F. M. DALLA VECCHIA

A CAUDAL SEGMENT OF A LATE TRIASSIC PTEROSAUR (DIAPSIDA, PTEROSAURIA) FROM NORTH-EASTERN 1TALY

/UN SEGMENTO CAUDALE DI UNO PTEROSAURO (DIAPSIDA, PTEROSAURIA) DAL TRIASSICO SUPERIORE DELL'ITALIA NORD-ORIENTALE

Abstract - For the first time, a relatively complete and articulated mid-distal segment of a caudal vertebral column of a Triassic pterosaur is reported. The specimen, which preserves also both the terminal wing phalanges, comes from the middle Norian Dolomia di Forni Formation of Friuli (NE Italy). The tail lacks the dorsal and ventral bundles of wire-like processes of the zygapophyses and hemapophyses typical of Jurassic long-tailed pterosaurs. The strutture of the tail in some long-tailed pterosaurs is considered and a group of Triassic pterosaurs without the bundles of the zygapophyseal and hemapophyseal processes is identified. This absence is a primitive feature for pterosaurs.

Key words: Triassic pterosaur, Caudal vertebrae, Late Triassic, Norian, Dolomia di Forni, Friuli.

Riassunto breve -*tiene descritto per la prima volta un segmento medio-distale relativamente completo ed articolato della colonna vertebrale caudale di uno pterosauro triassico. Il reperto, che presenta anche entrambe le falangi alari terminali, proviene dalla Dolomia di Forni (Norico medio) del Friuli (Italia nord-orientale). La coda è priva dei fasci dorsali e ventrali di processi filiformi rispettivamente delle zigapofisi e delle emapofisi tipici degli pterosauri a coda lunga del Giurassico. E discussa la struttura della coda di alcuni pterosauri a coda lunga ed è identificato un gruppo di pterosauri triassici privi dei fasci di processi zigapofiseali ed emapofiseali. Questa assenza dei fasci è un carattere primitivo per gli pterosauri.*

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

Introduction

Despite their rarity, pterosaur bones and skeletons are relatively well-represented in the record of fossil reptiles from the Norian of northern Friuli (Carnia, Udine province, NE Italy). The holotype of *Preondactylus buffarinii* WILD (WILD, 1984), the holotype of *Eudimorphodon rosenfeldi* DALLA VECCHIA (DALLA VECCHIA, 1995), another fragmentary remain of *Eudimorphodon* (DALLA VECCHIA, 1994), a gastric eject with pterosaurian bones (DALLA VECCHIA et al., 1989), an isolated, large fourth wing phalanx (DALLA VECCHIA, 2000)

and some other specimens under preparation and study are all found in the Norian of this area. Other reptiles found here include 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 specimen of *Langobardisaurus* (Moscio, 1997; RENESTO & DALLA VECCHIA, 2000); other two partial skeletons of the same genus; and the holotype of *Langobardisaurus? rossii* BIZARRINI & Muscio (BIZARRINI & Muscio, 1995), actually a reptile of uncertain affinity.

The specimen which is the object of this paper was found in 1994 by Mr. Ruggero Tonello, who recognized its scientific importance and donated it to the Museo Friulano di Storia Naturale of Udine.

I use here the term "rhamphorhynchoids" as indicating the taxa grouped in the order Rhamphorhynchoidea of the Linnean taxonomy (WELLNHOFER, 1978), aware of the fact that Rhamphorhynchoidea is a paraphyletic group.

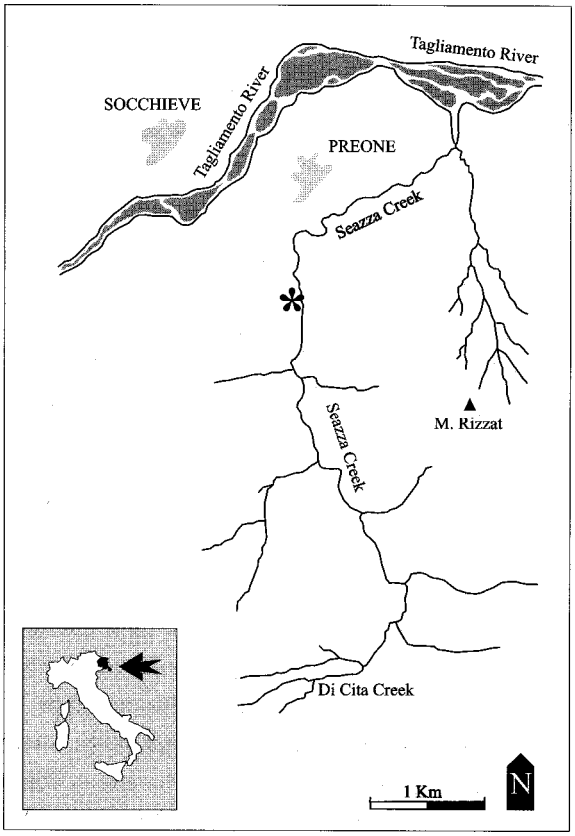


Fig. 1 - Location of the finding site (asterisk).
Posizione del luogo di rinvenimento (asterisco).

The taxonomic revision of some Triassic pterosaur specimens (MCSNB 3359, MCSNB 3496 and all the specimens of *Eudimorphodon ranzii* ZAMBELLI from Lombardy) is in progress (Dalla Vecchia, submitted and in progress), but here I consider the former attributions valid (excluding MCSNB 3496, see below), because the revision is not already published.

Abbreviations: BMNH = British Museum of Natural History, London, England; BSP = Bayerische Staatssammlung fiir Palaontologie und historische Geologie, Munich, Germany; MCSNB = Museo Civico di Scienze Naturali of Bergamo, Italy; MFSN = Museo Friulano di Storia Naturale, Udine, Italy; MPUM Museo di Paleontologia dell'Università di Milano, Italy; SMNS = Staatliches Museum fiir Naturkunde Stuttgart, Germany.

Geological and stratigraphical remarks

Dark, thinly bedded bituminous dolostones (Dolomia di Forni Formation) crop out in the Canna area, from the surroundings of Tolmezzo to the village of Forni di Sopra, extending as an east to west elongated band for more thatl 30 km. The depositionary environment was a small anoxic basin whose bottom conditions allowed the preservation of organic remains and articulated skeletons (DALLA VECCHIA, 1991). The fossilized organisms are both terrestrial (most of the reptiles and plants), marine nectonic (fish, some shrimp) or marine benthic (crustaceans, rare ophiuroids, rare gastropods and few pelecypods). They are all allochthonous, transported probably after the death from different life environments and deposited on the bottom of the basin. The basin was surrounded by a wide carbonate platform which was dominated by a tidal sedimentary environment (Dolomia Principale Formation, Hauptdolomit of German Authors).

The fossiliferous layers along the Seazza creek valley and Forchiar creek are in the lower-middle part of the Dolomia di Forni Formation (DALLA VECCHIA, 1991). According to ROGHI et al. (1995) their age, based on the conodont fauna, is Alaunian 2-3 (middle Norian).

The specimen here described was preserved on a block of dark dolostone found in a creekcut near a rock wall, placed in the Seazza creek valley along the road Preone-Valle di Preone at the bridge marked 552 m a.s.l. (fig. 1). This section, which is the outcrop Fl in the middle part of the lower member of the Dolomia di Forni according to DALLA VECCHIA (1991), is about 35 m thick and has been stratigraphycally and sedimentologically described in detailby DALLA VECCHIA (1990). Although the specimen was collected in the debris, it obviously comes from the overhanging rock wall. According to ROGHI et al. (1995), the outcrop is dated to the lowermost part of Alaunian 3.

Vertebrates found in the some section include a tail of *Megalancosaurus preonensis* (PINNA, 1988; RENESTO, 1994), a gastric eject with pterosaurian bones (DALLA VECCHIA et al., 1989), a coelacanth fish, several *Saurichthys* sp» and many small fish, mainly pholidophorids

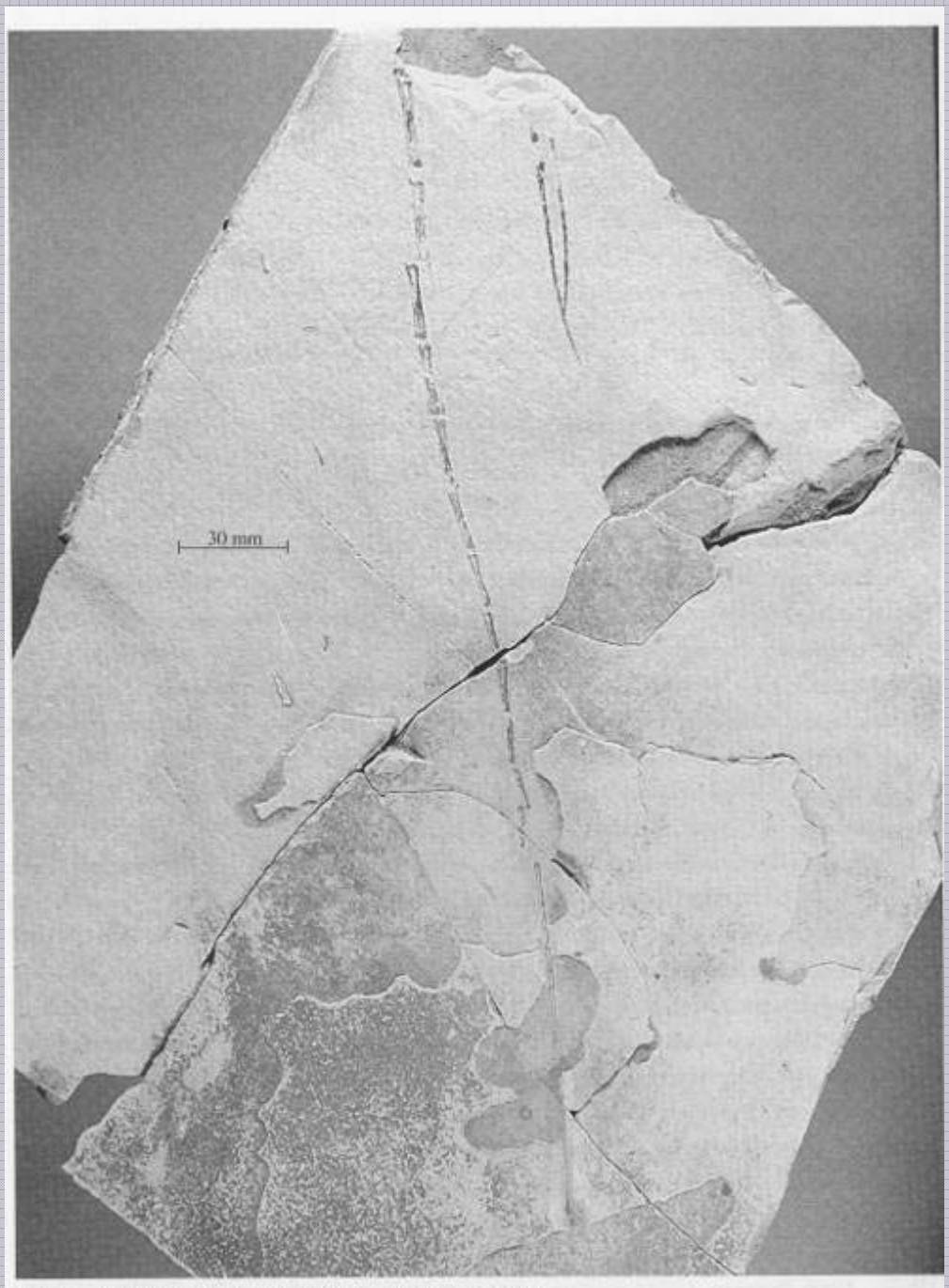
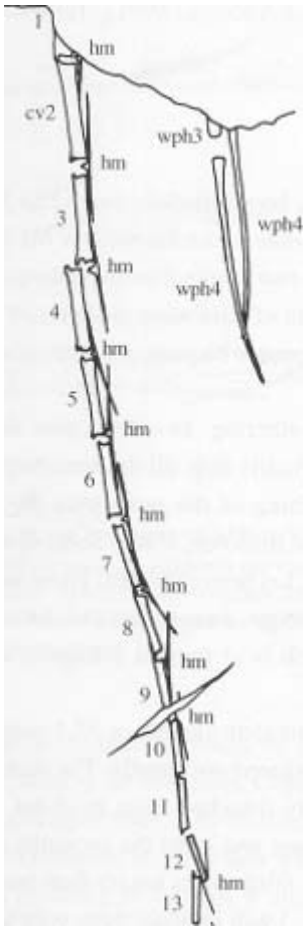


Fig. 2 - The specimen MFSN 19864. Scale bar = 30 mm.
- *L'esemplare MFSN 19864. Scala di riferimento = 30 mm.*



hm

I4

I5

16

I7

I8 19

20

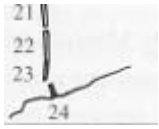


Fig. 3 - Drawing *of* the *specimen* MFSN 19864. Abbrevia*tions: ex* = caudal vertebra: *hm* = hemapophysis; *wph 3*-4 = *wing* phalanx 3-4: 1-24 = *progressive numhers of the* preserved caudal vcrtebrae. Scale bar = *30 mm.*

- *Disegno dell'esemplare iVIhSN 19864. Abbreviazioni: cv = vertebra caudale; hm = emapnfisi; ssph 3-4 = falange alare 3-4; 1-24 = numeri progressivi delle vertebre caudali convervate. Scala di riferimento* = 30 *mm.*

30 Inni

(cf. *Eopholidophorus forojuliensis* ZAMBELLI) (DALLA VECCHIA, 1991). Terrestrial plant remains have been also found (DALLA VECCHIA, 1991).

