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A REVIEW OF THE TRIASSIC PTEROSAUR RECORD

The Triassic pterosaur record has increased since the first description of a Triassic pterosaur (Zambelli, 1973). To date, remains of Triassic pterosaurs are reported from northern Italy, Austria, Greenland and possibly SW USA, Switzerland, Luxembourg, France and England.

Institutional acronyms: BSP = Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; MCSNB = Museo Civico di Scienze Naturali di Bergamo, Italy; MFSN = Museo Friulano di Storia Naturale, Udine, Italy; MGUH = Geological Museum, University of Copenhagen, Denmark; MPUM = Dipartimento di Scienze della Terra dell'Università di Milano, Italy; SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany.

MATERIAL

LOMBARDY, NORTHWESTERN ITALY

Pterosaur remains comes from the upper part of the Calcare di Zorzino (Alaunian, middle Norian; Jadoul *et al.*, 1994) and the basal part of the overlying Argilliti di Riva di Solto (Sevastian, late Norian; *ibidem*). *Eudimorphodon* and *Peteinosaurus* are the taxa identified.

Eudimorphodon is represented by the holotype of *E. ranzii* (MCSNB 2888), other three more or less complete specimens (Wild, 1978, 1994), an isolated tooth (Wild, 1978), and possibly by an isolated sternum (Renesto, 1993). MCSNB 2888 (Fig. 1) is a relatively large individual (the skull is 90 mm long) lacking most of the wing digit, hind limbs and tail. MPUM 6009 (Fig. 2), reported as "exemplar Milano" in Wild (1978), is a poorly preserved specimen without most of feet and pelvis, and with other skeletal parts represented by the impression of bones only. It is sensibly smaller (~50% of the linear lengths) than MCSNB 2888. I retain it in *Eudimorphodon*, but I consider dubious its conspecificity with MCSNB 2888 because of some remarkable osteological differences and lacking of definitive evidence of immaturity. MCSNB 2887 (Fig. 3) is a highly disarticulated skeleton preserving forelimb and hind limb elements, coracoids, some vertebrae and ribs, and comes from Cene quarry as MCSNB 2888 and MPUM 6009. It lacks the skull and the lower jaws, thus its attribution to *Eudimorphodon* is based on the long bone ratios, the outline of the deltopectoral crest, and the morphology of the pteroid which resembles that of MCSNB 2888. MCSNB 3345 is a single, large middle maxillary tooth similar to those of MCSNB 2888 (Wild, 1978). MCSNB 8950a,b (Fig. 4) is a partial skeleton without skull, lower jaws, most of the neck and tail, representing an individual the same size as MPUM 6009. It comes from the Argilliti di Riva di Solto Formation, thus it is slightly younger

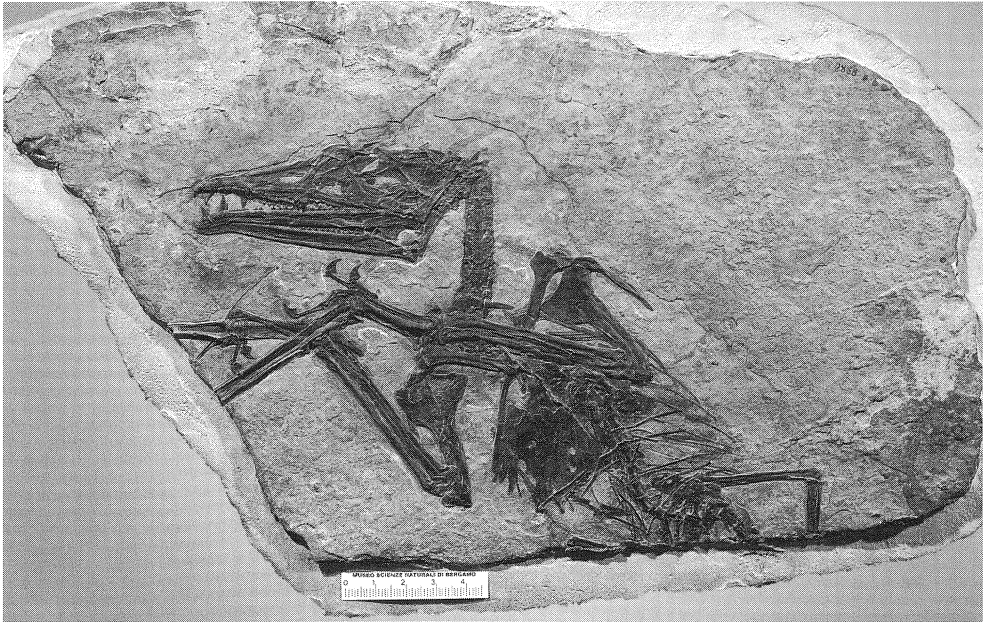


Fig. 1. MCSNB 2888, holotype of *Eudimorphodon ranzii*, Cene, Lombardy, Italy. Scale bar equals 45 mm.

