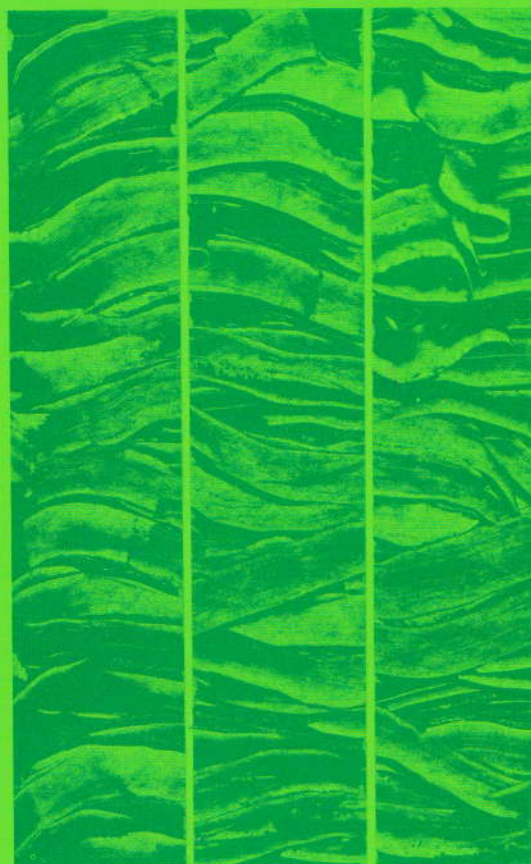


TWO HUNDRED YEARS OF PTEROSAURS

A symposium on the anatomy,
evolution, palaeobiology and environments
of Mesozoic Flying Reptiles

Toulouse, France
September 5-8, 2001



UNIVERSITE PAUL SABATIER - TOULOUSE III

Laboratoire de Dynamique des Bassins sédimentaires

S T R A T A

Série 1 - vol. 11

TWO HUNDRED YEARS OF PTEROSAURS

**A symposium on the anatomy,
evolution, palaeobiology and environments
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Réunion spécialisée

**de la Société Géologique de France,
de l'Association Paléontologique Française (APF),
de l'Association des Géologues du Sud-ouest (AGSO)
et des Associations Dinosauria et Paleo-Aquitania**

organisée par

**l'Université Paul Sabatier
Le Muséum d'Histoire Naturelle de Toulouse**

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PROGRAM

Tuesday 04th September

Afternoon (from 2 to 6 pm) : registration at the Muséum d'Histoire Naturelle de Toulouse.

06h30 pm : reception at the Toulouse City Hall

Wednesday 05th September

Morning session

Chairmen - Jean-Michel MAZIN and Eric BUFFETAUT

10.00-11.00 : Opening session

11.00-12.00 : Peter WELLNHOFER - Two hundred years of pterosaur research - a historical review.

12.00-14.00 **Lunch**

Afternoon session

Chairman - David MARTILL

14.00-14.30 : Natalie N. BAKHURINA - Hunting pterosaurs in Mongolia

14.30-15.00 : Alexander KELLNER - Pterosaurs of Gondwana

15.00-15.30 : Peter WELLNHOFER - A new Triassic pterosaur from the Northern Calcareous Alps.

15.30-16.00 : Eric BUFFETAUT, Dan GRIGORESCU & Zoltan CSIKI - Giant pterosaurs from the Maastrichtian of Romania

16.00-16.30 **tea-coffee**

16.30-17.00 : Fabio M.DALLA VECCHIA - Triassic pterosaurs : unravelling the puzzle

17.00-17.30 : Niels BONDE & Per CHRISTIANSEN - Anatomy and phylogenetic relationships of a Late Jurassic pterosaur from the Solnhofen limestone.

17.30-18.30 : Poster session

20.00 **Symposium Dinner**

Thursday 06th September

Morning session

Chairman - Dino FREY

09.00-09.30 : S. Christopher BENNETT - The evolution of the pterosaurian pectoral girdle

09.30-10.00 : David PETERS - The secondary sexual characteristic theory of pterosaur wing development

10.00-10.30 : David M.UNWIN - Pterosaur soft tissues: evidence, anatomy and palaeobiological significance

10.30-11.00 **tea-coffee**

11.00-11.30 : Lorna STEEL - Pterosaur bone histology : a re-examination of some of the earliest histological sections

11.30-12.00 : Deborah WHARTON - The pterosaur brain: an alternative view

12.00-13.30 **Lunch**

Afternoon session*Chairman - Christopher BENNETT*

- 13.30-14.00 : Carolina FUENTES VIDARTE, Federico MEIJIDE FUENTES, Manuel MEIJIDE CALVO - New Pterosaur traces in Spanish Lower Cretaceous (Berriasian, Oncala Mountain Range, Soria, Spain)
- 14.00-14.30 : Rubén A. RODRÍGUEZ-de la ROSA - Pterosaur tracks from the late Cretaceous of Northern Mexico: paleoecological and anatomical implications
- 14.30-15.00 : Jean-Michel MAZIN, Jean-Paul BILLON-BRUYAT, Pierre HANTZPERGUE & Gérard LAFAURIE - The Pterosaurian trackways of Crayssac (Lower Tithonian, south western France).
- 15.00-16.00 : film projection: "The Pterosaur Beach of Crayssac" (English version).
- 16.00-16.30 *tea-coffee*
- 17.30-24.00 : fieldtrip to "the Pterosaur Beach of Crayssac"

Friday 07th September**Morning session***Chairman - David UNWIN*

- 09.30-10.00 : Jean-Paul BILLON-BRUYAT & Jean-Michel MAZIN - What did pterosaurs on the coast of Crayssac (Lower Tithonian, SW France) ?
- 10.00-10.30 : Eberhard "Dino" FREY, H. TISCHLINGER, Marie-Céline BUCHY & David M. MARTILL - With bristles, claws and vessels - pterosaurs (almost) alive
- 10.30-11.00 *tea-coffee*
- 11.00-11.30 : Michael FASTNACHT, Natascha Heß, Eberhard FREY & Hans-Peter WEISER - Bites, Crests and Forces : how to engineer a pterosaur skull
- 11.30-12.00 : Matthew T. WILKINSON & Charles P. ELLINGTON - Gliding performance of Lower Cretaceous pterosaurs
- 12.00-14.00 *Lunch*

Afternoon session*Chairman - Peter WELLNHOFER*

- 14.15-15.00 : PADIAN Kevin - An integrative approach to pterosaurian locomotion
- 15.00-15.30 : ELVIDGE Daniel J & David M. UNWIN - A morphometric analysis of the hind limb of Pterosaurs
- 15.30-16.00 : Eberhard "Dino" FREY, Marie-Céline BUCHY & David M. MARTILL - "Schulter-" and "Tiefdecker" in pterosaurs continued: surprising consequences for flying and walking
- 16.00-16.30 *tea-coffee*
- 16.30-17.00 : Donald HENDERSON & David M. UNWIN - Investigating hypotheses of rhamphorhynchid pterosaur terrestrial locomotion with computer models.
- 17.00-17.30 : Jean-Michel MAZIN, Jean-Paul BILLON-BRUYAT & Pierre ROLLER - If they did, they were able to do it! A computational reconstruction of pterodactyloid terrestrial locomotion from trackways
- 20.00 : Public conference at the Museum d'Histoire Naturelle de Toulouse (in French and English)

Saturday 08th September

09.00-10.00 : Informal discussion and congress closure

10.00 : Fieldtrip to Espéraza.

POSTERS

BILLON-BRUYAT Jean-Paul, Eric BUFFETAUT & Dominique ABIT - New occurrence of pterosaur remains in the latest Jurassic of western France

BUFFETAUT Eric & Giovanni PINNA - First Late Cretaceous pterosaur from Italy: a metacarpian from the Santonian of the Trieste region

CLOWARD Karen & Kenneth CARPENTER - A new Scaphognathine (Rhamphorhynchidae) pterosaur from the Upper Jurassic Morrison Formation, USA

HENDERSON Donald & David M. UNWIN - Mathematical and computational modelling of a walking pterodactyloid pterosaur

JOUE Stéphane - Description of a *Ctenochasma* braincase, with systematic revision of Pterodactyloidea from the Tithonian of Germany and France

KNOLL Fabien - French Pterosaurs

MAZIN Jean-Michel, Jean-Paul BILLON-BRUYAT, Pierre HANTZPERGUE & Gérard LAFAURIE - Could they be the first rhamphorhynchid tracks? Yes!

MAZIN Jean-Michel, Eric BUFFETAUT & Jean-Paul BILLON-BRUYAT - A review of French Pterosaurs

PEREDA SUBERBIOLA Xabier, Nathalie BARDET, Stéphane JOUE & Sidi Mohammed IAROCHÈNE - The first pterosaur remains from the Latest Cretaceous Phosphates of Morocco

RENESTO Silvio - Gliding drepanosaurids: a case history

SANGSTER Sarah - Anatomy, Functional Morphology and Systematics of *Dimorphodon*

VULLO Romain - Two isolated teeth of pterosaurs from the Upper Jurassic (Lower Kimmeridgian) of La Rochelle (Charente-Maritime, western France).

FIELDTRIP TO THE PTEROSAUR BEACH OF CRAYSSAC (LOT)
EXCURSION SCIENTIFIQUE
SUR "LA PLAGE AUX PTEROSAURES DE CRAYSSAC" (LOT)

Thursday 06th September

Program

17.30 : travel from Toulouse to Crayssac by coach (around 1 h 30)
 19.15 : reception by the local authorities
 20.00 : presentation of the site (geology, sedimentology, history of the discoveries...)
 20.30 : "field dinner"
 21.30 - 24.00 : nocturnal visit and observation of the trackways and may be
 (probably!) your own discovery of a pterosaurian track...

 midnight : back to Toulouse.

FIELDTRIP TO THE ESPÉRAZA DINOSAUR MUSEUM (AUDE)
EXCURSION SCIENTIFIQUE
AU MUSEE DES DINOSAURES D'ESPERAZA (AUDE)

Saturday 08th September

Program

10.30 : travel from Toulouse to Espérazza by coach (about 1 h 30)
 12.00 : visit of the Espérazza Dinosaur Muséum
 13.00 : lunch in a local restaurant
 14.30: visit of a nearby fossil locality
 17.00 : back to Toulouse (arrival around 18.30).

FOREWORD

In 1801, Georges Cuvier interpreted a small skeleton from the lithographic limestones of northern Bavaria, which Collini had previously described as a marine animal, as that of a flying reptile. In the two hundred years that have elapsed since Cuvier's brilliant anatomical interpretation, pterosaurs have been found in many parts of the world, and their fossil record spans a large part of the Mesozoic era, from their emergence in the Triassic to their extinction at the Cretaceous-Tertiary boundary. Although Cuvier's "ptérodactyle" long remained the archetypal pterosaur, we now know that they came in all sizes, from that of a sparrow to that of a small airplane, and in many shapes, and the great diversity of pterosaurs is becoming more and more apparent as sometimes bizarre new forms are described. In addition, few other groups of extinct vertebrates have prompted so much speculation about their biology and mode of life. The long-enduring controversies about pterosaur locomotion have not yet come to a close, despite remarkable recent advances, notably in the field of ichnology.

The abstracts in this volume have been prepared on the occasion of a symposium held in Toulouse in September 2001 on the occasion of the 200th anniversary of Cuvier's identification of the "ptérodactyle". In the diversity of their approaches, they testify to the vitality of pterosaur research, and also give some idea of the unresolved problems which this remarkable group of extinct vertebrates still poses.

We would like to dedicate this symposium to our friend Peter Wellnhofer, who for the last thirty years has probably contributed more than anybody else to the progress and development of pterosaur research. He does us the great pleasure to attend this symposium and to present both some of the results of his current research and a historical review of research on pterosaurs. His work has been a constant source of inspiration to us and no doubt to all participants.

The Organisers

The authors are fully responsible for the form and contents of the abstracts in this volume. The organisers are grateful to Mrs Ronchini (Toulouse) for her help in the preparation of the abstracts volume.

HUNTING PTEROSAURS IN MONGOLIA

Natalie N. BAKHURINA

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Mesozoic sediments in the People's Republic of Mongolia have yielded many important remains of continental vertebrates including turtles, lizards, dinosaurs, birds, early mammals and pterosaurs. Pterosaurs have been recovered from three localities: Bakhar, in south central Mongolia, Tatal in western Mongolia and Hüren Dukh in central Mongolia (Bakhurina & Unwin 1995, Unwin & Bakhurina 2000). A tiny 'rhamphorhynchoid', possibly belonging to the Anurognathidae, was found in Middle Jurassic lake sediments at Bakhar by A. Ponomarenko. Early Cretaceous lacustrine beds at Tatal have yielded many well preserved, uncrushed bones of a medium-sized dsungaripterid (Bakhurina 1982, 1983, 1986) closely related to *Dsungaripterus* from Xinjiang, China. Finally, a large 5.5 m wingspan ornithocheirid represented by parts of the skull, spinal column and most of the principal limb bones was found in late Early Cretaceous sediments at Hüren Dukh by P. Narmandakh.

The Tatal locality is highly unusual from a taphonomical point of view because the fossil vertebrate assemblage is completely dominated by pterosaur remains, which occur in large numbers and are often well preserved. The first pterosaur remains were found in 1970 by the geologists V. Shuvalov and P. Khosbayar, but were not correctly identified until later (Bakhurina 1982). In 1979 Bakhurina was able to make a short visit to the Tatal area, a remote region of Western Mongolia, only after agreeing to cook for a team of seven for a whole field season, but the group did not find any pterosaur bones on this occasion.

In 1981 Bakhurina had the opportunity to lead a small group (part of the Joint Soviet-Mongolian Palaeontological Expedition) to search for Mesozoic fossil vertebrates, especially pterosaurs, in West Mongolia. Apart from the author, the five strong team included Igor Amelin, a skilful preparator, very experienced in the field and also an artist, Irina Martynova, a sculptor, and the late Nikolai Radkevitch, a driver, and Zinaida Shalneva, a cook, both with many years of experience in the field.

After a few days of unsuccessful exploration in the Tatal area, a tiny, two millimetre long pterosaur bone fragment, part of a carpal, was found by Irina in a surface wash. A few hours later Igor found a fragmentary tibia preserved 'in situ'. The pterosaur locality was established (Bakhurina, 1983). Later on, prospecting in a different level about 100 m away, Irina noticed a fragment of bone peeping out of the sediment which, after recovery, turned out to be a complete humerus. And, to his great surprise, Nikolai, when coming to collect the team to take them back to camp for supper, suddenly found himself standing on a pterosaur wing-finger. During this season the team explored outcrops across the entire area of Tatal, locating at least five or six different horizons with pterosaur remains. As a result, numerous remains, mainly the articular ends of postcranial bones, best able to withstand weathering and thus be preserved, were collected.