Description

The specimen is preserved on a slab of dark gray-brownish dolostone 450 x 320 x 23 mm stored at the Museo Friulano di Storia Naturale of Udine under the number MFSN 19864. It consists of a portion of the caudal vertebral column, two terminal wing phalanges, one complete and the other partially preserved, and a fragment of third wing phalanx, ali presumably belonging to the same individuai (figs 2-3). These appear to be parts of an articulated skeleton lost with the missing part of the slab.

All the elements have been affected by weathering. In some ,cases the bone has completely disappeared, leaving just a relief in the matrix (e.g. all the hemapophyses). This kind of preservation is probably due to the crushing of the bone plus the differential compaction of the sediment on it and around it (cf. DE BUISONJÉ, 1985). Some distai vertebrae were stili covered by the rocky matrix when the fossil has been collected. These were prepared with steel needles under a Wild 5 binocular microscope. Diagenesis and dolomitisation of the matrix strongly affected the bone tissue, which is at present a fragile, scaly, nearly transparent reddish-brown substance.

One terminal wing phalanx is practically complete (length = 57.5 mm; maximum width = 3 mm at the proximal end), but partly weathered proximally. The distai end of the corresponding wing phalanx 3 is preserved slightly detached from its distai articulation. The other, incomplete wing phalanx 4 is 51 mm long and lacks the proximal portion. The shaft of the wing phalanx 4 is thin, straight for two thirds of its length than curved distally.

Twenty four vertebrae are present on the slab. I will indicate them with numbers 1 to 24 from proximal to distai, but of course those numbers are not referring to the actual position according to the sequence of the complete caudal segment of the vertebral column, because the proximal portion is inissing. The tail is not completely disarticulated, but nearly all the centra are not strictly connected. Each centrum of the first nine vertebrae, and most of the others, is slightly separated from the preceding and the following (see fig. 4). The segment of vertebrae 4-23 is slightly displaced dorsally with respect to the proximal segment 1-3 (figs 3-4) and vertebra 13 is slightly drifted away anterodorsally from the originai connection to vertebrae 12 and 14 (fig. 3). This demonstrates that the vertebrae were not rigidly interlocked to one another.

Caudal vertebra 1 is only preserved distally. Most of vertebra 24 is preserved. The longest element is vertebra 2, with a 24 mm long centrum and a minimum dorsoventral height of 3.5 mm. Posteriorly the centrum length decreases regularly until centrum 23 which is only 4.5

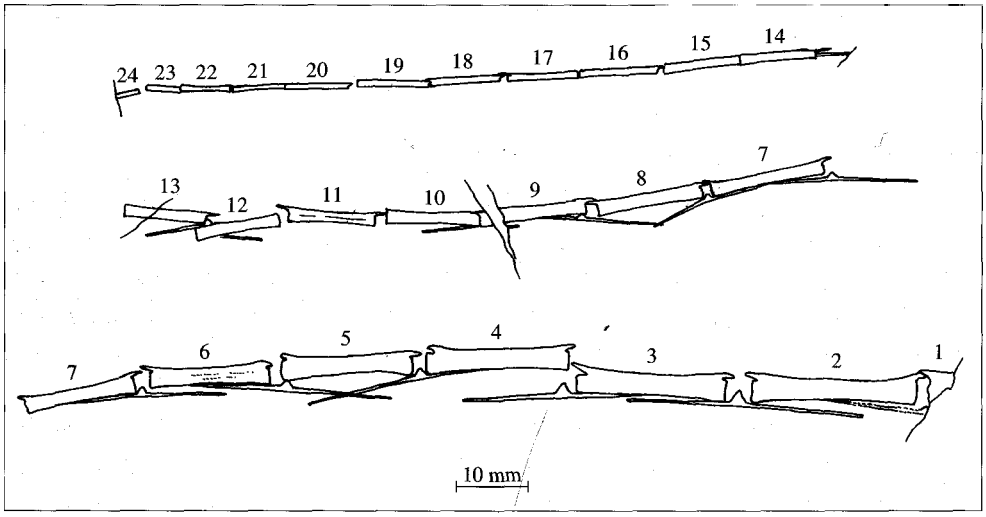


Fig. 4 - The caudal vertebrae of MFSN 19864. Vertebra 7 is reported in both the first and second vertebral string to maintain the continuity of articulation. Scale bar = 10 mm. *Vertebre caudali dell'esemplare MFSN 19864. La vertebra 7 è riportata sia nella prima sia nella seconda fila di vertebre per mantenere la continuità dell'articolazione. Scala di riferimento = 10 mm.*

mm long (tab. I). Centra 2 through 11 are elongated with a faint constriction in the middle and a slight flaring at the both ends. Centra 12 to 23 are stick-like and the last 10 elements (14 to 23) forni a straight "rod". The total length of the preserved tail segment, as the sum of the length of each centrum, is 300.5 mm. The 22 complete elements measure 291.8 mm.

Centra posterior to number 8 are collapsed showing that they were hollow inside. Long longitudinal ridges along the lateral side of some centra are visible as in those of other Triassic pterosaurs (WnD, 1978; see also fig. 12). These ridges probably result from the complete collapse and flattening of the centra.

The hemal arches have the typical shape described by WELLNHOFER (1975a, Fig. 7; here fig. 5) and WILD (1978, Fig. 12) in long-tailed pterosaurs, with a triangular main body inserting between two consecutive centra and long filiform processes projecting anteriorly and posteriorly. They are completely preserved between vertebrae 2 and 9. Only parts of the anterior and posterior filiform processes are visible between the vertebrae 9-10, 12-13 and in the vertebra 14. The filiform processes are not grouped in bundles along the ventral side of the tail. The absence of the bundles is also suggested by the fact that each hemapophysis has a different orientation with respect to the axis of the corresponding vertebrae, i.e. centra and filiform processes are not parallel to each other in most cases. Thus hemapophyses were free to rotate ventrally and were not bound by

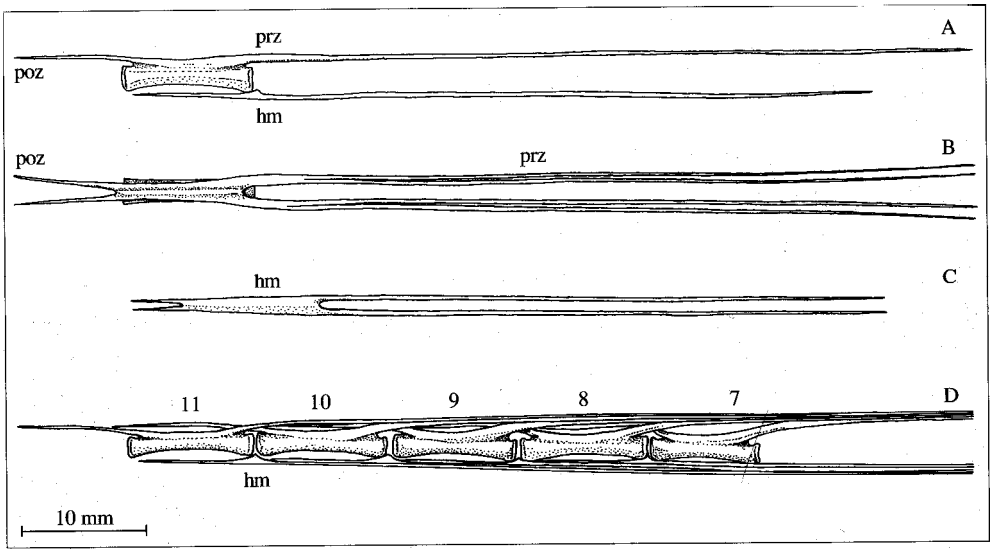


Fig. 5 - The structure of the mid-caudal vertebral column in *Rhamphorhynchus.* Numbers refer to the position of each element in the tail. A) Single l lth vertebra with hemapophysis, right latera view; B) the lame in dorsal view; C) the hemapophysis in ventral view; D) a string of articulated 7th to l lth vertebrae in right lateral view. After WELLNHOFER, 1991, modified. Abbreviations: hm = hemapophysis; poz postzygapophysis; prz = prezygapophysis. Scale bar = 10 mm.
La struttura della parte mediana della colonna vertebrale caudale in Rhamphorhynchus. *numeri si riferiscono alla posizione di ciascun elemento nella coda. A) Una singola 11 vertebra con emapofisi, in vista laterale destra;* ***B)*** *la stessa vertebra in vista dorsale; C l'emapofisi in vista ventrale; D) una fila di vertebre 7°-11 ° in articolazione naturale, vista laterale destra. Da* WELLNHOFER, *1991, modificato. Abbreviazioni: hm = emapofisi; poz = postzigapofisi; prz = prezigapofisi. Scala di riferimento = 10 mm.*