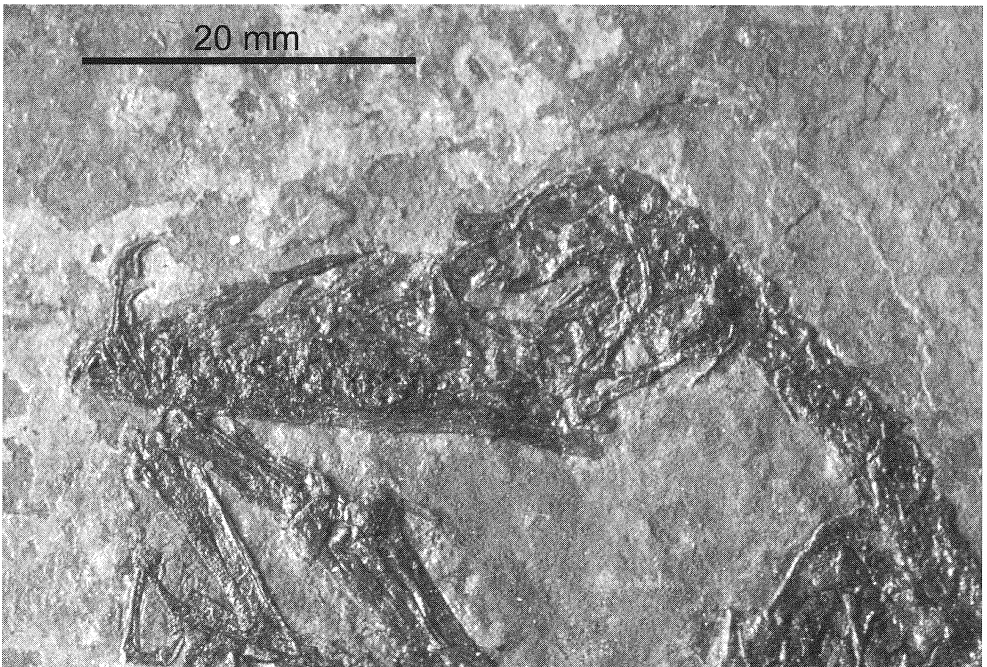


Fig. 2. MPUM 6009, *Eudimorphodon* sp., Cene, Lombardy, Italy. Particular of the skull and lower jaw. Scale bar equals 20 mm.

than the other specimens. It shows some evidence of osteological immaturity (Wild, 1994). Its attribution to *Eudimorphodon* is based mainly on the square shape of the deltopectoral crest of humerus, which however is not an autapomorphy of the genus, being present also in *Campylognathoides*. The latter is Toarcian (late Early Jurassic) in age and is found in southern Germany, thus an attribution of MCSNB 8950a,b to *Eudimorphodon*, that lived during Triassic times and in Lombardy, appears more probable. Unfortunately, the long bone ratios, differing in some respects from those of MPUM 6009, and the possible immature condition, do not help in supporting this interpretation.

A relatively large, incomplete and isolated sternal plate (MPUM 7039; Fig. 5) found in the Calcare di Zorzino of Endenna/Zogno site (Renesto, 1993) resembles that of MCSNB 2888. However, since we do not know the sternum of other Triassic pterosaurs and some differences occur between MPUM 7039 and the sternum of MCSNB 2888, I prudently consider it as cf. *Eudimorphodon*.

Peteinosaurus zambellii is represented by the holotype (MCSNB 2886; Fig. 6), a partial, highly disarticulated skeleton preserving partial lower jaw rami, few skull bones, some wing phalanges and other autopodial bones, a tibia+fibula, part of an ischiopubic plate and few other bones. MCSNB 3496 (Fig. 7) has also been attributed to *Peteinosaurus* (Dalla Vecchia, 2003). It preserves the pelvis and the sacrum, part of the tail, parts of the hind limbs and few other bones. MCSNB 3359 (Fig. 8) was originally indicated as the paratype of *Peteinosaurus zambellii*, but Dalla Vecchia (2003) prudently considers it as ?*Peteinosaurus* because it does not show indisputable diagnostic characters of the genus. It is a nearly complete and articulated skeleton lacking the neck and the skull. All three specimens come from Cene quarry and show some features of osteological immaturity (Dalla Vecchia, 1998, 2003).

Three articulated wing phalanges (MCSNB 4562; Fig. 9) from Endenna/Zogno (Padian, 1980; Wild, 1984) considered as *Preondactylus* by Wild (1984), are prudently attributed to an indeterminate large pterosaur by Dalla Vecchia (1998).

FRIULI-VENEZIA GIULIA, NORTHEASTERN ITALY

Specimens comes from the Dolomia di Forni (Forni Dolostone), a basinal unit of late Alaunian (late middle Norian) (Roghi *et al.*, 1995) age, cropping out in northern Friuli (Carnia). *Preondactylus* and *Eudimorphodon* are the taxa identified to date.

Preondactylus buffarinii Wild is represented by the holotype (MFSN 1770; Fig. 10), originally a nearly complete skeleton, now mostly preserved as impression of the bones. A partial skull (MFSN 25161) still under preparation, is most probably a second *Preondactylus* specimen. Both specimens come from the same section along the Seazza Creek, near the village of Preone (Udine).

A gastric eject with broken pterosaurian bones (MFSN 1891; Fig. 11) also from the Seazza creek valley was attributed with some doubts to *Preondactylus buffarinii* (Dalla Vecchia *et al.*, 1989). The broken nature of the bones and the increased knowledge of Triassic pterosaurs suggest to consider it as Pterosauria indet..

Eudimorphodon is represented by the holotype of *E. rosenfeldi* (MFSN 1797; Fig.



Fig. 3. MCSNB 2887, *Eudimorphodon* cf. *ranzii*, Cene, Lombardy, Italy. Scale bar equals 45 mm.



Fig. 4. MCSNB 8950a, *Eudimorphodon* sp., Ponte Giurino/Berbenno, Lombardy, Italy. Scale bar equals 45 mm.

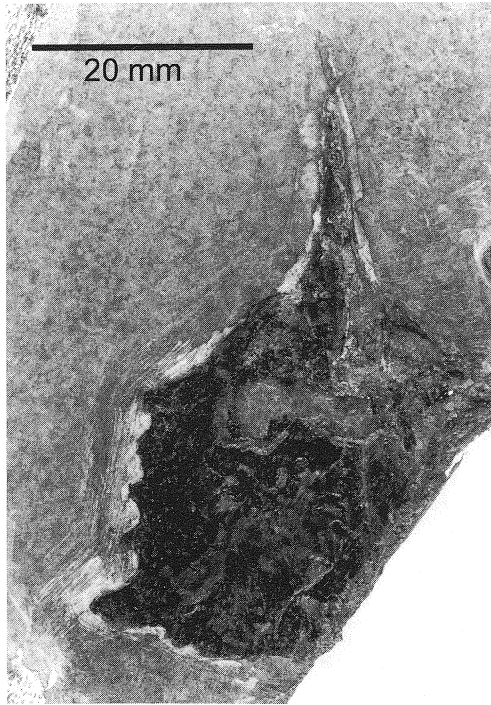


Fig. 5. MPUM 7039, isolated sternal plate, cf. *Eudimorphodon*, Zogno, Lombardy, Italy. Scale bar equals 20 mm.