In 1982 a group of six, including the late Namsrai-Gua, an experienced and skilful Mongolian preparator and writer, Igor Amelin and the author made a second visit to Tatal. On the very first day Namsrai-Gua found elongate wing-finger bones preserved 'in situ' and this site became the main focus for excavation during this season. Intensive collecting yielded a superb, well preserved only slightly compressed skull and lower jaw, and other fragments of skulls, jaws, vertebrae, wings, pelves and hind limbs (Bakhurina 1986, 1993, Bakhurina & Unwin 1995). Generally the bones were disarticulated, but in some cases had not been transported far. Remains of psittacosaur, a theropod, a sauropod and a lizard were also found in the same sediments.

On both visits to Tatal, during travel to and from the locality and back to Ulaanbaatar, and even during the excavations, the weather was exceptionally bad: heavy rain, hail and sand storms met the expedition everywhere. There was even an outbreak of Black Death in the region, although we were unaware of this until later. Collecting fragile material in such conditions was a strenuous task. We depended on every hour of good weather to expose the fossil bones and to let them dry, but often had to protect them by covering them up or urgently removing them so that they were not destroyed by the sudden appearance of 'mu baina' (bad weather). On some occasions it was only enough to sneeze for the paper thin walls of the bones to disappear.

The success of these two field seasons was possible thanks to the great enthusiasm of everybody involved and also to support and encouragement from the late Valerii Reshetov, Ekaterina Dmitrieva, Rinchen Barsbold, Alexander Tyuvaev, Leonid Tatarinov and Vladimir Zhegallo.

Finally, in 1989, a group of Mongolian palaeontologists, including the late Namsrai-Gua and Altangerel Perle revisited Tatal and collected further pterosaur material including an associated, but incomplete skeleton of a small individual. Tatal was not the only locality at which Namsrai-Gua collected pterosaurs. In 1982 he took part in the collection of the pterodactylid from

Hüren Dukh and, as we were astonished to learn during our work at Tatal, had also been involved in the discovery, in the mid-1960s, of Sordes from the Late Jurassic of Kazakhstan.

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THE EVOLUTION OF THE PTEROSAURIAN PECTORAL GIRDLE

S. Christopher BENNETT

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The pectoral girdle of basal pterosaurs (e.g., *Eudimorphodon*, *Peteinosaurus*) consisted of a long strap-like scapula that passed posteriorly over the ribcage, an elongate strut-like coracoid that articulated with the sternum, the scapula and coracoid fused at an acute angle and together forming a deep saddle-shaped glenoid fossa for articulation with the humerus, and a broad sternum formed of coossified paired clavicles, interclavicle, and paired sternal plates (Wild, 1978, 1993). The pectoral girdle is superficially similar to that of extant birds (e.g., *Aquila*, *Corvus*), and that similarity lead to it being interpreted as functionally like that of birds (Padian, 1983a, b). It was proposed that *M. supracoracoideus*, originating on the coracoid and sternum and having the direction of its pull reversed by a pulley-like acrocoracoid process, was the primary elevator of the wing in pterosaurs, and therefore the dorsal muscles of the pectoral girdle were relatively unimportant. This interpretation has been generally accepted, yet has not been examined critically.

The essential morphology of the pterosaurian pectoral girdle did not change as the pterodactyls evolved and eventually replaced the rhamphorhynchoids. However, in the large pterodactyls the pectoral girdle was modified from the condition in basal pterosaurs in that the posterior end of the scapula was rotated medially and articulated with the notarium formed of fused anterior dorsal vertebrae. Although this unusual condition was first described over 100 years ago (Marsh, 1876; Seeley, 1891), little has been done to understand its functional morphology and it is generally described as simply strengthening the pectoral girdle.

I reconstructed the pectoral musculature of representative pterosaurs in order to examine the functional morphology of the basal pterosaurian pectoral girdle and the structural and functional changes that took place during the evolution of the advanced pectoral girdle of large pterodactyls. The reconstructions were based on comparisons of pterosaurian pectoral osteology and muscle and ligament attachment scars with the known osteology and myology of extant archosauromorphs.

The reconstruction of the pectoral musculature of a representative basal pterosaur (*Campylognathoides*) suggests that *M. supracoracoideus* was not an elevator of the wing, but instead depressed and flexed the humerus anteriorly as in extant non-avian archosauromorphs. Wing elevation apparently relied on *M. deltoideus* and other dorsal muscles of the pectoral girdle. Thus, the pterosaurian pectoral girdle was not functionally like that of extant birds.

The reconstruction of the pectoral musculature of a representative large pterosaur with an advanced pectoral girdle (*Anhanguera*) suggests that the rotation of the scapula straightened the pull of *M. deltoideus*, improving its function in wing elevation. Likewise, the reconstruction suggests that the scapulonotarial joint would have permitted the scapula to act as a strut to resist compressive forces of muscles originating on the vertebral column and inserting on the humerus. As such it would mirror the function of the coracoid in resisting compressive forces of sternal muscles inserting on the humerus. It is probable that without the scapula braced against the vertebral column the great forces produced by wing elevators originating on the vertebral column could have pulled the scapulocoracoid medially and produced undesirable deformations of the ribcage. I argue that selection for improved function of *M. deltoideus* in wing elevation lead to medial rotation of the scapula. Subsequently, the approximation of the scapula and notarium lead to fixation of the posterior end of the scapula to the third and fourth notarial vertebrae, and finally to the evolution of a synovial joint between the scapula and supraneural plate of the notarium.

The advanced pectoral girdle of large pterodactyloids has been viewed either as a synapomorphy of a single clade of large pterodactyloids or as a correlate of large body size that evolved in parallel in several separate lineages of pterosaurs. Cladistic analyses that included pectoral characters (Bennett, 1989; Kellner, 1996) support a single origin of the advanced pectoral girdle, whereas cladistic analyses that excluded pectoral characters based on the *a priori* assumption that the advanced pectoral girdle might have evolved in parallel (Unwin, 1995; Unwin and Lü, 1997) support multiple origins of the advanced pectoral girdle. At present, no other evidence suggests that the advanced pectoral girdle evolved independently in several lineages of pterosaurs, and the distribution of other postcranial characters (e.g., exapophysial articulations, notarium) supports the interpretation of the advanced pectoral girdle as a synapomorphy of a single clade of large pterodactyloids.

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WHAT DID PTEROSAURS ON THE COAST OF CRAYSSAC (LOWER TITHONIAN, SW FRANCE) ?

Jean-Paul BILLON-BRUYAT & Jean-Michel MAZIN

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The Crayssac site (Lower Tithonian, Lot, southwestern France), corresponds to an ancient mudflat situated in the intertidal area. It reveals an abundant marine and continental fauna (near than fifty taxa and ichnotaxa), including a rich arthropodian and reptilian ichnofauna (trackways of turtles, crocodilians, pterosaurs and theropod dinosaurs). Vertebrate bones (fish, crocodilians...) are frequently excavated, but the pterosaur ones are scarce and isolated.

Conversely, pterosaurian ichnites are the most common, with hundreds of isolated prints and more than twenty trackways, made by quadruped pterosaurs. Numerous but also well diversified, these trackways lead to identify five ichnospecies (*cf.* Mazin & Billon-Bruyat in this volume): four assigned to pterodactyloids and one to a rhamphorhynchid. According to the print and trackway measurements, trackmakers range from sparrow- to seagull-sized pterosaurs. A very well preserved fourth metacarpal has been found, indicating the presence of a large pterosaur with a wing span close to three meters, but any matching print has been discovered.

Trackways are first hand evidence of biological activity in their original position, an autochthony which proves the presence of pterosaurs at low tide in this intertidal area. Moreover, pterosaur trackways occur on each excavation bed, which indicates their regular frequentation of this environment. Also, different pterodactyloid ichnospecies occur on the same surface which suggests the simultaneous presence of several species. Several footprints present impressions of webs between the toes, like skin traces described on some pterosaur foot skeletons (Wellnhofer 1991), an adaptation to life in water as in swimming birds (Kardong 1998, Kristoffersen 2001).

What did pterosaurs in this coastal environment? The most obvious reason seems for foraging, with an abundance of pterosaurian populations linked to the availability of important marine food resources, as in extant marine vertebrates (Duhamel 2001). Pterosaurs could feed on mudflat- and aground-preys at low tide, with a potential diet composed of fish, crustaceans, molluscs, etc.. The trackways demonstrate an important range of gaits (standing around, walking, running), which is not inconsistent with foraging. Up to now, no "feeding-mark", for example pick- or burrow-traces, has been observed.

The position of pterosaurs in these coastal trophic levels, chains and web of Crayssac is difficult to precise but the absence of preserved plants shows that the role of pterosaurs in the food web is exclusively that of predators (opportunistic or specialized), or scavengers. It is noteworthy that pterosaur dentition shows that all known pterosaurs are supposed to be carnivorous (Wellnhofer 1991), and that no one extant sea birds is herbivorous (Hémery 2001). Conversely, pterosaurs were probably themselves targeted by other predators (theropod dinosaurs, crocodilians), even so no predation trace is discernible on the rare pterosaur bones.

Were they regular visitors or seashore-dwellers? There is no direct evidence to answer but the potential marine food resources suppose that these pterosaurs could depend exclusively on sea resources for feeding, a fundamental energetic criterion defining certain extant birds as sea birds (Hémery 2001). In this way, "sea pterosaurs" can be recognized. Extant sea birds can be encountered in three main biogeographical zones (Hémery 2001): the littoral zone (birds which remain close to and in sight of the shoreline), the neritic or inshore zone (birds which can stay several months above the continental shelf without returning to land) and the oceanic or offshore zone (birds which live beyond the continental shelf and return to land just for breeding). Inshore and offshore birds have physiologic and morphologic features to feed and stay a long time in salt water (e.g. salt glands, hydrophobic body covering, endothermy). As far as known, such characteristics have never been recognized from pterosaur fossils. According to that, the pterosaurs of Crayssac can be tentatively assimilated to shore-dwellers.

The numerous and diversified trackways of Crayssac demonstrate clearly a high frequentation of small- to middle-sized pterodactyloid pterosaurs in an ancient intertidal area. Predators or scavengers, they could be on the ground to feed on mudflat- and aground-preys at low tide. Probably seashore-dwellers, the coastal life style of pterosaurs revealed by the trackways of Crayssac appears complementary to the data given by fossils such Solnhofen skeletons.

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NEW OCCURRENCE OF PTEROSAUR REMAINS IN THE LATEST JURASSIC OF WESTERN FRANCE

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Pterosaur finds have been numerous in the Late Jurassic of western France during the last decade (see the review of French pterosaurs, Mazin *et al.*, this volume), resulting both from professional systematic excavations and amateur discoveries. We report here hollow bones identifiable as pterosaurian (distal end of an ulna, proximal end of a first flight digit phalanx, distal end of a femur, and shaft fragments), from the Tithonian of the Atlantic island of Oléron (Charente-Maritime), belonging to the private collection of one of us (D. A.).

Pterosaur specimens were discovered in two calcareous beds along the sea cliff (separated by a thickness of some 14m), at the northwestern tip of the island, more precisely at the locality known as "La pointe de Chassiron", corresponding to an ancient coastal environment, along the coast of the opening Atlantic ocean. This area has yielded abundant remains of marine and continental vertebrates, including fish, turtles, crocodilians, lepidosaurs, pterosaurs and theropod dinosaurs. The detrital elements show that water from a near land area flowed into this coastal depositional environment. Consequently, this fossiliferous accumulation reveals a taphocoenosis and the original habitat of the pterosaurs cannot be precisely defined. As the majority of other vertebrate fossils, pterosaur remains are isolated and incomplete. This fragmentation of pterosaur bones is the result of transport before burial (no predation traces are discernible), as suggested by the slight abrasion of articular regions and by the presence of several shaft debris.

The lower level has revealed a distal left ulna, a slightly bowed bone with a well preserved articular head and a clear but crushed groove for the radius. As described by Seeley (1901), the distal articular surface of the ulna "shows on the one margin a concavity, followed by a prominent boss, and an oblique articulation beyond the boss" (from medial to lateral side).

Laterally to this oblique articulation, a dorsally oriented crest is observable. The preserved length is 70 mm. The shaft width, at the proximal end of the bone, is 6.5 mm (dorsoventrally) and 10 mm (mediolaterally). The articular head width is 23.5mm. By comparison with the ulna of "*Pterodactylus*" *maximus* (from Kuhn 1967), the original length of the ulna can be estimated at some 200 mm, showing that a sizeable part is missing. Based on the length of the radius, which is very slightly shorter than the ulna, the specimen is comparable in size to "*Pterodactylus*" *grandis* (radius length 185 mm, Wellnhofer 1970), one of the largest Jurassic pterosaurs with a wing span of about 2.5 m.

In the upper level, two articular heads and four unidentified shaft fragments have been found. First, a proximal right first phalanx of a fourth (wing) finger, presenting the two bowled glenoid fossae to accommodate the typical pterosaurian pulley-like joint of the distal end of the fourth metacarpal. The bony wall of the shaft is damaged, but the internal cast clearly shows that the cross-section is triangular and that there is no longitudinal furrow on the flight membrane side, which permits to assign this phalanx to the Pterodactyloidea. The preserved length is 41mm. The shaft width cannot be precisely measured because of the missing parts of the bony wall, but an estimate leads to 6 mm (dorsoventrally) and 10 mm (mediolaterally). The width of the articular head is 22.5 mm. Compared to the first flight digit phalanx of *Dsungaripterus* (from Wellnhofer 1978), the original length of the phalanx can be estimated at some 210mm, meaning that a sizeable part is missing. This length is comparable to *Pterodactylus longicollum* as well as to "*Pterodactylus*" *grandis* (Wellnhofer 1970), suggesting a wing span ranging from 1.45 to 2.5m.

The other identifiable bone from this level is a distal end of a left femur, curving slightly laterally and presenting the characteristic femoral distal joint, oriented ventrally to the longitudinal axis of the shaft. The two condyles are worn, separated by a well marked medially oriented incisura, and the external condyle presents a lateral prominence. The articular region appears somewhat offset medially to the shaft (in anterior view), because of a post mortem fracture on the shaft, filled with sediment. The preserved length is 31.5 mm. The shaft has a roughly circular cross-section, up to 5 mm in diameter. The width of the articular head is 11 mm. By comparison with the femur of *Pterodactylus longicollum* (Wellnhofer 1970), the original length of the femur can be estimated at some 80mm, showing that a sizeable part is missing and leading to an estimated wing span near 1m.

These three specimens indicate the presence of middle to large-sized pterosaurs in the Tithonian of western France, by comparison with other Late Jurassic forms (Wellnhofer 1991). This discovery also adds a western locality to the already wide geographical range of large pterosaurs in Europe during the Tithonian. The phalanx and the femur, found in the same bed, suggest the association of two individuals of significantly different sizes (respectively 1.45m to 2.5m and 1m in wing span), probably belonging to different species. The discovery of

numerous pterosaurian teeth (Mazin *et al.*, in prep.), will permit to improve our knowledge of the biodiversity of pterosaurs from Oléron island.

