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F. M. DALLA VECCHIA

AN *EUDIMORPHODON* (DIAPSIDA, PTEROSAURIA) SPECIMEN FROM THE NORIAN
(LATE TRIASSIC) OF NORTH-EASTERN ITALY

UN ESEMPLARE DI *EUDIMORPHODON* (DIAPSIDA, PTEROSAURIA) DAL NORICO
(TRIASSICO SUPERIORE) DELL'ITALIA NORD-ORIENTALE

Abstract - The second specimen (MFSN 1922) of the ramphorhynchoid pterosaur *Eudimorphodon* from the Dolomia di Forni Formation (Late Triassic, Norian) of Carnia region (Udine Province, Friuli Venezia Giulia Autonomous Region, NE Italy) is here described. The first specimen is the holotype of *Eudimorphodon rosenfeldi* DALLA VECCHIA. The incomplete preservation of the new specimen does not allow a specific attribution. Part of a mandibular ramus with tricuspid, quinticuspid and a lesser number of quadricuspid teeth is preserved in MFSN 1922, along with part of the vertebral column, ribs, an humerus and an incomplete wing phalanx. Traces of the wing patagium are also present. The enamel on the multicuspid tooth is smooth as in all specimens of *Eudimorphodon* excluding the holotype of *E. ranzii* ZAMBELLI. Unlike the Late Jurassic *Rhamphorhynchus* the number of mandibular teeth in *Eudimorphodon* increases with increase in the size of the lower jaw.

Key words: Triassic pterosaur, *Eudimorphodon*, Late Triassic, Norian, Dolomia di Forni, Friuli.

Riassunto breve - Viene descritto il secondo esemplare (MFSN 1922) dello pterosauro ramforincoideo *Eudimorphodon* scoperto nella Dolomia di Forni (Norico) della Carnia (Udine, Friuli Venezia Giulia). Il primo è l'olotipo di *Eudimorphodon rosenfeldi* DALLA VECCHIA. La conservazione parziale del nuovo esemplare non consente una attribuzione specifica. MFSN 1922 consiste in parte di un ramo mandibolare con denti tricuspidati, pentacuspidati e in minor numero tetracuspidati, parte della colonna vertebrale, costole, un omero e una falange alare incompleta. Sono presenti anche tracce del patagio alare. Come in tutti gli esemplari di *Eudimorphodon*, tranne l'olotipo di *E. ranzii* ZAMBELLI, lo smalto dei denti multicuspidati è liscio. Diversamente da *Rhamphorhynchus* del Giurassico Superiore, il numero dei denti mandibolari di *Eudimorphodon* aumenta con l'incremento delle dimensioni della mandibola.

Parole chiave: Pterosauro triassico, *Eudimorphodon*, Triassico superiore, Norico, Dolomia di Forni, Friuli.

Introduction

Although rare, pterosaurs are the most common fossil reptiles in the Dolomia di Forni (Forni Dolostone; Upper Triassic), a lithostratigraphic unit cropping out in the Carnia region of northern Friuli, Udine Province, NE Italy. *Preondactylus buffarinii* WILD

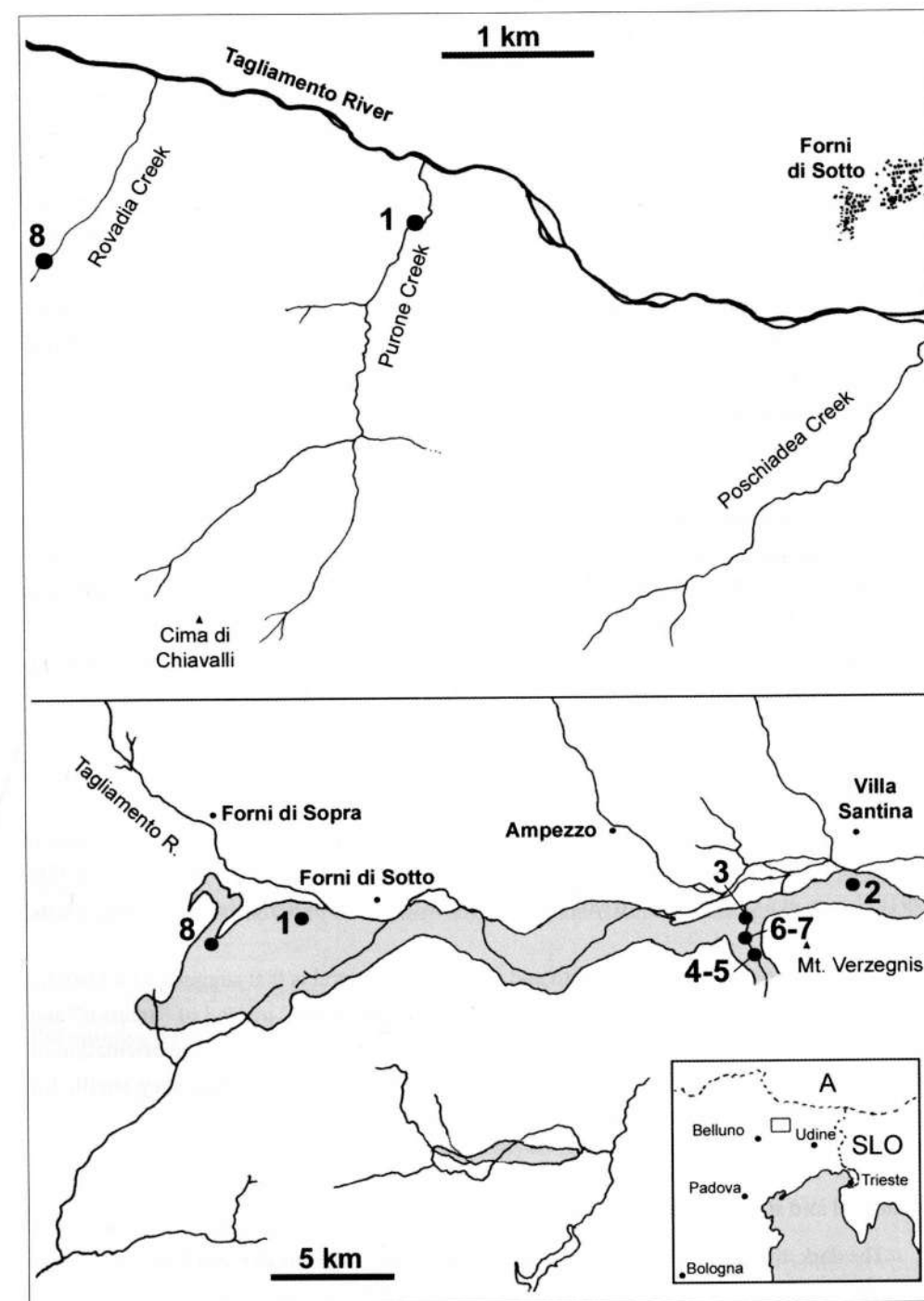
is represented by the holotype (MFSN 1770; WILD, 1984; DALLA VECCHIA, 1998), and probably by a partial, still undescribed skull (MFSN 25161). A gastric eject with pterosaurian bones (MFSN 1891) was also attributed with doubt to *Preondactylus buffarinii* based on estimated bone lengths and ratios and its provenance (DALLA VECCHIA et al., 1989). All these specimens come from the Seazza Creek valley, near the village of Preone (fig. 1). *Eudimorphodon* ZAMBELLI is represented by the holotype of *E. rosenfeldi* DALLA VECCHIA briefly described in DALLA VECCHIA (1995) on the base of a nearly complete, articulated skeleton (holotype, MFSN 1797). The specimen was found along the Forchiar Creek, northern flank of Mt Lovinzola, Enemonzo township. A partial *Eudimorphodon* skeleton (MFSN 21545) was found in 1997, along the Seazza Creek valley, but this specimen is not available for study and hopefully it will be described in the future.

Another fragmentary specimen of *Eudimorphodon* (MFSN 1922) was found by Dr. Corrado Rosenfeld and Mr. Sergio Spizzamiglio during the summer 1989 in a boulder along the Purone Creek, Forni di Sotto township (fig. 1). Other pterosaur material consists of a segment of the caudal vertebral column with two terminal wing phalanges (MFSN 19864) from Seazza Creek valley (DALLA VECCHIA, 2002) and an isolated wing phalanx 4 (MFSN 19836; DALLA VECCHIA, 2000b) from the Rovadia Creek.

