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A NEW PTEROSAUR (REPTILIA, PTEROSAURIA) FROM THE UPPER
TRIASSIC (NORIAN) OF FRIULI, ITALY

UN NUOVO PTEROSAURO (REPTILIA, PTEROSAURIA) DEL TRIASSICO
SUPERIORE (NORIANO) DEL FRIULI, ITALIA

Dedicated to Prof. Dr. E. Kuhn-Schnyder
on his 80th birthday

Abstract — A new Upper Triassic pterosaur, *Preondactylus buffarinii* n. gen., n. sp., is described from the Norian of the Preone valley, province of Udine, Italy. The specimen differs from the well-known Upper Triassic pterosaurs *Eudimorphodon* and *Peteinosaurus* mainly in possessing single-cusped *Dorygnathus*-like teeth and in the ratios of the bones of the postcranial skeleton. By means of this method a second uncomplete specimen from the Norian of Endenna, province of Bergamo, Italy, is referred to the new species as cf. *Preondactylus buffarinii*. *Preondactylus* belongs to the family Rhamphorhynchidae. The arboreal theory of the origin of flight in pterosaurs and their supposed eosuchian relationships are reconsidered.

Key words: Pterosauria, Upper Triassic, Udine, Bergamo, Origin of flight, Relationships.

Riassunto breve — Viene descritto un nuovo pterosauro del Triassico superiore, *Preondactylus buffarinii* n. gen., n. sp., proveniente dal Noriano della Val Preone (provincia di Udine, Italia). Questo esemplare differisce dai più conosciuti pterosauri del Triassico superiore, *Eudimorphodon* e *Peteinosaurus*, soprattutto nel possedere denti monocuspidati simili a quelli del *Dorygnathus*, e nei rapporti delle ossa dello scheletro post-craniale. In base a questo metodo viene descritto un secondo esemplare incompleto proveniente dal Noriano di Endenna (provincia di Bergamo, Italia) che viene riferito alla nuova specie come cf. *Preondactylus buffarinii*. Il *Preondactylus* appartiene alla famiglia Rhamphorhynchidae. Viene riconsiderata la teoria arboricola dell'origine del volo nei pterosauri e la loro supposta parentela con gli eosuchi.

Parole chiave: Pterosauri, Triassico Superiore, Udine, Bergamo, Origine del volo, Relazioni di parentela.

Introduction

In spring 1982 Mr. Nando Buffarini of Udine found an almost complete skeleton of a pterosaur in the Norian shaly limestones and dolomites of the Preone valley, province of Udine. The specimen was discovered south of the church in the small village of Madonna Peraries on the Northeast-slope of the Monte Pezzet. The black bones of the skeleton were imbedded in a two to three mm thick yellow-brown marl covering the dolomitic limestone. The specimen broke in several parts during excavation and small pieces were lost. As Mr. Buffarini and his wife fit the parts together and washed them, the marl and the bones were almost completely removed, with the exception of parts of the left hand and foot. Therefore, the skeleton is now preserved only as a natural mould on the surface of the slab (fig. 1). To prepare this specimen

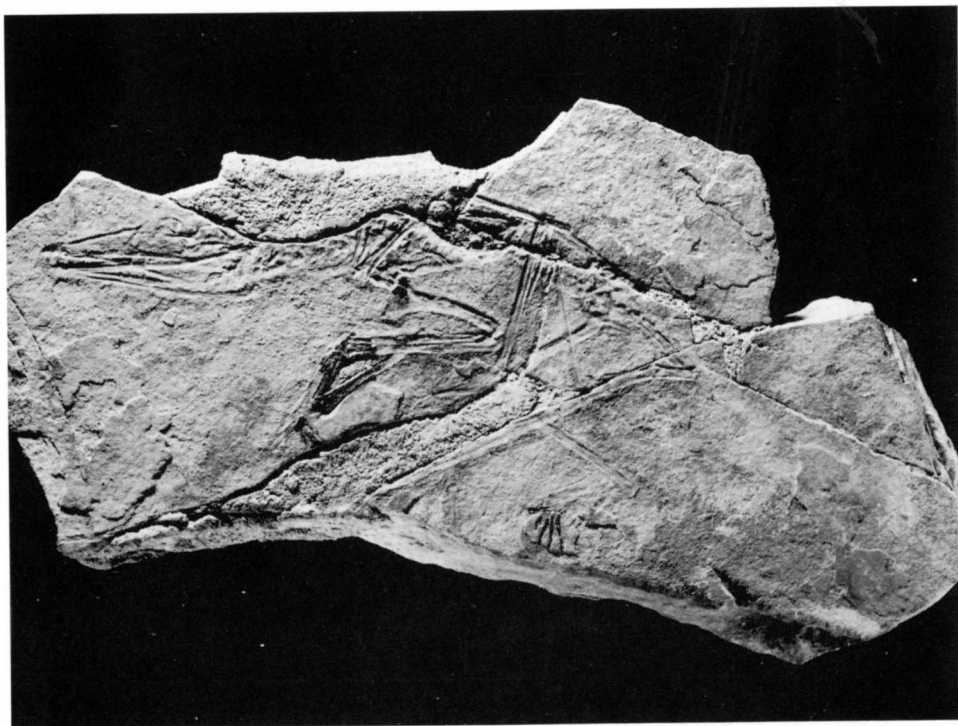


Fig. 1 - *Preondactylus buffarinii* n. gen., n. sp.; no. 1770 MFSN. Natural mould with preserved bones in the carpus and foot. Norian, Val Preone, province of Udine, Italy.
- *Preondactylus buffarinii* n. gen., n. sp.; n. 1770 MFSN. Impronta con le ossa preservate del carpo e del piede. Noriano, Val Preone, provincia di Udine, Italia.