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FIRST CRETACEOUS PTEROSAUR FROM ITALY : A WING METACARPAL FROM THE SANTONIAN OF VILLAGGIO DEL PESCATORE (TRIESTE)

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Italy currently has the best record of Triassic pterosaurs in the world, but no pterosaur remains of a later age had hitherto been reported from that country. We report here the discovery of a typical wing metacarpal from the Santonian of Villaggio del Pescatore, near Duino (Trieste, northeastern Italy), which is the first record of a Cretaceous pterosaur from that country.

The specimen was found in the course of systematic excavations at a site which has also yielded fishes and remarkably preserved skeletons of crocodilians and hadrosaurian dinosaurs. The fossils are preserved on slabs of grey laminated limestones which appear to have been deposited in a lagoonal to lacustrine environment. The age of the deposit is considered as Santonian.

The only pterosaur specimen so far discovered is an isolated left fourth metacarpal, visible in posterior view on two slabs of limestone, missing the middle part of the shaft because of dissolution at the level of a crevice. The bone has undergone considerable compression, but its proximal and distal ends are sufficiently well preserved to warrant identification. The much compressed proximal end shows a proximal articular surface (with the carpus) which is perpendicular to the axis of the shaft, and a ventral ridge, the sharpness of which is clearly exaggerated by crushing. The distal end shows the typical pterosaurian pulley-like articular region for the first phalanx of the fourth digit. This is formed by two main prominent rounded condyles on the dorsal and ventral sides, with a third smaller condyle in the middle. This middle condyle appears to be absent in some pterosaurs, such as *Pteranodon* (Bennett, 2001), and present in others (see, for instance, Wellnhofer, 1991a, for a description of *Santanadactylus araripensis*, a species referred to *Anhangura* by Kellner & Tomida, 2000, in which this feature is present). A deep depression at the base of the middle condyle may correspond to a pneumatic foramen, as in *Pteranodon* (Bennett, 2001). The whole articular region is somewhat offset dorsally.

Although the specimen is clearly pterosaurian, a more precise attribution is made difficult by the fact that the middle part is missing so that the total length of the bone can only be estimated. What is left of the shaft shows that it tapered gradually, from a width of 26 mm at the proximal end to only 13 mm just proximal to the distal condyles (the width of the distal articular region is 20 mm). This suggests that a sizeable portion of the shaft is missing. Informations available about the circumstances of the find, taken together with the proportions of the proximal and distal parts, suggest that the missing part may have been about 100 mm in length, in which case the total length of the bone was probably about 190 mm. However, a greater length cannot be excluded.

Whatever its exact original length may have been, the metacarpal from Villaggio del Pescatore clearly was an elongated and slender bone, much longer than broad. This type of long wing metacarpal, which contrasts with the much shorter metacarpals of the "rhamphorhynchoids", is found in pterodactyloid pterosaurs, and there is no doubt that the specimen from Villaggio del Pescatore can be referred to the Pterodactyloidea. Several families of pterodactyloid pterosaurs, including the Ornithocheiridae, the Pteranodontidae, the Nyctosauridae and the Azhdarchidae, occurred in the later part of the Late Cretaceous (Wellnhofer, 1991), and identifying an isolated and incomplete metacarpal at the family level is not easy. It can only be hoped that further discoveries at Villaggio del Pescatore will provide more complete pterosaur material, which may warrant a more precise identification.



Fig.1 – Left fourth metacarpal of a pterosaur from the Santonian of Villaggio del Pescatore, Trieste, Italy (Museo Civico di Storia Naturale, Trieste). Ventral view. Scale bar : mm.

The wing span of the pterosaur from Villaggio del Pescatore can only be very roughly estimated, because of uncertainties about the original length of the metacarpal. Using the skeletal reconstruction of *Pteranodon* provided by Bennett (2001, fig.124) as a model, and supposing that the original length of the metacarpal was 190 mm, a wing span of 2.50 metres would seem likely. However, using pterodactyloids with a relatively shorter wing metacarpal as a basis for reconstruction results in higher wing span estimates. On the basis of the reconstruction of *Anhanguera piscator* by Kellner and Tomida (2000), an estimated wing span of about 3.80 m is obtained for the pterosaur from Villaggio del Pescatore. Obviously, it is not

easy to obtain a reliable wing span estimate on the basis of the scanty material available, but it appears that the pterosaur from Villaggio del Pescatore was at most a middle-sized animal, especially by comparison with the largest known Late Cretaceous pterosaurs.

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GIANT PTEROSAURS FROM THE UPPER CRETACEOUS OF TRANSYLVANIA (WESTERN ROMANIA)

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Pterosaur remains have already been reported from the Upper Cretaceous of Transylvania (western Romania), but have not been described in detail, and are not unusually large. We report the discovery in the Maastrichtian of Transylvania of uncrushed cranial and postcranial bones of gigantic pterosaurs, which may have exceeded the size of *Quetzalcoatlus northropi*, and are remarkable for the robustness of the skull bones. The best material consists of associated skull elements (occiput, right suspensorium), an incomplete left humerus and unidentified bone fragments, clearly belonging to a single individual (palaeontological collection of the Faculty of Geology and Geophysics, University of Bucharest, n° FGGUB R1083.), from chocolate-coloured siltstones of the Densus-Ciula Formation at Valioara, in the northwestern part of the Hateg Basin of Transylvania. In addition, a 385 mm long femur (FGGUB R1625), lacking both articular ends, has been found in the Densus-Ciula Formation at Tustea, SE of Valioara. The Densus-Ciula Formation is referred to the late Maastrichtian on stratigraphical and palaeontological grounds (Grigorescu, 1992).

Because of their size, the skull elements from Valioara were previously misidentified as those of a large theropod dinosaur. However, the incomplete humerus is clearly pterosaurian, showing a large wing-shaped deltopectoral crest and the bases of the medial process and the articular head. The preserved proximal part is 236 mm long, with a maximum shaft diameter of 90 mm. The skull bones, including parts of the right quadrate, pterygoid, quadratojugal and jugal, and the posterior part of the braincase, also show distinctive pterosaur features. The articular region for the mandible on the quadrate is helical, with an oblique groove separating two offset, rounded condyles. This peculiar type of jaw articulation is known in various pterosaurs (Wellnhofer, 1980). Lateral to the quadrate articulation, the thin plate-like quadratojugal and part of the jugal are preserved; the jugal shows the ventral edge of a very large infratemporal fenestra. Medial to the articulation, the pterygoid process of the quadrate merges into the pterygoid; no suture is visible, and the bones were very firmly fused. The pterygoid forms a robust rod of bone, some 45 mm in diameter, which is bifurcated anteromedially to form the bevelled posterior border of the choana. The posterior part of the palate was highly vaulted. The individual bones of the remarkably massive occiput are completely fused. The occipital condyle is hemispherical and its diameter (55 mm) is greater than that of the foramen magnum (43 mm). Ventrally, the basioccipital forms a transversely

concave rugose plate which provided an insertion for strong neck muscles. The supraoccipital bears a median ridge also indicating the insertion of powerful muscles. Above the strong paroccipital process, there is a large post-temporal opening, as usual in pterosaurs.

The humerus resembles that of the Azhdarchidae, with a long and gently curved deltopectoral crest unlike the distinctly warped crest of the Pteranodontidae, and a thickened proximal articular head. Comparison of the skull elements from Valioara with the Azhdarchidae is not easy, because the only azhdarchid in which some parts of the posterior region of the skull are known is *Quetzalcoatlus* sp., the "small" species of *Quetzalcoatlus*. In it, the skull is much more lightly built than in the Romanian form, and the articular surfaces of the lateral condyle of the quadrate are set at a marked angle, unlike the condition in the Valioara specimen. In the latter, the helical condyles of the quadrate are more reminiscent of the condition in *Pteranodon*, but they are even more smoothly rounded. In *Quetzalcoatlus* sp. there is a deep notch posterior to the lateral condyle, for the reception of a process on the posterolateral edge of the glenoid fossa of the mandible. No such notch is present on the specimen from Valioara. The Romanian pterosaur thus appears to be a very large non-pteranodontid pterosaur, with a jaw articulation markedly different from that of *Quetzalcoatlus*, which apparently justifies the erection of a new taxon.

The humerus from Valioara was probably as long as, or slightly longer than that of the type of *Quetzalcoatlus northropi* (540 mm). This suggests that the Romanian pterosaur had a wing span comparable to that of *Quetzalcoatlus northropi*. Wing span estimates for the latter range from 11 or 12 metres to 15 and even 20 metres. A conservative estimate of the wing span of the Romanian pterosaur would thus be about twelve metres or slightly more. The available material shows that the skull must have been about 500 mm wide at the level of the jaw articulation. On the basis of skull proportions in other long-snouted Late Cretaceous pterosaurs, an estimated total skull length of about 3 metres is suggested. The Romanian pterosaur thus would have had one of the longest skulls in any non-marine vertebrate.

Whereas pterosaur skulls are usually very lightly built, consisting of thin bony struts and plates, the skull of the Romanian pterosaur was robustly built, with stout bones bearing strong ridges for muscle insertions. It was doubtless made lighter by large openings, but the elements of the palate and occiput are remarkably large and robust, especially by comparison with other large pterosaurs such as pteranodontids and *Quetzalcoatlus* sp. It is generally accepted that very large pterosaurs such as *Pteranodon* were able to fly because the combination of a lightly built skeleton and a vast wing span resulted in low wing loading. The Romanian form had a much more robust skull than *Pteranodon*. Unless it was a flightless pterosaur, which seems unlikely because its humerus is very similar to that of normal flying pterosaurs, the weight of its huge skull must somehow have been reduced to enable it to take off. As this was not done by reducing the volume of the bones, the answer probably lies in their internal structure. In Late Cretaceous pterosaurs, pneumatisation of post-cranial elements is fairly well known, but details of skull pneumatisation are usually obscured by the widespread crushing affecting most

cranial remains, and little is known beyond the fact that the skull bones of pteranodontids consist of "thin plates with internal reticulate reinforcing ridges" (Bennett, 2001). In the uncrushed skull elements from Valioara, although the vacuities are now filled with matrix, the internal structure is well preserved. The outer layer is a thin compact cortex, usually less than one millimetre in thickness. Inside, the bones consist of very numerous, elongated alveoli, usually a few millimetres in width and up to more than 10 mm in length, separated from one another by a dense network of extremely thin bony trabeculae. The resulting unusual structure, consisting of numerous closely packed "cells", is rather reminiscent of expanded polystyrene, and like it probably provided a very light but rigid material forming robust, strain-resistant bones without inducing excessive weight. Apparently, this peculiar structure sufficiently reduced the weight of the skull to make flight possible for an animal with such an enormous head.

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ASPECTS OF THE DETAILED ANATOMY OF *RHAMPHORHYNCHUS*

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The Late Jurassic pterosaur *Rhamphorhynchus* sp. is common in the lithographic shales of Solnhofen (Late Jurassic: Tithonian) and is also found in slightly older strata of Southern Germany (Wellnhofer 1991), and several hundred have been collected over the years. The Solnhofen and several other bavarian localities are famous for the excellent state of preservation of many of the fossils, including flying creatures such as insects, pterosaurs and the Urvogel *Archaeopteryx*. Several of the better preserved pterosaurs have remains of soft tissues as well, including parts or all of the cheiropatagium. Previously 5 species of *Rhamphorhynchus* were recognized (Wellnhofer 1975a, b; 1991) but in recent years other researchers have questioned this number, considering many of the characters previously used to differentiate species as ontogenetic, and have assigned all to the species *R. muensteri* (Bennett 1995, 1996a; Unwin pers. comm. 2001). The current specimen is part of the collections of the Geological Museum in Copenhagen, and was originally assigned to *R. muensteri* by Wellnhofer (1975b) and, thus, whether or not the above view prevails, the species name of this particular specimen is going to remain unchanged. Wellnhofer (1975b: p. 155) noted that it was the hitherto smallest known specimen of *R. muensteri*, and the lack of fusion in several parts of the skeleton supports the notion that the specimen was not fully adult. For instance, several of the articulating facts of the long bones were not co-ossified with the shafts and the pubes and ischia have not fused into an ischiopubis. Other bones, however, particularly in the manus, appear much better ossified.

The largest collection of *Rhamphorhynchus* specimens is found in the Bayerische Staatssammlung in München, and many of these are well preserved. Nonetheless the present specimen reveals a plethora of anatomical details which cannot be recorded from most other specimens, in part due to the excellent state of preservation of the current specimen, but mainly due to the procedure in which it was prepared. Initially, the specimen was considered of limited value, mainly exposing the long flight finger and a seemingly insignificant scatter of bones. No soft parts appear to have been preserved, neither on the slab nor the counterslab. Accordingly, during a practical laboratory course in the early 1960'ties under the supervision of Dr. Eigil Nielsen, then the only vertebrate palaeontologist in Denmark, the slabs were prepared by the senior author, then a student, and the specimen exposed by Toombs' & Rixon's acetic acid (5-10%) transfer method after being encased in artificial resin.

Surprisingly, both slabs proved to contain a completely uncrushed, albeit disarticulated skeleton, in an exquisite state of preservation. The skeleton lacks, among others, the tail, one wing and smaller parts of the braincase, but apart from this most of the skull and the remainder of the postcranium are displayed three dimensionally and in great detail. The state of preservation and exposure is such that the skeleton looks near extant and despite the great thinness of most bones they do not appear particularly fragile. As a matter of fact when the specimen was taken out several ribs appeared slightly elastic. Subsequently a few bones have broken free, possibly due to vibrations caused by the subway running below the museum and due to the room in which the fossil has been on display for the past nearly 3 decades lacking humidity or temperature control. The latter factors are often a liability with acid prepared skeletons - even fragile skeletons of extant animals will suffer damage due to these factors. Only 3 other pterosaurs from the Solnhofen have been acid transfer prepared, and more recently, one less well preserved specimen in New York (Wellnhofer 1975b); additionally there are two incomplete and/or more crushed specimens of *R. longicaudus* in Copenhagen.

The Copenhagen *Rhamphorhynchus* is possibly the most well preserved pterosaur from the lithographic limestone, as also noted by Wellnhofer (1975b), and display a multitude of features hitherto unrecognized in this species. Among others is a large longitudinal muscle insertion on the humerus, possibly for attachment of the wing finger extensor muscles. In most other pterosaurs this scar is smaller, or a part of the epicondyle. The pelvis and sternum have been described in some detail and figured by Wellnhofer (1975a,b) and the exquisitely preserved vertebral column has also been discussed briefly. The cervical vertebral column is ventrally exposed, and show the central and zygapophysial articulations in great detail. Small exapophyses are present on some of the vertebrae. The pneumatization is extensive and in a vertebra where the lamella is not preserved it is possible to study the internal air chambers of the vertebra. Cervical pneumatization apparently was of the camerate type (Britt 1997) with large and relatively simple internal cavities. Such exquisite features are clearly impossible to expose by means of mechanical preparation. Large pneumatopores are visible below the transverse processes and extend into the hollow centra which are divided into a few elongate camerae, bordered by paper-thin bony walls. There is hardly any spongiosa proper left in the vertebra.