Non-pterosaurian tetrapods from the Dolomia di Forni consist of the holotype of *Megalancosaurus preonensis* CALZAVARA, MUSCIO & WILD (CALZAVARA et al., 1981) and two isolated tails referred to this species (PINNA, 1988; RENESTO, 1994; 2000), a nearly complete large specimen of *Langobardisaurus* RENESTO (holotype of *L. tonelloi* MUSCIO; MUSCIO, 1997; RENESTO & DALLA VECCHIA, 2000), a partial skeleton of *Langobardisaurus* (RENESTO et al., 2002) and a very small one still to be prepared, and the holotype of "*Langobardisaurus*" *rossi* BIZARRINI & MUSCIO (BIZARRINI & MUSCIO, 1995), which is actually not a prolacertiform (RENESTO & DALLA VECCHIA, in progress).

Fig. 1 - Location of the finding site of MFSN 1922 and the other pterosaur specimens in the Dolomia di Forni Formation. The outcrop of the formation is marked in gray. Legend: 1 = *Eudimorphodon* sp., MFSN 1922; 2 = *Eudimorphodon rosenfeldi*, MFSN 1797, holotype, Forchiar Creek, Enemonzo; 3 = *Eudimorphodon* sp., MFSN 21545, Seazza Creek, Preone; 4 = *Preondactylus buffarinii*, MFSN 1770, holotype; 5 = *Preondactylus buffarinii*, MFSN 25161; 6 = MFSN 1891; 7 = MFSN 19864; 8 = MFSN 19836.

- Posizione del luogo di rinvenimento di MFSN 1922 e degli altri esemplari di pterosauri della Dolomia di Forni. Le zone di affioramento della formazione sono evidenziate in grigio. Legenda: 1 = *Eudimorphodon* sp., MFSN 1922; 2 = *Eudimorphodon rosenfeldi*, MFSN 1797, olo tipo, Rio Forchiar, Enemonzo; 3 = *Eudimorphodon* sp., MFSN 21545, Rio Seazza, Preone; 4 = *Preondactylus buffarinii*, MFSN 1770, olo tipo; 5 = *Preondactylus buffarinii*, MFSN 25161; 6 = MFSN 1891; 7 = MFSN 19864; 8 = MFSN 19836.



Along with *Eudimorphodon rosenfeldi*, two other *Eudimorphodon* species have been named: *E. ranzii* ZAMBELLI (type-species; ZAMBELLI, 1973; WILD, 1978; 1994), from the middle and possibly upper Norian of Lombardy, northern Italy, and *E. cromptonellus* JENKINS JR., SHUBIN, GATESY & PADIAN (JENKINS jr. et al., 2001) from the Norian/Rhaetian of Greenland. The holotype of *E. ranzii* is MCSNB 2888; other relatively complete specimens from the Norian of Lombardy reported in literature as *Eudimorphodon* are MPUM 6009 (mentioned as "Exemplar Milano" in WILD, 1978), MCSNB 2887 and MCSNB 8950.

E. cromptonellus is represented by the holotype (MGUH VP 3393), a small immature individual. *Eudimorphodon* is found also in the middle Norian Seefeld Schichten of Tyrol (Austria) (BSP 1994I 51; *E. cf. ranzii* according to WELLNHOFER, 2001).

The *Eudimorphodon* specimen MFSN 1922 is here described and compared to the other *Eudimorphodon* specimens from Friuli, Lombardy, Greenland and Austria.

Institutional abbreviations: BSP = Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CM = Carnegie Museum of Natural History, Pittsburgh, USA; 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.

Terminology

I use here the term "rhamphorhynchoidea" as indicating all of the genera included in the suborder Rhamphorhynchoidea in the Linnnean systematic (WELLNHOFER, 1978; 1991; UNWIN et al., 2000), aware of the fact that Rhamphorhynchoidea is a paraphyletic group.

The terminology utilized for teeth and dentition in general is that suggested by EDMUND (1969) and PEYER (1968). In particular, I use "mesial" and "distal" instead of "anterior" and "posterior" to indicate the relative position of a tooth in the tooth row and the orientation of single parts of the tooth. I use the terms "cusps", and "cuspules" when very small, for topographically separate elevations on tooth crown.

Geological and stratigraphical remarks

The dark, thinly-bedded, bituminous dolostone of the Dolomia di Forni Formation crops out in the Carnia region from the environs of the town of Tolmezzo to the village of Forni di

Sopra, extending as an east to west elongated band for more than 30 km (fig. 1). The depositional environment was a small, anoxic marine basin whose bottom condition allowed the preservation of organic remains and articulated vertebrate skeletons (DALLA VECCHIA, 1991; 1994). The fossilized organisms are both terrestrial (reptiles and plants), marine nectonic (fishes, some shrimps) or marine benthic (crustaceans, rare ophiuroids, rare gastropods and pelecypods). They were all allochthonous, transported after death from different life environments and deposited at the basin bottom.

The basin was surrounded south, west and east, by a wide carbonate platform represented by the Dolomia Principale Formation, "Hauptdolomit" of German Authors, which is mainly Norian in age. Terrestrial vertebrates, above all dinosaurs, left their footprints in the tidal flat facies of the Dolomia Principale (DALLA VECCHIA & MIETTO, 1998), suggesting that the inner platform was at least partly emergent. The northern margin of the outcrop of the basinal dolostone is marked by faults and contacts older Triassic units.

The fossiliferous layers along the Seazza Creek valley belong to the lower member of the Dolomia di Forni (sensu DALLA VECCHIA, 1991). The size-trend in the conodont *Epigondolella slovakensis* (KOZUR) suggests an Alaunian 2-3 (*Himavites hogarti* - *Halorites macer* ammonoid Zones) dating for the Seazza Creek section and that of the nearby Forchiar Creek (where *Eudimorphodon rosenfeldi*, MFSN 1797, was found) (ROGHI et al., 1995). Alaunian, which is divided into three parts (Alaunian 1 is the oldest, 3 the youngest) represents the middle Norian (GRADSTEIN et al., 1995, fig. 8). The specimen MFSN 1922 was found on an isolated block in the bed of the Purone Creek and its stratigraphic position cannot be detailed further. The Purone Creek is in the western part of the Dolomia di Forni outcrop, relatively far from the Seazza Creek section (fig. 1). However, samples from the upper part of the Dolomia di Forni in the closer Poschiadea Creek and other western sections of the Dolomia di Forni contain the conodonts *Epigondolella slovakensis* and *E. postera* together (CARULLI et al., 1998; 2000), also suggesting an Alaunian 3 dating for the upper part of the unit.

Paleontological description

Reptilia LINNAEUS, 1758

Diapsida OSBORN, 1903

Pterosauria KAUP, 1834

Eudimorphodon ZAMBELLI, 1973

Type-species: *Eudimorphodon ranzii*

Holotype: MCSNB 2888, Calcare di Zorzino, middle Norian, Cene (Bergamo, northern Italy)

Eudimorphodon sp.
(figs. 2-5)

1994 Rhamphorhynchoidea indet. - SIRNA, DALLA VECCHIA, MUSCIO & PICCOLI, pag. 264

1994 *Eudimorphodon* sp. A - DALLA VECCHIA, pages 144-149, figs 1.48-1.49

2000a *Eudimorphodon* sp. - DALLA VECCHIA, pages 328, 334

MFSN 1922 is a partial, rather disarticulated skeleton (figs. 2-3) preserved on a fragment of dark-gray dolostone. The bones have a dark brown colour and a scaly aspect. Because of weathering, most of the bones are in a poor state of preservation. Some teeth were still covered by rock and have been freed under the binocular microscope using thin steel needles.

There is a segment of the vertebral column comprised of at least six still articulated dorsal vertebrae with the relative ribs more or less in natural connection. Another vertebra without articulated ribs is present distally in this segment. A detached and isolated dorsal vertebra and some fragmentary portions of dorsal ribs are also present anterior and close to the segment. Some dorsal ribs are grouped in a band parallel to the vertebral string and the probable remains of at least two vertebrae are found close by. A stronger rib is preserved between this group and a lower jaw ramus. There is a poorly preserved, but practically complete humerus and a wing phalanx without most of its proximal extremity and its distal portion. Remains of the wing patagium can be observed near the phalanx. Part of a mandibular ramus with teeth is preserved between the wing phalanx and the stronger dorsal rib. Some small bone fragments belong to unidentifiable elements.

