entirely above the premaxillary tooth row, (1) displaced posterior to the premaxillary tooth row.
12. Antorbital fenestra, position (Unwin 2004, char. 9): (0) lies level with the external naris, (1) lies lower than the external naris.
13. Antorbital fenestra, shape (Unwin 2004, char. 10, modif.): (0) length twice the height or less (1) length more than twice the height.
14. Antorbital fenestra confluent with external naris (Unwin 2003, char. 24): (0) absent, (1) present.
15. Orbit, shape (Unwin, 2004, char. 11): (0) similar width to depth, (1) 1.5 times higher than wide.
16. Orbit, relative size (Unwin 2004, char. 12): (0) larger than antorbital fenestra, (1) smaller than antorbital fenestra.
17. Supratemporal fenestra, relative size (Unwin 2004, char. 13): (0) smaller than other skull openings, (1) larger than other skull openings except orbit.
18. Quadrate, orientation (Unwin 2004, char. 14): (0) vertical or subvertical, (1) inclined backwards of 120° or more.
19. Palatal elements, shape (Unwin 2004, char. 15, modif.): (0) relatively broad and flat, (1) reduced to very thin bars of bone.

20. Dentary, relative length (Unwin, 2004, char. 16, modif.): (0) 60% length of lower jaw or less, (1) more than 60% length of lower jaw.
21. Rostral end of the dentary, shape (Unwin 2004, char. 17): (0) straight, (1) slightly bent ventrally.
22. Mandibular rami fused at the relatively long symphysis (Unwin 2004, char. 18, rephrased): (0) absent, (1) present.
23. Mandibular tips fused into a short symphysis with forward projecting prow and several large, fang-like, procumbent teeth forming a fish grab (Unwin 2004, char. 19): (0) absent, (1) present.
24. Ratio of mandibular length:height at mid-ramus: (0) higher than 9, (1) lower than 9.
25. 'Coronoid' process: (0) gently rounded, (1) gently rounded with two low peaks, (2) pointed, (3) practically absent.
26. Retroarticular process, orientation: (0) posteriorly directed or slightly ventrally directed but short, (1) long, low and posteroventrally directed, making with the dentary axis an angle of about 35°.
27. Large oval foramina every 2-3 teeth, in a row parallel to the tooth row along the laterodorsal margin of the dentary: (0) absent, (1) present.
28. Cup-shaped structures (large foramina) on the dorsolateral side of the rostral part of the dentary: (0) absent, (1) present.
29. Maxillary and dentary teeth: (0) present, mandibular teeth with a size similar or slightly smaller than that of maxillary teeth, (1) present, mandibular teeth much smaller than maxillary teeth, (2) absent.
30. Maxillary teeth, much enlarged below the dorsal process: (0) absent, (1) present.
31. Teeth small, peg-like, widely spaced (Unwin 2004, char. 22): (0) absent, (1) present.
32. Distal dentary teeth, cutting margin: (0) with cusps, cuspules or serrations, (1) without cusps, cuspules or serrations (smooth).
33. Tri- to quinticuspid teeth: (0) absent, (1) present.
34. Teeth in the maxilla distal to the dorsal process large, triangular, serrated and decreasing in size distally: (0) absent, (1) present.
35. Teeth in the rostrum, number (Unwin 2004, char. 24): (0) more than 11 pairs, (1) less than 11 pairs.
36. Rostral teeth, number and shape (Unwin 2004, char. 25): (0) more than nine relatively straight pairs of teeth, (1) nine or less relatively straight pairs of teeth.
37. Mandibular dentition, number (Unwin 2004, char. 26): (0) more than six tooth pairs, (1) six or less, widely spaced, vertically oriented tooth pairs.
38. Heterodont mandibular dentition (sensu Unwin 2003) (Unwin 2004, char. 27): (0) present, (1) absent.
39. Mid-cervical vertebrae, shape (Kellner 2003, char. 45): (0) short, subequal in length, (1) elongated (much longer than high).
40. Ribs in mid-cervical vertebrae (Unwin 2004, char. 28 and Kellner 2003, char. 46): (0) present, (1) absent.
41. Dorsal+sacral vertebral series (Unwin 2004, char. 29): (0) longer than ulna, (1) similar length to ulna.
42. Caudal vertebral series (Unwin 2004, char. 31): (0) longer than the dorsal series, (1) shorter than the dorsal series.
43. Filiform processes of caudal zygapophyses (Unwin 2004, char. 30; modif.): (0) absent, (1) present, (2) absent because of tail reduction.
44. Rectangular sternum with short cristospine and short lateral processes on each posterolateral corner (Unwin 2004, char. 32): (0) absent, (1) present.
45. Coracoid, relative length (Unwin 2004, char. 33): (0) less than 66% length of scapula, (1) 66% or more length of scapula.
46. Coracoid, shaft shape: (0) relatively broad and flat, (1) strut-like, narrow and slender in the middle.
47. Forelimb (h+u+mcIV+ phalanges of digit IV), relative length (Unwin 2004, char. 34): (0) less than 2.5 times the length of hind limbs (fe+ti+mtIII), (1) 2.5 times the length of hind limbs or more.