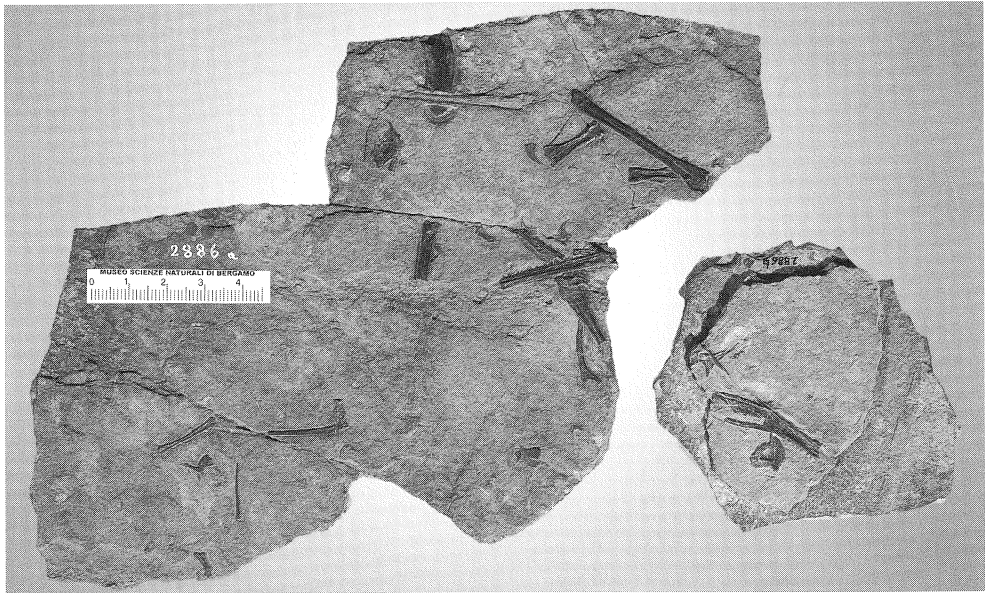


Fig. 6. MCSNB 2886, holotype of *Peteinosaurus zambellii*, Cene, Lombardy, Italy. Scale bar equals 45 mm.

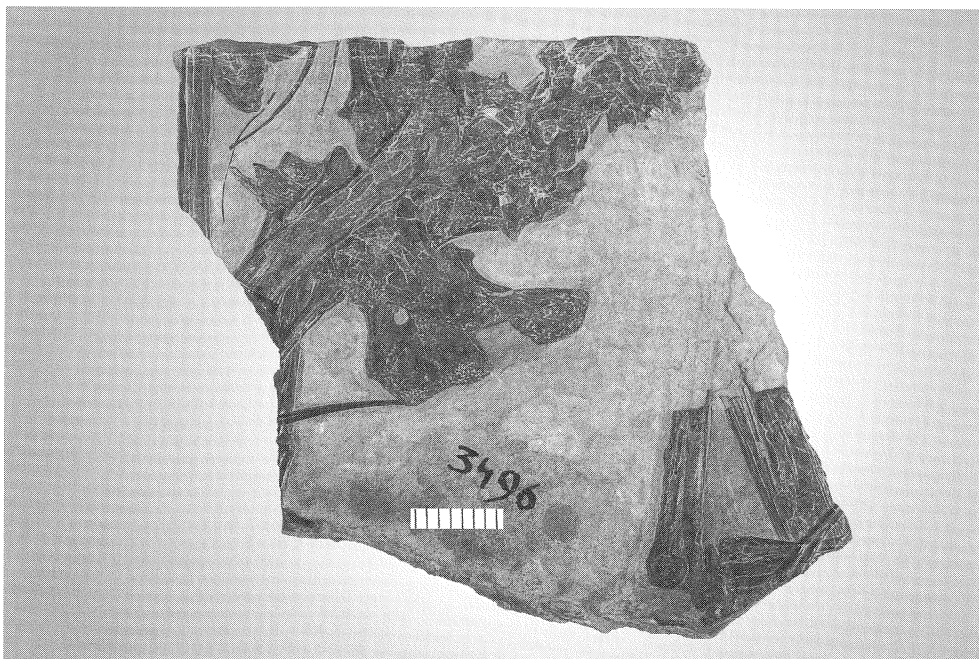


Fig. 7. MCSNB 3496, *Peteinosaurus zambellii*, Cene, Lombardy, Italy. Scale bar equals 8 mm.



Fig. 8. MCSNB 3359, ?*Peteinosaurus zambellii*, Cene, Lombardy, Italy. Scale bar equals 45 mm.

12), a specimen without sacrum, tail, most of the pelvis and part of the skull and lower jaw (Dalla Vecchia, 1995).

A second fragmentary and disarticulated specimen of *Eudimorphodon* (MFSN 1922; Fig. 13) preserves an humerus, part of the thoracal vertebral column with ribs, part a wing phalanx with few traces of the patagium and an incomplete lower jaw ramus with teeth (Dalla Vecchia, in press).

A third, disarticulated *Eudimorphodon* skeleton (MFSN 21545; Fig. 14) shows both lower jaw rami, many disarticulated skull elements, vertebrae and ribs, most of the fore and hindlimbs, and part of the pelvic and shoulder girdle. Unfortunately, its study has not been allowed yet and hopefully it will be described in the future. A recently discovered specimen (MFSN 26823), still unprepared, and showing only three articulated wing phalanges, is possibly another *Eudimorphodon* specimen, as suggested by the length ratio of wing phalanges ($wph2/wph1$ is 0.90; it is 0.91 in MFSN 1797 and 1.10 in MFSN 1770).