Osteological description

Lower jaw (fig. 4)

The partial mandibular ramus lacking both the extremities is 31.5 mm long. Most of the

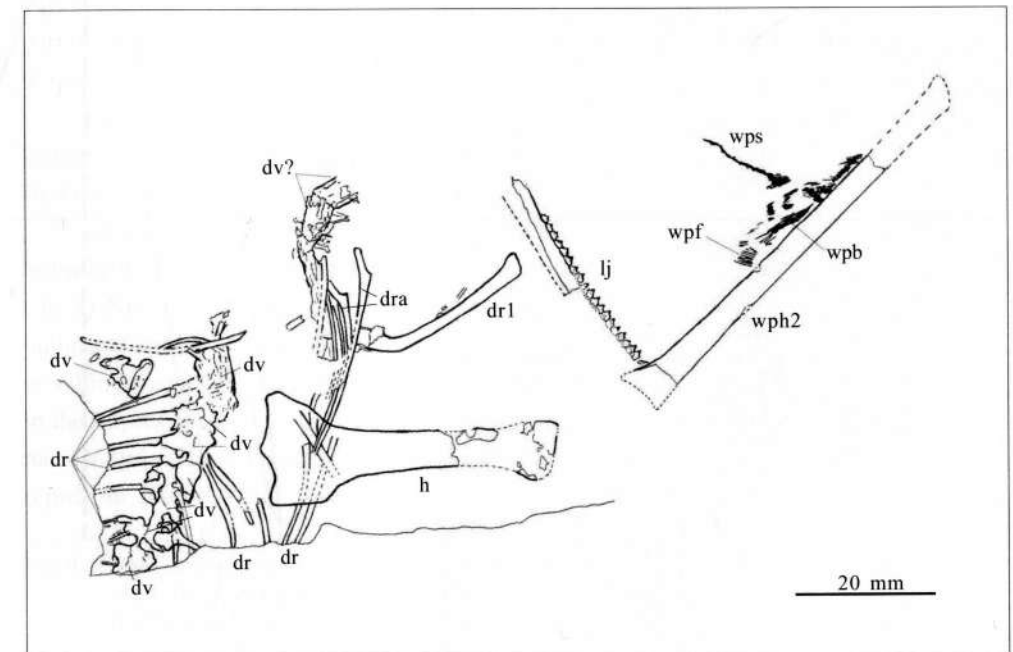
Fig. 3 - *Eudimorphodon* sp., MFSN 1922. Interpretative drawing. Abbreviations: dr = dorsal rib; dr1 = first dorsal rib; dra = anterior dorsal rib; dv = dorsal vertebra; h = humerus; lj = lower jaw; wpb = bundle of wing patagium fibers; wpf = wing patagium fibers (actinofibrils); wph2 = wing phalanx 2; wps = wing patagium in cross-section. Scale bar equals 20 mm.

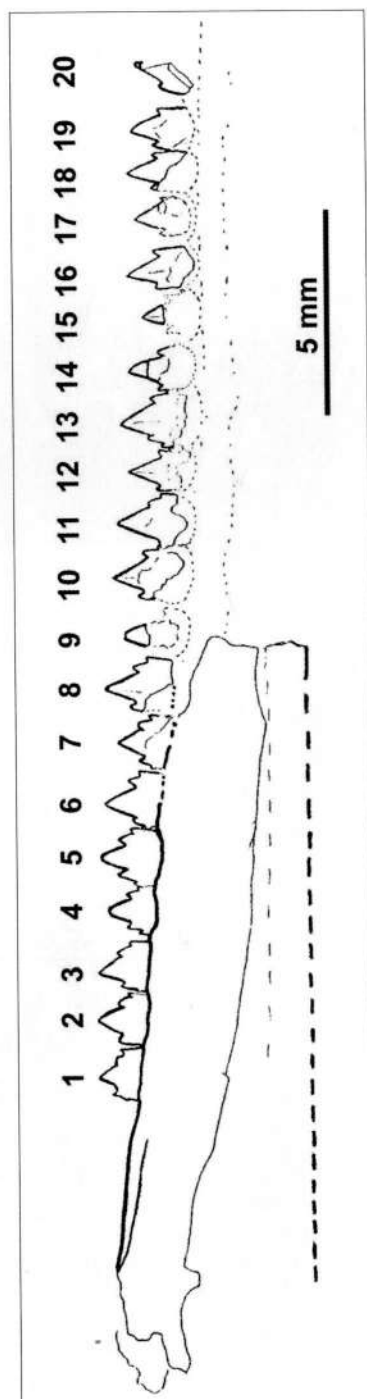
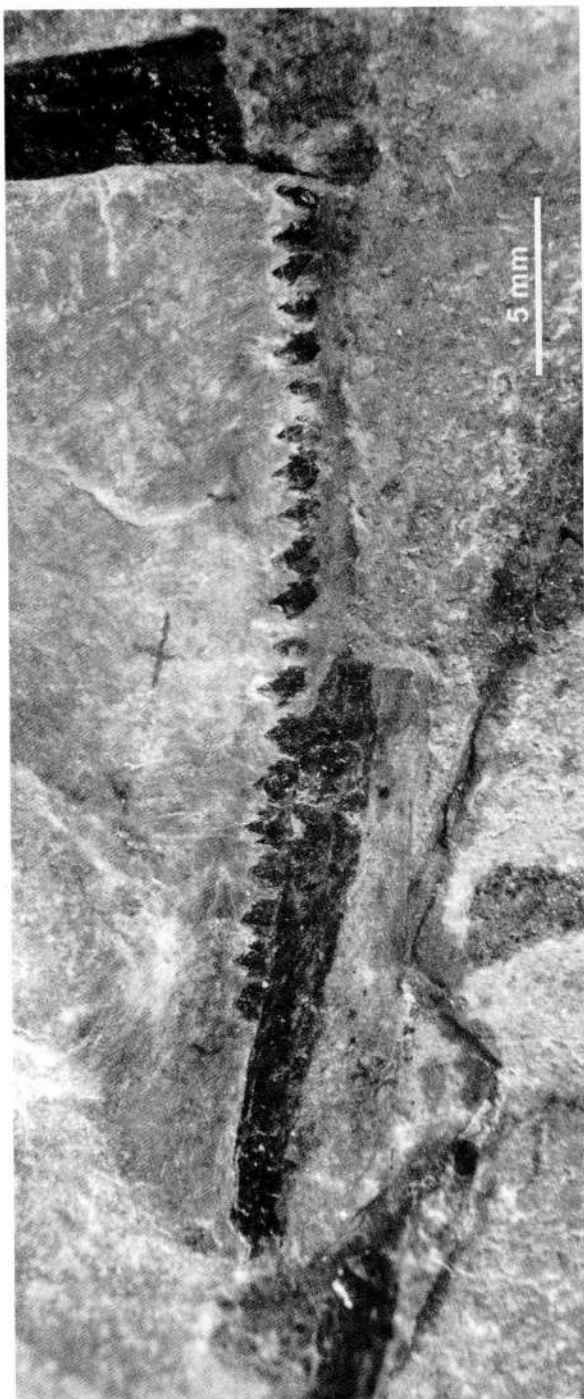
- *Eudimorphodon* sp., MFSN 1922. Disegno interpretativo. Abbreviazioni: dr = costola dorsale; dr1 = prima costola dorsale; dra = costola dorsale anteriore; dv = vertebra dorsale; h = omero; lj = ramo mandibolare; wpb = fascio di fibre del patagio alare; wpf = fibre del patagio alare (actinofibrille); wph2 = falange alare 2; wps = patagio alare in sezione. Scala di riferimento = 20 mm.



Fig. 2 - *Eudimorphodon* sp., MFSN 1922. As for scale see figure 3.

- *Eudimorphodon* sp., MFSN 1922. Per la scala di riferimento si veda la figura 3.





bone was lost and only its impression remains. It is impossible to state whether it is the right or left ramus and whether it is exposed labially or lingually. The general outline of the ramus can be recognized, but the single elements are not identifiable.

There are 20 teeth, representing the middle-posterior portion of the mandibular dentition. The posterior part of the lower jaw becomes sensibly deeper caudally because the ventral margin of the ramus is straight and parallel to the axis of elongation, whereas the dorsal one is inclined. The portion between the most distal tooth and the posterior, artificial, end of the lower jaw, is 7 mm long. The dorsal margin of this tract of the lower jaw is the original, unbroken margin up to 4.17 mm posterior the last tooth, where it then is broken. This margin is inclined and it does not reach the apical part of the presumably present coronoid process, suggesting that the preserved part is anterior the coronoid process. Therefore, a relatively long diastema is without doubt present before the point of the coronoid process.

Dentition

The total number of the teeth must be estimated because the anterior part of the lower jaw is not preserved. The rostral tip of the lower jaw could not have extended beyond the last preserved tooth for more than 9 mm, corresponding to the split away and missing proximal part of the wing phalanx (the proximal part of the mandibular ramus overlapped the proximal part of the phalanx, see fig. 3), because there are no traces of the lower jaw in the rock beyond that split piece of dolostone.