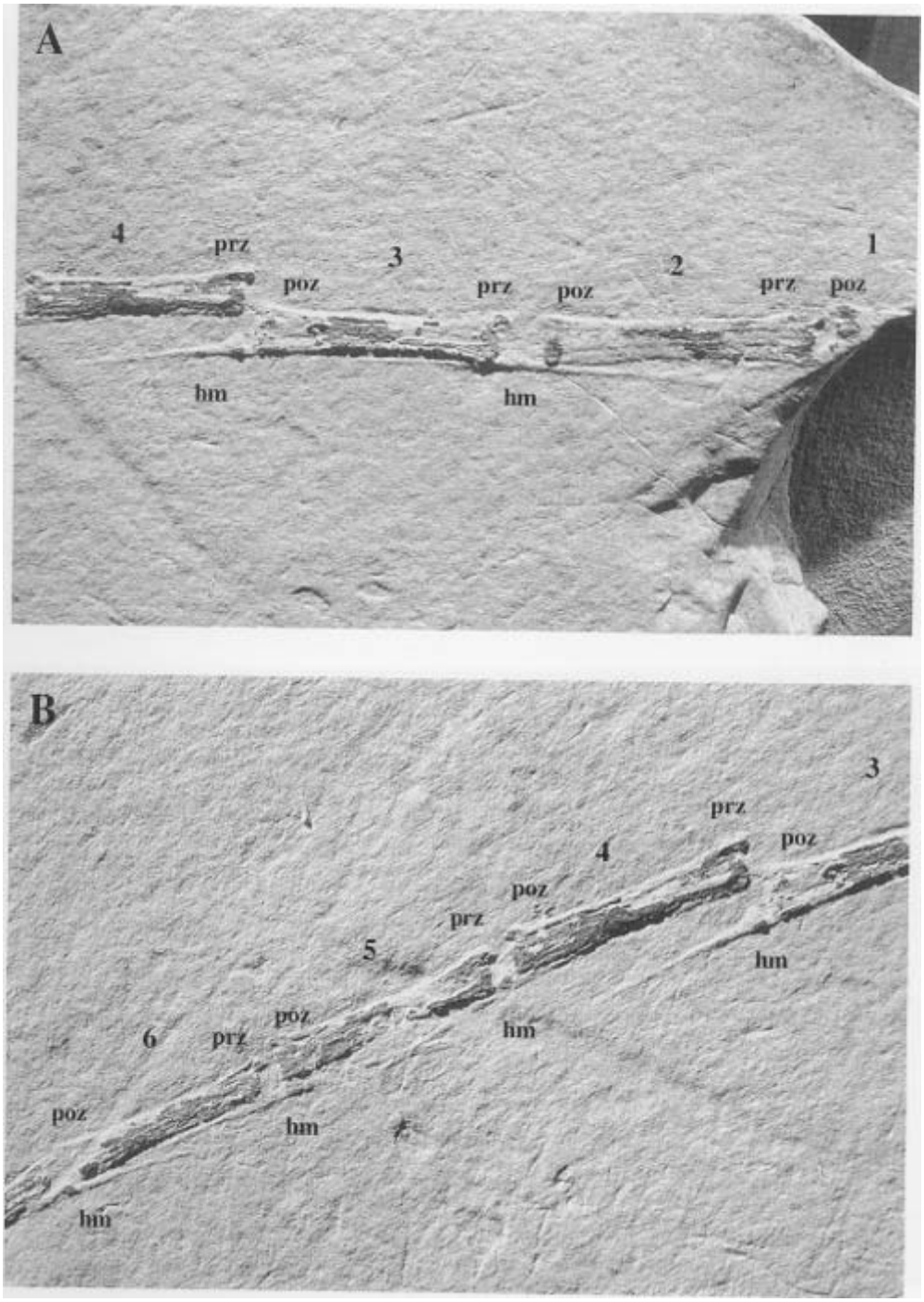
each other. Each process is not longer than the overlying centrum, i.e. it lies below just one centrum and does not reach other centra.

Unlike the ventral side, no filiform processes of the zygapophyses are visible in the dorsal side of the tail, i.e. there-is no evidence of the existence of a bundle of zygapophysea filiform processes (see below). When apparently present dorsally, the filiform processes actually belong to displaced hemapophyses. Pre- and postzygapophyses project beyond the end of the centrum, but they are relatively short (see for example vertebrae 6-7, 7-8, 8-9, 15-16 and 17- 18; figs. 4, 6). They are anteroposteriorly directed (sometimes slightly dorsally) and pointed

Discussion

The tail of long-tailed pterosaurs

The most accurate description of the caudal vertebrae of a long-tailed pterosaur regards the Late Jurassic *Rhamphorhynchus H. v.* MEYER (WELLNHOFER, 1975a, p. 15-17, Fig. 7;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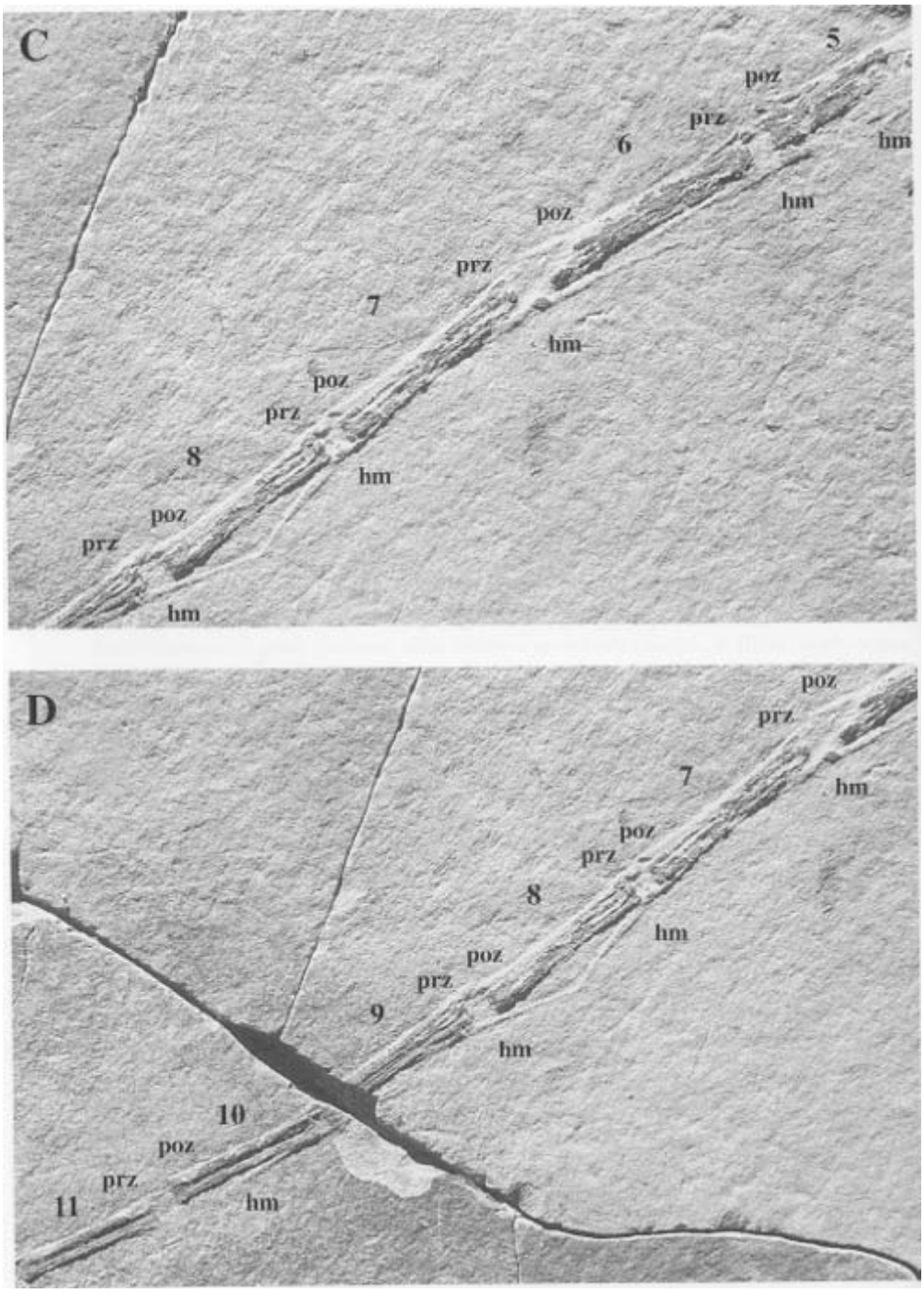
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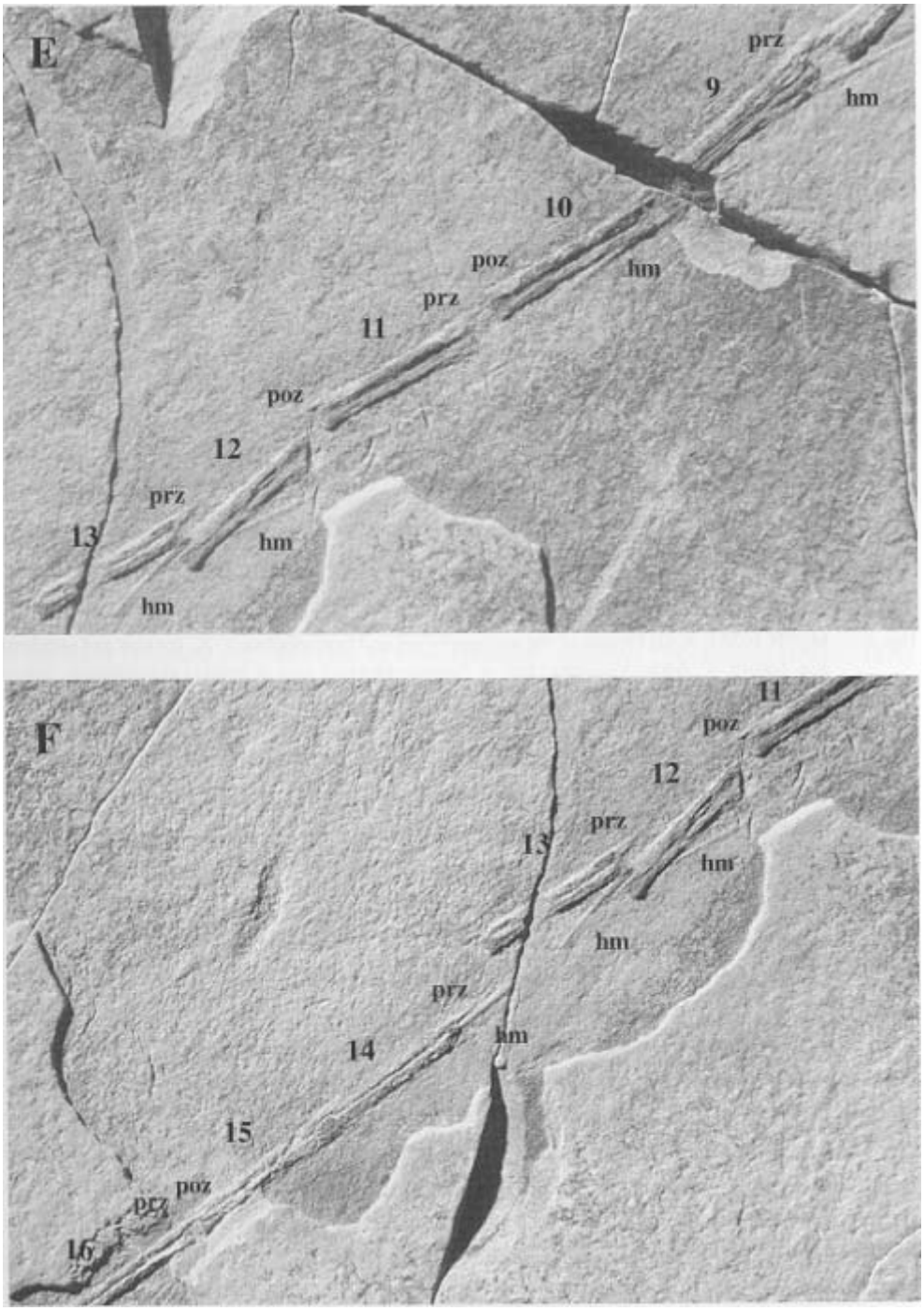
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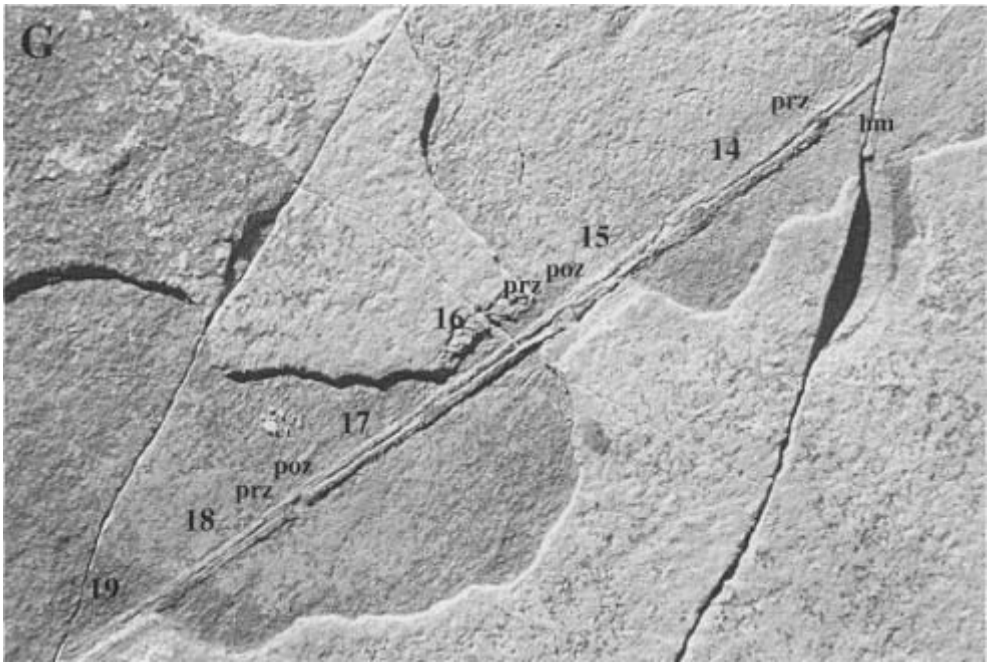


Fig. 6 - MFSN 19864. A-G) Details of the zygapophyses and hemapophyscs. As for .site and numhers sec figure 4. Ahhreviations: hm = hemapophysis; poz = postzygapophysis; prz = prezygapophysis.