for study, Mr. N. Adorf, preparator of the Staatliches Museum für Naturkunde Stuttgart, took a silicon rubber impression. It shows all the skeletal details that are important for description and comparison (fig. 2). By illuminating the specimen from different directions and different angles, I drew the skeleton under the Wild M5 binocular glass with the help of a drawing mirror (fig. 3).

In September 1982, when I first studied this specimen and took its measurements, I recognized this pterosaur as different from the hitherto known Norian genera *Eudimorphodon* and *Peteinosaurus* (ZAMBELLI, 1973; WILD, 1978). Although the new specimen shows similarities to *Eudimorphodon* (from the Norian of Cene near Bergamo) in the shape of the skull, especially the enlargement of two maxillary teeth between the antorbital fenestra and the orbit; it differs from the latter genus principally in the morphology of the teeth and the ratios of the postcranial bones.

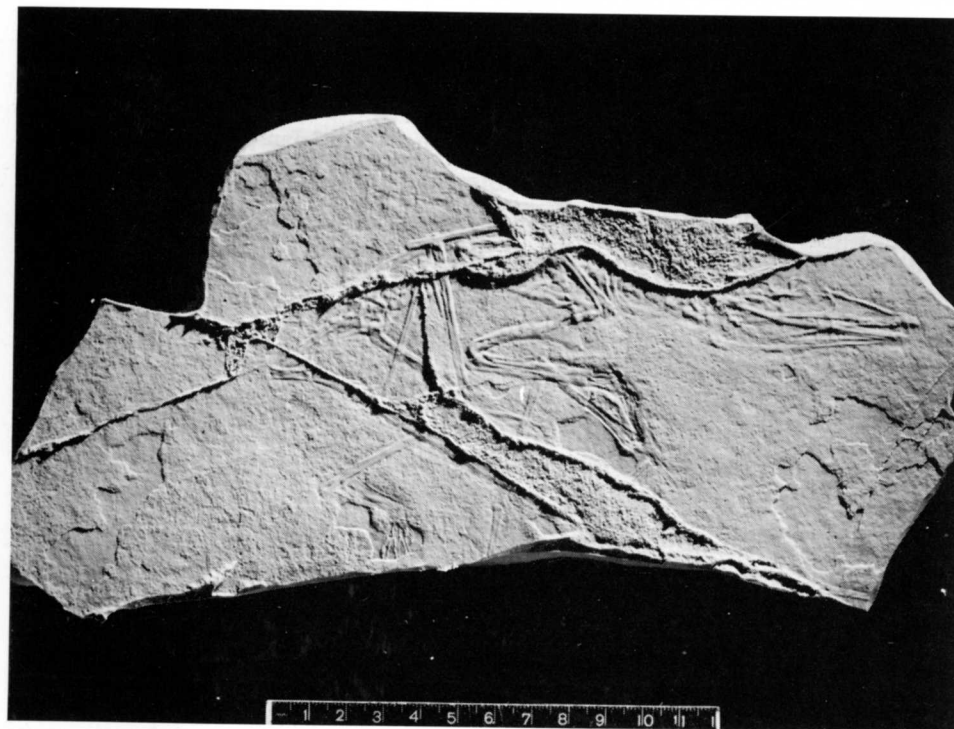


Fig. 2 - *Preondactylus buffarinii* n. gen., n. sp.; no. 1770 MFSN. Silicon-rubber impression of the type specimen.
- *Preondactylus buffarinii* n. gen., n. sp.; n. 1770 MFSN. Calco in gomma di silicone dell'esemplare-tipo.

Beyond all doubt, the new specimen has single-cusped teeth, which was also confirmed by the finder, Mr. Buffarini. When he discovered the specimen he immediately checked the dentition to see if the teeth were multi-cusped as in *Eudimorphodon*, but this was not the case.

In autumn 1982 the new pterosaur specimen was acquired by the Museo Friulano di Storia Naturale of Udine. The director of this museum, dr. C. Morandini, kindly offered me the privilege of describing the specimen. I am greatly indebted to him and also to my friends dr. G. Muscio, curator for geology and paleontology at the museum in Udine, and dr. M. Calzavara in Udine, for permitting the study of this specimen to the Staatliches Museum für Naturkunde Stuttgart at Ludwigsburg and for providing all possible assistance during my stays in Udine in 1982 and 1983. Finally I wish to thank Mr. N. Buffarini and his wife for their permission to study the specimen even before its acquisition by the Udine museum, and for their kind hospitality during my visits in Udine.