Most likely the camerae were filled by air diverticulae as in extant avialans, where the cervical vertebrae are pneumatized by diverticulae arising from the paired cervical airsacs, and this might also have been the case in pterosaurs. However, caution must be exercised when ascribing homology to the airsacs in pterosaurs and avialans. Pterosaurs are usually considered the sister taxon of the The Dinosauromorpha (e.g. Benton 1999) or are in a trichotomy with the Dinosauria and *Lagosuchus* (e.g. Gauthier 1986). The Ornithischia and primitive Saurischia appear not to show signs of postcranial pneumaticity. However, in extant Aves the anterior and posterior air diverticulae, although large, appear never to pneumatize bones, and, thus, would be unrecognizable in a fossil. Parsimoniously this implies that a synapomorphy of the

Ornithodira might be a more well developed lung system with air diverticulae. An advanced lung system may have implications on the paleophysiology of Ornithodira, and is also in accordance with the known distribution of integumentary structures. An implication of the monophyly of Ornithodira might further be the possibility of homology of pterosaur "hair" with dinosaurian cryptoptile feathers. If the Pterosauria, as recently advocated are not closely related to the Dinosauria, but instead are outside the Archosauria (Bennett 1996b) this implies that homology of the air diverticulae in pterosaurs and theropods must be seriously questioned, and implies a more primitive lung system in stemgroup Dinosauria.

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A NEW SCAPHOGNATHINE (RHAMPHORHYNCHIDAE) PTEROSAUR FROM THE UPPER JURASSIC MORRISON FORMATION, USA

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A partial rostrum and mandibles from the Morrison Formation, Wyoming, are the first identifiable cranial remains of a scaphognathine pterosaur. The rostral fragment is 13.5 cm, suggesting a skull length of ~27 cm; this in turn indicates a large individual with a wing span of about 3 m. Sutures are not visible implying a mature individual. The alveolar border is scalloped laterally (as seen in dorsal view), as well as dorso-ventrally (as seen in lateral view). The alveoli are widely spaced and of different sizes indicating heterodont dentition. The mandibular fragment shows closely spaced alveoli of nearly uniform size. Referral of this pterosaur to the Scaphognathinae is based upon similarities with *Scaphognathus* from the Solnhofen Limestone of Bavaria. These similarities include: near vertical scalloping around the root of the rostral teeth implying non-procumbent teeth, a pair of alveoli at the tip of the rostrum (which is slightly damaged) indicating that teeth extended to the tip of the rostrum, and large antorbital (i.e., preorbital) fenestra. It does differ from *Scaphognathus crassirostris* in that the tip of the lower jaw is pointed as in *Rhamphorhynchus*. The discovery of this scaphognathine pterosaur increases the number of "giants" soaring in the Jurassic skies of North America, the other being the pterodactyloid *Kepodactylus* with a 2.5 m wing span.

TRIASSIC PTEROSAURS : UNRAVELLING THE PUZZLE

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Most of the Triassic pterosaurs (*Eudimorphodon*, *Peteinosaurus*, *Preondactylus* and a new genus) come from marine anoxic basin deposits of late-middle Norian age in Northern Italy (Lombardy and Friuli) and southwestern Austria (Tyrol). Pterosaurs from Lombardy have been found in the uppermost Calcare di Zorzino Formation (late Alaunian) and basal Argilliti di Riva di Solto Formation (early Sevatian), while the specimens from Friuli come from the Dolomia di Forni Formation (late Alaunian) and those from Tyrol from the Seefeld Schichten (late Alaunian).

The taxonomy of Triassic pterosaurs is highly problematic.

Eudimorphodon is the most common and widespread genus resulting present in Lombardy (Calcare di Zorzino and Argilliti di Riva di Solto; Wild, 1978; 1994), Friuli (Dalla Vecchia, 1995), Tyrol (P. Wellnhofer, pers. comm.) and Greenland (Jenkyns et al., 1994). It is diagnosed mainly on features of its multicusped dentition. Teeth identified as belonging to *Eudimorphodon* are also reported from SW USA, Switzerland, Belgium and Luxembourg (for a review, Dalla Vecchia, 1994). Two species (*E. ranzii* and *E. rosenfeldi*) have been described from Northern Italy and one or two more are going to be described (F. Jenkyns and P. Wellnhofer, pers. comm.s). However, the Lombardian specimens attributed to *E. ranzii* show some differences to each other and it is hard to state whether different species are represented in the sample or the species *E. ranzii* has a high degree of ontogenetic and/or individual variability. The holotype *E. ranzii* represents an individual much larger than all other *Eudimorphodon* specimens (excluded an isolated sternum) and could be a very old individual. The specimen MCSNB 3496 identified as *E. ranzi* by Wild (1978) actually belongs to *Peteinosaurus*. The immature specimen MCSNB 8950 from the Argilliti di Riva di Solto (all other Lombardian specimens are from the Calcare di Zorzino) can be identified as *Eudimorphodon* only on the base of the shape of the deltopectoral crest of humerus, lacking the skull and lower jaw. Some features in the humerus and tibia distinguish *E. rosenfeldi* of Friuli from all the Lombardian specimens of *Eudimorphodon*.

Peteinosaurus zambellii has been based on two immature specimens from the Calcare di Zorzino of Lombardy (Wild, 1978). The diagnostic features of the holotype (MCSNB 2888) are found in the lower jaw, lower jaw dentition and fibula. These characters cannot be seen in the other specimen indicated by Wild as *Peteinosaurus* (MCSNB 3359), because it lacks skull and lower jaw and distal end of both fibulae is covered. The only important long bones preserved in both specimens are tibia and wing phalanx 1. The ratio of the lengths of these bones is actually similar in both specimens, but it is the same also in *Preondactylus* and *Dimorphodon*. Actually, MCSNB 2886 and MCSNB 3359 were originally grouped in the same taxon only because they do not belong to *Eudimorphodon*. The reconstruction of the tarsus of MCSNB 2886 by Wild (1978) is not the only possible and an alternative one is proposed.

Preondactylus buffarinii from the Dolomia di Forni of Friuli is based on the holotype (1770 MFSN) represented nearly completely by the only print of the bones (Wild, 1984; Dalla Vecchia, 1998). This specimen is probably an immature individual (Dalla Vecchia, 1998). The ratios of the long bones lengths suggest a relationship with ?*Peteinosaurus* (MCSNB 3359) and with *Dimorphodon* (Dalla Vecchia, 1998). The shape of the deltopectoral crest of humerus is similar in these three taxa. The diagnostic features of *Preondactylus* are found in the skull, lower jaw and dentition. Unfortunately, the fine details of the crowns cannot be identified because of the poor preservation. As far as it can be seen, the pattern of lower jaw dentition does not differ so much from that of the holotype of *Peteinosaurus* as figured by Wild (1978) (Dalla Vecchia, 1998). The only way to definitely state whether the latter and 1770 MFSN belong to two different genera is to find a *Peteinosaurus* skull or a well preserved *Preondactylus* lower jaw.

A new genus from Tyrol is clearly distinguished from all others on the base of its peculiar multicusped dentition and the presence of a sagittal cranial crest.

At least three characters are found in Triassic pterosaurs which are not present in more recent pterosaurs.

1) Multicusped dentition - *Eudimorphodon* and the new genus have multicusped teeth on both maxillary and dentary teeth. *Peteinosaurus* has posterior mandibular teeth with small accessory cusps. Is this a primitive feature for pterosaurs or a converging adaptation of Triassic pterosaurs to a peculiar diet ?

2) Very enlarged maxillary teeth below the ascending process of the maxilla - Also in some Jurassic pterosaurs (e. g. *Dimorphodon* and *Campylognathoides*) the maxillary teeth below the ascending process of the maxilla are the largest of the maxilla, but in *Eudimorphodon ranzii* (holotype), *Preondactylus* and the new genus one or two of these teeth are much more developed than in Jurassic taxa. Apparently a small specimen of *Eudimorphodon* from Lombardy lacks this feature. Is it a sexual feature or other, it disappeared in the Jurassic.

3) Absence of elongate pre- and postzygapophyses in the caudal segment of the vertebral column. *Eudimorphodon* and the new genus lack the typically elongated caudal pre- and postzygapophyses which contributed to create a «sheat» stiffening the tail in most long-tailed pterosaurs. The situation in *Preondactylus* is unclear, but also this taxon seems to lack them. In the new genus, also the anterior and posterior processes of the hemapophyses are not overlapping. On the other side *?Peteinosaurus* MCSNB 3359 and *Peteinosaurus* MCSNB 3496 have the «sheat». The absence of very elongated pre- and postzygapophyses in the caudal vertebrae is a primitive feature, as suggested by their absence in Jurassic long-tailed pterosaurs and in all supposed pterosaur relatives (no consensus exists about pterosaur ancestry). Thus, there are two pterosaur groups in the Late Triassic, one more primitive than the other under this point of view.

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A MORPHOMETRIC ANALYSIS OF THE HIND-LIMBS OF PTEROSAURS

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Ternary diagrams were used to investigate the hind limbs of pterosaurs. The relative lengths of the components plotted as a tight compact cluster with no outliers. The femur exhibits the smallest range of variation while the tibia and metatarsal III have similar ranges. Rhamphorhynchoids and pterodactyloids occupy a similar size and range in morphospace although their positions are different: certain rhamphorhynchoid species have longer metatarsal III than any pterodactyloid and some pterodactyloids have shorter metatarsal III than any rhamphorhynchoid. The groups have a large area of overlap centered about their most primitive clades. The distribution of clades within the pterosaur groups indicates a trend in rhamphorhynchoids for an increasingly long Metatarsal III preceding crownward on the cladogram. By contrast, in pterodactyloids the crownward trend, is in the opposite direction to that of rhamphorhynchoids. The pterosaur morphospace overlaps that of birds and bats. Compared to these groups the hind limb elements show low morphological disparity. The general range of morphological disparity overlaps those of bats, and birds with rather poor terrestrial ability. The results of this study are consistent with the proposals that pterosaurs were terrestrial quadrupeds, and that the fore and hind limbs were involved in the flight apparatus.

BITES, CRESTS AND FORCES : HOW TO ENGINEER A PTEROSAUR SKULL

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The enormous variety of skull shapes is one of the outstanding characteristics of pterosaurs. Mainly the morphology of the dentition and the occurrence of crests formed by bone and/or soft tissue certainly have had an impact on the life style of pterosaurs.

The aim of the study is to work out the biomechanical options for the crests and to reconstruct possible biomechanical reasons for the evolution of edentulous pterosaurs. Therefore, the following questions have to be settled :

- What is the mechanical effect of the crests ?
- What is the constructional difference of skulls with and without teeth with respect to the force transmission inside the skull. What consequences does this have for the architecture of the skull and the velocity of the occlusion during the bite ?
- Does the reconstruction of maximum loading cases allow predictions on the arrangement of jaw musculature and optional spaces for air sacs inside the skull ?
- Which biomechanically founded modifications of the morphology of the skulls permits a complete reduction of the dentition ?
- Do the crests have any hydrodynamical effects ?
- What can be said about the mechanical properties of potential prey items with respect to the various skull constructions?

The studies are based on the analysis of the *Konstruktionsmorphologie* of the different types of pterosaur skulls by using the finite element method (FEM). FEM is a numerical method originally developed in engineering sciences, to analyse the static and dynamic behaviour of complex structures.

The first step for the analysis was to determine the interaction between tooth and jaw. This is necessary to find out in which way forces are transmitted during bite. The tooth and its implantation were discretized in a separate, numerically intensive model. The model was further simplified in order to minimize the computation time when simulating the entire jaw including the dentition. Comparative analyses were undertaken to evaluate the mechanical effects of the specific pterosaurian tooth structure with an enamel cap with enamel running down the carinae).

In the next step, a model for a whole skull was created. To generate an as far as reasonable accurate model of the skull, a three-dimensionally preserved skull of *Anhanguera* sp. was scanned with a 3D-Laser Scanner. Internal structures were investigated by CT-Scans. Furthermore, the jaw adductor musculature was reconstructed to estimate the forces acting during the bite. The results of these studies and the finite element analysis of the jaw will be the base for further studies on models of different pterosaur skull morphologies.

“SCHULTER“ AND “TIEFDECKER“ IN PTEROSAURS CONTINUED : SURPRISING CONSEQUENCES FOR FLYING AND WALKING

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The shoulder construction of ornithocheirid type pterosaurs differs from that of azhdarchid type pterosaurs mainly in the position of the fossa glenoidea. In the ornithocheirid type the fossa is situated level with the notarium resulting in a wing attachment above the centre of gravity. As a consequence the ornithocheirid flight apparatus is comparable with a self stabilising “Schulterdecker” aircraft. In the azhdarchid type the fossa lies level with the sternum. The wings are attached level with or slightly below the centre of gravity. The azhdarchid type pterosaurs had the option to destabilise their flight by holding the wings laterally or ventrolaterally and increase their manoeuvrability as it is seen in “Tiefdecker” aircrafts. They also could fly under stable conditions by holding the wings dorsolaterally, as is also the case in “Tiefdecker” with their wings in a V-position (Frey *et al.* 2000). This fundamental difference between the ornithocheirid and the azhdarchid flight apparatus helps to explain the differences in the proportions of the wing bones, the mobility of the wing, the wing size with respect to the size of the hind limbs, the relief of the scapulocoracoid as well as the shape and position of the processus deltoideus. Due to the restricted wing mobility ornithocheirid type pterosaurs mostly relied on gliding and must have produced a front wing track at least twice as wide as the hind limb track. The high mobility of azhdarchid type wings allowed to fly with wing beats and to glide. Due to the better foldability of the wings the wing tracks must have been only slightly wider than the hind limb tracks.

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WITH BRISTLES, CLAWS AND VESSELS PTEROSAURS (ALMOST) ALIVE

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Recent finds of pterosaurs from the Solnhofen limestone (late Jurassic, Bavaria, Germany) and the Crato limestone (early Cretaceous, Brazil) yield surprising details of some soft part structures (Frey & Tischlinger 2000). Scaly sole pads, webbing and huge claw sheaths preserved on the pes of a *Pterodactylus* from Bavaria (Germany) and an undescribed azhdarchid from Brazil allow a precise reconstruction of the pes anatomy. The sole pads hitherto are only known from pterosaurs of the Pterodactyloidea type. They apparently are restricted mostly around the heel onto the lateral part of the pes. The pad is covered with rounded scales and includes the fifth metatarsal completely. The webbing is marked by a fine striation which runs subparallel to the digits. The striation is caused by fibre bundles, probably from connective tissue that show the same diameter and phosphatic preservation as is seen in the wing membrane. The webbing reaches the bases of the claw phalanges. A pes of this type would produce a footprint which is coincident with some already published trace fossils which have been referred to pterosaurs (e.g. Stokes 1957, Mazin *et al.* 1995). Especially one of the footprints known from Crayssac and depicted in Mazin *et al.* (1995) shows the relief of the planta three dimensionally including the imprints of the scalation on the sole pad, the webbing and the enormously long claws. Combining the anatomy of the foot sole with the footprints would yield a precise interpretation of the mechanics of the terrestrial locomotion in pterodactyloid pterosaurs.