48. Humerus, relative length (Unwin 2004, char. 35, modified): (0) shorter than femur or as long as femur, (1) longer than femur.
49. Proximal end of humerus with angular, sub-symmetric profile (Unwin 2004, char. 36): (0) absent, (1) present.
50. Deltopectoral crest of humerus, shape (Unwin 2004, char. 37): (0) small, (1) large and subtriangular with apex directed proximally, (2) relatively short, rounded and extremely proximally placed, (3) large and hatched-shaped (square), (4) large and tongue-shaped, with necked base, (5) 'pterodactyloid'.
51. Ulna, relative length (Unwin 2004, char. 38): (0) less than 1.5 times length of humerus, (1) 1.5 times length of humerus or more.
52. Ulna, relative length (Unwin 2004, char. 39): (0) as long as tibia or shorter, (1) longer than tibia.
53. Pteroid: (0) absent, (1) very short (less than 1/6 ulnar length), rod-like and slightly arched, (2) relatively short (but more than 1/6 ulnar length), straight and with an expanded proximal extremity and a tapering or expanded distal extremity, (3) slender, elongated and angled (boomerang-like), (4) robust, with the proximal part bent (handle-like) and the shaft more or less tapering, (5) slender, long and straight, (6) very long, slender and distally pointed, with the proximal part more or less bent.
54. Metacarpals I-III, length (Unwin 2004, char. 40, modified): (0) metacarpal I < metacarpal II < metacarpal III, (1) metacarpal I < metacarpal II = metacarpal III, (2) all the same length, (3) reduced proximally (i.e., two or all of them do not reach the carpus).
55. Metacarpal IV-humerus ratio (Unwin 2004, char. 41 modif.): (0) less than 35%, (1) more than 35% but less than 80%, (2) more than 80%.
56. Manus and pes unguals, relative size (Unwin 2004, char. 43): (0) similar sized, (1) manual unguals two times or more the size of pedal unguals.
57. Manual digit IV, relative size (Unwin 2004, char. 44): (0) equal or less than 65% total forelimb length, (1) more than 65% total forelimb length.
58. Phalanx 1 of digit IV, relative size (Unwin 2004, char. 45): (0) less than 35% finger length, (1) 35% finger length or more.
59. Phalanx 2 of digit IV, relative size (Unwin 2004, char. 46): (0) shorter than length of ulna, (1) as long as the length of ulna or more.
60. Proportional length of the first phalanx of digit IV relative to the metacarpal IV (Kellner 2003, char. 66): (0) both small and reduced, (1) both enlarged with the phalanx over twice the length of the metacarpal, (2) both enlarged with the phalanx less than twice the length of the metacarpal.
61. Proportional length of the phalanx 1 of digit IV relative to tibia/tibiotarsus (Kellner 2003, char. 67, modified): (0) phalanx much shorter than tibia, (1) phalanx elongated but shorter than tibiotarsus, (2) phalanx elongated, longer than tibiotarsus, but less than twice its length, (3) phalanx elongated about or longer than twice the length of tibia.
62. Proportional length of the phalanx 2 of digit IV relative to the phalanx 1 (Kellner 2003, char. 68): (0) both short or absent, (1) elongated, with the second phalanx about the same size or longer than the first, (2) elongated, with the second phalanx up to 30% shorter than first, (3) elongated, with the second phalanx more than 30% shorter than first.
63. Proportional length of the third phalanx of digit IV relative to the first phalanx (Kellner 2003, char. 69): (0) both short or absent, (1) extremely elongate, phalanx 3 about the same length or longer than phalanx 1, (2) extremely elongate, phalanx 3 shorter than phalanx 1.
64. Proportional length of the third phalanx of digit IV relative to the second phalanx (Kellner 2003, char. 70): (0) both short or absent, (1) extremely elongate, phalanx 3 about the same length or longer than phalanx 2, (2) extremely elongate, phalanx 3 shorter than phalanx 2.
65. Fourth phalanx of manual digit IV: (0) short and stout, (1) extremely elongate and slender like the other phalanges, (2) much shorter respect to the other, elongate, phalanges or lost.
66. Preacetabular iliac process, relative length (Unwin 2004, char. 47): (0) as long as postacetabular process or shorter, (1) longer than postacetabular process

67. Angle of caput femoris to shaft (Unwin 2004, char. 50): (0) 145° or less, (1) more than 145°

68. Fibula, relative length (Unwin 2004, char. 51, modified): (0) same length as tibia, (1) shorter than tibia.

69. Fibula, distal end: (0) More or less expanded with free distal articulation, (1) Distal end slightly expanded and fused above the lateral tibiotarsal condyle, (2) tapering to a point or very thin, without condyles or expansions.