- *MFSN 19864. A-G) Particolari delle zigapofasi ed emapofisi. Per le dimensioni e i numeri si veda la figura 4. Abbreviazioni: bar = craapotisi; lao; = postz.igapofisi; prz = prezigapofisi.*

here fig. 5). After that description it has been assumed that the tail *bauplan* of all long-tailed pterosaurs has the sante peculiar construction (see WFLLNHOIER, 1978; 1991).1 agree that the *bauplan* may be similar, but there are certain relevant differcnces which suggest that we should avoid over-generalization.

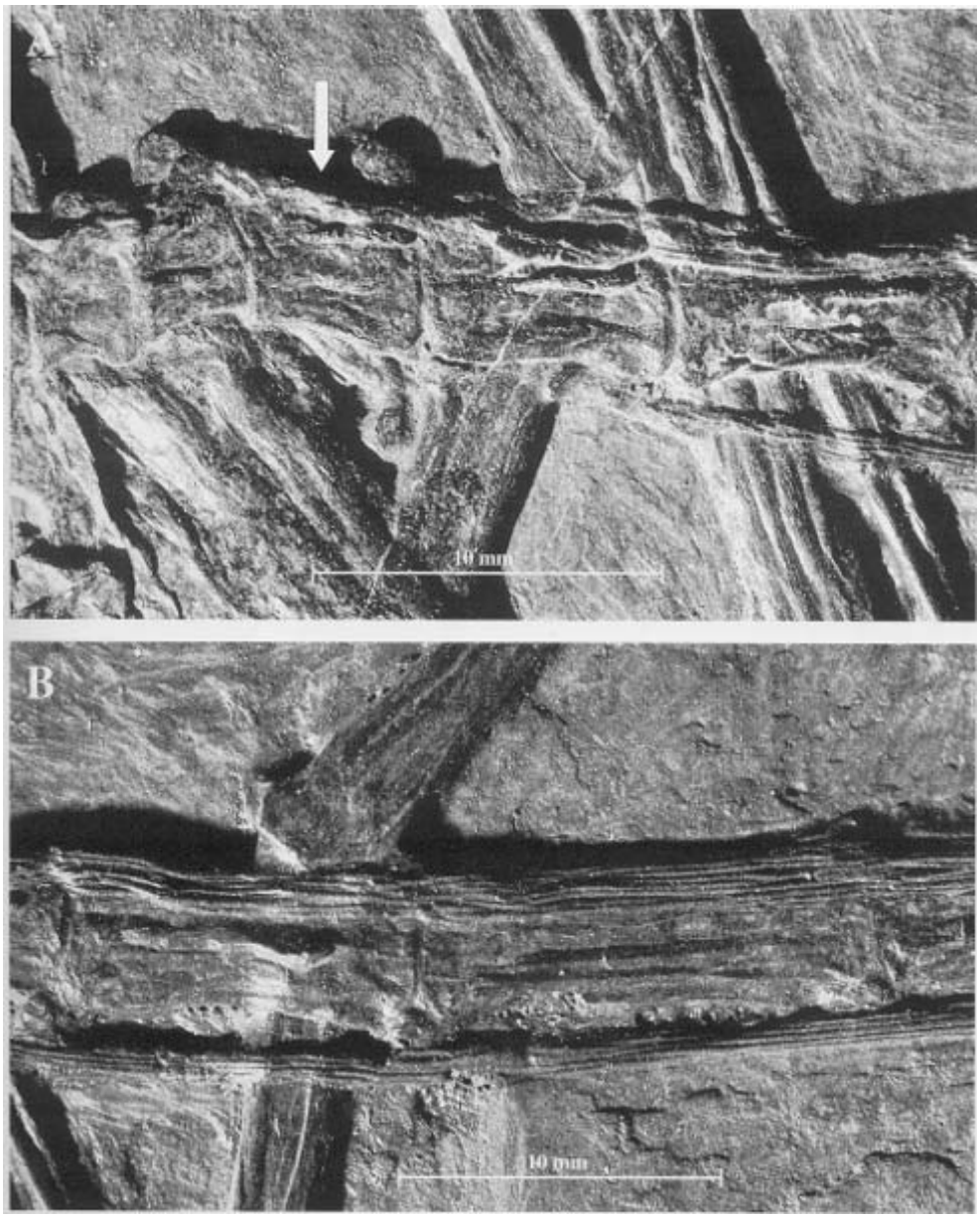
According to WELI.NHOFF.R (1975a), *Rharraphorhynchus* has 40 caudal vertebrae as average. The centra of the first five to six bave a length similar to that of the dorsal centra, while the subsequent centra are very elongated. The elongation inereases from the 5th to the 8-9th vertebra, remains constant in the succeeding five vertebrae and then decreases posteriorly. The longest centra are nearly threc times the length of a dorsal centrum. Beginning at the 7th vertebra the hernapophyses have a triangular portion which inserts bctween adjacent centra and develop two anterior and two posterior processes. These processes are extremely elongated and filiform. The anterior processes are much longer than the posterior ones. The zygapophyses are also very elongated and filiform processes appear from the 7th vertebra posteriorly. The prezygapophyseal processes are much longer than

the postzygapophyseal ones. Thus the bundles surround dorsally and ventrally the tail beginning from the 5th and 6th vertebra. In a typical cross-section at mid-tail there is a dorsal bundle of 26 iygapophyscal processes and a ventral bundle of 12 hemapophyseal processes. The last five vertebrae, which are embedded in the tip of the tail vane, are very small and less elongated than the others.

Extremely elongated pre- and postzygapophyses and elongated anterior and posterior processes of the hemal arches in caudal vertebrae are convergently found also in the dista] tail of the theropod dinosaur *Deinonvchus anthirropus* OsTRONI (Early Cretaceous of U.S.A.) and are considered a diagnostic featurc of the Dromeosauridae (OsrRovl, 1990). However, compared to the long-tailed pterosaurs, the caudal centra of the Dromeosauridae are only moderately elongated (see OsTRONI, 1990). In both cases, the bundles create a stiffer tail, supposed to be useful in the locomotion of the animai (HANII.Ev, 1990: OSTROM, 1990).

The tail of the so called "Pittsburgh specimen" of the late Liassic *Ca.mpvlognathoides liasicus* (QuENSTEDT) (WELLNHOFER, 1974) preserves 33 vertebrae. According to WELLNHOFER (ibidem, p. 14) the total number was probably 38. The length of each vertebra increases from the I st to the 9th, and the 9th to 14th are the longest. The bundles begin with vertebra 5. As in *Rhamphorhynchus,* the last vertebrae are not involved in the bundles.

An isolated pterosaurian tail with 30 articulated vertebrae (1 st to 30th; BMNH 41346) is tbc most complete tail attributed to *Dimorphodon macronvx* (BucKi.AND) (O\N EN, 1870, Pl. XIX, Fig. 4). This attribution is due to the fact that the specimen was found in the Blue Lias of Lyme Regis, where the only pterosaurian taxon identified to date has been *Dimorphodon,* and from the saure cliff as BMNH 41212, the most complete specimen of *Dimorphodon* (OwEN, 1870, p. 54). No other bone is found with the tail to support that identification. BMNH 41212 preserves only some traces of a small portion of the caudal bundles, whereas the holotype (BMNH 1034) has only a short proximal segment of the tail, probably the first 8 or 9 vertebrae and part of another one (BUCKLAND, 1835, Pl. 27. Fig.] k, a-a'; OWLN, 1870, Pl. XIX, Fig. 3). OWI[R]N (1870, Pl. XX) in his natural-size reconstruction of *Dimorphodon rnacronvx* "attached" the tail BMNH 41346 to the body of BMNH 41212. The comparison of the corresponding vertebrae of BMNH 1034 and BMNH 41346 (ibidem. Pl. XIX, Figs 3 and 4) shows that the lattei is somewhat smaller than the former. Furthermore, BMNH 41212 is largcr than BMNH 1034 (UN);\IN, 1988). As a result of this, the reconstruction of *Dimorphodon niacmnv-x* by Owen has probably been figured with a relatively shorter tail than it would have had in reality. This may have led to errors from subsequent authors who took that reconstruction as a reference. According to OwuN (1870, p. 55) the tail vertebrae of BMNH 41346 "progressively increase to a length of 1 ineh at the twelfth, begin to shorten gradually after the fiftenth". Actually, in plate XIX, figure 4 of OWEN (1870) the 13th and 14th vertebra] centra appetir to be the Iongest. The filiform processes begin with the 7th



ig. 7 - Segments of the tali of MCSNB 3359 *(Peteinosaurus aml °liii* accordino to WII.D, 1978). A) lst to 5th vertebra, B) the 6th, 7th and pari of 8th vertebra. The filiform processes of the zygapophyses are present from the 3rd vertebra on (arrow). Scale bar = I O mm.

- *Segmenti emulali dell'esemplare MCSNB 3359* (Petcinosaurus zambellii *per* WnD, *1978).* A) *1°-5° vertebra. B) 6`', 7° e parte dell'8° vertebra.* I *processi filiformi delle:igapo/isi sono presenti a partire dalla 3° vertebra (freccia). Scala di riferimento = IO mm.*

vertebra. The 8th vertebra is surrounded ventrally and dorsally by bundles. The first five vertebrae are subequal in length and the last preserved (30th) is stick-like. Thus, on the basis of the structure of the terminal segment of the caudal vertebral column in *Rhamphorhynchus*, at least five small distai vertebrae are missing in BMNH 41346. Otherwise, the distai termination of the tail BMNH 41346 was different from that of *Rhamphorhynchus*.

In the caudal vertebral column of MCSNB 3359 from the Norian of Cene, Lombardy, attributed by WILD (1978) to *Peteinosaurus zambellii*, the vertebrae increase in length from the I st to the 9th, and centrum 9 is the longest. The 6th and 9th centra are respectively about 2.7 and 4 times the length of a mid-dorsal centrum. Filiform zygapophyseal processes *appear* asearly as the 3rd vertebra (apparently in the postzygapophysis, see WILD, 1978, Pl. 14) and hemapophyses form a bundle beginning from the 5th vertebra (fig. 7A). At least four *filiform* processes with the same size (dorsoventral height is slightly less than 0.2 mm) are visible ventrally in the 6th vertebra, while five zygapophyseal processes are found dorsally (fig. 7B). 'entrai to the 8th and 14th vertebrae there are 6 and 5 processes in a bundle respectively, whereas dorsally they are 8 and 7 or 8. Thus the number of processes in a bundle appears to be lower than in *Rhamphorhynchus*. Hemapophyseal processes are proximally wider than dorsoventrally high.