The specimen was covered by a special lacquer, which was cleaned by acetone and alcohol to make the natural moulds of the bones clearly visible. The preserved bony parts of the left carpal region and left foot were prepared under the Wild M5 binocular glass with sharpened insect-needles, as I described in 1978 (p. 178). I want to thank Mr. N. Adorf for making the silicon-rubber imprints and Mr. H. Lumpe of the Staatliches Museum für Naturkunde Stuttgart for the photographs.

Systematic Paleontology

Class	<i>Reptilia</i>
Subclass	<i>Archosauria</i>
Order	<i>Pterosauria</i>
Suborder	<i>Rhamphorhynchoidea</i>
Family	<i>Rhamphorhynchidae</i> SEELEY, 1870.

For the definition of the family see WELLNHOFER (1978).

Genus ***Preondactylus*** n. gen.

Type species: ***Preondactylus buffarini*** n. sp.

Etymology: Preon (Italian), after the locality in the valley of Preone in Friuli, Northern Italy (also called Val Preon); dactylus (Greek) for finger, regarding the elongated wing-finger, which supports the wing-membrane.

Diagnosis: Long-tailed pterosaur with a wing-span of approximately 130 to 160 cm; teeth single-cusped, conical, the anterior ones recurved backwards as in *Dorygnathus*; about 25 to 28 teeth in the upper and lower jaw rami; two enlarged maxillary teeth between the antorbital fenestra and the orbit, as in *Eudimorphodon*; skull resembling that of *Eudimorphodon*, but with a larger naris situated more anteriorly; sutures of the bones of the lower jaw distinct from those in *Eudimorphodon* and more similar those in *Dorygnathus*; dentary only almost half the length of the complete lower jaw; distinct retroarticular process; presumably 8 cervical vertebrae, 14 dorsals, less than 4 sacrals, and more than the preserved 11 caudals, perhaps as many as 20; scapula and coracoid not fused; humerus shorter than femur (a ratio unknown in any other pterosaur), wing-phalanx 1 shorter than humerus and femur (also unknown in any other pterosaur) and much shorter than the ulna and the tibia; femur + tibia longer than humerus + ulna; at least 4 carpals, the proximal two, probably ulnare and radiale, are unfused; pteroid short, rod-like; fibula of about 2/3 the length of the tibia, fused to the latter; ?2 tarsals; phalangeal formula of the pes: 2 3 4 5 2.

Distribution: Upper Triassic, Norian, valley of Preone in the region of Friuli, and Endenna, province of Bergamo, Italy.

Preondactylus buffarini n. sp.

Synonymy: 1984 «Neuer, noch unbenannter Flugsaurier». WILD, Naturwiss., 71: 1, fig. 4.

Etymology: In honor of the finder of this specimen, Mr. Nando Buffarini, Udine.

Type and only specimen: No. 1770 MFSN (Museo Friulano di Storia Naturale of Udine).

Horizon: 3-30 cm thick, laminated, bituminous dolomitic limestones and dolomites of the «Dolomia di Forni» sensu CALZAVARA et al. (1980: 51); lower middle part of the «Dolomia Principale»; probably Middle Norian.

Locus typicus: About 200 meters South of the small village of Madonna Peraries in the valley of Preone at the Northeast-slope of the Monte Pezzet.

Diagnosis: see diagnosis of the genus.