70. Metatarsals, arrangement: (0) tightly bound in a single unit and parallel to each other, (1) spreading.

71. Metatarsal IV, relative length (Unwin 2004, char. 52, modif.): (0) sub-equal to length of metatarsals I-III or slightly longer, (1) roughly as long as metatarsal I and slightly shorter than II and III, (2) sensibly shorter than metatarsals I-III.

72. Pedal digit V, phalangeal count (Kellner 2003, char. 73): (0) with three or four phalanges, (1) with two phalanges, (2) with one or no phalanx (extremely reduced).

73. Pedal digit V, phalanx 2 shape: (0) short and stout, (1) elongated, thin and straight or slightly curved, approximately as long as phalanx 1, (2) shorter than phalanx 1 and of the penultimate phalanges of digits III and IV, (3) thin, straight, shorter than phalanx 1, but longer than the penultimate phalanges of digits III and IV, (4) elongated, thin and bent (angled) at midlength, (5) lost in the reduction of the whole digit.

Appendix 2

Character state data matrix

Macrocnemus bassanii
1001000000 1- - -0-1000 0000200000 0100000110 0000100000
0000000000 0000001000 000
Ticinosuchus ferox
0000000000 0000000000 0000000000 0000000000 0000000000
0000000000 0000000000 000
Herrerasaurus ischigualastensis
0000000000 0100000000 0000000001 0000000000 0000000000
00000000-0 0000200000 025
Preondactylus buffarinii
10?100?10? 1000?????0 000000?011 0?01000000 000?000001
00211?0001 11111?0??0 01?
Austriadactylus cristatus
1000100100 10000000?? ??0000??11 0001000000 ?00???????
0???????1? ??1/211????0 ???
BSP1994 I 51
?0???????? ???000???1 ?00010???1 001?000000 ?00000??03 ??????????
1????1?00? ???
'Eudimorphodon' cromptonellus
?0???0???? 10?0?????1 0000??0000 000000000? ?00?000001
00?01?0011 11111?0??? ???
MCSNB 3359
?????????? ?????????? ?????????? ?????????? 001?100101 0121111001
11111??120 011
Peteinosaurus zambellii
?0???????? ?????????1 10000?0??? 000?0000?? ?010?????? ???0?1???1
11??1?0010 ?11

Dimorphodon macronyx
0000001001 1000110001 1000000010 0100000000 001?111101
0020110001 1111100020 111
Campylognathoides spp.
1001000000 1000001101 1000300000 0100000000 0011111103
0120111011 3122111000 1/212
Eudimorphodon ranzii
1001000000 1000001101 1000200001 0010000000 0??111?103
01401????1 2/31/2???10??? ???
MCSNB 8950
?????????? ?????????? ?????????? ????????00 1001001103
0120/1111011 2111110??0 111
Carniadactylus rosenfeldi
1011000000 1100001101 0?00200000 0010000000 100??01103
0130111011 22111??020 111
Caviramus schesaplanensis
?0???????? ???????1?1 00010111?? 001?000??? ?????????? ??????????
?????????? ???
'Raeticodactylus' filisurensis
1012100000 110000?1?1 0?01011100 001000000? ??????1103
01?0100011 22111?0??0 ?1?
Dorygnathus banthensis
1011000000 1110000101 0110300000 0100100000 0010111104
1120110001 21111100/11/20 214
Sordes pilosus
101?000000 1000000101 0100?0??00 0100111100 0010111104
11?2110001 111111012? 214
Scaphognathus crassirostris
1012000000 1100000101 0100300000 0100111100 00101110/104
11?2110001 2112110121 214
Rhamphorhynchus muensteri
1012000000 1110001101 0/1110300000 0100100100 0010111104
1152111011 3222110121 214
Anurognathus ammoni
0100011010 0000001011 0000300000 1100110101 0120011112
0112010101 22222101?0 013
Jeholopterus ningchengensis
01??01?0?? ????????1? ??0?????00 1?00????01 112?011111
011?010101 2222210120 013
Batrachognathus volans
0100011011 000011??11 0000??0000 110000010? ?1201?1112
?1???1???? ?????1?120 0/113
Dendrorhynchoides curvidentatus
01??01101? 0?0?????1? ??0??????0 110?????01 112?111112
0112010011 2222?1?120 011
Pterodactylus antiquus
1012022001 1001000101 0100300000 0100000111 01201110/105
00/162210002 1/2222110121 225
Pteranodon longiceps
10120220- - 10-10-0101 0100300020 0-00111111 11201110/105
0163210112 222211012? 225
Anhanguera spp.
10121220- - 10-11-0101 0110300000 0100000011 ?120111105
1163210??? ????111??? ???