The manus of the Crato azhdarchid preserved huge claw sheath in combination with a webbing which was hitherto unknown. The webbing is preserved as goethitic stain between the digits of the left manus and shows no trace of a striation. The fact that on the same specimen the fibrils of the wing membrane are preserved three dimensionally allows the conclusion that the membranes forming the leading edge of the wings likely consisted of a different type of skin.

The manus from the *Crato azhdarchid* should have caused an imprint with short, stubby digits but enormously long claws. Such trace fossils are not known until now, not even from Crayssac. The imprint of a manus depicted next to the pes in Mazin *et al.* (1995) does not belong to the pes on the same plate. Traces of a webbing between the digits are reported from Stokes (1957) and can now be verified. The presence of a webbing between the digits of the manus might be a hint on the presence of a large propatagium as suggested by Frey & Rieß (1981).

The *Pterodactylus* specimen shows a head crest consisting of a central layer of fibres which on both sides was covered by a layer on an unknown type of tissue preserved as phosphatic dust and a wrinkled skin similar to that described for the wing membrane (Martill & Unwin 1989). This is consistent with what is known from some tapejarid pterosaurs from Brazil in which parts of the crest are mineralised (Frey & Tischlinger 2001). The diameter and the preservation of the fibres that support the soft part crests are coincident with that of the wing membrane fibres.

In a new specimen of *Rhamphorhynchus* the multilayered nature of the wing membrane is visible. Besides the wing membrane support fibres, hitherto known as "actinofibrils" (Wellnhofer 1987), fibrous structures in phosphatic preservation are visible that form a loose meshwork running obliquely to the fibres. The membrane also contains the remnants of a hitherto unknown vessel system that resembles strikingly the tracheoli in insect wings. Such a vessel system has now been identified in most *Rhamphorhynchus* wings with membrane preservation. The vessels might represent blood vessels which form loops similar to the arcades of the mesenteric vessel system in Mammalia. The vessel with the largest diameter runs subparallel to the brachium. Possibly these structures represent a system of blood vessels that could have been used as a cooling device for the wing. This assumption is supported by the fact that they are situated on the ventral side of the wing membrane. Dorsal to the vessel layer there is a layer of loose meshwork of a phosphatised fibrous tissue. This meshwork can be derived from connective tissue or muscle fibres or both. The wing membrane support fibres ("actinofibrils") form the dorsal most preserved layer in the new *Rhamphorhynchus* specimen. In the fragment of wing membrane from the Santana Formation described by Martill & Unwin (1989) and reinterpreted by Kellner (1994) as a fragment of the skin from the body or arm, a muscle layer is visible that is situated directly ventral to a layer of large bundles of connective tissue fibres which show the same spacing and diameter as is seen in the wing membrane support fibres. The muscle fibres are seen in oblique section while the supposed wing membrane support fibres are cut in an almost 90° cross-section. Under the light of the anatomy of the wing membrane of the new Solnhofen *Rhamphorhynchus* specimen it appears likely that the interpretation by Martill & Unwin (1989) assuming that the Santana pterosaur skin specimen represents a fragment of a wing membrane is correct.

The role of webs and head crests with respect to flight has to be newly investigated. The webbing of the pedes could have been used as a twin rudder when oriented vertically during flight and as an air brake when rotated into a horizontal position during landing. On land it could prevent the animals from sinking into muddy soft grounds. The role of the crests is at the moment under investigation (Fastnacht *et al.*, this volume).

The latest discoveries of pterosaurian soft parts allow details studies on the anatomy and aspects of the physiology of pterosaurs to a detail which is exceptional for an extinct animal (fig 1).

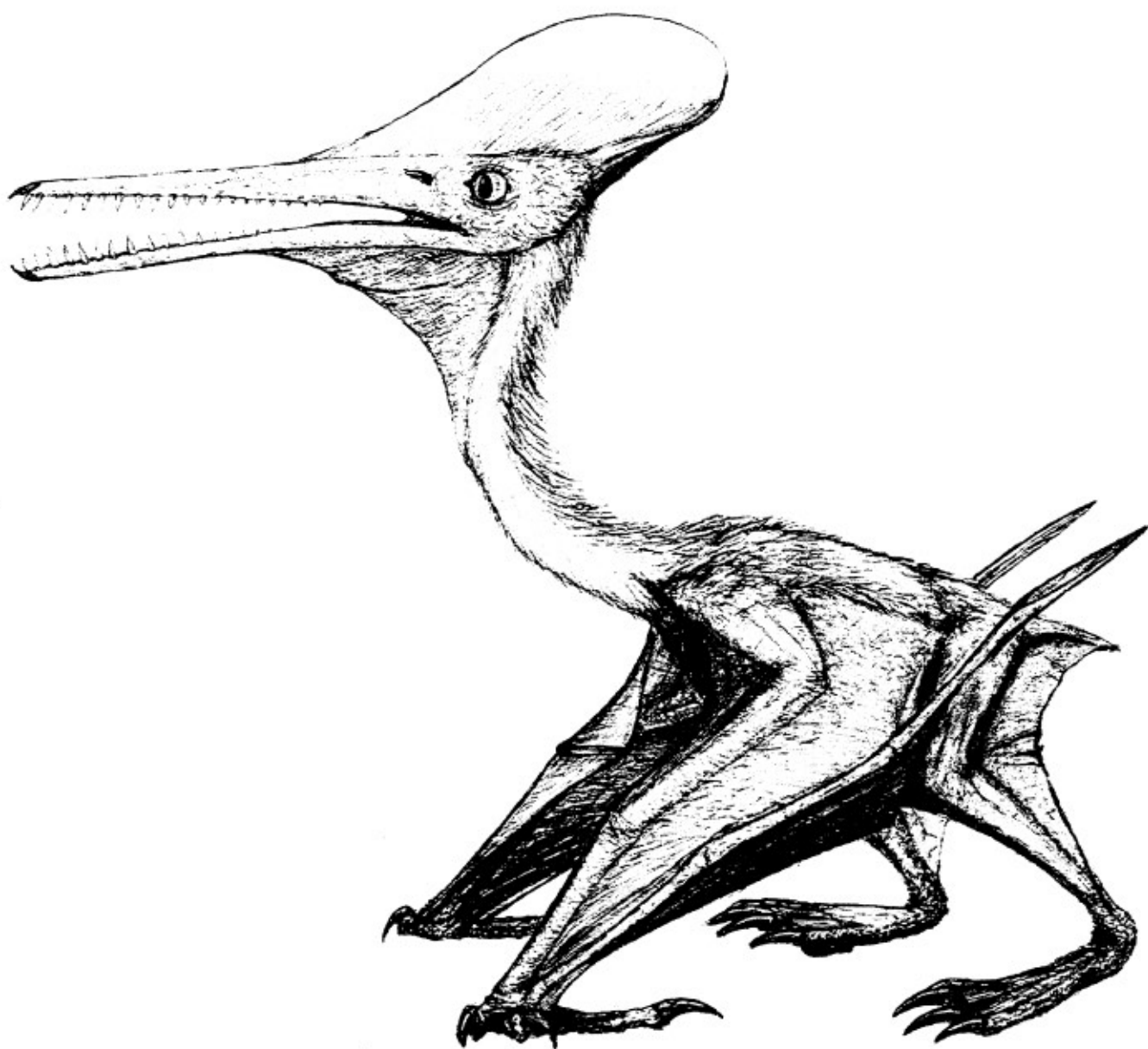


Fig. 1 - *Pterodactylus antiquus* in stance according the latest knowledge of the soft parts.

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A NEW SPECIES OF *PTERAICHNUS* FOR THE SPANISH LOWER CRETACEOUS : *PTERAICHNUS CIDACOI*

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The Cameros Basin is extraordinarily rich in ichnite sites of dinosaurs and other vertebrates from the Lower Cretaceous, and its Sorian slope has yielded an extraordinarily rich Pterosaur ichnite site. (Meijide Calvo, 1999; Pascual Arribas & Sanz Pérez, 2000), unique in its extension and diversity, mainly because of the long lapse of time covered by its stratigraphy.

The La Fuente Mingo site in Valloria (Oncala Range, Soria) lies on the right bank of the Cidacos River. It's a great, 210 m² flagstone which shows Teropod Dinosaur tracks (*Therangospodus oncalensis*, Moratalla, 1993), bird tracks (*Archaeornithipus meijidei*, Fuentes Vidarte 1996), and more than 250 Pterosaur tracks..

Stratigraphically, the site belongs to the lower stretch of the Oncala group by Tischer (1966), within the Weald of Cameros Basin in Soria (Lower – Middle Berriasiense). Its paleo-environmental reconstruction shows a lagoon area of shallow, more or less permanent, salt waters.

Most of the Pterosaur tracks are hand tracks, with very few foot tracks, although some of the tracks which have been classified as undetermined (50) may be claw tracks.

The hand is a three-fingered and asymmetrical one, and of small size, between 3,0 and 6,0 cm long. Finger I has an anterior orientation, is usually l-shaped, is the shortest of the three and has a clearly defined nail; finger II has a lateral orientation and is longer than finger I; finger III points backwards, is slightly sinuous and is the longest one. The length ratio is 1: 1, 3: 2. Their average angulation is: I^II, 57°; II^III, 48°; I^III, 105° (fig. 1).

The foot is plantigrade and four-toed. The heel is rounded and the sole is very wide. The fingers are not clearly marked; only the claws are clearly visible. They protrude and are separate and curved. Average foot length is 5,0 cm, average width is 3,0 cm, and the fl/fw ratio is 1,6. Lack of traces makes it impossible to establish a complete comparison with the *P. saltwashensis*, (Stokes 1957), *P. stokesi* (Lockley et al 1995), *P. palaciei-saenzi* (Pascual & Sanz, 2000) ichnospecies. However, if attention is focused on the meristic features mentioned earlier, we can see that the hand tracks from our site are considerably different from the rest, not only in size but also in finger length ratio and in interfinger angulation. As for the foot tracks, the rounded shape of the heel differs greatly from the subtriangular shape of the three other species.

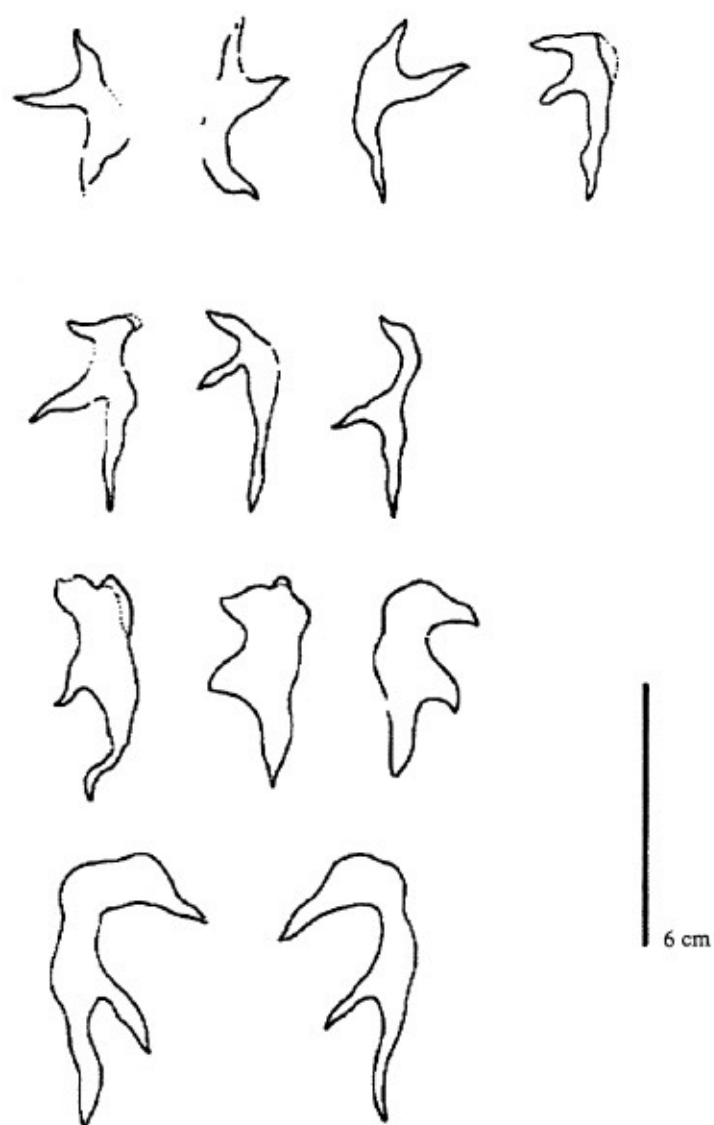


Fig. 1 - Pterosaur tracks (mainly hand tracks) of the La Fuente Mingo site.

Consequently, since it has been possible to establish a thorough biometry of these tracks, and their general morphology is different from what has been described in other sites, we believe that the Valloria ichnites belong to a new ichnospecies of the genus *Pteraichnus* for whose classification we propose the name *Pteraichnus cidacoi*.

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INVESTIGATING HYPOTHESES OF RHAMPHORHYNCHID PTEROSAUR TERRESTRIAL LOCOMOTION WITH COMPUTER MODELS

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Previously, studies of pterosaurian walking were dependent upon analyses of preserved trackways and interpretations of the mechanics of severely flattened fossil bones. Additionally, previous analyses treated the skeletal remains in a static way. We decided to use a scheme that used a dynamic, three-dimensional computer model to investigate the mechanics and dynamics of pterosaurian terrestrial locomotion. The model consists of three-dimensional bone forms that are animated by an underlying (internal) network of nodes. The nodes represent the limb joints, and the spatial positions of the nodes and their axes of rotations are specified as three dimensional coordinates and vectors, respectively. All limb motions are controlled by systems of differential equations. With the bones forms represented as three-dimensional solids, the ranges of motion of the limbs at the shoulders and hips, and degrees of flexion and extension of the more distal limbs joints can be investigated both visually and quantitatively. Additionally, the computer can record any aspect of the geometry of the model, and three-dimensional "recordings" for a given limb and joint configuration can be collected for different models, and the results presented graphically. A final feature of the model is its ability to calculate and record the fractions of the body weight carried by each limb at every stage of step-cycle. Different limbs stances and gaits give different loading patterns of the hands and feet. The ability to track limb loadings could be useful in interpreting fossil trackways attributed to pterosaurs.