For practical purposes, teeth are numbered in this paper from the last distal tooth to the last preserved tooth mesially, the reverse with respect to the conventional use, because the first teeth are not preserved.

All teeth are strictly spaced, still located in their alveoli, and there are no empty alveoli. Some crowns are apicobasally higher than others, but there are no teeth that have just erupted (fig. 4). No one tooth is entirely preserved, only the last distal seven show a relatively complete outline, while the others are partially preserved, sometimes represented mostly by an impression or a thin phosphatic film. Regardless, the original outline of the crown can be recognized also in the impressions. In no case can the base ("root") be observed. Crowns are labiolingually narrow and multicusped (tricuspid, quinticuspid and sometimes quadricuspid). The central (apical or primary) cusp, which is always markedly more developed than the others, is

Fig. 4 - *Eudimorphodon* sp., MFSN 1922, lower jaw ramus. Above: Photograph. Below: Drawing, scale bar equals 5 mm. Legend: 1-20 = teeth 1-20 (reverse numeration).
- *Eudimorphodon* sp., MFSN 1922, ramo mandibolare. Sopra: fotografia. Sotto: disegno, scala di riferimento = 5 mm. Legenda: 1-20 = denti 1-20 (numerazione invertita).

conical and pointed, with a subcircular apical cross-section and sharp mesial and distal margins. The apical part of the primary cusp is completely preserved in most teeth. Accessory cuspules occur along the mesial and distal edges of the crown. The tooth surface is smooth, without apicobasal ridges of enamel. The primary cusp is sometimes symmetrical and straightly pointing upward, while in other cases it is slightly asymmetrical and curved backward (i.e., the mesial margin is convex, while the distal is straight; e.g., tooth 1, 6-8, 12-14, 19). The basal (lower) cuspules in quinticuspid teeth are much smaller than the upper accessory cuspules. The cuspules in tricuspid teeth are either slightly splayed from the central axis of the tooth or parallel to it. The basal cuspules in quinticuspid teeth are splayed from the central axis, whereas the upper cuspules are only slightly splayed or parallel to the axis. The cuspidation pattern can be seen in figure 4 and table I. There are five tricuspid teeth mesially, whereas the posterior are quinticuspid or quadricuspid.

Taking accurate measurements is in some cases prevented by the incomplete preservation of the teeth. Teeth range in mesiodistal length from 0.92 to 1.34 mm, and in apicobasal height from 0.97 to 1.60 mm. The last seven distal teeth are either mesiodistally longer than apicobasally high or as long as high. For example the last tooth is 1.17 mm long mesiodistally and 1.09 mm high apicobasally, and tooth 3 is 1.34 mm long and 1.34 mm high. This reverses anteriorly: tooth 16 is 0.99 mm long and 1.22 mm high, and tooth 18 is 0.93 mm long and 1.24 mm high. Most of teeth do not show traces of wear, but teeth 4-5 and 9 have the apex of the primary cusp worn away or broken.

A detailed description of each tooth follows. The letter "h" indicates the apicobasal height of the crown, i.e., the part of the tooth rising up from the dorsal margin of the dentary. When the basal part of the crown is preserved as print only, the print of the dorsal margin of the dentary is taken as basal reference point. The mesiodistal length (l) reported for each tooth is the measurement of the preserved part, which in incompletely preserved teeth is slightly lower than the original one. I mark with an asterisk where the measurement of l is affected in this sense.

Tooth 1: The outer portion is missing. H is 1.09 mm, l is 1.17 mm, h/l is 0.93. There is a large primary cusp slightly curved backward, an upper mesial accessory cuspule which is broken, low and blunt. That cuspule is placed higher than the upper distal cuspule. The lower mesial accessory cuspule is small, whereas the distal one appears to be extremely small. An asymmetry is observed in the sizes of the cuspules, with a higher development of the mesial ones. There is a very small diastema between this tooth and the following one.

Tooth 2: Most of the outer part of the crown is missing. H is 1.18 mm, l is 1.18 mm, h/l is 1.00.

The tooth is quadricuspid. The primary cusp is higher apicobasally than that of tooth 1, and is less markedly asymmetric and curved backward. The upper mesial accessory cuspule is slightly larger than the upper distal one and is placed slightly higher in the crown. The lower mesial cuspule is much smaller than the upper one.

Tooth 3: Most of the outer surface of the crown is missing. H is 1.14 mm, l is 1.16 mm, h/l is 0.98. The tooth is quadricuspid and similar to tooth 2, with one distal and two mesial cuspules. The crown is slightly asymmetric and curved backward. There is a small diastema between this tooth and tooth 4.

Tooth 4: Most of the surface of the crown is missing. It is slightly lower than teeth 2 and 3. H is 0.97 mm, l is 1.24 mm, h/l is 0.78. The crown is symmetric and quinticuspid. The lower accessory cuspules are splayed and much smaller than the upper. The apical part of the primary cusp is not pointed and probably is worn away or broken.

Tooth 5: Most of the outer part of the crown is missing. This quinticuspid tooth is larger than the distal teeth. H is 1.34 mm, l is 1.34 mm, h/l is 1.00. The primary cusp is apically worn or broken; the upper mesial accessory cuspule is slightly higher than the distal. The lower mesial accessory cuspule is larger than the distal and is splayed.

Tooth 6: The outer part of the crown is missing, excluded the primary cusp which is slightly asymmetric and smooth. H is 1.24 mm, l is 1.33 mm, h/l is 0.93. There are a lower mesial and an upper distal accessory cuspule. It is impossible to discern whether a lower distal cuspule was present, because the corresponding part of the crown is missing. The lower mesial cuspule is very small. The mesial upper cuspule is placed higher than the distal. There is a small diastema between this tooth and tooth 7.

Tooth 7: The preservation is the same as in tooth 6. The crown is lower than that of teeth 5-6 and 8, the primary cusp is slightly asymmetric, and the upper accessory cuspule has the size of that of tooth 6. The lower mesial accessory cuspule is well-developed and splayed; the distal one is only partly preserved. H is 1.12 mm, l is 1.30 mm, h/l is 0.86.

Tooth 8: Only the mesioapical part is preserved. Its size is the same as in tooth 6. H is 1.46 mm, l is 1.32 mm*, h/l is 1.11. The primary cusp is slightly asymmetric and the whole crown is slightly rotated backward. The upper mesial cuspule and the upper distal are more or less the same size; the lower mesial cuspule is splayed, the lower distal cannot be seen because that part of tooth is not preserved.

Tooth 9: Only the point of the primary cusp, apically worn, is preserved, along with a film of

the central part of the crown. This tooth is lower than teeth 8 and 10. H is 1.33 mm. The probable lower accessory mesial cuspule is present as a faint print.

Tooth 10: Only the mesioapical portion is preserved. H is 1.60 mm, l is 1.31* mm, h/l is 1.22. The external surface of the primary cusp's tip shows a smooth surface. The primary cusp is symmetric, but the whole tooth is slightly inclined toward the rear. The upper mesial accessory cuspules and the distal ones have the same size and are placed at the same height along the cutting margins as in tooth 8. The lower distal accessory cuspule cannot be seen because that part of tooth is missing; according to the print of that part of the crown a lower distal cuspule could be absent. The lower mesial cuspule is splayed. Therefore this tooth is quadricuspid or quinticuspid.

Tooth 11: It is preserved like tooth 10 and the surface of the primary cusp is smooth. H is 1.43 mm, l is 1.20 mm*, h/l is 1.19. The primary cusp is symmetric. The upper and lower mesial accessory cuspules are preserved (the upper is broken), while the distal cuspules are not preserved because that part of the tooth is missing. Therefore this tooth is quadricuspid or quinticuspid.

Tooth 12: The distobasal part is missing. It is lower than teeth 10-11 and 13; H is 1.28 mm, l is 1.09 mm*, h/l is 1.17. The primary cusp is slightly curved backward. It is completely preserved and is smooth, and there are upper mesial and distal accessory cuspules. A lower accessory cuspule was probably present mesially and is covered by tooth 13. The possible distal lower accessory cuspule cannot be seen since that part of tooth not is preserved. Therefore this tooth is quadricuspid or quinticuspid.

Tooth 13: This tooth is higher than tooth 12 and 14. H is 1.51 mm, l is 1.30 mm*, h/l is 1.16. The basal part not is preserved, the primary cusp is complete, asymmetrical and with a smooth surface. The upper accessory mesial and distal cuspules have more or less the same size; the lower mesial and distal are decidedly smaller and splayed, the lower mesial is in part covered by the preceding tooth.