MCSNB 3496 from the Norian of Cene has been considered to belong to *Eudimorphodon* by Wu.D (1978), but it is actually *Peteinosaurus* (DALLA VECCHIA, 2001, and submitted). The most complete centrum of the two partial, articulated caudal vertebrae preserved as bone has atotal length of 14-15 mm and is about 4 mm high. The elongation of the centrum and the presence of a sma111ateral process *on* it, compared to the condition in the caudal vertebrae of MCSNB 3359, suggest that this is probably the 6th or 7th vertebra. Four to five filiform pre- and postzygapophyseal processes are visible in the partially preserved dorsal bundle (fig. 8). Four or five filiform hemapophyseal processes are exposed ventrally at the articulation between the two centra, ten are visible below the centrum.

However, recently it has become evident that some Triassic pterosaurs have *a* tail without bundles. The zygapophyses of the elongated middle caudal vertebrae are relatively short and the hemapophyses have elongated, rod-like processes which do not overlap to forni bundles (DALLA VECCHIA, 2001; DALLA VECCHIA et al., 2002).

Contra Wn.D (1978, p. 204-205) none of the specimens attributed to *Eudimorphodon* have bundles. Only the first three caudal vertebrae and part of the 4th vertebra are preserved in the holotype of *E. ranzii* (MCSNB 2888) (fig. 9A) and they are exposed in ventral view, thus nothing can be said about the presence or absence of the bundles in this specimen. A hemapophysis preserved on,the ventral side of the 3rd centrum appears to be Y-shaped.

Two long mid-caudal vertebrae and a more proximal one (probably the 4th or 5th) are

found separated and isolateti in MCSNB 2887 *(E. ranzii* according to Wtt.). 1978). suggesting that the tail was totally disarticulated and the bundlcs were not developed (fig. 9B). The zygapophyses do not show filiform processes. 1'he "ossified tendons" identified by WII.o (1978, Pl. 8) near the coracoids and the sternum cannot be confidcntly identified as elongated caudal pre- and postzygapophyses and are probably rib shafts.

The lenght of the preserved portion of the tail is 150 mm in MPUM 6009 (also known as Exemplar Milano, *E. ranzii* by Wn.D, 1978). The two best preserved vertebrae are probably the Iongest of the tail and have centra of siniilar Iength: 16 mm, 4.5 times the length of a mid-dor.sal centrum (WILD, 1978, p. 204). It is not possible to be cure about the numher of preceding caudal vertebrae, but probably they are the 8th and 9th or 9th and IOth. They have short pre- and postzygapophyses (the postzygapophysis appears to be slightly longer than the prezygapophyses, but unfortunately they are partly covered by the left wing phalanx 4) and the wire-like hemapophyseal processes do not forni a bundle (fig. 10). Segments of these processes are preserved ventrally.

Only the lst to Sth vertebrae and part of the 6th are preserved in MCSNB 8950

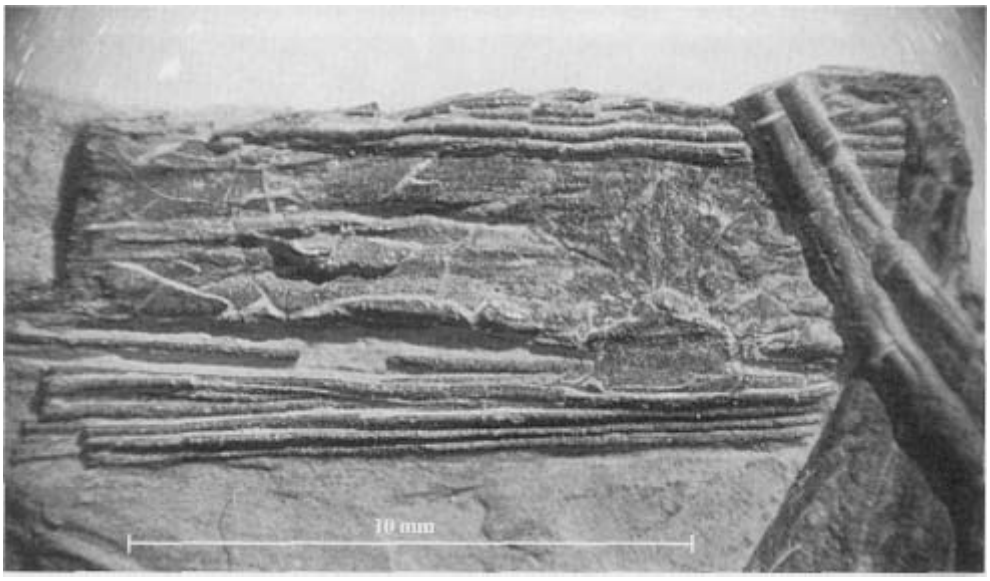


Fig. 8 Mid-tail vertebrae (from left to right, po~oaly 6th and 7th or 7th and 8th vertebrae) of MCSNB 3496, *PeteinovaLa'aS'<<<rurhellii (Eudinsorpodon ranzii* in WILD, 1978). Note the bundles. Scale bar = 10 mm.

Vertebre della parte centrale della coda (da sinistra a destra le probabili vertebre 6° e 7° o 7° e 8' dell'esemplare MCSNB 3496, Peteinosaurus zambellii (Eudimorpodon ranzii *in* WILD, *1978). Si notino ifa.sci di processi filiformi delle:igapofisi ed emapo/i.si. Scala di riferimento = l0 mm.*

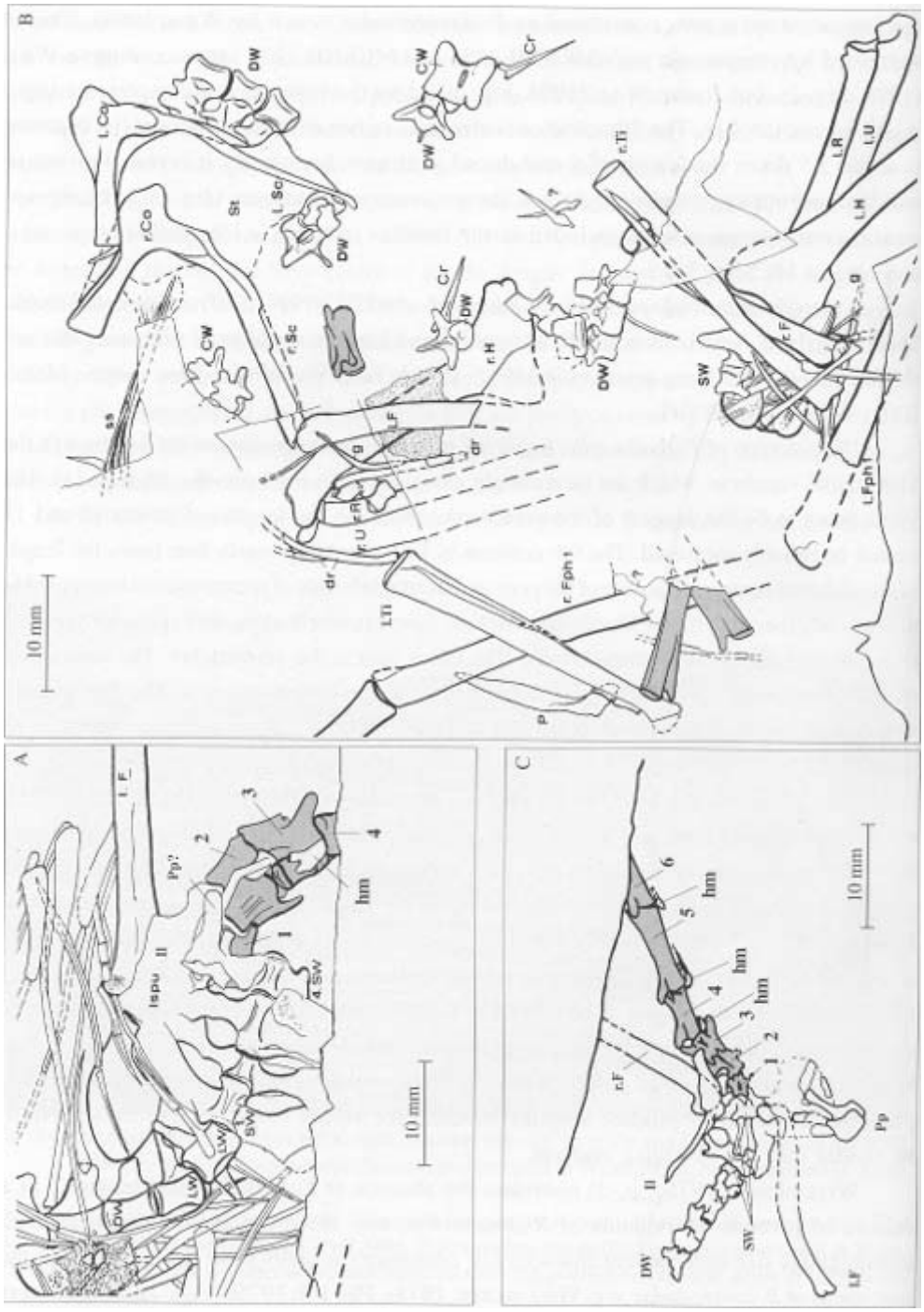
(an immature specimen, considered as Eudimorphodon ranzii by WILD, 1994). This is suggested by comparison with MCSNB 2888 and MCSNB 3359 and according to WILD (1994, Fig. 2), but contra WILD (1994, Fig. 5 and text) where the last complete vertebra is considered the 4th). The 5th vertebra is already a rather elongated element (its centrum is about 3.5 times the length of a mid-dorsal centrum), but clearly it is not involved in bundles and its zygapophyses do not show elongated processes (fig. 9C). Elongated caudal vertebrae are always included in the bundles in Jurassic long-tailed pterosaurs, and also in MCSNB 3359.

A recently described specimen of *Eudimorphodon* (BSP 1994151) from the Late Triassic Seefeld Beds of Austria does not have bundles and has hemapophyseal processes that are shorter than the overlying centra as in MFSN 19864 (Peter Wellnhofer, pers. comm., March 2001; WELLNHOFER, 2001).

The holotype of *Preondactylus buffarinii* preserves an impression of the 1st through the llth caudal vertebrae, which are increasingly elongated from the 1st to the 7th (fig. 11). The 9th appears to be the longest of the preserved centra, but the lengths of centra 10 and 11 cannot be reliably measured. The 9th centrum is 14.5 mm long, nearly four times the length of a mid-dorsal centrum. Because of the poor and incomplete state of preservation it is impossible to know whether the 7th to llth caudal vertebrae have extremely elongated zygapophyses, but theie are no traces of the ventral bundle. The tail is bent at the 4th vertebra. The centrum of the 6th vertebra is nearly 3.5 times the length of a mid-dorsal centrum. The 5th and 6th vertebrae do not show any traces of bundles and their pre- and postzygapophyses appear to be short (fig. 11). All this suggests a possible absence of the bundles in this genus also.

Austriadactylus cristatus DALLA VECCHIA, WILD, HOPF & REITNER (SMNS 56342) from the Seefeld Beds of Austria does not have extremely elongated pre- and postzygapophyses in the l st to 18th caudal vertebrae (DALLA VECCHIA et al., 2002; here fig. 12). The longest preserved centrum is the 9th, which is 3.5 times the length of a posterior dorsal centrum. However; centra 7 and 8 are only partially preserved (DALLA VECCHIA et al., 2002, Fig. 1) and could be longer than 9. Zygapophyses are similar in overall size and shape to those in MFSN 19864 and they seem to be relatively slightly longer in the mid-posterior portion of the tali than in the mid-anterior one, suggesting that the development of extreme elongation began posteriorly. The hemapophyses have relatively robust, rod-like anterior and posterior processes which do not produce a ventral bundle. Like MFSN 19864, each process seems to be shorter than the overlying centrum.