MATHEMATICAL AND COMPUTATIONAL MODELLING OF A WALKING PTERODACTYLOID PTEROSAUR

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Well preserved fossil remains combined with mathematical modelling were used to develop an animated, three-dimensional model of a pterosaur walking quadrupedally. Key components of the model include: accurate determination of the centre of mass (CM) of the body; coordination of the step cycles of the fore and hind limbs; transverse motions of the body to maintain stability during walking; and the generation of synthetic trackways for comparison with fossil trackways.

Determination of the CM took into consideration the lung volume, the high degree of pneumaticity of the head and neck, and the requirement that the CM should be close to the inferred centre of lift. Hands and feet were made to follow predetermined parabolic trajectories, and the required flexions and extensions at the shoulders, elbows, hips, knees, and ankles were determined by numerically solving systems of coupled differential equations subject to the constraints imposed by the hand and foot trajectories. An important criterion for stability was that the CM always remain within a triangle of support defined by the three limbs in contact with the ground at any one time. Satisfaction of this constraint throughout a step-cycle required rolling the body from side-to-side such that the CM followed a sinusoidal path. Given that tetrapods are primitively "rear-wheel drive", the legs were used to control the required lateral/medial motions and set the pace. The corresponding motions of the shoulders and arms passively followed the motions imposed on the body by the legs.

DESCRIPTION OF A *CTENOCHASMA* BRAINCASE WITH A SYSTEMATIC REVISION OF TITHONIAN PTERODACTYLOIDEA OF EUROPE

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The pterosaur skull, because of lightening of its structure, is composed by very thin bones, extremely fragile, making it rare and often crushed. Seeley (1901) was the first to describe pterosaur endocranial material, but the specimen studied was very fragmentary. Newton (1889), Edinger (1941), Lewy et al (1992) and especially Kellner (1996) benefited from better material. Until now, except Kellner (1996), the brain of pterosaurs is considered as occupying the totality of the endocast, with an organisation of its different parts relatively closed to birds one. Kellner (1996), established in *Tapejara wellnhoferi* that the brain occupied one third of the totality of the endocast, this one exhibiting an important trabecular system in a pneumatic cavity.

A new specimen of *Ctenochasma*, from the Tithonian of the vicinity of Saint Dizier (eastern France), composed by a skull and associated mandible, is broken longitudinally, exhibiting the endocast. The brain of this animal is contained in a bony outer layer, surrounded with a pneumatic cavity. The optic lobes seem to be well developed, with a lateral position, under the telencephalon, reminding the configuration of bird brain. This convergence could be explained by a same adaptation, a good sight for the fly.

Thus, the brain of *Ctenochasma* seems organised as previously supposed, with an organisation closer to birds than to reptile one, but its size, smaller than previously thought, is closer to reptile than to birds.

This new specimen has been compared with other Pterodactyloidea from the European Tithonian, known mainly by some small size species, with juveniles, and large size species without juvenile, with the use of a simple biometrics analysis, based on skull length and tooth number.

This analysis shows the alignment of some « small » species with « large » species on the graph. Thus, it is suggested that *Ctenochasma gracile* and *Ctenochasma porocristata* are senior synonym of *Pterodactylus elegans*, and *Pterodactylus antiquus* of *Pterodactylus kochi*, a view previously suggested by Bennett (1996). However, this study could not reveal if *Pterodactylus micronyx* is a juvenile of *Ctenochasma roemeri* or to the *Ctenochasma* of Saint Dizier.

The genus *Pterodactylus* is composed by *P. longicollum*, *P. antiquus* and *P. micronyx*, and the genus *Ctenochasma* by *C. elegans*, *C. roemeri* and *C. sp.* (the Saint Dizier specimen).

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A REVIEW OF THE PTEROSAUR RECORD FROM GONDWANA

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Pterosaur deposits from Gondwana are rare. Since the first discoveries from the Late Jurassic Tendaguru Beds of Tanzania, published by Reck in 1931, a total of 30 localities are known so far: 15 from South America, 9 from Africa, 5 from Oceania, and 1 from India. This number might be greater, since in some areas the precise sites are not known and have been here counted as one (e.g., Santana Formation, Brazil; Cretaceous red beds of Hamada du Guir, Morocco). Furthermore some occurrences, if confirmed, will increase the Gondwanan record of those flying archosaurs (e.g., Antarctica, Bahia Series of Brazil).

South American pterosaurs have only been reported in the following countries: Brazil, Argentina, Chile, Peru and recently Venezuela. From those, the most important come from the Araripe Basin, Brazil. The outcrops of the Crato Member have furnished about 30 specimens, most still undescribed. Among those are the pteranodontoid *Arthurdactylus* and the tapejarid *Tapejara* (the oldest toothless flying reptile known to date). The Romualdo Member has furnished over 350 specimens, most preserved in three dimensions. The main localities are situated around Santana do Cariri (e.g., Cancão, Mina Pedra Branca), Porteirás, and Serra da Mãozinha. So far 17 different species have been described, but most are based on incomplete material and it is likely that some may represent the same taxon. Two major groups have been identified, each with several species : the Anhangueridae and the Tapejaridae. The Anhangueridae comprise pterosaurs with wingspans varying from 3 to 6 meters, recognized by sagittal crests confined to the anterior part of the snout (premaxilla and dentary) and their particular dentition. The Tapejaridae are represented by four species, with wingspans ranging from about 1,5 (*Tapejara*) to over 6 (*Tupuxuara*) meters. These toothless pterosaurs share the following synapomorphies: large sagittal crest present over the skull (projecting backwards) and the large nasoantorbital fenestra. The sole other pterosaur remain known from Brazil is a partial humerus from the Gramame Formation (Maastrichtian, Pernambuco-Paraíba Basin), attributed to "*Nyctosaurus*". Although this specimen represents a nyctosaurid pterosaur, it is too incomplete to confirm this generic identification.

Argentina has 9 pterosaur localities, including the oldest record from South America: an isolated tibia from the Late Jurassic (Tithonian) Picún-Leufú Formation, Neuquén. This province has yielded the sole other Jurassic pterosaur from South America so far: *Herbstosaurus* (Lotena Formation). The main Argentinean pterosaur locality is the "Loma del *Pterodaustro*", formed in a lacustrine environment during the Early Cretaceous (Lagarcito Formation). This site has furnished several isolated bones and occasionally some incomplete skeletons, all attributed to *Pterodaustro guinazui* (considered a member of the Archaeopterodactyloidea). Most specimens represent animals with a wingspan of 1,5 m but very small individuals (wingspan of 0.2m) have been reported too. Argentina has also furnished the only pterosaur tracks known from South America so far; several tracks referred to *Pteraichnus* were found near at the Lake Ezequiel Ramos Mexiá, in Neuquén.

Pterosaurs from Chile consist of several isolated elements from La Carreta (Sierra de Candeleros, Antofagasta); first referred to *Pterodaustro*, they are presently regarded to represent a new dsungaripterid taxon. The second Chilean occurrence comes from Cerro la Isla, 80 km east of Copiapó (Northern Chile) and consists of numerous isolated bones. Further records of pterosaur remains in South America are consists of an incomplete large pteranodontoid humerus from the (?) Albian Chulec Formation (Huallanca, Huanco) and an undescribed pteranodontoid scapula-coracoid from the Cretaceous strata of Venezuela.

The pterosaur record in Africa is also scarce. The oldest come from the Late Jurassic Tendaguru Beds of Tanzania and comprise of several isolated elements referred to the clades Rhamphorhynchidae, Pterodactylidae, and Dsungaripteridae ; these assignments have to be confirmed by more material. The best taxon known from this deposit is based on a small lower jaw, *Tendaguripterus*, that was classified in the Germanodactylidae (here considered a member of the Archaeopterodactyloidea). Further elements suggest the presence of Azhdarchidae in this deposit.

More recently pterosaur remains have been unearthed in several localities of Hamada du Guir, near the town Taouz in Morocco. Most common are isolated teeth, some referred to the Anhangueridae. Siroccopteryx, based on the anterior part of a skull, also represents this clade. Isolated remains of Azhdarchidae, Tapejaridae, and Pteranodontidae (?) were also reported, making the Cretaceous red beds of this country the most diverse pterosaur concentration in Africa known to date. The remaining pterosaur records from Africa consist of isolated elements from Congo (Pterodactyloidea indet.), an elongated cervical azhdarchid vertebra and other elements from the Campanian-Maastrichtian strata of Senegal, and azhdarchid specimens from Ruseifa (Jordan). A partial wing was reported from Lebanon (part of the African continent during the Mesozoic) and fragmentary remains were also found in Cretaceous strata of Israel.

In Australia, most pterosaur remains come from the marine strata of the Toolebuc Formation (Albian, western Queensland). Among those is a lower jaw, similar to some specimens found in the Cambridge Greensand (Cenomanian, England) and a pteranodontoid scapulocoracoid.

Further Australian pterosaur record consists of a partial skull from the marine Allaru Mudstone (Albian, Hughenden, Queensland), which was tentatively referred to the Anhangueridae.

Up to date, the pterosaur record of Gondwana is concentrated in Cretaceous strata with a limited number coming from Jurassic deposits. The absence of any Triassic record so far, despite the existence of very fossiliferous continental deposits (e.g., Santa Maria Formation, Brazil; Ischigualasto Formation, Argentina) suggests that, if present, pterosaurs were very rare in Gondwana at that time.

The richest Gondwanan pterosaur localities so far are the Romualdo Member of the Santana Formation (Brazil), the Cretaceous red beds from Morocco, and the Lagarcito Formation (Argentina). If all named taxa are valid, the first one counts for over half of the described species (19 from 31). Morocco also has a great potential to present a great pterosaurian diversity, but the characterization of individual taxa might be difficult since most reported specimens consist of isolated bones.

Interesting to note is the fact that where pterosaurs have been found in great abundance, they tend to be the most abundant represented tetrapod. Such observation, which cannot be explained by taphonomic reasons alone, has also been made in other deposits of Laurasia, particularly those found near shorelines (e.g., Solnhofen, Germany) or representing marine depositional environments (Niobrara Chalk, North America). The absence of avian remains in those deposits suggests that pterosaurs dominated the Mesozoic coastal regions and that avian faunas might have been more confined in inland areas.

FRENCH PTEROSAURS

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French pterosaurs, although mentioned as early as the mid-nineteenth century, have been the subject of relatively few papers. This is not surprising in view of the fact that the evidence is rare and, more often than not, fragmentary. However, in recent years, several papers have dealt with interesting pterosaur remains from the French Jurassic as well as from the Cretaceous. Besides skeletal elements [Buffetaut *et al.*, 1996; Buffetaut *et al.*, 1997; Buffetaut *et al.*, 1998], remarkable trackways have been the subject of noteworthy studies [Mazin *et al.*, 1995; Mazin *et al.*, 1997].

An exhaustive inventory of the pterosaur material attested so far in France is at press at the time of writing this abstract [Knoll & Bouveur, 2001]. It shows that, although few remarkable finds have been reported, pterosaurs are known in France from a number of sites ranging in age from the Late Triassic ('Rhaetian') to the Late Cretaceous (Maastrichtian) (Tab. 1). However, the French pterosaur record, contrary to the dinosaur one [Buffetaut *et al.*, 1991], remains, except, to some extent, for the terminal Jurassic (Kimmeridgian - Tithonian), rather poor.

As is observed elsewhere, the stratigraphical concentrations of the French pterosaur record are clearly biased by secondary factors (such as the low resistance of pterosaurian skeletal elements to transportation and burial). These peaks merely reflect statistically the discovery of pterosaur fossils in France from different horizons to date and, thus, do not correlate, with any degree of certainty, to actual pterosaur palaeoecological significance during the Mesozoic.

Stages	Localities	Taxa
Rhaetian	Varangéville (Meurthe-et-Moselle)	Campylognathoididae ¹ : aff. <i>Eudimorphodon</i> sp.
	Saint-Nicolas-de-Port (Meurthe-et-Moselle)	Campylognathoididae ¹ : <i>Eudimorphodon</i> sp.
Hettangian	Hettange-Grande area (Moselle)	? Pterosauria indet.
Callovian	Le Wast (Pas-de-Calais)	Pterosauria indet.
	Villers-sur-Mer area (Calvados)	? Rhamphorhynchidae ² indet.
Oxfordian	Lisieux area (Calvados)	? Rhamphorhynchidae ² indet.
Kimmeridgian	Cape de la Hève (Seine-Maritime)	? Rhamphorhynchidae ² indet.
		? Pterodactylidae ³ indet.
		Dsungaripteridae ⁴ : <i>Normannognathus wellnhoferi</i>
	Boulogne-sur-Mer area (Pas-de-Calais)	? Rhamphorhynchidae ² indet.
		? Pterodactylidae ³ indet.
	Fumel (Lot-et-Garonne)	? Pterodactylidae ³ indet.
	Cerin (Ain)	? Pterodactylidae ³ indet.
Tithonian	Cran aux Œufs (Pas-de-Calais)	? Rhamphorhynchidae ² indet.
		? Pterodactylidae ³ indet.
	Crayssac area (Lot)	? Rhamphorhynchidae ² indet.
		? Pterodactylidae ³ indet.
		? Dsungaripteridae ⁴ indet.
	Saint-Dizier area (Haute-Marne)	Pterodactylidae ² : <i>Ctenochasma micronyx</i>
	Canjuers (Var)	Pterodactylidae ³ : <i>Gallodactylus canjuersensis</i>
	Montrouge (Pas-de-Calais)	Pterosauria indet.
Hauterivian	Attancourt area (Haute-Marne)	? Ornithocheiridae ³ indet.
Albian	Louppy-le-Château (Meuse)	? Ornithocheiridae ³ indet.
	Grandpré (Ardennes)	? Ornithocheiridae ³ indet.
	Le Gaty (Aube)	? Ornithocheiridae ³ indet.
	Boulogne-sur-Mer area (Pas-de-Calais)	? Ornithocheiridae ³ indet.
Coniacian	Lezennes-Lez-Lille (Nord)	Pterosauria indet.
Campanian	Notre-Dame-du-Thil (Oise)	? Pterosauria indet.
Maastrichtian	Campagne-sur-Aude area (Aude)	Pterosauria indet.
	Fontjoncouse (Aude)	Pterosauria indet.
	Mérigon (Ariège)	Azhdarchidae ⁶ indet.

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Table 1. French pterosaur record. For each locality, there will be no mention of a Pterosauria indet. when a taxon of lower level has been recognized there. Excepted for the Tithonian of the Crayssac area where, besides teeth and bones, pterodactyloid (*Pteraichnus* spp.) and possible rhamphorhynchid trackways have been discovered, all records are based on skeletal elements only.

¹ *Campylognathoides zitteli*, *Eudimorphodon ranzii*, their most recent common ancestor and all descendants.

² *Rhamphorhynchus longicaudus*, *Scaphognathus crassirostris*, their most recent common ancestor and all descendants.

³ *sensu* Knoll [2000].

⁴ *sensu* Knoll & Bouveur [2001].