A long segment of the caudal vertebral column preserved along with two terminal wing phalanges (MFSN 19864; Fig. 15) does not show the elongated zygapophyses that make a bundle in long-tailed Jurassic pterosaurs. This is a feature observed in *Eudimorphodon*, *Austriadactylus* and possibly in *Preondactylus* (Dalla Vecchia, 2002). Its taxonomic attribution cannot be detailed further. An isolated wing phalanx 4 (MFSN 19836; Fig. 16), 137 mm long, belongs to an indeterminate pterosaur with a rather large size, comparable to that of the largest Late Jurassic rhamphorhynchoids (Dalla Vecchia, 2000).

TYROL, NORTHWESTERN AUSTRIA

Two pterosaur remains have been found in the Seefelder Schichten (Seefeld Beds), a basal unit of probable Alaunian age approximately coeval to the Dolomia di Forni. One is the holotype of *Austriadactylus cristatus* Dalla Vecchia, Wild, Hopf & Reitner (SMNS 56342; Fig. 17), a partial articulated skeleton preserving skull and lower jaw, most of the tail and presacral vertebral column, part of the forelimbs and hind limbs, and parts of the pelvic and shoulder girdle.

The second (BSP 1994I 51) is a disarticulated *Eudimorphodon* specimen preserving a jugal, isolated teeth, two partial lower jaw rami, cervical, dorsal and caudal vertebrae, ribs, sternum, scapulocoracoids, humerus, first wing phalanx, pelvis and tibia+fibula. It was identified as *E. cf. ranzii* by Wellnhofer (2001), but the many osteological differences with MCSNB 2888 would suggest a different specific attribution.

EASTERN GREENLAND

The only pterosaur (MGUH VP 3393) is an *Eudimorphodon* specimen from the lowermost Ørsted Dal Member of the Fleming Fjord Formation (Jenkins *et al.*, 2001). The age of that level is probably late Norian (Clemmensen *et al.*, 1998, fig. 3). *Eudimorphodon cromptonellus* is based on a rather small (sensibly smaller than MPUM 6009) and disarticulated specimen preserving most of the lower jaws, parts of the skull, some vertebrae, part of the shoulder girdle, hind limbs and forelimbs. It is the best candidate as an immature individual among *Eudimorphodon* specimens, because

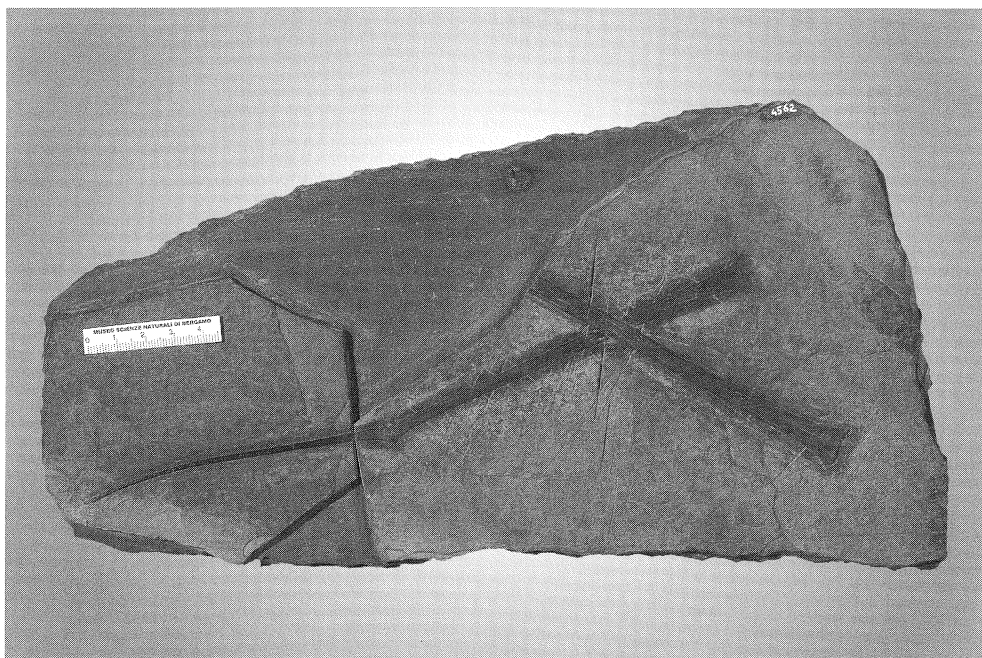


Fig. 9. MCSNB 4562, Pterosauria indet., Zogno, Lombardy, Italy. Scale bar equals 45 mm.