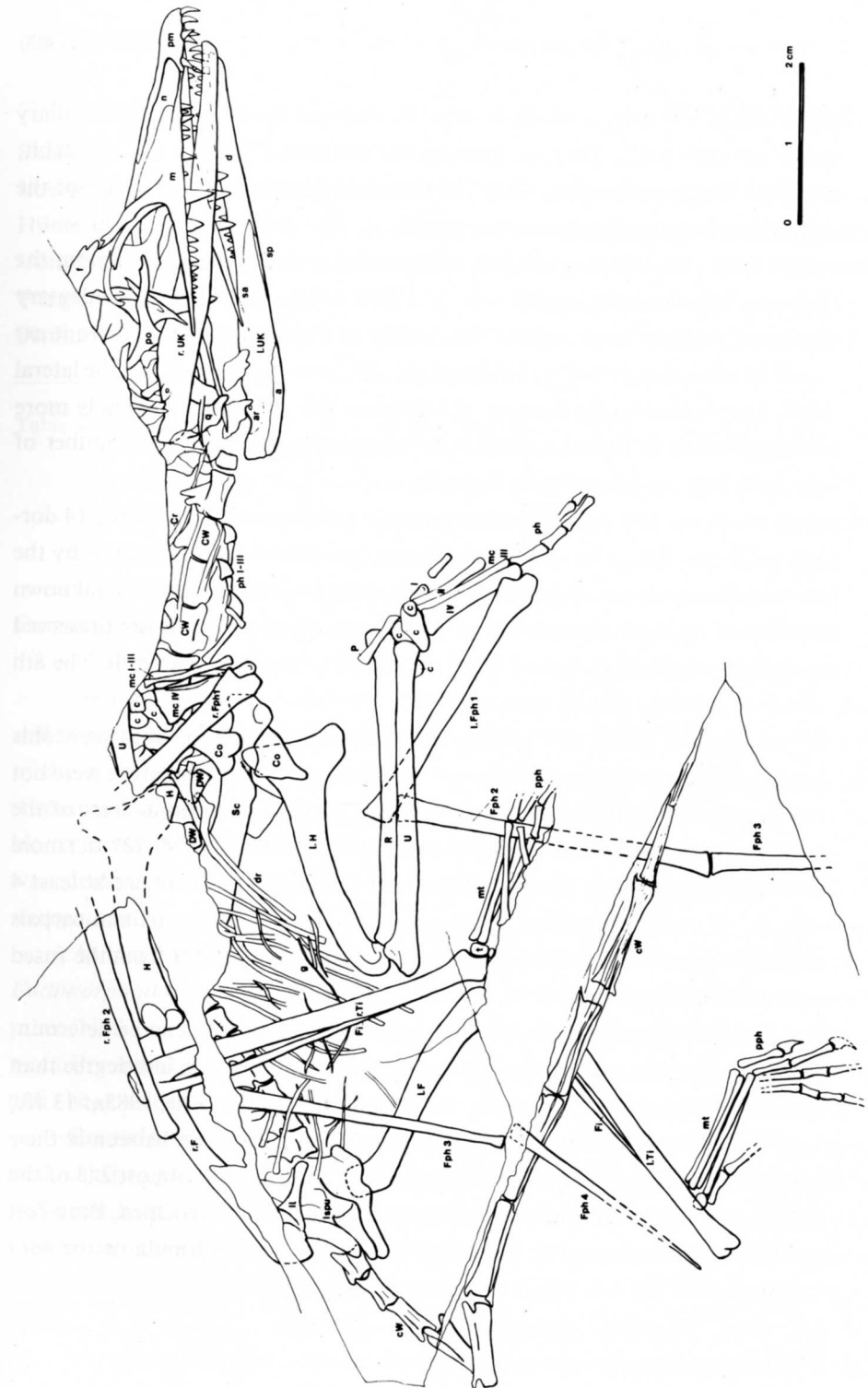
Description

Although the bones of the skeleton are not preserved, the specimen clearly lies on its left side, presenting the right view (figs. 1-3). The right wing and right hind-limb are moved out of their natural articulation: they are not covered by the body, but have turned to overlap the latter. The tail is bent cranially at one of the first elongated caudal vertebrae, so that it overlies the left tibia and the left wing-phalanx 2.

Skull: On the silicon-rubber impression the skull is visible from the right side (fig. 2). Its posterior part is missing because the slab is fractured. Few skull bones are identifiable: the premaxilla has 4 posteriorly recurved teeth. It possesses a long dorsal nasal process. It borders the naris, which is situated more anteriorly than in *Eudimorphodon* (WILD, 1978: 184, fig. 1). The maxilla bears 19 conical teeth; their different sizes are due to tooth succession. The gap between the teeth of the right premaxilla and maxilla is caused by the loss of teeth during growth, as can be seen in the more complete dentition of the left upper

Fig. 3 - *Preondactylus buffarinii* n. gen., n. sp.; no. 1770 MFSN. Drawing of the skeleton according to the silicon-rubber impression. Abbreviations: a = angular; ar = articular; c = carpal; Co = coracoid; Cr = cervical rib; CW = cervical vertebra; Cw = caudal vertebra; d = dentary; dr = dorsal rib; DW = dorsal vertebra; F = femur; f = frontal; Fph 1-4 = wing-phalanges 1-4; Fi = fibula; g = gastrale; H = humerus; Il = ilium; Ispu = ischiopubis; l. = left; m = maxilla; mc I-III = metacarpals I-III; metacarpal IV = wing-metacarpal; mt = metatarsal; n = nasal; P = pteroid; ph = phalanges of manus; pm = praemaxilla; po = postorbital; pph = phalanges of pes; q = quadrate; R = radius; r. = right; sa = surangular; Sc = scapula; sp = splenial; t = tarsal; Ti = tibia; U = ulna; UK = lower jaw.

- *Preondactylus buffarinii* n. gen., n. sp.; n. 1770 MFSN. Disegno dello scheletro in base al calco in gomma di silicone. Abbreviazioni: a = angolare; ar = articolare; c = carpale; Co = coracoide; Cr = costola cervicale; CW = vertebra cervicale; Cw = vertebra caudale; d = dentario; dr = costola dorsale; DW = vertebra dorsale; F = femore; f = frontale; Fph 1-4 = falangi alari 1-4; Fi = fibula; g = gastrale; H = omero; Il = ilio; Ispu = ischiopube; l. = sinistra; m = mascella; mc I-III = metacarpali I-III; metacarpale IV = metacarpale alare; mt = metatarsale; n = nasale; P = pterioide; ph = falangi dell'arto superiore; pm = premaxillare; po = postorbitale; pph = falangi dell'arto inferiore; q = quadrato; R = radio; r. = destro; sa = soprangolare; Sc = scapola; sp = spleniale; t = tarsale; Ti = tibia; U = ulna; UK = mascella inferiore.



jaw, which, however, is partly covered by the right lower jaw. Two maxillary teeth are enlarged in the zone between the antorbital fenestra and the orbit, as in *Eudimorphodon* (loc. cit.). The complete dentition of one ramus of the upper jaw is estimated to about 28 teeth.