⁵ *Anhanguera blittersdorffi*, *Pteranodon longiceps*, their most recent common ancestor and all descendants.

⁶ *Tapejara wellnhoferi*, *Quetzalcoatlus northropi*, their most recent common ancestor and all descendants.

THE PTEROSAURIAN TRACKWAYS OF CRAYSSAC (SOUTH-WESTERN FRANCE)

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At the end of the 1980s, a new Late Jurassic site was discovered at Crayssac (Quercy, south-western France) by Gérard Lafaurie, a French amateur palaeontologist. Among several vertebrate remains (fish and crocodilian bones), he found a small slab bearing some vertebrate imprints, which were been described as crocodilian tracks (Hantzpergue and Lafaurie, 1994). After some prospecting fieldtrips, a first excavation was undertaken in 1994, during which several similar short trackways were been found and interpreted as quadrupedal pterodactyloid pterosaur tracks, referred to the ichnogenus *Pteraichnus*, formerly described by Stokes in 1957 (Mazin *et al.*, 1995). In the same years, further prints and trackways similar to those of *Pteraichnus* were reported from North America (Logue, 1994 ; Hunt *et al.*, 1995 ; Lockley and Hunt, 1995 ; Lockley *et al.*, 1995) as well as from Europe (Lockley *et al.*, 1995). Thus, by the year 1995, little doubt existed concerning the status of these tracks, although they had been controversial for a long time (see Padian and Olsen, 1984) and, in the following years, many pterosaurian tracks were been reported from several sites in the world.

Seven years of excavation have followed the first campaign of 1993 in the Late Jurassic quarry of Crayssac. They revealed an incredibly rich paleontological site yielding mainly vertebrate and invertebrate prints in a Jurassic littoral mud flat, under tidal influence. These include tracks of: crustaceans, theropod dinosaurs, turtles, crocodilians, pterosaurs, as well as enigmatic vertebrate trackways (Mazin *et al.*, 1997). Among them, the pterosaurian imprints are so numerous that some levels yield 20 to 50 isolated pes and manus prints per square metre, which led us to nickname the site "the Pterosaur Beach of Crayssac".

Up to now, 22 true pterosaurian trackways (with more than four well preserved paces) have been discovered at Crayssac and carefully prepared, directly in the field. They consist of from 6 to 42 successive paces, and the printmakers range from small sparrow-sized pterosaurs to sea-gull-sized animals.

On the basis of the present ichnological sample, we can discriminate two major kinds of trackways. The most common ones (21 out of the 22 excavated trackways) show tridactyl manus prints and tetradactyl pes prints. They are referred to pterodactyloid pterosaurs. The second kind, with tridactyl manus prints and pentadactyl pes prints can be tentatively referred to "rhamphorhynchoid" pterosaurs, represented by only one short trackway and some isolated prints (see "Could they be the first rhamphorhynchid tracks?", Mazin *et al.*, this volume).

All the pterodactyloid trackways from Crayssac can be referred to the ichnogenus *Pteraichnus* Stokes 1957. But a great variability exists, and almost all trackways show different features (size, imprint outlines, relative location of hands and feet...), pointing out the classic difficulties in ichnological systematics. The temptation to refer each trackway to a new ichnospecies could be great. Taking into account the numerous causes of variability (such as the animal size, its stance and gait, or the competence of the substratum), we refer the pterodactyloid trackways of Crayssac to four new ichnospecies.

All the pterosaurian trackways from Crayssac are quadrupedal, without exception. Three trackways have been used to provide a computational reconstruction of pterodactyloid terrestrial locomotion. The model agrees with the hypothesis put forward by Bennett (1997).

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IF THEY DID IT, THEY WERE ABLE TO DO IT! A COMPUTATIONAL RECONSTRUCTION OF PTERODACTYLOID TERRESTRIAL LOCOMOTION FROM TRACKWAYS

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The debate on the terrestrial locomotion of pterosaurs started early in the history of palaeontology and is still alive today, leading to consider the pterosaurs either as quadrupedal or bipedal walkers. Beyond this opposition, a second debate concerns pterosaur terrestrial abilities, which have been considered as either restricted or good.

In recent years, a new look at pterosaurian terrestrial locomotion has been made possible by the discovery of quadrupedal trackways. However, though pterosaurs can be considered as quadrupedal vertebrates when walking, the problem of their locomotion cycle and abilities remains, because of the particular anatomy of these animals.

Two approaches can be used in order to decipher the biomechanics of vertebrate terrestrial locomotion. The first and most commonly used one, consists in the animation of a 3D skeleton on which all the supposed joint constraints limit the movements. The animator decides what will be the motion of all the joints, estimated from skeletal anatomy. Modern softwares are able to calculate the accumulation of all motion along a chain of segments, such as a limb. This method necessitates a good knowledge and a good control of all the constraints for each joint, which is often difficult with fossils.

The other approach proceeds in the opposite direction, because it uses the trackways, when they are available and correctly identified. A trackway being the result of a biological motion, it should be possible to reconstruct the cycle of locomotion from it if we can force a scaled model to walk "in" its tracks. Indeed, if pterosaurs made a certain type of trackways, this means that they were able to walk like that!

Concerning pterosaurs, the first attempt at such a trackway approach was proposed by Bennett (1997) who concluded that pterosaurs, at least those which made the known tracks, used a diagonal walk step cycle.

Because they are numerous, well preserved, long and diverse, the pterosaurian trackways of Crayssac provide a good experimental material to reconstruct the terrestrial locomotion cycle of pterosaurs.

A first attempt was made by one of us, using graphic models drawn for each step of the cycle along a trackway. The subsequent animation of this two-dimensional model was obtained by acceleration of a succession of images, exactly as in a traditional cartoon. This quite empiric method led us to agree with the hypothesis of Bennett (1997). Furthermore, it also led us to consider that pterosaurs were not so limited when on the ground: they were able to walk and run without serious difficulties.

A second computational development, which is the aim of this paper, was made by our team. It is a true 3D reconstruction of pterosaurian locomotion based on trackways and processed through a specialized software (Lightwave 6.5b). The work has been conducted through four successive stages and is based on the synchronisation of two groups of items (a skeleton and mobile targets) with each imprint, successively when the body moves along the trackway.

The first stage consisted in building a 3D model of a pterosaur. This skeleton is made of linear items (objects) organized in chains. Each object corresponds to a skeletal segment (at least for the limbs) and received rotation limitations in the three spatial directions: heading (x-z axis), pitch (x-y) and bank (y-z). The chain of objects (segments) representing the skeleton, has been hierarchised with parents and child items, and when an object moves all the others are affected by this motion and move themselves according to their location and constraints. The skeleton has been exactly adjusted to the size of the original trackmaker, by using the foot length. The skeletal proportions have been based on the genus *Pterodactylus*, the most common and the most generalized pterodactyloid known in the Late Jurassic of Western Europe. This model can be used as a skeletal object or as a restored body with general outlines.

The second stage consisted in the analysis of the trackway itself, on which the line which corresponds to the projection of the centre of gravity on the ground during locomotion (the "body way") has been calculated from the relative position of the tracks along the trackway. The same calculation has been made for the shoulder ways and the hip ways. The aim of these

calculations is to reconstruct these five motion lines in order to synchronise the relative location of the body, shoulders and hips for each step of the motion along the trackway.

The third stage consisted in using the inverse kinematics process (or goal-directed motion) to correlate the skeleton motion to the trackway constraints by using target objects. These objects (single virtual points) are in fact the only active objects in the reconstruction (the trackway is fixed and the skeleton passively moves to follow the targets to which it is attached). The target movement between two successive prints has been calculated to follow a low parabolic curve, with an acceleration at the beginning of the motion and a deceleration at the end. Once the motion of the four targets (two hands and two feet) has been calculated for the whole trackway, the four limbs are attached to them, and the skeleton follows the targets, as a puppet which should be animated by its extremities.

The fourth stage of the study consisted in the adjustment of the items (skeleton and targets) in order to respect the real succession of tracks along the trackway. The trackway is a biological object, showing variability, whereas the theoretical motion has been calculated from averages. For example, the target and the limb can disconnect if the target continues its motion and the limb is too short to follow it. The animator must modify the former data in order to force such a limb to follow the target and to reach the track in time. As, as explained above, all the items of the skeleton are linked, the whole body modifies its general motion correlatively to this new situation. The same adjustment is done for each track.

When the model is completed and fully animated, its careful observation lead to some interesting conclusions:

- 1) The animated models confirm the alternate diagonal walk described by Bennett (1997). We have to note, from the trackway morphologies, that the foot never passes under the arm.
- 2) The terrestrial abilities of these pterosaurs are much more extensive than formerly supposed. Depending on the studied trackways, they were able to walk (slowly or quickly) as well as to run, with stages when two or three limbs are off the ground. This was supposed on the basis of the general morphology of some trackways with long strides, and is confirmed by this study.
- 3) Consequently, the stances are variable, from almost horizontal when the pterosaur runs to semi-erect when it is walking.

- 4) As already known from skeletal morphology, the centre of gravity is located in the fore part of the body, but can be projected forwardly out of the quadrilater of sustentation when running.
- 5) As observed on the trackways, the hand trackways are generally wider than the foot trackways, but some trackways show hand and foot trackways of equal width. It could be suggested that the hands are far out of the body axis when the animal is walking and, conversely tend to be closer to the body axis when running. In fact, our ~~animated~~ models show that this assumption is wrong. Most of the running trackways show wide hand trackways, whereas the walking trackways more commonly show narrow hand trackways. This probably has to be correlated to the stance of the animal, which was more erect when walking slowly.

Finally, beyond the scientific study of the reconstructed skeleton, it is pleasant to “dress” the model with flesh and skin, to cover it with short coloured hair, and to observe a true pterosaur walking on the mud of the Pterosaur Beach of Crayssac...

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COULD THEY BE THE FIRST RHAMPHORHYNCHID TRACKS ? YES !

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Among the numerous tracks and trackways which have been found in the Late Jurassic of Crayssac, most are clearly referable to the pterodactyloid ichnogenus *Pteraichnus* Stokes 1957 (see "The pterosaurian trackways of Crayssac", this volume). However, several isolated small prints and one short trackway show features which indicate a pterosaurian from their general characters, but without pterodactyloid features. They were tentatively referred to a possible rhamphorhynchoid by Mazin *et al.*, 1997, and new scarce discoveries allow to confirm this first hypothesis.

The general morphology of the trackway is that of a small quadrupedal animal, with different manus and pes print morphologies. It consists of nine successive paces. The measurements of the trackway reveal that the hand trackway is notably wider than the foot trackway, a feature which can be encountered only in pterosaurs among known vertebrates.

The hands prints are tridactyl, with short and straight digits, parallel and forwardly oriented. This feature is absolutely different from the *Pteraichnus* hand print, but not so different from the predictive pterosaur manus print proposed by Unwin (1989). A pit is marked posteriorly to the digits, which should correspond to the impression of the fourth metacarpal.

The pes prints are quite strange, pentadactyl and very different from the *Pteraichnus* ones. Three short digit prints, parallel and forwardly oriented, correspond to digits II to IV. Digit I, also forwardly oriented, is quite separate from the three others. The fifth digit print is postero-laterally curved and hooked. A transverse imprint is marked at the base of the digits, which ends with a deeper pit at the base of the fifth digit. There is no trace of a heel. Such a print morphology reveals a digitigrade stance for the foot.

The relative width of the hand and foot trackways, the tridactyl hand prints, the pentadactyl foot prints, and the morphology of the foot prints, altogether lead us to consider this trackway as that of a quadrupedal and digitigrade non-pterodactyloid pterosaur.

It is notable that there is no observable tail trail.

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A REVIEW OF FRENCH PTEROSAURS

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Since the first mention of pterosaurs from France (bone fragments from the Hettangian of Hettange) by Terquem in 1846, a number of discoveries have augmented our knowledge of French pterosaurs. Although complete specimens are very scarce, the French record is good from a stratigraphic point of view, as shown by the list below, which gives the geological age, the geographical location, the type of material, the systematic identification (when possible), the main references, and the place where the material is kept (when known).

Triassic

Norian/Rhaetian : Varangéville, Saint-Nicolas-de-Port (Meurthe-et-Moselle). Teeth, *Eudimorphodon* - Godefroit (1995), Godefroit & Cuny (1997) - Institut royal des Sciences naturelles de Belgique, Brussels.

Jurassic

Hettangian : Hettange (Meuse) - Bone fragments, Pterosauria indet. - Terquem (1846), Gervais (1848-1852) - Musée, Metz (?).

Toarcian : Nancy (Meurthe-et-Moselle) - Partial skeleton, *Dorygnathus* cf. *banthensis* - Delsate & Wild (2000) - Private collection.

Callovian : Vaches Noires cliffs (Calvados) - Limb bones, "rhamphorhynchoid" - Buffetaut (in prep.) - Private collection.

Callovian : Boulonnais (Pas-de-Calais) - Unidentified bones, Pterosauria indet. - Sauvage (1880) - Lost.

Oxfordian : Cordebugle (Calvados) - Limb bones, teeth. - Pterodactyloidea and Pterosauria indet. - Buffetaut et al. (1985), Buffetaut (in prep.). - Private collections.

Kimmeridgian : Cerin (Ain) - Limb bones, pterodactyls. - Meyer (1852, 1860), Lortet (1892), Buffetaut et al. (1990). - Musée Guimet d'Histoire Naturelle and Université Claude Bernard, Lyon.

Kimmeridgian : Fumel (Lot-et-Garonne) - Unidentified fragments, Pterosauria indet. - Sauvage (1902). - Museum, Agen.

Kimmeridgian : Cap de la Hève (Seine-Maritime). - Type jaws of *Normannognathus wellnhoferi* (pterodactyloid), "rhamphorhynchoid" limb bones. - Buffetaut *et al.* (1998), Buffetaut (in prep.). - Musée Cantonal de Géologie, Lausanne, Muséum d'Histoire Naturelle, Le Havre, and private collection.

Kimmeridgian : Boulonnais (Pas-de-Calais) - Limb bones, pterodactyloids. - Sauvage (1873). - Lost.

Tithonian : Boulonnais (Pas-de-Calais) - Limb bones, Pterosauria indet. - Cuny *et al.* (1991) - private collection.

Tithonian : Canjuers (Var) - Type skeleton of *Gallodactylus canjuersensis* - Fabre (1974, 1976, 1981) - Muséum National d'Histoire Naturelle, Paris.

Tithonian : Saint-Dizier region, exact location unknown (Haute-Marne) - Skull of *Ctenochasma*. - Taquet (1972). - Musée municipal, Saint-Dizier.

Tithonian (Lower) : Crayssac (Lot) - Isolated pterodactyloid bones, pterodactyloid trackways, rhamphorhynchid trackways - Mazin *et al.* (1995, 1997), Mazin & Billon-Bruyat (in prep.), Billon-Bruyat & Mazin (in prep.) - Université de Poitiers, Université Claude Bernard, Lyon, Muséum d'Histoire Naturelle de Toulouse.