Tooth 14: Only the apical part of the primary cusp is preserved completely, while the remaining part of the crown is represented only by a phosphatic film. H is 1.24 mm, l is 1.14 mm*, h/l is 1.07. The primary cusp is asymmetric. There are upper accessory mesial and distal cuspules. The print of the crown suggests the presence of a lower mesial cuspule. The part possibly bearing the distal one is missing.

Tooth 15: It is lower than the two adjacent teeth. H is 1.04 mm, l is 1.20 mm*, h/l is 0.87. Only the apical part of the primary cusp is completely preserved and is symmetric. Part of the crown is represented only by a thin phosphatic film. The upper accessory cuspules are preserved as print. There is a small lower mesial

accessory cuspule. Therefore this tooth is quadricuspid or possibly quinticuspid.

Tooth 16: The basal part of the crown is partially missing. H is 1.22 mm, l is 0.99 mm, h/l is 1.23. The primary cusp is smooth and symmetric. The upper accessory cuspules have the same size, and the distal is slightly splayed. A true lower accessory mesial cuspule is absent, but there is a bump in the margin just below the upper cuspule. The part bearing a possible lower distal cuspule is missing, but the print of the crown suggests its absence. Therefore this tooth is tricuspid. There is a small diastema between this and tooth 17.

Tooth 17: Only a phosphatic film and the sectioned primary cusp are preserved. Two accessory cuspules are visible. The tooth is slightly lower than teeth 16 and 18. H is 1.03 mm, l is 0.92 mm, h/l is 1.12.

Tooth 18: Only the mesioapical portion is preserved, while the rest is represented by a print. H is 1.24 mm, l is 0.93 mm, h/l is 1.33. The crown is symmetric with three cusps, and the accessory ones have a similar size.

Tooth 19: H is 1.13 mm, l is 0.96 mm, h/l is 1.18. The apical half is completely preserved; the primary cusp has a smooth surface and is slightly asymmetric. The crown is tricuspid, accessory cuspules are placed at the same height and the mesial is slightly splayed.

Tooth 20: Three cusps are probably present; only the distal half of the crown is preserved and is slightly inclined mesially. H is 1.17 mm. Teeth 19 and 20 are separated by a diastema longer (0.30 mm) than the very small diastema present between the other teeth.

Axial skeleton

Dorsal vertebrae

The string of seven dorsal vertebrae is so poorly preserved that is difficult to identify the single elements, and the same is true for all other remains identified as vertebrae (fig. 3). The ribs still connected to the vertebrae of the string seem to be holocephalous. This indicates that it is the posterior segment of the dorsal vertebral column (see below). The most caudal element could be a "lumbar" vertebra, according to WILD (1978). If the string has 7 articulated elements and one more is separated (fig. 3), probably only six dorsals are missing, assuming that the total dorsal count is 14 as in MCSNB 2888 (12 thoracic and 2 "lumbar", WILD, 1978). The possible vertebral remains found near the two-headed ribs (fig. 3) could be the first two dorsals, but it cannot be ruled out that they represent the posterior cervicals.

Dorsal ribs

One rib is much more robust than the others and is identified as the first dorsal rib because it is very similar to the first dorsal rib of MCSNB 2888 (WILD, 1978, pl. 2). The length of the visible part is 25 mm. The proximal segment is markedly curved medially, whereas the remaining part is nearly straight (fig. 3). The distal end is slightly expanded and the proximal part is so poorly preserved that it is not possible to identify the tuberculum and the capitulum, which probably are also covered by other ribs. Another rib preserves a two-headed articular part and a long portion of the shaft, which is thin and only slightly curved (fig. 3). A second two-headed dorsal rib shows only the proximal part. In both cases, the capitulum is much more developed than the tuberculum, with the latter not projecting from the shaft. At least other six ribs, some of which lie beneath the humerus, are represented by thin and nearly straight fragments of shafts.

Appendicular skeleton - Forelimb

Humerus

The distal part of this element is represented only by small fragments of bone, while the remainder is a thin phosphatic film. Regardless, the element is complete and 41 mm long, because the distal extremity is expanded as it is in the humeri of all pterosaurs in the area of the radio-ulnar condyles. The proximal part of humerus is wide and the deltopectoral crest is square, rather narrow and with a straight preaxial margin which is parallel to the shaft (the whole crest is 10 mm long, the portion with the straight margin is 7.7 mm long). The head of the humerus is rather poorly preserved and the drawing of figures 3 and 6 is based on a faint impression and phosphatic traces. The shaft is elongated and straight, but it is strongly crushed and this could have influenced its curvature. The ratio of the humeral length against the maximum proximal width is 2.58.

Wing phalanx

The preserved part of this bone is 44 mm long. The proximal extremity has nearly completely split away, but a splint of the postaxial margin of the bone and the impression of the remainder portion show that it had the typical asymmetrical proximal expansion of wing phalanges 2-4. The distal segment of the bone was also lost. The width of the phalanx just before the proximal expansion is 3.80 mm, it is 3.19 mm at mid-shaft, and 3.00 mm at the broken distal end. The minimum width (2.80 mm) is reached 11.5 mm before the broken distal end. Thus the width of the shaft remains rather constant, and the shaft is perfectly straight.

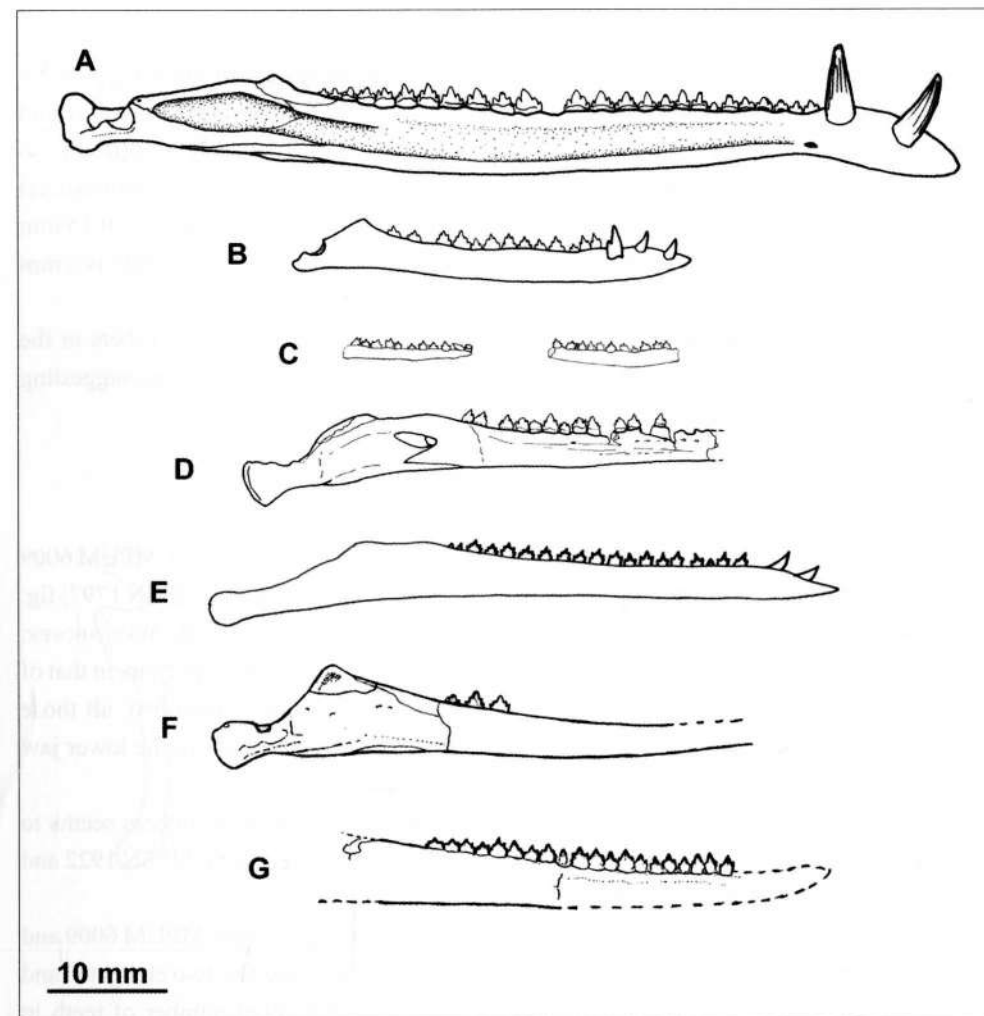


Fig. 5 - Lower jaws of *Eudimorphodon* specimens. A) *E. ranzii*, holotype, MCSNB 2888; B) MPUM 6009; C) *E. cromptonellus*, holotype, MGUH 3393, right (right) and left (left) ramus; D) BSP 1994I 51; E) MFSN 21545 (this drawing is only indicative of mandibular size and teeth number); F) *E. rosenfeldi*, holotype, MFSN 1797; G) MFSN 1922. A and B after WILD (1978), C after JENKINS et al. (2001), D after WELLNHOFER (2001), all redrawn with a same anteroposterior polarity. Scale bar equals 10 mm.