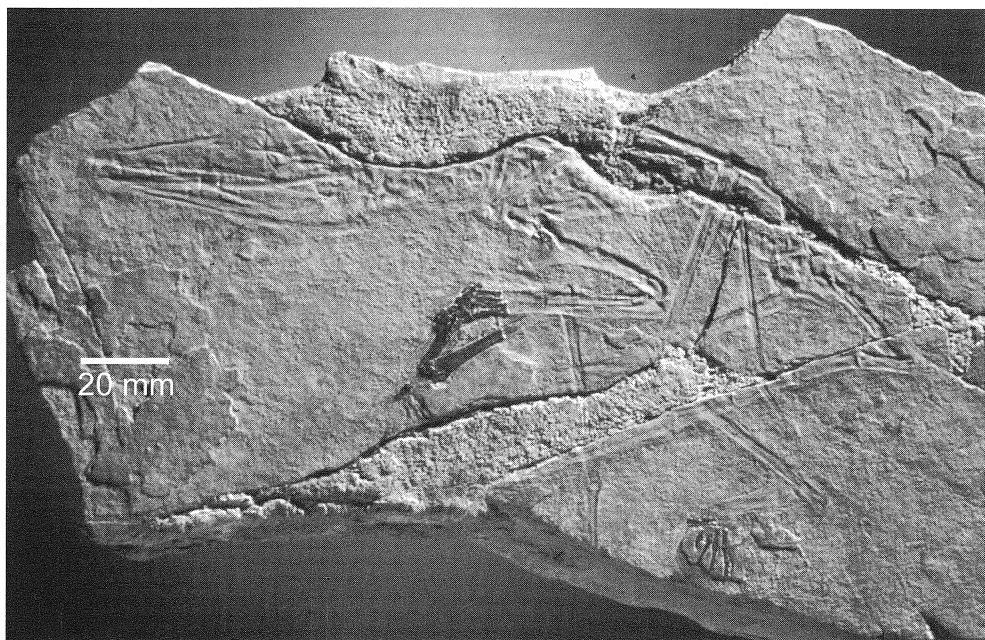


Fig. 10. MFSN 1770, holotype of *Preondactylus buffarinii*, Seazza Creek, Friuli, Italy. Scale bar equals 20 mm.

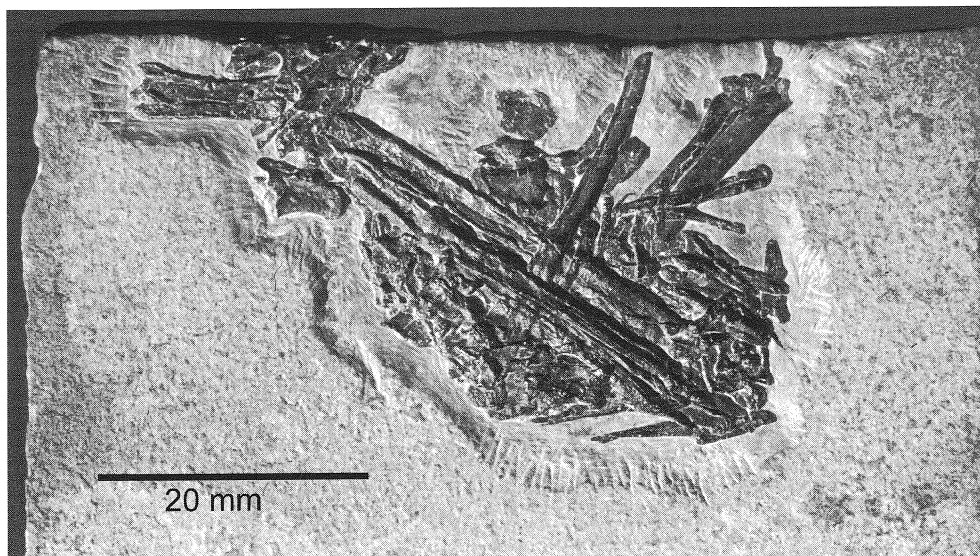


Fig. 11. MFSN 1891, Pterosauria indet., Seazza Creek, Friuli, Italy. Scale bar equals 20 mm.

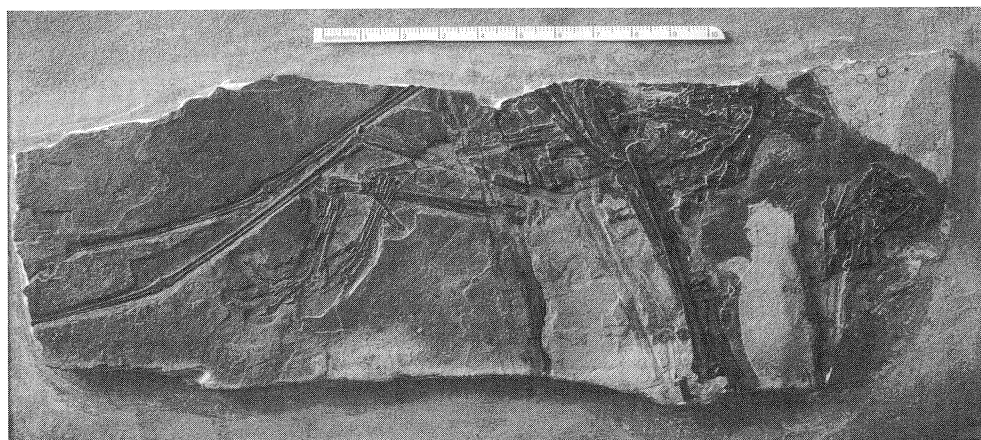


Fig. 12. MFSN 1797, holotype of *Eudimorphodon rosenfeldi*, Forchiar Creek, Friuli, Italy. Scale bar equals 100 mm.



Fig. 13. MFSN 1922, *Eudimorphodon* sp., Purone Creek, Friuli, Italy. Scale bar equals 20 mm.