Lower jaw: Both rami of the lower jaw are loosened at the symphyseal region; the left one, seen from the medial side, is shifted a little posteriorly. The dentary is almost half the length of the jaw, unlike in *Eudimorphodon*, where it extends to more than 2/3 of the length of the jaw, however only seen on the lateral side. The retroarticular process of the lower jaw of **Preondactylus** is more elongated than in *Eudimorphodon*. In comparing both rami, the number of the teeth can be estimated at about 25.

Postcranial skeleton: The vertebral column consists of probably 8 cervicals, 14 dorsals (of which 2 may be lumbar vertebrae), less than 4 sacrals (judged by the narrow distance between the last dorsals and the first caudals) and an unknown number of caudals, possibly about 20. The anterior 11 caudals are preserved and are increasingly elongated from the fourth to about the eleventh. The 8th and 10th caudals are the longest.

Of the shoulder girdle, one scapula and the proximal ends of both coracoids are known. The scapula and the coracoid are separated and therefore were not fused. In its proportions and in the features of the deltopectoral crest of the humerus, the anterior limb resembles *Peteinosaurus* (WILD, 1978: 227 ff.) more than *Eudimorphodon*. The pteroid is short and rod-like. There are at least 4 carpals, of which the medial distal one is the largest. Both proximal carpals (probably ulnare and radiale) are not fused and thereby differ from the fused ones in *Eudimorphodon*.

Few bones of the pelvis, which is compressed dorsolaterally, can be determined. The femur has a distinctly inclined proximal end, but to a less degree than in *Eudimorphodon*, *Dorygnathus* and *Dimorphodon* (PADIAN 1983a: 13 ff., figs. 7e, 28). The tibia and fibula are obviously fused, as can be seen at their proximal end, as in nearly all pterosaurs. The fibula extends almost 2/3 of the length of the tibia. This bone ends distally in a bicondylar trochlea. Both feet are incompletely preserved; nevertheless the phalangeal formula of the foot confirms with 2-3-4-5-2 the rhamphorynchoid condition.

Like other pterosaurs, **Preondactylus** has gastralia.

The measurements are given in tab. I.

Skull:	5,6*	Tibia:	4,95
Lower jaw:	5,4	Wing-phalanx 1:	3,08
Humerus:	3,2	Wing-phalanx 2:	3,9
Ulna/Radius:	4,2/4,1	Wing-phalanx 3:	3,9
Wing-metacarpal:	1,9	Wing-phalanx 4:	2,8*
Femur:	3,4	Metatarsals I-IV:	1,6*

Table I - Length (in mm) of bones of **Preondactylus buffarinii** n. gen., n. sp.; no. 1770 MFSN; * = uncertain.

- *Lunghezza (in mm) delle ossa di Preondactylus buffarinii* n. gen., n. sp.; n. 1770 MFSN; * = incerto.

Comparisons

As was shown first by OWEN (1870), later by NOPCSA (1922), WIMAN (1925) and in particular WELLNHOFER (1968, 1970, 1974, 1975) and other authors, the ratios of the bones in pterosaurs are useful for distinguishing different species, especially if specimens are partially preserved or lack the skull. With this method it is also possible to recognize juvenile and adult specimens of the same or different species, as was demonstrated in the Upper Triassic pterosaurs *Eudimorphodon* and *Peteinosaurus*.

As mentioned already, **Preondactylus** shows similarities to the Upper Triassic *Eudimorphodon* in the shape of the skull and the enlarged maxillary teeth between praeorbital fenestra and orbit. On the other hand also relations seem to exist between **Preondactylus** and *Peteinosaurus*, mainly in the morphology of the humerus and the considerably long hind-limb.

Preondactylus differs from *Eudimorphodon* and *Peteinosaurus* in the dentition, consisting of slightly enlarged and recurved premaxillary and conical maxillary teeth, which are only single-cusped. Further differences are revealed in the far anteriorly situated naris of **Preondactylus**, the bones of the lower jaw and probably also of the skull. The silicon-rubber impression, however, gives no information on this account.

Striking differences between **Preondactylus**, the Upper Triassic and Lower

Jurassic pterosaurs, as *Dimorphodon*, *Dorygnathus* and *Campylognathoides* become evident by the ratios of the postcranial bones (tab. II). No other pterosaur is known, which has such an unproportionally long hind-limb as **Preondactylus**. This depends on the unusual length of the femur and tibia, demonstrated by the ratios of humerus/femur, humerus/tibia, ulna/tibia, wing-phalanx 1/femur and wing-phalanx 1/tibia. However, the hind-limb is not only exceptionally long, but also the wing is extraordinarily short, as can be seen in the relatively short humerus, lower arm and wing-phalanx 1. The ratios of the wing-metacarpal and the other wing-phalanges do not vary to such an extent from those of other pterosaurs, as does especially the short wing-phalanx 1.