- Rami mandibolari degli esemplari di *Eudimorphodon*. A) *E. ranzii*, olotipo, MCSNB 2888; B) MPUM 6009; C) *E. cromptonellus*, olotipo, MGUH 3393, ramo destro (a destra) e sinistro (a sinistra); D) BSP 1994I 51; E) MFSN 21545 (questo disegno è solo indicativo delle dimensioni della mandibola e del numero di denti); F) *E. rosenfeldi*, olotipo, MFSN 1797; G) MFSN 1922. A e B da WILD (1978), C da JENKINS et al. (2001), D da WELLNHOFER (2001), tutte ridisegnate con una stessa polarità anteriore-posteriore. Scala di riferimento = 10 mm.

Wing patagium

Traces of a dark substance are found along the postaxial margin of the wing phalanx and in the same plane with it (fig. 3). Part of this thin film is still covered by dolostone and is seen as a cross-section. Thin fibers, parallel to each other, are clearly identifiable in some places, although poorly preserved. Each fiber is represented by a faint bidimensional trace of black substance. Single fiber segments are at maximum 1.7 mm long, 0.10-0.15 mm wide and spaced 0.12 to 0.20 mm to each other. A bundle of closely grouped fibers is 6 mm long.

The fibers are the actinofibrils of the actinopatagium (BENNETT, 2000). Fibers in the different preserved patches of patagium of MFSN 1922 show a varying orientation, suggesting that the patagium was creased.

Discussion

The lower jaw is completely preserved in the holotype of *E. ranzii* (fig. 5A), MPUM 6009 (fig. 5B), and MFSN 21545 (fig. 5E), partly in the holotype of *E. rosenfeldi* (MFSN 1797; fig. 5F), partly in the specimen of *Eudimorphodon* from Seefeld (BSP 1994I 51; WELLNHOFER, 2001; fig. 5D), and nearly completely, as far as it concerns the tooth-bearing portion, in that of *E. cromptonellus* (MGUH VP 3393; fig. 5C). Like the specimen here described, all those specimens have tricuspid and quinticuspid (sometimes quadricuspid) teeth in the lower jaw (MFSN 1797 preserves evidence only of distal, quinticuspid teeth).

The toothless margin between the last distal tooth and the coronoid process seems to be proportionally shorter in MCSNB 2888 and above all MPUM 6009 than in MFSN 1922 and MFSN 1797 (the condition in BSP 1994I 51 is not clear).

Comparing the lower jaw of MFSN 1922 with those of MCSNB 2888, MPUM 6009 and the still undescribed element of MFSN 21545, it is clear that at least the first two elongated and monocuspidate "caniniform" teeth are missing and thus the minimum number of teeth in MFSN 1922 is 22. As the first two "caniniform" teeth are widely spaced, the tip of the jaw is edentulous and sometimes (MFSN 21545) there is a diastema between the first tricuspid tooth and the distal "caniniform" tooth, it is plausible that tooth 20 is the first tricuspid tooth or at maximum the second. Therefore the maximum tooth count is 23. The large specimen MCSNB 2888 has 28 teeth in the lower jaw, whereas the smaller MPUM 6009 has 17 teeth, and MFSN 1922 has an intermediate number.

MFSN 1922 had probably a slightly larger lower jaw than MFSN 1797, and was intermediate between those of MCSNB 2888 (74.5 mm long) and MPUM 6009 (34 mm long) (fig. 5A-B, F-G). Humeri of MFSN 1922 and MFSN 1797 have practically a similar length, 41 mm and 42 mm respectively (fig. 6F-G); the humerus is 26 mm long in MPUM 6009 and 47 mm in MCSNB 2888.

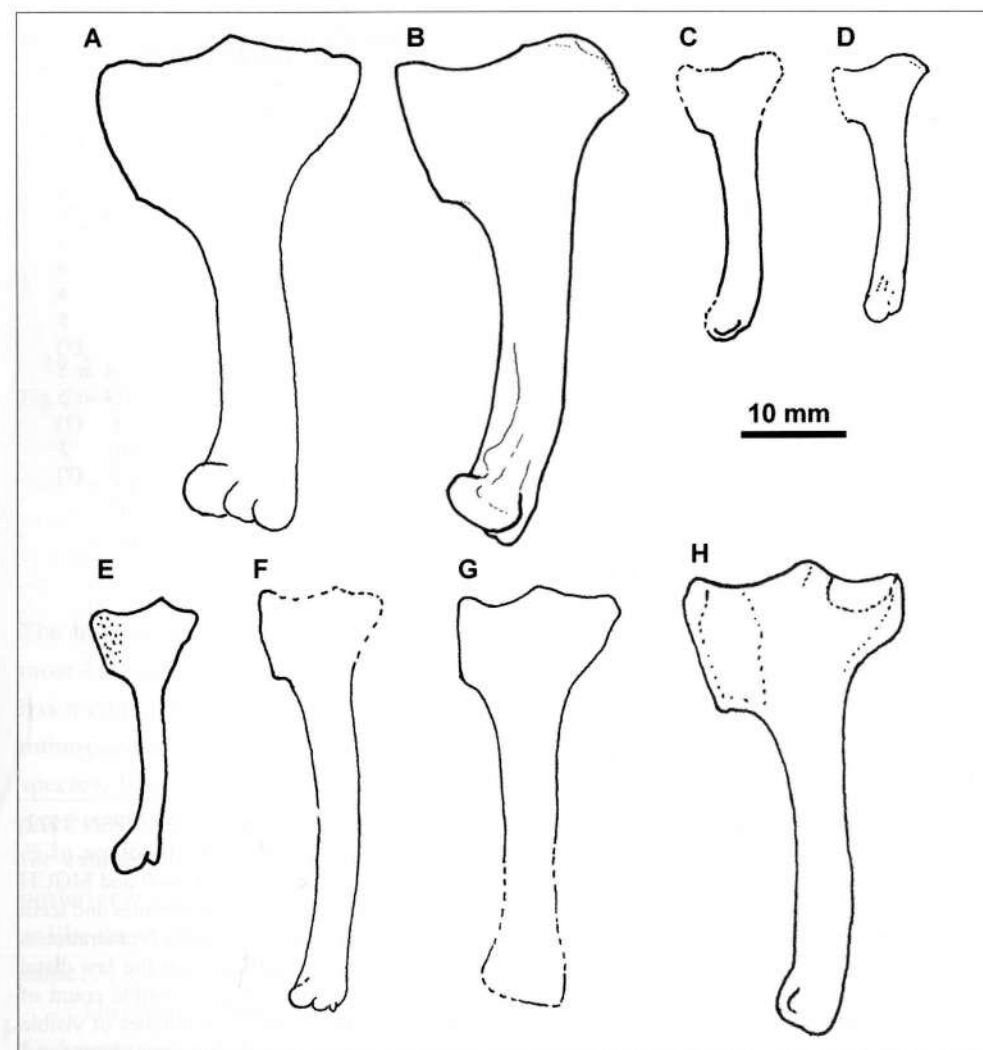


Fig. 6 - Humeri of *Eudimorphodon* and *Campylognathoides*. A) *E. ranzii*, holotype, MCSNB 2888, right humerus; B) *E. ranzii*, MCSNB 2888, left humerus; C) MCSNB 2887; D) MPUM 6009; E) MCSNB 8950; F) *E. rosenfeldi*, holotype, MFSN 1797, preliminary reconstruction based on both humeri; G) MFSN 1922; H) *Campylognathoides liasicus*, CM 11424. A, B, C, D redrawn after WILD (1978), E redrawn after WILD (1994), H redrawn after WELLNHOFER (1974). Scale bar equals 10 mm.