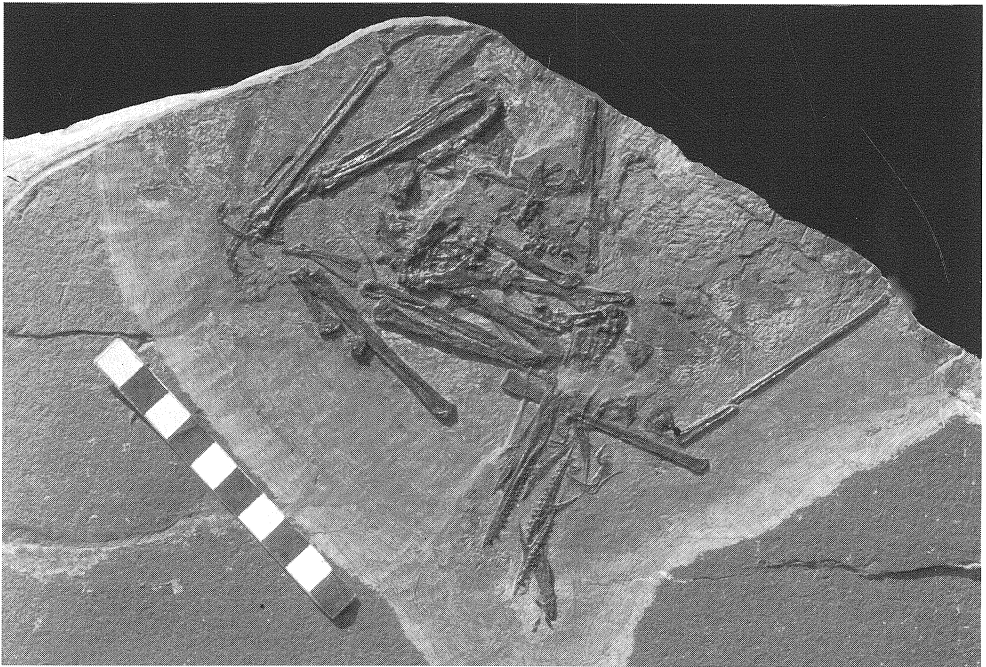


Fig. 14. MFSN 21545, *Eudimorphodon* sp., Seazza Creek, Friuli, Italy. Scale bar equals 100 mm.

of unfusion of several skeletal elements. Jenkins *et al.* (2001) exclude it as an immature of *E. ranzii* because of the comparison with MPUM 6009 and MCSNB 8950, which they consider juveniles of that species. However, the synonymy of *E. cromptonellus* and *E. ranzii* cannot be excluded if they are not *E. ranzii*.

OTHER REMAINS

Multicuspid teeth attributed to *Eudimorphodon* have been reported from some Late Triassic localities in North America and Europe.

Previous reports by Chatterjee (1986) of *Eudimorphodon* bones and teeth from the Cooper Member of Dockum Formation (lower Norian) of Texas are probably unsubstantiated (S. Chatterjee, pers. comm.). Murry (1986, pp. 116, 129) reports as *Eudimorphodon?* sp. a fragmentary lower jaw, a fragmentary upper jaw and several isolated teeth from the Dockum Group of Texas, probably late Carnian in age. He also mentions that isolated teeth "possibly referable to pterosaurs" and "similar to the genus *Eudimorphodon*" (p. 129), more or less coeval with those from Texas, have been found in the Chinle Formation of Arizona according to Jacobs & Murry (1980). An isolated humerus from the "middle" Carnian of New Mexico has been reported as "*Pterosauria gen. et sp. nov.*" by Hunt & Lucas (1993), but it is not described nor figured, and, as far as I know, it was never mentioned again.

Clemens (1980) reports the presence of multicuspid teeth possibly belonging to *Eudimorphodon* and *Peteinosaurus* (figured in Peyer, 1956) in the "Rhaetian" bone-bed of Hallau, NE Switzerland. Hahn *et al.* (1984) attributed to *Eudimorphodon* three pentacuspid teeth from a bone-bed at Rinckebierg locality near Medernach (Luxembourg), middle Norian in age (Duffin, 1993; Cuny *et al.*, 1995). Subsequently, Cuny *et al.* (1995) reports about other 19 *Eudimorphodon* teeth from the same site. Finally, Godefroit (1997) identifies teeth aff. *Eudimorphodon* sp. in the "Rhaetian" of Varangéville, Meurthe-et-Moselle, and Godefroit & Cuny (1997) describe teeth of *Eudimorphodon* sp. from the "Rhaetian" (late Sevatian-Rhaetian, according to Benton, 1994) of Saint-Nicolas-de-Port, Meurthe-et-Moselle, both in France.

All those isolated teeth should be reconsidered under the light of the whole new record of pterosaurs, and amniotes in general, with a multicuspid dentition.

Two small wing metacarpals of an indeterminate pterosaur are reported from the Norian or "Rhaetian" fissure infillings of Gloucestershire (United Kingdom) according to Fraser & Unwin (1990).

Hollow, not diagnostic bone fragments from Upper Triassic horizons in Germany (Oppel, 1858a,b; Defner & Fraas, 1859; Meyer, 1859-60; Huene, 1902; Plieninger, 1907), England (Dawkins, 1864) and USA (Cope, 1870; Huene, 1921) have been attributed to pterosaurs, but they could belong to other tetrapods with delicate, hollow bones (small theropods, prolacertiforms, *Icarosaurus* etc.), and to date most of them have been lost. Also some fragmentary vertebrae from Germany (Huene, 1902) are too poorly preserved to allow a positive identification as pterosaurian.

SYSTEMATIC REMARKS

The systematic identification of the specimens is problematic because of the small size of the sample and the not overlapping preserved portions of the specimens.