Preondactylus does not show closer relationships either to *Peteinosaurus* and its closely related *Dimorphodon* or to *Eudimorphodon* and its Lower Jurassic descendant *Campylognathoides* (WILD, 1978: 242 ff.). *Peteinosaurus* and the Lower Jurassic *Dimorphodon* belong to the family Dimorphodontidae. This is characterized by the high skull and the heterodont, probably insectivorous dentition, consisting of 2 to 5 larger anterior teeth and about 40 posteriorly following ones. They are laterally compressed, sharp-pointed and possess a distinct anterior and posterior cutting-edge. *Eudimorphodon* has unique heterodont, multi-cusped teeth, which can be recognized in a simplified single-cusped pattern in *Campylognathoides*. Both genera represent independent families, which, however, are closely related.

Although it does not become evident by all ratios of the bones (tab. II), I suppose relationships between **Preondactylus** and *Dorygnathus*. This latter genus represents the family Rhamphorhynchidae in the Lower Jurassic (WELLNHOFER, 1978: 33 f.). The assumption that **Preondactylus** belongs to the Rhamphorhynchidae is based on the proportions of the phalanges of the wing-finger, as for example the ratio of wing-phalanx 1/humerus, wing-phalanx 1/ulna, wing-phalanx 2/wing-phalanx 1 and wing-phalanx 3/wing-phalanx 2. Additionally, the ratios of humerus/wing-metacarpal, humerus/tibia, tibia/femur, wing-phalanx 1/femur, and wing-phalanx 1/tibia correspond in **Preondactylus** and *Dorygnathus* (and also in *Rhamphorhynchus*), rather than in **Preondactylus** and other pterosaurs (tab. II). The dentition of **Preondactylus**, with its slightly enlarged and recurved anterior teeth, resembles that of *Dorygnathus*. So it turns out to be very probable that **Preondactylus** is an early member of the family Rhamphorhynchidae, which therefore extends from the Upper Triassic to the Upper Jurassic. The presence of this family in the Upper Triassic was already supposed (WILD, 1978: 246 ff.; fig. 47) and is now confirmed.

	u/h	h/mcIV	u/mcIV	h/f	h/ti	u/f	u/ti	ti/f	f/mcIV	ti/mcIV	h	u	mclV	f	ti	wph1/wph1	wph2/wph1	wph3/wph2	wph3/wph4	wph3/wph1
<i>Preond.</i>	1,31	1,68	2,21	0,94	0,65	1,23	0,85	1,45	1,78	2,61	0,96	0,73	1,62	0,90	0,62	1,27	0,98*	1,39+	1,27	
<i>Eudim.</i>	1,36	2,09	2,84	1,26	0,99	1,65	1,34	1,27	1,64	2,10	1,53	1,12	3,17	1,92	1,51	0,94	1,09	1,03	0,94	
<i>Petein.</i>	1,25	2,26	2,82	1,04	0,79	1,30	0,98	1,32	2,17	2,88	1,11	0,89	2,53	1,16	0,88	1,0	1,08	1,34	1,08	
<i>Dimorph.</i>	1,17	2,10	2,01	1,27	0,84	1,27	0,88	1,44	1,63	2,81	1,15	0,98	2,04	1,25	0,86	1,14	1,16	—	1,30	
<i>Dorygn.</i>	1,60	2,04	3,26	1,20	0,92	1,93	1,48	1,35	1,65	2,23	1,23	0,77	2,50	1,49	1,11	1,21	1,01	1,25	1,13	
<i>Campyl.</i>	1,20	2,23	2,66	1,31	1,07	1,50	1,21	1,28	1,77	2,26	1,98	1,60	4,27	2,41	1,91	1,08	0,89	1,26	0,84	
<i>Rhamph.</i>	1,62	1,83	2,99	1,31	0,95	2,11	1,54	1,35	1,40	1,93	2,52	1,56	4,57	3,27	2,37	0,92	0,90	0,99	0,83	

Table II - Mean ratios of different postcranial bones in Triassic and Jurassic pterosaurs (after WILD 1978: 241, tab. 6). Ratios of *Dimorphodon* partly modified according to PADIAN (1983a: 6, tab. I); *) = Specimens no. 1770 MFSN and no. 4562 MCSNB; +) = uncertain.

- *Rapporti medi fra le ossa nei pterosauri triassici e giurassici (dopo WILD, 1978: 241, tab. 6). I rapporti per Dimorphodon sono parzialmente modificati in accordo con PADIAN (1983a: 6, tab. I); *) = esemplare n. 1770 MFSN e n. 4562 MCSNB; +) = incerto.*

Cf. *Preondactylus buffarinii*

In 1980 PADIAN restudied the pterosaur fauna of Cene and described a new, hitherto unknown incomplete wing-finger of a large pterosaur. It was found in the valley of Bruciata near the village of Endenna, province Bergamo. This specimen is housed in the Museo Civico di Scienze Naturali of Bergamo (= MCSNB) as no. 4562. It is the only pterosaur known from that locality. Based on the ratios of the wing-phalanx 2/wing-phalanx 3, Padian argued that this specimen could belong neither to *Eudimorphodon* nor to *Peteinosaurus* and therefore possibly represented a new species or genus. Due to the very incomplete preservation of this specimen, a single wing-finger, Padian did not name it. The ratio of wing-phalanx 3/wing-phalanx 2, compared to those of *Peteinosaurus*, *Eudimorphodon* and *Dimorphodon*, and the stratigraphic occurrence in a series of Norian shaly limestones below those of Cene (Zambelli, pers. comm.), leads me to confirm Padian's view: 1. that the pterosaur wing from Endenna represents a new rhamphorhynchoid pterosaur and 2. that it is very probably conspecific with *Preondactylus buffarinii*.