- Omeri di *Eudimorphodon* e *Campylognathoides*. A) *E. ranzii*, olotipo, MCSNB 2888, omero destro; B) *E. ranzii*, MCSNB 2888, omero sinistro; C) MCSNB 2887; D) MPUM 6009; E) MCSNB 8950; F) *E. rosenfeldi*, olotipo, MFSN 1797, ricostruzione preliminare basata su entrambi gli omeri; G) MFSN 1922; H) *Campylognathoides liasicus*, CM 11424. A, B, C, D ridisegnati da WILD (1978), E ridisegnato da WILD (1994), H ridisegnato da WELLNHOFER (1974). Scala di riferimento = 10 mm.

	MFSN 1922	MCSNB 2888	MPUM 6009	MGUH 3393	BSP 1994I 51
1	5	5	5	*5/(?)	3
2	4	5	5	5/(?)	5
3	4	5	(5?)	5/3	(?)
4	5	5	5	3/5	5
5	5	2/5	5	5/3	4
6	4 or 5	5	5	5/3	4 or 5
7	5	5	5	4/3	5
8	4 or 5	5	5	3?/3	4
9	(5?)	5	3/5	4 or 5/3	4
10	4 or 5	5	3	3/3	5
11	4 or 5	5	5	4 or 5/3	(?)
12	4 or 5	5	3	(?)/2	4 or 5
13	5	5	3	(?)/1	4 or 5
14	4 or 5	4/5	3		(?)
15	4 or 5	5	2		3
16	3	3/5	1		(?)
17	3	3	1		
18	3	5			
19	3	3			
20	3	3			
21	(3?)	3/5			
22	(1?)	3			
23	(1?)	3/5			
24		3			
25		3			
26		3			
27		1			
28		1			

Tab. I - Cuspitation pattern of teeth in the lower jaw of *Eudimorphodon* specimens MFSN 1922, MCSNB 2888 (holotype of *E. ranzii*), MPUM 6009, MGUH 3393 (holotype of *E. cromptonellus*) and BSP 1994I 51. The pattern of MCSNB 2888, MPUM 6009 and MGUH 3393 is reported for both right and left (r/l) mandibular rami. The count of cusps and teeth number of BSP 1994I 51 is deduced from the drawing in WELLNHOFER (2001). Numeration is reversed respect to the conventional use of teeth numbering, starting from the last distal tooth. Legend: (?) = empty alveolus or missing tooth; (1?) (3?) (5?) = possible count of cusps based on the condition in other specimens or close teeth; 3? = number of visible cusps in a not completely erupted tooth; 4 or 5 = count of the cusps uncertain between 4 and 5 because of the poor or partial preservation of the tooth; * = possibly not the last distal tooth.

- Formula delle cuspidi dei denti mandibolari negli esemplari di *Eudimorphodon* MFSN 1922, MCSNB 2888 (olotipo di *E. ranzii*), MPUM 6009, MGUH 3393 (olotipo di *E. cromptonellus*) e BSP 1994I 51. È riportata la formula di entrambi i rami mandibolari (destra e sinistra) di MCSNB 2888, MPUM 6009 e MGUH 3393. Il conto delle cuspidi e il numero di denti di BSP 1994I 51 è stato dedotto dal disegno di WELLNHOFER (2001). La numerazione è invertita rispetto a quella convenzionale ed inizia dall'ultimo dente distale. Legenda: (?) = alveolo vuoto o dente mancante; (1?) (3?) (5?) = possibile conto di cuspidi basato sulla condizione presente in altri esemplari o denti vicini; 3? = numero delle cuspidi visibili in un dente non ancora spuntato completamente; 4 o 5 = conto delle cuspidi incerto tra 4 o 5 a causa del cattivo o parziale stato di conservazione; * = forse non è l'ultimo dente distale.

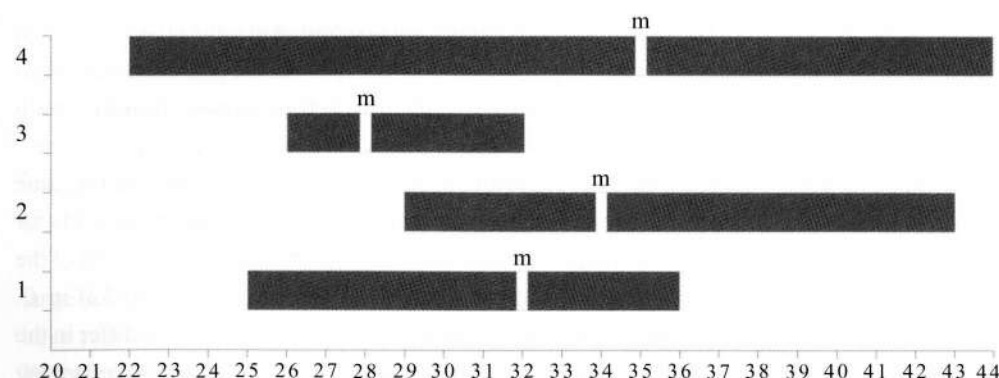


Fig. 7 - Teeth number range in different species of the gekkonid *Coleonyx*. Legend: 1 = *C. brevis*; 2 = *C. elegans*; 3 = *C. mitratus*; 4 = *C. variegatus*; 20-44 = teeth number; m = mean. After EDMUND (1969).

- Variazione nel numero dei denti in specie diverse del gekkonide *Coleonyx*. Legenda: 1 = *C. brevis*; 2 = *C. elegans*; 3 = *C. mitratus*; 4 = *C. variegatus*; 20-44 = numero dei denti; m = media. Da EDMUND (1969).

The smallest specimen, MGUH VP 3393 (see fig. 5C; humerus is 18.15 mm long), has at most 4 mandibular teeth less than MPUM 6009, which has 17 teeth (tab. I). MFSN 21545 has a complete right mandibular ramus that is 53 mm long, with 21 teeth (two mesial monocusped, 19 multicusped). Considering the genus *Eudimorphodon* and not the single species, because of the scarce sample, there seems to be a general increase in tooth number with the increase in lower jaw length. This also happens in some living reptiles, for example in iguanids where "as many as four teeth per year can be added to the posterior end of the tooth row in rapidly growing animals" (EDMUND, 1969, p. 154). This is unlike the condition in *Rhamphorhynchus* where the tooth count in the lower jaw is the same (7) in all specimens (WELLNHOFER, 1975).

This relationship between jaw length and tooth number does not appear to be linear in *Eudimorphodon*. The length of the lower jaw of MCSNB 2888 is 2.19 times that of MPUM 6009, but the number of teeth is only 1.65 times. The length of the lower jaw of MCSNB 2888 is 1.41 times that of MFSN 21545 and the number of teeth is 1.33 times. The length of the lower jaw of MFSN 21545 is 1.56 times that of MPUM 6009, but the number of teeth is only 1.23 times. Apparently, MPUM 6009 has more teeth than it should have if teeth number would increase linearly with lower jaw length. This is partly due to the relatively short portion of the lower jaw posterior to the last tooth in MPUM 6009 compared to that of both MCSNB 2888 and MFSN 21545 (fig. 5). However, a comparatively higher number of teeth is evident also in the small MGUH VP 3393 with respect to MPUM 6009 (fig. 5B-C). Actually, in living reptiles with an increase of teeth number with growth, the number is not strictly

proportional to body size. The example of *Iguana iguana* is reported in table II. Additionally, tooth number is not linearly correlated with the body length also in the gekkonid *Tarentola annularis*, although there is an average increase of teeth with the increase of body length (EDMUND, 1969, p. 162).

We should also consider that we are possibly dealing with different species of the same genus, which could differ in the tooth number at a same stage of growth, because of, for example, a slower increase in tooth number with growth. Samples from different species of the Gekkonid *Coleonyx* show an intraspecific variation in tooth number from 6 (26-32) in *C. mitratus* to 22 (22-44) in *C. variegatus* (EDMUND, 1969, p. 162). Different species differ in the minimum and/or maximum tooth number observed in the sample, but there is a wide overlapping of the specific ranges (fig. 7).

These observations suggest caution in using tooth count for any systematic and ontogenetic conclusion when the sample is small, made of specimens from different localities, and surely belonging to different populations, that possibly lived also in different times (although not sensibly different from the geological point of view), as is the case for *Eudimorphodon*.

It is noteworthy that four of the seven specimens have a similar size, i.e., the most represented size class in the sample is by far that of MFSN 1922. The sample is too small to have a statistical significance, but I must observe that the medium-size class is that with the highest number of specimens also in the more significant sample of *Rhamphorhynchus* according to BENNETT (1995).