WELLNHOFER (1975c, p. 3) considers the absence of "ossified caudal tendons" as a feature of juvenile individuals of *Rhamphorhynchus.* However, many specimens with unambiguous size-independent characters of immaturity actually have the bundles (see the specimens of *R. longicaudus,* e.g. WELLNHOFER, 1975a, Pls. 1-5; 1975b, Figs. 18-23). BENNETT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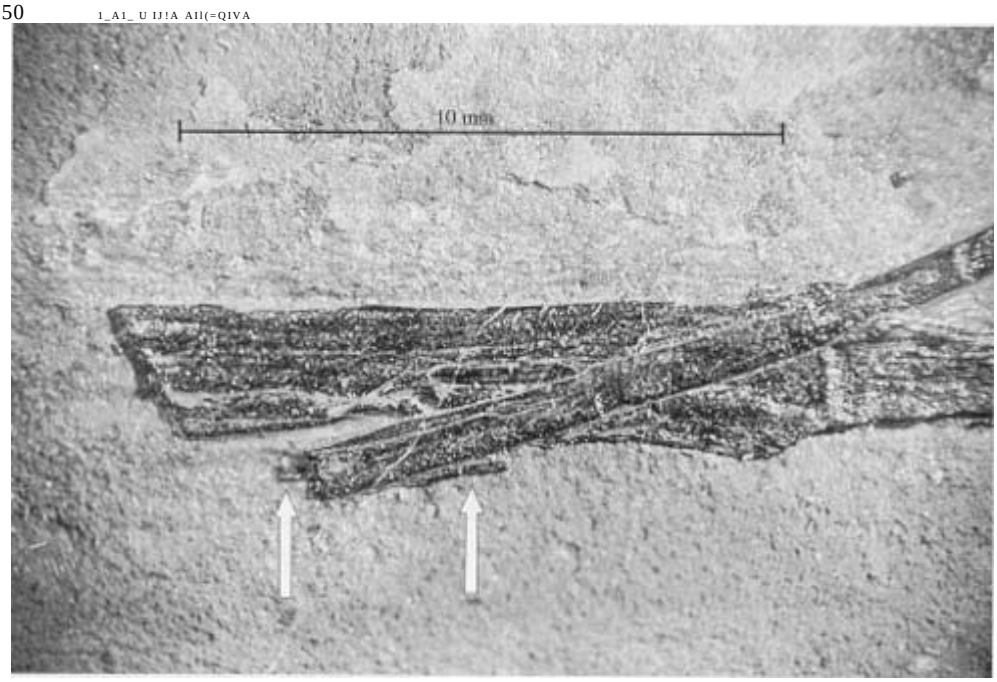
(1995) does not consider the presence or absence of the caudal bundles an ontogenetic feature of *Rhamphorhynchus.* Probably the "ossified caudal tendons" lack only in the the youngest individuals. MPUM 6009 has a fused scapulocoracoid, thus it is not a very young pterosaur (BENNETT, 1995). SMNS 56342 is a large specimenwithout size-independent features of irnmaturity and BSP 1994I 51 also lacks indisputable size-independent features of immaturity (pers. obs.). Therefore, the absence of the bundles in the Triassic specimens is not due to their growth stage.

When in 1996 I noticed the absence of the bundles of zygapophyseal and hemapophyseal processes in MFSN 19864, my firstthought was that they were missing due to weathering. However, it was not clear to me why some single hemapophyses with anterior and posterior elongated processes are preserved without bundles and why no remains of wire-like processes are preserved dorsally. The zygapophyses appeared to be rather short, single hemapophysis were not parallel to the centra and the vertebrae were slightly disarticulated, as opposed to other long-tailed pterosaurs in which the tail is usually preserved as a single block tightly bound by zygapophyseal and hemapophyseal processes (e.g. WELLNHOFER, 1975b, Pl. 13 (27), Fig. 1, P1.29 (15), Fig. 2; 1975c, Pl. 4 (30), Fig. 3; 1991, pp. 73 lower, 76, 82 lower). The absence of bundles in *Eudimorphodon, Austriadactylus* and possibly *Preondactylus* suggests that their absence is MFSN 19864 is not an artifact of preservation, but a feature of some early pterosaurs.

Because the first entirely preserved element of the tail segment specimen, MFSN 19864, is the longest, it is as minimum the 8th to 14th vertebra. If that vertebra is actually the longest of the whole tail, the missing proximal segment should include 7 to 13 elements

Fig. 9 - Caudal vertebrae in *Eudimorphodon ranzi.* A) Holotype (MCSNB 2888), B) MCSNB 2887, C) MCSNB 8950. A-B, after WILD (1978), C after WILD (1994), modified. Caudal vertebrae are marked in gray colour and numbered. Abbreviations (after WILD, 1978, 1994): Co = coracoid, Cr = cervical rib, CW = cervical vertebra, dr = dorsal rib, DW = dorsal vertebra, F = femur, Fphl = wing phalanx 1, g = gastralia, H = humerus, hm = hemapophysis, Il = ilium, Ispu = ischiopubic plate, 1. = left, LW = "lumbar" vertebra, P = pteroid, Pp = prepubis, R = radius, r. = right. Sc = scapula, ss = presumed "ossified tendons" of the tail (actually probably rib shafts), St = sternum, SW = sacral vertebra, Ti = tibia, U = ulna. Scale bar = 10 mm.
Vertebre caudali in Eudimorphodon ranzi. *A) Olotipo (MCSNB 2888), B) MCSNB 2887, C) ICSNB 8950. A-B, da* WILD *(1978), C da* WILD *(1994), modificato. Le vertebre caudali sono evidenziate in grigio e numerate. Abbreviazioni (da* WILD, *1978, 1994): Co = coracoide, Cr costa cervicale, CW vertebra cervicale, dr = costa dorsale, DW = vertebra dorsale, F = femore, Fphl = falange alare 1, g = coste gastrali,* ***H*** *= omero, hm = emapofisi, Il = ileo, Ispu = placca ischiopubica, 1.= sinistra, LW = vertebra "lombare ", P = pteroide, Pp = prepube;R = radio, r = destra, Sc = scapola, ss = presunti "tendini ossificati"della coda (in realtà si tratta probabilmente di diafisi di coste), St = sterno, SW = vertebra sacrale, Ti tibia, U = ulna. Scala di riferimento = 10 mm.*



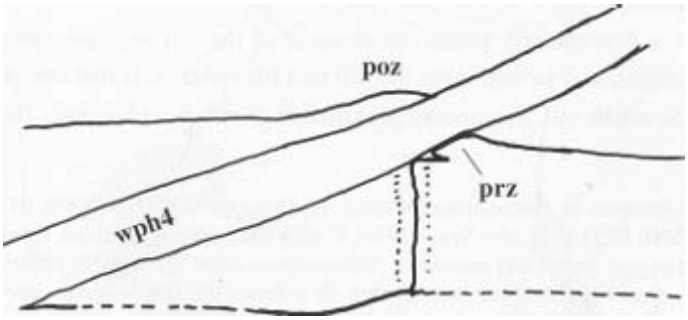


Fig. 10 Mid-caudal vertebrae of *Eudirnorphodon* (MPUM 6009). A) from left to right, the 8th or 9th vertebra and part of the 9th or I Oth vertebra; the arrows point to the remains of the filiform hemapophyseal processes. Note the absence of the bundles. B) The short zygapophyses, separated and partly covered by the left orina phalanx 4. Abbreviations: poz. = postzygapophysis; prz = prezygapophysis; wph 4 = wing phalanx 4. Scale bar = I O mm.

Vertebre caudali mediane in Eudimorphodon. *(MPUM 6009). A) 1)a sinistra a destra, la vertebra 8° o 9° e parte della 9° o 10° vertebra; le frecce indicano i resti dei processi filiformi delle emapofisi. Si noti l'assenza dei fasci di processi filiformi delle zigapofisi ed emapgfisi. B) Le corte zigapofisi, separate e in parte coperte dalla falange alare 4 sinistra. Abbreviazioni: po = postzigapnfrsr; prz = prezigapofisi; wph 4 = falange alare 4. Scala di riferimenti) = 10 mm.*

(see tab. II). Thus the number of the caudal vertebrae from the first element to the last preserved should be 30 to 36. As noted above, the last five caudal centra in *Rhamphorhynchus* are very smali, shorter and higher (i.e. cylindrical more than stick-like) with respect to the precedings. The last preserved vertebrae of MFSN 19864 are stick-like, thus it could be presumed, on the basis of the *Rhamphorhynchus* model, that at least the last five vertebral elements are missing. Therefore the minimum total vertebral number in the complete MFSN 19864 tail is estimated between 35 and 41.

Making a comparison between the wing phalanx 4 length, the length of the preserved

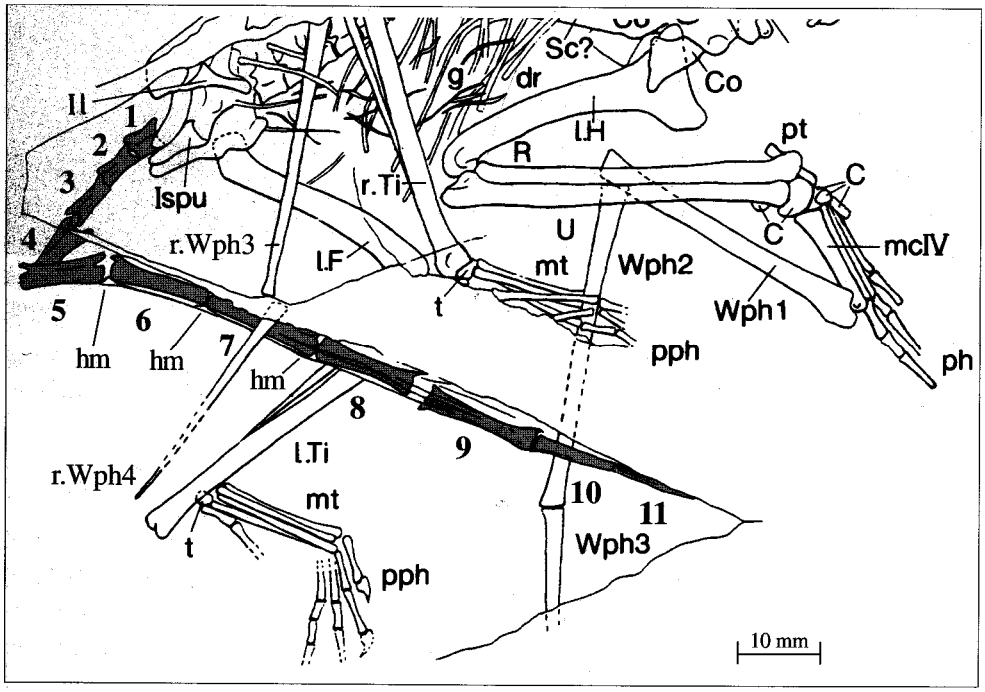


Fig. 11 - Caudal vertebrae of *Preondactylus* (1770 MFSN). After DALLA VECCHIA (1998) based on WILD (1984, Fig. 3). Caudal vertebrae are marked in grey colour and numbered. Abbreviations: C = carpals, Co = coracoid, dr = dorsal rib, F = femur, g = gastralia, H = humerus, hm = hemapophysis, l = ilium, Ispu = ischiopubic plate, 1. = left, mclV = wing metacarpal, mt = metatarpal, ph = manual phalanges, pph = pedal phalanges, pt = pteroid, R = radius, r. = right, Sc = scapula, t = tarsal, Ti = tibia, U = ulna, Wph = wing phalanx. Scale bar = 10 mm.