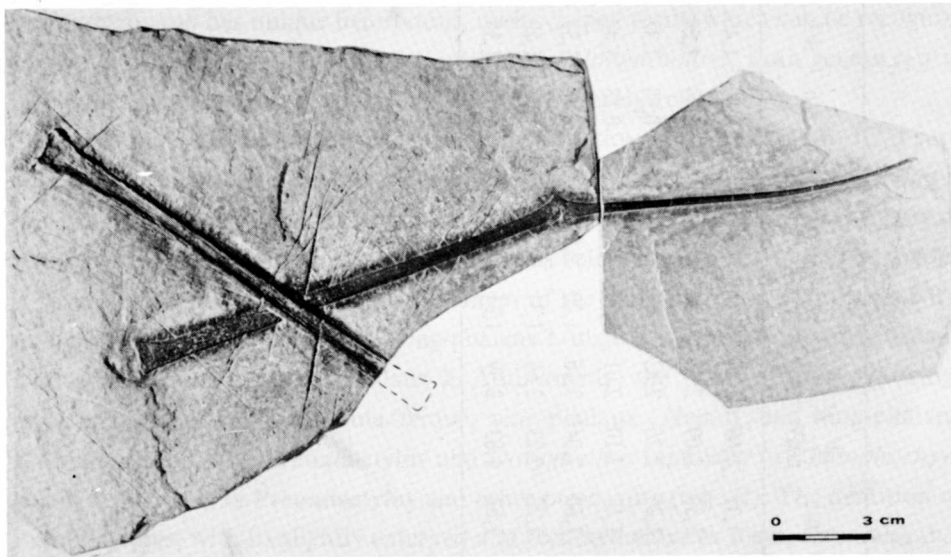


Fig. 4 - Cf. *Preondactylus buffarinii* n. gen., n. sp.; no. 4562 MCSNB. Incomplete wing-finger, Norian, Endenna, province of Bergamo, Italy.
- Cf. *Preondactylus buffarinii* n. gen., n. sp.; n. 4562 MCSNB. Dito alare incompleto, Noriano, Endenna, provincia di Bergamo, Italia.

A restudy of that specimen, after thorough preparation and a more exact fitting of both pieces of the slab (fig. 4), essentially confirms Padian's data: wing-phalanx 4 = 107 mm, wing-phalanx 3 = 134 mm and the incomplete wing-phalanx 2 = 123 mm. The width of the shaft of the wing-phalanx 2 at the fracture is 7 mm, the minimal width, however — 70 mm behind the proximal end of the bone — is 6 mm. This shows that the shaft is slightly expanded towards its distal end and that this must have been laid short behind the fracture. Compared with the corresponding wing-phalanx 2 of other pterosaurs, the length of the complete bone must have reached at least 130 mm and at the most about 150 mm (see also PADIAN, 1980: 123, tab. II). The length of this wing-phalanx was most probably 140 mm (fig. 4), what corresponds with Padian's result, achieved by means of the ratio method. The comparison of the ratio of wing-phalanx 3/wing-phalanx 2 in the type of *Preondactylus buffarinii* with the corresponding ratios in *Eudimorphodon*, *Peteinosaurus*, *Dimorphodon* (PADIAN, 1983a: 6), *Dorygnathus*, *Campylognathoides*, *Rhamphorhynchus* and of the Endenna specimen shows that the latter must be assigned most probably to *Preondactylus* (tab. III). Since the type of *Preondactylus buffarinii* and the Endenna specimen differ in size and the latter pterosaur is known only by an incompletely preserved wing, it is defined as cf. *Preondactylus buffarinii*.

Genus or species	wph 3/wph 2
<i>Preondactylus buffarinii</i> ; no. 1770 MFSN	1,00
cfr. <i>Preondactylus buffarinii</i> ; no. 4562 MCSNB	0,96
<i>Eudimorphodon ranzii</i> *	1,09
<i>Peteinosaurus zambellii</i> *	1,08
<i>Dimorphodon macronyx</i> **	1,16
<i>Campylognathoides</i> *	0,89
<i>Dorygnathus</i> *	1,01
<i>Rhamphorhynchus</i> *	0,90

Table III - Ratios of wing-phalanx 3/wing-phalanx 2 (wph 3/wph 2) of the specimens mentioned in the text. *) = After WILD (1978: 245, tab. 8, according to OWEN 1870 and WELLNHOFER 1975); **) = after WILD (1978) and PADIAN (1983a: 6, tab. 1).
- *Rapporti falange alare 3/falange alare 2 (wph 3/wph 2) negli esemplari citati nel testo.* *) = Dopo WILD (1978: 245, tab. 8, in accordo con OWEN 1870 e WELLNHOFER 1975); **) = dopo WILD (1978) e PADIAN (1983a: 6, tab. 1).