The formula of the cusps in MFSN 1922 differs in some aspects from that of the two individuals of *Eudimorphodon* from Lombardy, as can be seen in table I. However, the formula of the cusps also differs in the right and the left ramus of the same individual (WILD, 1978, fig. 27). Furthermore, a certain variability of cuspidation pattern along the lower jaw is stressed by comparison with *E. cromptonellus* (JENKINS jr. et al., 2001, fig. 3, pp. 154-155; tab. I) and BSP 1994I 51 (WELLNHOFER, 2001, figure without number). Thus a count of tricuspid, quinticuspid and quadricuspid teeth characteristic for *Eudimorphodon* does not exist. The first tricuspid tooth in MFSN 1922 is tooth 16, the same as the right lower jaw (using the reverse numeration) of MCSNB 2888, whereas it is tooth 17 in the left. The number of teeth in the distal continual series of non-tricuspid teeth is rather similar in MFSN 1922 and MCSNB 2888. However, mesial to the first tricuspid there are other quinticuspid teeth (18 right, 18, 21 and 23 left) in MCSNB 2888, while in MFSN 1922 five tricuspid teeth follow. MPUM 6009 has 17 mandibular teeth, the first tricuspid is tooth 9 in the right ramus and tooth 10 in the left ramus (using the reverse numeration), but pentacuspid teeth are found also in position 11. The small MGUH VP 3393 has at least 13 mandibular teeth (JENKINS jr. et al., 2001), and a small

tricuspid tooth is found in position 3, whereas the most mesial multicuspid tooth has 4 or 5 cusps (see tab. I). I cannot see a clear relationship between the relative number of tricuspid and quinticuspid teeth and the size of the individual. We can only reliably say that in Alpine *Eudimorphodon* specimens teeth are prevailing quinticuspid in the posterior part of the jaw and tricuspid in the anterior part, with a lower number of quadricuspid and sometimes also bicuspid teeth.

Crowns of multicuspid teeth of all the six *Eudimorphodon* specimens, excluding the large holotype of *E. ranzii* (MCSNB 2888), have smooth enamel. Mesial teeth of MCSNB 2888 have marked apicobasal ridges of enamel, but faint ridges are present also in distal teeth. When only MCSNB 2888 and MPUM 6009 were known, WILD (1978) considered smooth against ridged tooth surface as an ontogenetic feature, with MCSNB 2888 an adult and MPUM 6009 a juvenile. In fact, living reptiles sometime show an ontogenetic change of tooth shape related to a shift in their alimentary habits (e.g., *Varanus niloticus*, *Conolophus*, *Amblyrhynchus*). However, other explanations are possible and are listed below along with the ontogenetic ones.

- 1) Ontogenetic change (A): MCSNB 2888 is an adult and the others are all immature (subadults or juveniles); enamel ridging occurred when the adult stage was reached. This introduces the further problem of a rigorous definition of adulthood or sexual/osteological maturity that is not further discusses here.
- 2) Ontogenetic change (B): MCSNB 2888 is an old individual, the others are younger, but most of them are "adults". The ridged surface occurs in old individuals as a useful character connected to a change in their diet or simply as a neutral one. Being older, the individual is

size	pmx	mx	d
very small	7	16	17
small	5	19	19
small	7	19	19
medium	5	24	25
medium	7	26	29
large	7	30	29
very large	7	27	29

Tab. II - Tooth counts in a sample of *Iguana iguana*. After EDMUND (1969, tab. I). Note that the author did consider only the size, not the ontogenetic "adult", "subadult" or "juvenile" stage of the individuals. Abbreviations: d = dentary teeth; mx = maxillary teeth; pmx = premaxillary teeth.

- Conto dei denti in un campione di *Iguana iguana*. Da EDMUND (1969, tab. I). Si noti che l'autore considera solo le dimensioni degli esemplari, non gli stadi ontogenetici "adulto", "subadulto" o "giovane". Abbreviazioni: d = denti nel dentale; mx = denti nel mascellare; pmx = denti nel premaxillare.

possibly larger than younger individuals in an animal with indeterminate growth. There are examples in living reptiles. Describing the dentition of the iguanid squamates *Conolophus* and *Amblyrhynchus*, EDMUND (1969, p. 154) reports "In the young ... the crown is very strongly trilobate. ... In older individuals the crown is trilobate, but the individual lobes are broader and the emarginations between much less pronounced. In an old individual the constriction below the crown continues occlusad to merge with the single, narrow spatulated tip, all traces of the anterior and posterior lobes having disappeared". Note that Edmund does not consider adult or juvenile stages, but young, older and old, suggesting that the final change in shape occurs as a gerontic feature.

- 3) Individual feature: The ridged teeth are a feature of that individual only, falling in the range of intraspecific variation. The character could be related to an unusual large size of MCSNB 2888 due to individual genetic factors or particular environmental conditions (ANDREWS, 1982). Intraspecific giantism seems to be present in pterosaurs (UNWIN, 2001) like in many living reptiles.
- 4) Species specific feature: MCSNB 2888 and therefore *E. ranzii* is a species separate from that/those represented by all others *Eudimorphodon* specimens, and "apicobasally ridged teeth" is an autapomorphy of *E. ranzii*.

The problem cannot be solved on the base of dentition alone, and the fossil record is too scarce to support confidently one explanation more than another. There is no way to make any statement about the ontogenetic stage of MFSN 1922, because it is too incompletely preserved. An analysis of the ontogenetic features in *Eudimorphodon* specimens is in progress and will be published elsewhere.

According to WILD (1978) the 11 thoracal ribs following the first thoracal rib are all two-headed in MCSNB 2888, but with a capitulum and tuberculum only slightly separated from each other. However, later WILD (1994, p. 102) observes in MCSNB 8950 that "the first 3 dorsal ribs ... are still double-headed, the caudally following dorsal ribs are single-headed". According to WELLNHOFFER (1978, p. 12) the 11-12 anterior dorsal ribs of pterosaurs are two-headed ribs that posteriorly could become single-headed. Dorsal ribs 1-6 are two-headed whereas 7-13 are holocephalous in *Dorygnathus* according to ARTHABER (1919, p. 34, fig. 20). The two-headed ribs in MFSN 1922 belong to the anterior pairs and the longest one is surely among the most anterior.

A square deltopectoral crest of the humerus is found in all specimens attributed to *Eudimorphodon* (pers. obs.), excluding the very small and skeletally immature holotype of *E. cromptonellus* (MGUH VP 3393), where it is subtriangular (JENKINS jr. et al., 2001). A square deltopectoral crest is present also in *Campylognathoides* (QUENSTEDT) from the Lower Jurassic of Germany (fig. 6H). Larger individuals have shorter and stouter humeri

than smaller ones because the proximal part is comparatively wider in order to accommodate a larger muscular mass for flight. This is observed in MCSNB 2888 and MPUM 6009 (fig. 6) where the ratio of the humeral length against maximum proximal width is 2.23-1.88 (apparently variable in the right and left humeri) and about 2.80, respectively. The ratio in MFSN 1922 (2.58) follows the same trend, intermediate between that of the large MCSNB 2888 and the small MPUM 6009.

By comparison with MFSN 1797 and the wing phalanges of other *Eudimorphodon* specimens (MPUM 6009, MCSNB 8950, MFSN 21545), the partially preserved wing phalanx can be identified as a wing phalanx 2 (the most stout and straight among wing phalanges), because it is relatively stout, it shows a reduced distal tapering, any curvature is practically absent, and the expanded shape of the proximal extremity is asymmetrical.

Conclusions

The specimen MFSN 1922 is attributed to the genus *Eudimorphodon* because of the tricuspid to quinticuspid teeth in the lower jaw. No other pterosaur has this kind of dentition. Additionally, an humerus with a quadrangular deltopectoral crest like that in MFSN 1922 is found only in *Eudimorphodon* and the Late Liassic *Campylognathoides*.

MFSN 1922 shows some general similarity with the holotype of *E. rosenfeldi* (similar size, smooth crown surface and a long diastema between the last distal tooth and the point of the coronoid process) and also has in common the stratigraphic and geographic provenance. However, the main diagnostic features of *E. rosenfeldi*, the comparatively long tibia, the short and wide shaft of the coracoid, and the rod-like and angled pteroid, cannot be checked in MFSN 1922. Thus, the specimen cannot be confidently attributed to this species. The detailed osteological description and revision of the holotype of *E. rosenfeldi* is still in progress. Also the systematic of *Eudimorphodon* needs a revision, which is also in progress.

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Author's address - Indirizzo dell'Autore:

- Dr Fabio M. DALLA VECCHIA
Museo Friulano di Storia Naturale
Via Marangoni 39, I-33100 UDINE
Museo Paleontologico Cittadino
Via Valentinis 134, I-34074 MONFALCONE (GO)
e-mail: fabdalla@tin.it