'Vertebre caudali di Preondactylus *(1770 MFSN). Da* DALLA VECCHIA (1998) *basato su* WILD *(1984, Fig. 3).* ***Le*** *vertebre caudali sono evidenziate in grigio e numerate. Abbreviazioni: C = tarpali, Co = coracoide, dr = costa dorsale, F = femore, g = coste gastrali,* ***H*** *= omero, hm = emapofisi, Il = ileo, Ispu = placca ischiopubica, 1. = sinistra, mclV = metacarpale alare, mt = metatarsale, ph = falangi della manus, pph = falangi del pes, pt = pteroide, R = radio, r = destro, Sc = scapola, t = tarsale, Ti = tibia, U = ulna, Wph = falange alare. Scala di riferimento = 10 mm.*

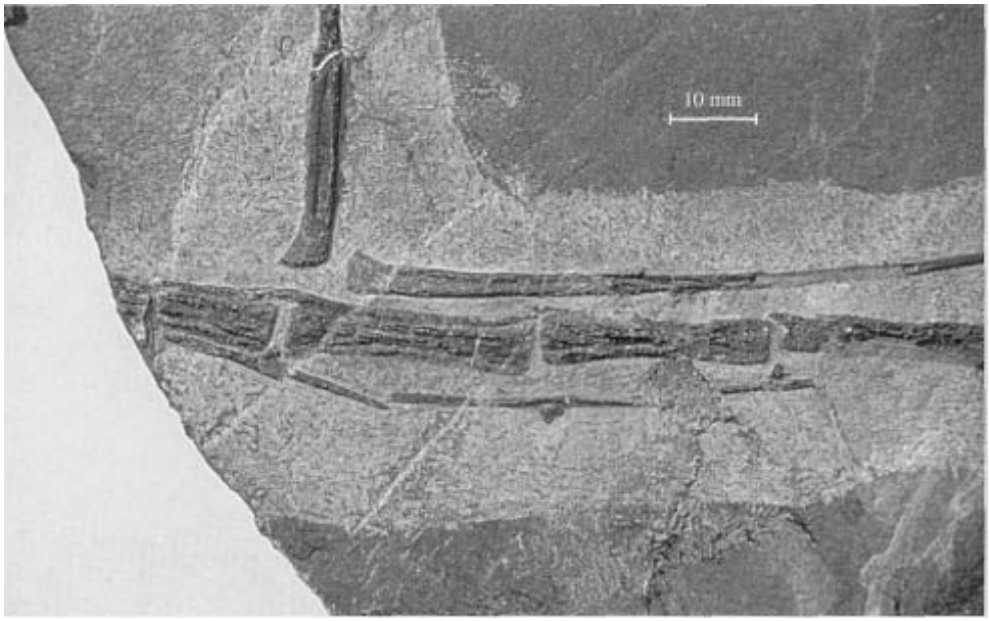


Fig. 12 - Segment of the mid laìl (from left to right: the 8th to I Ith vertehrae) of */lustriadactylus cri.status* (SMNS 56342). The hemapophyses are visible under the centra; above, a wing phalanx 4. Scale bar = 10 mm.

- *Segmento della parte centrale della coda (da sinistra cr destra: 8°-11 ° vertebre) di* Austriadactylus cristatus *(SMNS 56342). Le emapo/isi sono visibili sotto i centri vertebrali; sopra si nota una falange alare 4. Scala di riferimento = IO aura.*

tail segment and the length of the longest vertebral element between *Campylognathoides liasicus* and MFSN 19864 shows that the tail of the lattcr was relatively longer with relatively longer elements. In fast the longest caudal centrum of MFSN 19864 is 160% the length of the longest element in the Pittsburgh specimen of *Campylognathoides liasicus.* while the terminal wing phalanx is only 83% as long. The tail of MFSN 19864 is 291.8 mm (considering the 22 complete elements from the longest on), while in *Campylognathoides liasicus* (the only non-Triassie early rhamphorhynchoid where the tail is sufficiently complete and has been descrihed in a certain detail) the segment of 20 elements from the longest (14th) on is only 175.3 mm long. The presence in *Eudimorphodon* of middle caudal vertehrae comparatively longer than those of the Jurassic pterosaurs was noted by WILD (1978, p. 204). The presence of comparatively longer middle caudal vertebrae in Triassie pterosaurs is supported by data in table 11, partieularly in regard to the length of the longest centra.

The ratio of the length of the first 15 caudal vertehrae to the skull length is about 2.8 in *Austriadactvlus cristatus* (D.AII.A VECCHIA et al., 2002). The saure ratio is 2.4 in *Dorvgnathus*

banthensis (ITHEODORI) (WIMAN, 1925), 2.17 in *Campylognathoides liasicus* (WELLNHOFER, 1974) and around 1.5-1.6 *in Rhamphorhynchus longicaudus* (MONSTER) (WELLNHOFER, 1975b). The ratio of the length of the whole caudal vertebral segment to the skull length is about 1.85 in *Sordes pilosus* SHAROV based on the figure of the holotype in SHAROV (1971), but it is at least 3 based on the photograph of the specimen in WELLNHOFER (1991, p. 101). The same ratio is 2 in t he small specimen of *Scaphognathus crassirostris* (GoLDFuss) with 37 caudal vertebrae (WELLNHOFER, 1975b). The poorly known Anurognathidae *(Anurognathus ammoni* DÒDERLEIN, Late Jurassic of Germany; *Batrachognathus volans* RIABININ, Late Jurassic of Kazakhstan; *nendrorhynchoides curvidentatus* (JI S., Jr Q. & PADIAN), Lower Cretaceous of China) seem to bave a very reduced tail. *Anurognathus ammoni* seems to have only 11 short caudal vertebrae WEu raro x,1975b).

Taxonomic remarks The caudal segment and the wing phalanges 4 alone are not sufficient to unambiguosly determine the taxonomic position of the specimen. Two taxa are recorded in the Dolomia di Forni: *Preondactylus buffarinii* and *Eudimorphodon rosenfeldi*. The holotype of *Preondactylus buffarinii* was found in the same valley as MFSN 19864, but in a stratigraphical level placed about 150-200 m above it. The holotype of *Eudimorphodon rosenfeldi* comes from the nearby (4 km) Forchiar creek at about the same stratigraphical Jevel as MFSN 19864 (see RoGHI et al., 1995, Fig. 5).

Probably both *Preondactylus buffarinii* and *Eudimorphodon rosenfeldi* Jack the bundles of extremely elongated zygapophyseal and hemapophyseal processes, thus their absence in MFSN 19864 does not allow to exclude one of the two taxa. The terminal wing phalanx of MFSN 19864 resembles that of *Eudimorphodon* (WILD, 1978; 1994; DALLA VECCHIA, 1994) rather than the short and straight one of *Preondactylus* (see WILD, 1984). However, only one wing phalanx 4 of *Preondactylus* is known and it is very poorly preserved. Furthermore, the shape of the terminal wing phalanx does not seem to have a taxonomical relevance in early pterosaurs.

Based on the length of the wing phalanx, MFSN 19864 appears to belong to a slightly urger individuai than the other pterosaur specimens found in the Dolomia di Forni (cf. tab. I), except for a single very large wing phalanx 4 (MFSN 19836, 137 mm long). Unfortunately, e terminai wing phalanx is not a good tool to estimate size, because its length has a rtain degree of variability even within single species (PADIAN, 1980, p. 121). Anyway, it is eful for a gross estimation. It is 112% the length of the same wing phalanx of the holotype *Eudimorphodon rosenfeldi* (tab. 11) which has a wing span of 700 mm. Thus our specimen obably had a slightly larger wing span of 780 mm, if we just scale the linear proportion with that of the wing phalanx 4.

1	2	3	4	5	6	7	8	9	10	11	12 -
6*	24	22		20.7	19.5	18	16.5	15	14.5?	14	12	12?

13	14	15	16	17	18	19	20	21	22	23	24
11.7	11.5	11.2	11	10.75	10	9.75	8.75	8 -	6.5	4.5	2.7*

Tab. I - Length of the vertebral centra of MFSN 19864. Legenda: * = incomplete element, ? = uncertain measurement. Measurements are in millimeters.
*Lunghezza dei centri vertebrali del reperto MFSN 19864. Legenda: * elemento incompleto; ? = misura incerta. Le misure sono in millimetri.*

						6
Preondactylus buffarinii	lst-12nd	-113.5	?9th	14.5	28	32
Peteinosaurus zambellii	lst-16th	-197	9th	16	35	39
Eudimorphodon ranzii	lst-18th	150	8th-9th or 9th-10th	16	34	26.3
Eudimorphodon rosenfeldi	—	—	*?*	*?*	51.5	40.5
Austriadactylus cristatus	lst-18th	-365	?9th	28	85.5	-75
MFSN 19864	22+2 inc.	301.3		24	57.5	—
Dimorphodon macronyx	lst-30th	533.4	13th-14th	28		—
*Dorygnathus banthensis**	lst-23th	249	9th-llth	16	71	61
*Dorygnathus banthensis***	8th-17th	140	10th	17	72	61
Campylognathoides liasicus	lst-33th	325	9th-14th	15	69.6	50.3
Campylognathoides zitteli	lst-35th	584.5	8th-9th	35	121.5	70+

Tab. II - Data concerning caudal vertebrae and wing phalanx 4 in some Triassic and Early Jurassi long-tailed pterosaurs. 1) Number of preserved caudal vertebrae, 2) length of the preserve segment of the caudal vertebral column, 3) number of the longest caudal vertebra, 4) lengt of the longest caudal vertebra, 5) length o the wing phalanx 4, 6) length of the humerus a approximate parameter of individuai size (WILD, 1984). *Peteinosaurus zambellii* is represente by MCSNB 3359 (pers. obs.); *Eudimorphodon ranzii* is represented by MPUM 6009 (pers obs.); *Dimorphodon macronyx* according to OWEN (1870), specimen BMNH 41346
Dorygnathus banthensis according to WIMAN, 1925 (* exemplar Uppsala; ** exemplar Berlin
Campylognathoides liasicus after WELLNHOFER (1974), exemplar Pittsburgh; *C. zitteli*, holotype after PLIENINGER (1895) with humeral length estimated (+) according to WELLNHOFER (1974 Measurements are in millimeters. Legenda: inc. = incomplete elements, + = estimated leng *I dati riguardano le vertebre caudali e la falange alare 4 in alcuni pterosauri a coda lung del Triassico e Giurassico Inferiore. 1) numero di vertebre caudali preservate, 2) lunghezz del segmento conservato della colonna vertebrale caudale, 3) numero della vertebra caudal più lunga, 4) lunghezza della vertebra caudale più lunga, 5) lunghezza della falange alare 6) lunghezza dell'omero come parametro approssimato delle dimensioni individuali (W 1984).* Peteinosaurus zambellii *è rappresentato dall'esemplare MCSNB 3359 (oss. pers.)* Eudimorphodon ranzii è *rappresentato dall'esemplare MPUM 6009 (oss. pers.);* Dimorphod macronyx *secondo* OWEN *(1870), esemplare* ***BMNH*** *41346;* Dorygnathus banthensis *second* WIMAN, *1925 (* exemplar Uppsala; ** exemplar Berlin);* Campylognathoides liasicus *d* WELLNHOFER *(1974), "exemplar Pittsburgh"; C.* zitteli, *olotipo, da* PLIENINGER *(1895) con l stima della lunghezza totale dell'omero (+) secondo* WELLNHOFER *(1974). Le misure sono i millimetri. Legenda: inc. = elementi incompleti, + lunghezza stimata.*

Concltsions

MFSN 19864 is a further evidence that some Triassic pterosaurs lack the bundles of extremely elongated zygapophyseal and hemapophyseal processes.

I consider the absence of the bundles as a primitive feature because they are absent ;ra all supposed pterosaur relatives (WILD, 1978; PADIAN, 1984; GAUTHIER, 1986; SERENO 1991; BENNETT, 1996; PETERS, 2000) and are present in all Jurassic long-tailed pterosaurs. PETERS (2000; p. 306, Fig. 9A-B) identifies as elongated hemapophyses some structures in the supposed ventral side of the caudal vertebrae of *Sharovipteryx mirabilis* (SHAROV). Peters considers *Sharovipteryx* the sister-taxon of Pterosauria. Unfortunately, few is clear in the photograph of figure 9A. The drawing of figure 9B shows that the supposed hemapophyses differs from those of the long-tailed pterosaurs, because they are expanded at both ends and lie just "under" the centrum without the median triangular portion which inserts between two adjacent centra. The hemal arches of the reptiles are usually intercentral in position. This suggests that the supposed hemapophyses represents the ventral part (or the left lateral if the tail is exposed dorsally) of the collapsed vertebral centra. This was also the interpretation of GANS et al. (1987). The apparent separation from the upper part is possibly due to the splitting of the bone, or by the matrix filling of the groove caused by the collapse. In any case, even if they were actually hemapophyses, they would be derived with respect to the intercentral position found in early pterosaurs.