Conclusions

With regard to the long hind-limb and short wing, *Preondactylus* is the most primitive pterosaur known up to now. The femur has the same length as the humerus and the tibia has almost twice the length of the humerus. The tibia exceeds not only the lower arm, but also each single wing-phalanx. This is also found in *Peteinosaurus*, but not in such an extent as in *Preondactylus*. The ratio of the length of the complete wing-finger to that of the humerus (as a measure for size and growth in pterosaurs according to WELLNHOFER 1968: 119 and 1974: 28) is 2,36 in *Preondactylus* and 4,35 in *Peteinosaurus*. These ratios and those of the wing-phalanx 3/wing-phalanx 2, wing-phalanx 3/wing-phalanx 1 and wing-phalanx 2/wing-phalanx 1 in *Preondactylus*, *Peteinosaurus* and *Dimorphodon*, as the most ancestral pterosaurs (the last wing-phalanx can be ignored, since its length varies at the free end) demonstrate: 1. That the elongated hind-limb is a primitive character, derived from their ancestors; 2. That the development of the wing by elongation of the wing-bones starts distally and runs proximally. In geological younger pterosaurs are not only elongated the proximal wing-phalanges, but also the wing-metacarpal and lower arm.

The long hind-limb and short wing of early pterosaurs raises the question of a terrestrial origin of flight in pterosaurs versus the more conservative arboreal theory. PADIAN (1983a, b; 1984) is the opinion that the flight in pterosaurs evolved from early bipedal theropods in a stage of transition from thecodonts to dinosaurs. His conclusion is based on the proportions of the hind-limb, the elongated metatarsals, the length of the tibia, the supposed parasagittal gait (contra WELLNHOFER, 1975, 1978) and digitigrade stance, the morphology of the femur with a distinct head, the supposed ventrally closed pelvis (contra WELLNHOFER s.o.), the bird-like knee-joint, the mesotarsal ankle and the reduction of the fibula already in early pterosaurs, as for example in *Dimorphodon*. Nearly all these characters are found in the advanced Upper Triassic thecodonts *Lagosuchus*, *Lagerpeton* (regarding the geological age of these genera, see PADIAN 1984: 164) and *Scleromochlus*. Unfortunately these thecodonts are very incompletely preserved. *Lagosuchus* and *Lagerpeton* are almost only known by the hind-limb and pelvis (ROMER, 1971, 1972a). *Scleromochlus* is inadequately described (ROMER, 1972b versus v. HUENE, 1914). Its geological age is Norian. At about the same time already three distinct groups of pterosaurs, early rhamphorhynchids, the dimorphodontids and the eudimorphodontids, were present. Therefore, *Scleromochlus* cannot be considered as an ancestor of pterosaurs, despite

its small size, large skull and elongated hind-limb. Furthermore the hand in *Scleromochlus* differs from that in early pterosaurs by its very small size, in the number of phalanges and the very short fourth finger (v. HUENE, 1914: 8; fig. 15, 16). The neck-vertebrae of *Scleromochlus* are shorter than the dorsals, quite distinct from what can be seen in pterosaurs. The few data and the geological age of *Scleromochlus* seem to be not sufficient at present for a detailed comparison with pterosaurs, to solve the problem of their origin.

The opposite view of an arboreal origin of pterosaurs was first expressed by v. HUENE in 1914 in his study on *Scleromochlus*. I also assume an arboreal (or better climbing) «prae-pterosaurian» stage in the evolution of flight in pterosaurs, since I believe that flight could have evolved only by falling, as the most simple form of flying. There seem to be relationships between pterosaurs and eosuchians (including the prolacertilians) in a number of characters, which are, to a great extent, not known in thecodonts, or only found in proterosuchians, which are too specialized to give rise to the pterosaurs: small size, since only small animals can take to the air; quadrate streptostylic; pterygoid bearing teeth; teeth of the jaws multi-cusped; dentition sub-theodont; lower jaw with coronoid; no external mandibular fenestra; elongated neck vertebrae; bony sternum or sternal plates; elongated fourth finger; ankle mesotarsal; metatarsal V hooked; fifth toe opposable (WILD, 1984). Eosuchians and their descendants do not have an antorbital opening. But there are advanced forms in the transition stage from eosuchians to archosaurs, which may have developed such a fenestra, as is supposed in *Heleosaurus* (CARROLL, 1976: 71 ff.). The much longer hind-limb than the fore-limb in bipedal thecodonts, as *Lagosuchus* and *Lagerpeton* and also in early pterosaurs, is — in my opinion — an ancestral feature, derived from the eosuchians. It is known in all archosaurs and lepidosaurs, which undoubtedly descended from the eosuchians. The erect stance and gait in pterosaurs cannot be bound conclusively to the «dinosaurian-avian» bipedality sensu PADIAN (1984), since this kind of stance and locomotion was evolved several times and independently in earth history, not only in different groups of archosaurs (PARRISH, 1984), but for example also in mammals.

The Triassic pterosaurs, too, possess sharp-pointed, «hooked» claws at the first three digits of the hand. These claws are compressed laterally, are slightly expanded dorsally and keeled ventrally. They have twice the length of the claws of the feet, which are only slightly «hooked» (WELLNHOFER, 1978: 27). This can be seen in all pterosaurs. Compared with climbing claws in birds, lacertilians and mammals, there