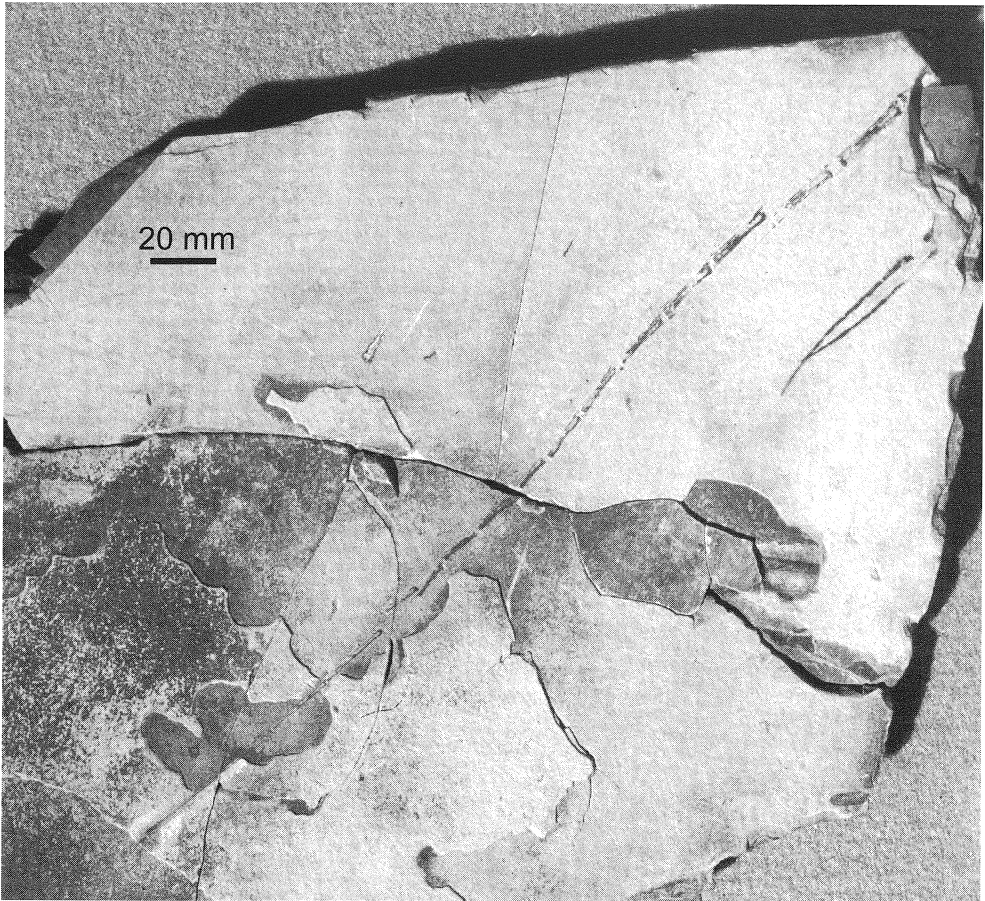


Fig. 15. MFSN 19864, Pterosauria indet., Seazza Creek, Friuli, Italy. Scale bar equals 20 mm.

Eudimorphodon

It is the best known and the most common Triassic pterosaur. All specimens differ to each other in some degree as for proportions and morphology of the skeletal elements. There is either an high specific diversification (each specimen is a separate species), a very high intraspecific variability, or a various combination of the two. The only apomorphy of the genus seems to be the presence of tricuspid, pentacuspid and to a lesser extent, tetracuspid lateral teeth, with multicuspoid teeth in the lower and upper jaw having a similar size. The concomitant presence of a square deltopectoral crest of humerus, absence of elongated pre and postzygapophyses in the tail (Dalla Vecchia, 2002), and a first wing phalanx just slightly longer than the ulna ($wph1/u$ is 1.04 in MPUM 6009, 1.16 in MFSN 1797; smallest and probably immature individuals are a possible exception), could diagnose specimens where skull and lower jaw are not preserved (Dalla Vecchia, 2003).

The large MCSNB 2888 has two enlarged maxillar teeth in correspondence of the

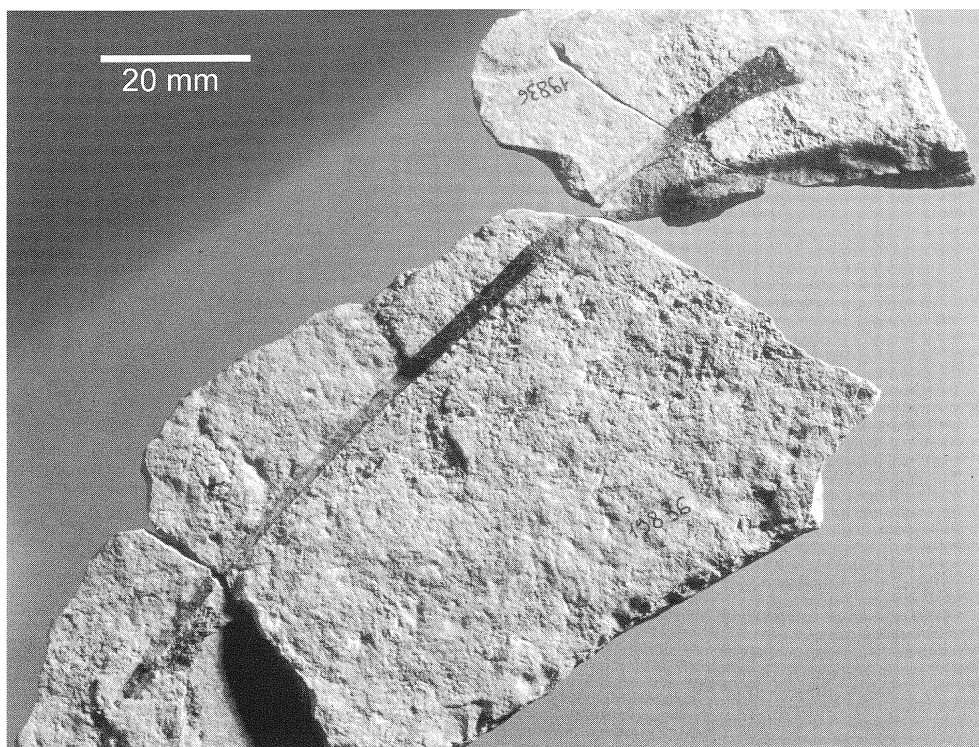


Fig. 16. MFSN 19836, isolated wing phalanx 4, Pterosauria indet., Rovadia Creek, Friuli, Italy. Scale bar equals 20 mm.

ascending process of maxilla. Also the holotype of *Austriadactylus cristatus* and *Preondactylus buffarini* have enlarged teeth in the same position. MPUM 6009, the holotype of *E. cromptonellus* and MFSN 21545 do not have them. It was hypothesized to be a sexual feature (Wild, 1978).