Probably the whole caudal vertebral series was relatively longer in Triassic pterosaurs than in Jurassic forms and there could be a trend toward a shortening during the rhamphorhynchoid evolutionary history, with the Late Jurassic rhamphorhynchoids having the connparatively shortest tail among long-tailed pterosaurs.

Detailed comparisons are actually made difficult by the incompleteness of the specimens and the lacking of accurate description of the caudal sections of the vertebral column for many specimens reported in literature. Thus a further detailed study is needed to confirm definitly thistrend.

Manoscritto pervenuto il 1.X.2001.

Acknowledgements

I thank Ruggero Tonello who found the specimen and deposited it at the Museo Friulano di Storia Naturale of Udine. I thank him also for the precious information about the piace of finding. I am w.lbt with the Museo Friulano di Storia Naturale of Udine, and in particular with the Director, ;Carlo Morandini, and the Curator of the Geological Section, Giuseppe Muscio, for the permission to study the specimen. I thank Peter Wellnhofer for the important personal communicàtions, Anna l?aganoni, Director of the Geopaleontological section of the Museo Civico di Scienze Naturali di Bergamo, for the photographs of the Lombardian specimens and the access to the collections under

her care, Silvio Renesto, University of Milano, for the photograph of MPUM 6009 and Elido Turco for the photographs of MFSN 19864. David Peters and Andrea Tintori have reviewed the manuscript. Thanks to David Peters allo for the correction of the English in a first version of the text. Of course, the responsibility for the interpretations and the possible mistakes is all mine.

References

BENNETT S.C., 1995 - A statistical study of Rhamphorhynchus from the Solnhofen Limestone of~ Germany: year-classes of a single large species. Journ. Paleont., 69: 569-580, Lawrence.

BENNETT S.C., 1996 - The phylogenetic position of the Pterosauria within the Archosauromorpha. Zoological Journ. Linnean Soc., 118: 261-308, London.

BIZARRINI E & Muscio G., 1995 - Un nuovo rettile (Reptilia, Prolacertiformes) dal Norico di Preone (Udine, Italia nord-orientale). Nota preliminare. Gortania - Atti Mus. Friul. St. Nat., 16 (1994): 67-76, Udine.

BUCKLAND W., 1835 - On the discovery of a new species of Pterodactyle in the Lias at Lyme Regis. Transactions of the Geological Society of London, 3 (2): 217-222, London.

BUISONJÈ P.H. DE-, 1985 - Climatological Conditions During Deposition of the Solnhofeil Limestone. In: ECHT M.K., OSTROM J.H., VIOHL G. & WELLNHOFER P. (Eds) - The Beginnings 3 of Birds. Proceedings of the International Archaeopteryx Conference Eichstàtt, 1984: 45-65.

CALZAVARA M., Muscio G. & WILD R., 1981 - Megalancosaurus preonensis n.g., n.sp., a new reptile from the Norian of Friuli, Italy. Gortania - Atti Museo Friul. St. Nat., 2: 49-64, Udine.

DALLA VECCHIA F.M., 1990 - Sedimentologia e paleontologia della Dolomia di Forni (Triassico superiore) nella valle del Rio Seazza (Preone, Carnia): ricostruzione paleoecologica e paleoambientale. Unpublish. grad. thesis, pp. 204, Bologna.

DALLA VECCHIA F.M., 1991 - Note sulla stratigrafia, sedimentologia e paleontologia della dolomia di Forni (Triassico superiore) nella valle del Rio Seazza (Preone, Friuli-Venezia Giulia). Gortania - Atti Mus. Friul. St. Nat., 12 (1990): 7-30, Udine.

DALLA VECCHIA F.M., 1994 - Studio sugli pterosauri triassici con note sulla loro datazione, habitat e storia evolutiva. Unpublish..Ph. D. thesis, pp. 249, Modena.

DALLA VECCHIA F.M., 1995 - A new pterosaur (Reptilia, Pterosauria) from the Norian (Late Triassic) of Friuli (Northeastern Italy). Preliminary note. Gortania - Atti Mus. Friul. St. Nat., 16 (1994): 59-66, Udine.

DALLA VECCHIA F.M., 1998 - New observations on the osteology and taxonomic status of Preondactylus buffarinii Wild, 1984 (Reptilia, Pterosauria). Boli. Soc. Paleont. It., 36 (3, 1997): 355-366, Modena.

DALLA VECCHIA EM., 2000 - A wing phalanx of a large basal pterosaur (Diapsida, Pterosauria) fronhi
the Norian (Late Triassic) of NE Italy. Boli. Soc. Paleont. It., 39 (2): 229-234, Modena.

DALLA VECCHIA F.M., 2001 - Triassic pterosaurs: unravelling the puzzle. Extended abstracts of "Two hundred years of Pterosaurs - A symposium on the anatomy, evolution, palaeobiology an d' environments of Mesozoic Flying Reptiles", Tolouse, France, September 5-8, 2001. Strata, 11, Série 1 (Communications): 33-35, Tolouse.

DALLA VECCHIA F.M., submitted - New morphological observations on Triassic pterosaurs. Proceedings of the symposium "Two hundred years of Pterosaurs - A symposium on the anatomy, evolution, palaeobiology and environments of Mesozoic Flying Reptiles".

DALLA VECCHIA F.M., Muscio G. & WILD R., 1989 - Pterosaur remains in a gastric pellett from Upper Triassic (Norian) of Rio Seazza valley (Udine, Italy). Gortania - Atti Mus. Friul. St. Nat., 10 (1988): 121-132, Udine.

DALLA VECCHIA F.M., WILD R., HoPF H. & REITNER J., 2002 - A crested rhamphorhynchoid pterosaur from the Late Triassic of Austria. Journ. Vert. Paleont., 22 (1): 196-199, Lawrence.

GANS C., DAREVSKI I. & TATARINOV L.P., 1987 - Sharovipteryx. A reptilian glider? Paleobiology, 13 (4): 415-426.

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

HAMLEY T', 1990 - Functions of the tail in bipedal locomotion of lizards, dinosaurs and pterosaurs. Mcm. Qd. Mus., 28 (1): 153-158, Brisbane.

MUSCIO G., 1997 - Preliminary note on a specimen of Prolacertiformes (Reptilia) from the Norian (Late Triassic) of Preone (Udine, North-Eastern Italy). Gortania-Atti Mus. Friul. St. Nat., 18 (1996): 33-40, Udine.

OSTROM J., 1990 Dromeosauridae. In: WEISHAMPEL D.B., DODSON P. & OsMóISKA H. (eds.) - The Dinosauria. University of California Press: 269-279, Berkeley.

JWEN R., 1,870 - A monograph of the fossi) Reptilia of the Liassic Formations. III. Monogr. Paleontogr. Soc.: 41-81, London.

ADIAN K., 1980 - Note of a new specimen of pterosaur (Reptilia: Pterosauria) from the Norian (Upper Triassic) of Endenna, Italy. Riv. Mus. Sc. Nat. "E. Caffi" Bergamo, 2: 119-127, Bergamo.

PADIAN K., 1984 - The origin of pterosaurs. In: REIF W.E. & WESTPHAL F. (eds.) - Third symposium in Mesozoic terrestrial ecosystems. Tiibingen 1984, Short Papers: 163-168, Stuttgart.

PETERS D., 2000 - A redescription of four Prolacertiform genera and implications for pterosaur phylogenesis. Riv. hai. Paleont. Strat., 106 (3): 293-336, Milano.

PINNA G., 1988 - Un nuovo esemplare giovanile di Drepanosaurus unguicaudatus del Norico della Val Preone (Udine). Atti Soc. Ital. Sci. Nat. Museo Civ. St. Nat., 128 (1-2): 80-84, Milano.

PLIENINGER F., 1895 - Campylognathus Zitteli. Ein neuer Flugsaurier aus dem Oberen Lias Schwabens. Palaeontographica, 41: 193-222, Stuttgart.

RENESTO S., 1994 - Megalancosaurus, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of Northern Italy. Journ. Vert. Paleont., 14 (1): 47-62, Lawrence.

RENESTO S., 2000 - Bird-like head on a chameleon body: New specimens of the enigmatic diapsid reptile Megalancosaurus from the Late Triassic of Northern Italy. Riv. Ital. Paleont. Strat., 106 (2): 157-180, Milano.

RENESTO S. & DALLA VECCHIA F.M., 2000 - The unusual dentition and feeding habits of the Prdlacertiform reptile Langobardisaurus (Late Triassic, Northern Italy). Journ. Vert. Paleont., 20 (3): 622-627, Lawrence.

ROGHI G., MIETTO P. & DALLA VECCHIA F.M., 1995 - Contribution to the conodont biostratigraphy of the Dolomia di Forni (Upper Triassic, Carnia, NE Italy). Mem. Sci. Geol., 47: 125-133, Padova.

SERENO P.C., 1991- Basal archosaurs: phylogenetic relationships and functional implications. Journ. Vert. Paleont. Memoirs, 2: 1-53, Lawrence.

SHAROV A.G., 1971 - New flying reptiles from the Mesozoic of Kazakhstan and Kirghizia. Transactions of the Paleontologica) Institute, 130: 104-113, Moscow (in Russian).

UNWIN D.M., 1988 - New remains of the pterosaur Dimorphodon (Pterosauria: Rhamphorhynchoidea) and the terrestrial ability of early pterosaurs. Modem Geology, 13: 57-68.

WELLNHOFER P., 1974 - Campylognathoides liasicus (Quenstedt) an Upper Liassic pterosaur from Holzmaden - the Pittsburgh specimen. Ann. Carnegie Museum, 45: 5-34, Pittsburgh.

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

WELLNHOFER P., 1975b - Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Siiddeutschlands. Teil Il, Systematische Beschereibung. Palaeontographica, A, 14[g]: 132-186, Stuttgart.

WELLNHOFER P., 1975c - Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke

Siiddeutschlands. Teil III: Palbkologie und Stammesgeschichte. Palaeontographica, 149: 1-30 Stuttgart.

WELLNHOFER P., 1978 - Pterosauria. In: WELLNHOFER P. (ed.) Handbuch der Paldoherpetologie, patf 19. Fischer, pp. 82, Stuttgart.

WELLNHOFER P., 1991 - The illustrated enciclopedia of Pterosauria. Salamander Book, pp. 192, London

WELLNHOFER P., 2001 - A Late Triassic pterosaur from the Northern Calcareous Alps. Extended abstracts of "Two hundred years of Pterosaurs - A symposium on the anatomy, evoluti(m. palaeobiology and environments of Mesozoic Flying Reptiles", Tolouse, France, Septembct 5-8, 2001. Strata, 11, Série 1 (Communications): 99-100, Tolouse.

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

WILD R., 1984 - A new pterosaur (Reptilia, Pterosauria) from the Upper Triassic (Norian) of Friulii Italy. Gortania - Atti Mus. Friul. St. Nat., 5: 45-62, Udine.

WILD R., 1994 - A juvenile specimen of Eudimorphodon ranzii Zambelli (Reptilia, Pterosauria) from the Upper Triassic (Norian) of Bergamo. Riv. Mus. Civ. Sc. Nat. "E. Caffi" Bergamo, 16 (1993): 91415, Bergamo.

WIMAN C., 1925 - ÍJber Dorygnathus and andere Flugsaurier. Bull. Geol. Inst; Uppsala, 19: 23-54; Uppsala.

Author's address - Indirizzo dell' Autore:
- Dr Fabio Marco DALLA VECCHIA
Museo Paleontologico Cittadino
Via Valentinis 134, I-34074 MONFALCONE
(GO) e-mail: fabdalla@tin.it