Peteinosaurus

The holotype is rather incomplete and its diagnostic features are the trimorphodon lower jaw dentition and in the unreduced fibula fused to the upper part of the lateral tibiotarsal condyle without a distal condyle (Dalla Vecchia, 2003). The second feature is observed in MCSNB 3496, originally considered as *Eudimorphodon ranzii*, that has the bundle of elongated pre and postzygapophyses in the tail, and was considered as *Peteinosaurus* by Dalla Vecchia (2003). The diagnostic features of *Peteinosaurus* holotype cannot be checked in the other specimen originally attributed to this genus (MCSNB 3359). MCSNB 3359 and MCSNB 2886 share a similar low $wph1/ti$ ratio, which however is distinctive of a larger group including *Preondactylus* and *Dimorphodon* (Dalla Vecchia, 2003). The “bundles” in the tail are surely present only in MCSNB 3496 and MCSNB 3359 among Triassic pterosaurs, but they are synapomorphic of all long-tailed Jurassic pterosaurs, including

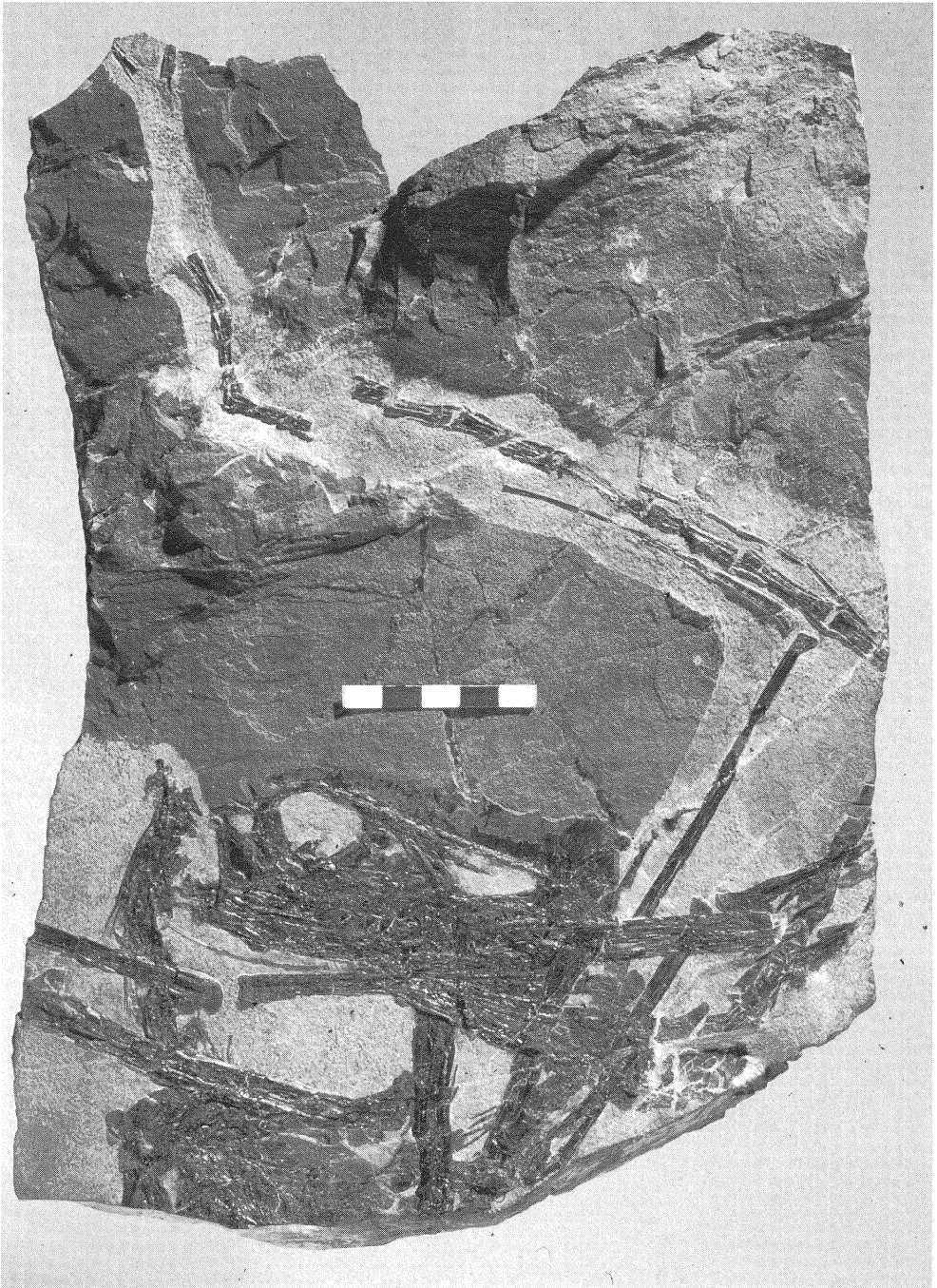


Fig. 17. SMNS 56342, holotype of *Austriadactylus cristatus*, Ankerschlag, Tyrol, Austria. Scale bar equals 50 mm.

Dimorphodon. Thus MCSNB 3359 should be prudently considered as ?*Peteinosaurus*.

Preondactylus

It continues to be a problematic taxon. I previously suggested an affinity with *Peteinosaurus* mainly on the base of long bones ratios, lower jaw teeth size and spacing, and shape of the humerus (Dalla Vecchia, 1998, 2003). Unfortunately, the skull of *Peteinosaurus* is unknown and the lower jaw and the dentition of *Preondactylus* holotype are preserved as faint impressions of the original bone. The new specimen MFSN 25161 would suggest a stricter relationship of *Preondactylus* with *Austriadactylus* based on the upper jaw dentition (Dalla Vecchia, work in progress). Unfortunately, this new specimen does not preserve the lower jaw, thus it does not allow a cross comparison with *Peteinosaurus* and *Austriadactylus*, both surely distinct by a different lower jaw dentition.

Austriadactylus

When firstly described it appeared as a very distinct genus, characterized by a peculiar upper and lower jaw dentition and a sagittal cranial crest (Dalla Vecchia *et al.*, 2002). As reported above, new information from *Preondactylus* would suggest a certain degree of affinity between the two taxa.

After 30 years from the first discovery we know more about Triassic pterosaurs, but what we need to know is by far much more.

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