Tithonian (Lower) : Oléron (Charente-Maritime) - Isolated limb bones, pterodactyloid indet. - Billon-Bruyat *et al.* (in prep.) - Private collection.

Tithonian (Portland facies) : Oléron (Charente-Maritime) - Teeth of *Rhamphorhynchus* sp., teeth of Pterodactyloidea - Mazin *et al.* (in prep.), Billon-Bruyat *et al.* (in prep.) - Université de Poitiers.

Tithonian or Early Berriasian (Purbeck facies) : Cherves de Cognac (Charente) - Teeth, isolated bones of pterodactyloids - Mazin *et al.* (in prep.), Billon-Bruyat *et al.* (in prep.) - Musée d'Angoulême, private collection.

Cretaceous

Hauterivian : Attancourt (Haute-Marne). - ulna and undescribed limb bones, Ornithocheiridae ? - Buffetaut & Wellnhofer (1983), Buffetaut (in prep.) - Musée municipal, Saint-Dizier.

Albian : Louppy (Meuse) - Neck vertebra, ornithocheirid (?) - Barrois (1875), Sauvage (1882) - Musée d'Histoire Naturelle, Lille.

Albian : Grandpré (Ardennes) - Teeth, Pterosauria indet. (?) - Barrois (1875), Sauvage (1882) - Muséum d'Histoire Naturelle, Lille.

Albian : Le Gaty (Aube) - Neck vertebra, *Ornithocheirus* sp. - Buffetaut *et al.* (1989) - Private collection.

Cenomanian (Lower) : Lussant (Charente-Maritime) - Teeth, Ornithocheiridae indet. - Vullo *et al.* (in prep.) - Private collections.

Senonian : Notre-Dame-du-Thil (Oise). - Unidentified bones, Pterosauria indet. (?) - Graves (1847), Gervais (1848-1852). - Location unknown.

Coniacian : Lezennes (Nord) - Limb bone, Pterosauria indet. - Barrois (1875). Muséum d'Histoire Naturelle, Lille.

Maastrichtian (Early) : Campagne-sur-Aude (Aude) - Wing bone fragments, Pterosauria indet. - Buffetaut (1998). - Musée des Dinosaures, Espéraza.

Maastrichtian (Early) : Cruzy (Hérault) - Neck vertebra, Azhdarchidae. - Buffetaut (in press) - Musée de Cruzy.

Maastrichtian (Late) : Fontjoncouse (Aude) - Wing bone fragments, Pterosauria indet. - Buffetaut *et al.* (1996). - Musée des Dinosaures, Espéraza.

Maastrichtian (Late) : Mérigon (Ariège) - Neck vertebra, Azhdarchidae - Buffetaut *et al.* (1997) - Musée des Dinosaures, Espéraza.

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**PTEROSAUR TRACKS IN ONCALA MOUNTAIN RANGE
(SORIA, SPAIN)
A NEW ICHNOSPECIES : *PTERAICHNUS VETUSTIOR***

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The High Lands area in Soria has turned out to be one of the greatest paleontological sites of vertebrate and invertebrate ichnites from the Spanish Cretaceous. This area is in stratigraphical contact with another, equally important, paleontological area: Enciso, in La Rioja region. Both of them, together with a small area in northern Burgos, make up a set of weald facies known as Cameros Basin. Within this basin, the Sorian slope of the Oncala Range is extraordinarily rich in Pterosaur ichnites (Meijide Calvo, 1999; Pascual Arribas & Sanz Pérez, 2000).

Valdelalosa I paleontological site lies on one of the richest Pterosaur areas in the Oncala Range, on one side of the road that goes from the village of San Pedro Manrique to the village of Fuentes de Magaña. Its stratigraphy belongs to the Oncala group Oncala by Tischer (1966), Huérteles IVb aloformation (Gómez-Fernández, 1992), which is dated middle-higher Berriasiense.

It's a long stratum, roughly 25 m long by 1-2 m wide, which stands at a slightly higher level than the road, formed by layers of grey limolitas. They originated in a more or less permanent muddy lagoon, and show more than 400 Pterosaur hand ichnites and some Pterosaur foot ichnites. The tracks don't show any clear trace or pattern.

The hand is three-fingered and strongly asymmetrical. The average length of its track is 7 cm and its average width 3,2 cm. The ratio hl/hw is 2,3. The first finger is the shortest (average length 2,3 cm); it's usually curved towards the outside and points to the terminal nail. The second finger (average length 3,8 cm) points to the outside and slightly curves backwards. The third finger is the longest (average length 6,2 cm), points backwards and is slightly sinuous. The length ratio for the three fingers is : 1: 1, 6 : 2,6. The average angulation is : $I^{\wedge}II$, $53,5^{\circ}$; $II^{\wedge}III$, 36° ; $I^{\wedge}III$, 88° (fig. 1).

The foot is plantigrade; its heel is rounded, and the anterior end is wide. It has four toes, all of them similar and almost parallel. Its average length is 11,5 cm and its average width 9,0 cm, so that the ratio l/w is 1,2.

The above features separate these tracks from the rest of the *Pteraichnus* species known. Given the great number of prints analyzed, and in spite of the lack of clear traces, we suggest creating a new ichnospecies for the Spanish Lower Cretaceous: *Pteraichnus vetustior*.

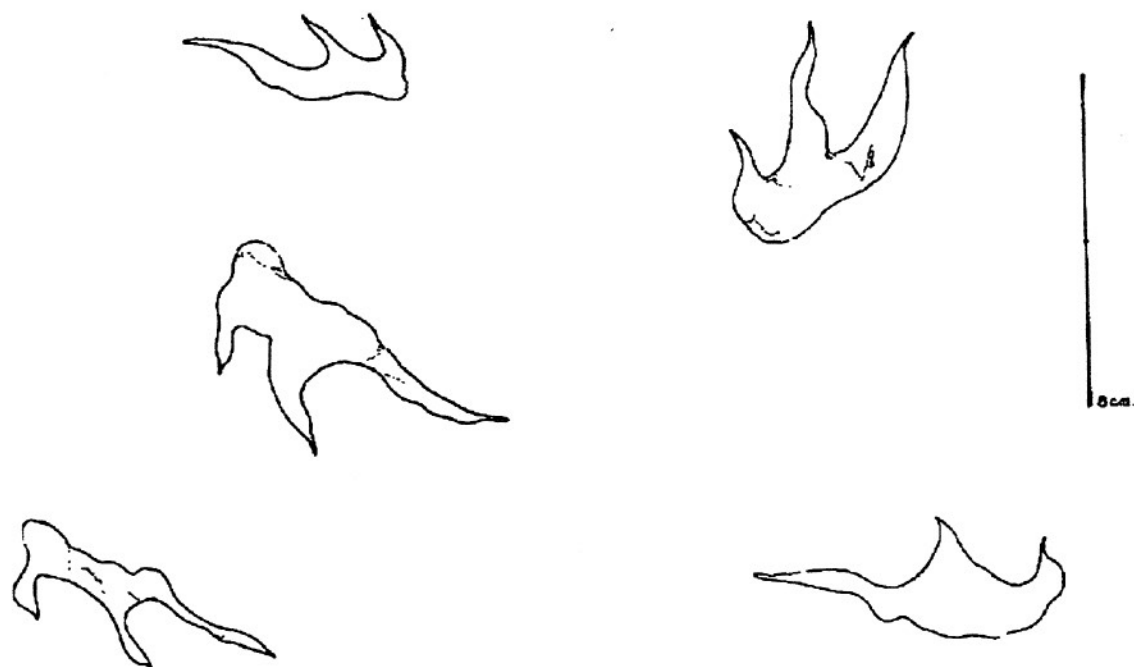


Fig. 1 - Pterosaur tracks in the Valdelalosa I formation.

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**PTEROSAUR TRACE IN ONCALA BERRIASIAN
(SORIA, SPAIN)
NEW ICHNOSPECIES : *PTERAICHNUS MANUELI***

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Pterosaur ichnite sites in Spain are scarce, with the exception of those found in Soria, in the Oncala Range (Meijide Calvo, 1999 ; Pascual Arribas & Sanz Pérez, 2000), where there are extensive sites with hundreds of prints. In addition, the ichnites from those sites are so different from those found in America and Europe that new ichnospecies can be established.

The site under study lies on the Serrantes ravine, within the Villar del Río municipal area, on the left bank of Cidacos River. Its stratigraphy belongs to the Oncala group (Tischer, 1966), within the lithographic set of the Cameros Weald, from the Lower-Middle Titonic-Berriasiense. The paleo-geographical reconstruction of the area shows a great alluvial plain with intermittently marshy areas which contact a great permanent saltwater lake.

The extensive ravine shows tracks and prints of Teropod and Ornitopod Dinosaurs and of birds (*Archaeornithipus meijidei*, Fuentes Vidarte 1996), and tracks of at least three types of Pterosaurs.

The trace under description is formed by the right-hand and right-foot tracks of a small-sized Pterosaur. (fig. 1) In spite of its small size, it's quite clear and enormously beautiful. The foot is plantigrade, elongated (21,0 mm average length) and relatively wide (9,0 mm average width). The fl/fw ratio is 2,3. The heel is rounded and slightly curved towards the outside of the trace ; it has four toes which are short and sharp, of similar size and slightly convergent.

The hand is three-fingered and asymmetrical, with an average length of 25,3 mm and an average width of 8,3 mm. The hl/hw ratio is 3. The first finger is the shortest one, the second finger is bigger than the first and smaller than the third, the ratio being 1 : 2, 5 : 3,5. The third finger is oriented towards the outside and the back of the trace and is almost parallel to the axis of movement. Average interfinger angulation is : I[^]II, 35°; II[^]III, 19°; I[^]III, 54°.

The Step and the stride are constant and measure, respectively, 5,0 y 13,0 cm ; the step angle of hands and feet is 150°.

All these data clearly show that the meristic and morphologic features of this trace are different from all previously described traces of the *Pteraichnus* ichnospecies (*P. saltwashensis*, Stokes 1957 ; *P. stokesi*, Lockley et al 1995 ; *P. palaciei-saenzi*, Pascual & Sanz 2000), so we suggest creating a new ichnospecies which we call *Pterichnus manueli*.

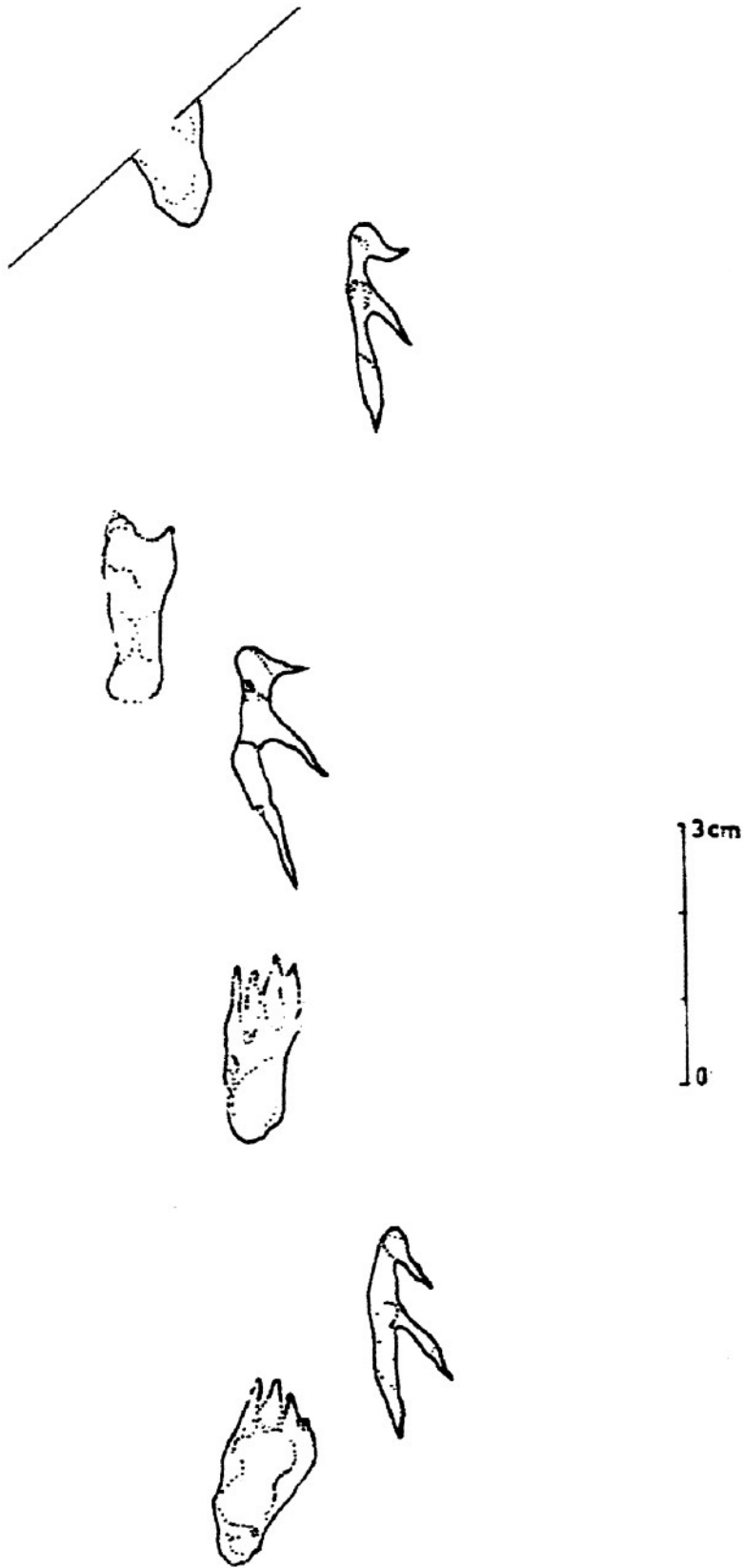


Fig. 1 - Right-hand and right-foot tracks of a small sized Pterosaur in the Villar del Rio municipal area

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AN INTEGRATIVE APPROACH TO PTEROSAURIAN LOCOMOTION

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There are as many views on pterosaurs as there are workers on pterosaurs; and about the only thing that we all agree on is that pterosaurs could fly. Different views on other questions stem partly from differences in perception or observation. Skull bones are especially vulnerable to differences in preservation and identification. Presumed remnants of soft parts represent different kinds of tissues to different workers. The potential for joint movements – which are always overestimated when considering bones alone – are often assessed differently. Trackways are regarded as pterosaurian by some, crocodilian by others, indeterminate by others. In all these cases, the incompleteness of information, the quality of preservation, and the lack of sufficient examples to settle the question are of paramount importance. Beyond all these difficulties, and perhaps most importantly, is the need to agree on scientific methods. This is necessary to test hypotheses about the evolution of features such as stance and gait, flight and locomotion, and further paleobiological questions.

The stance and gait of pterosaurs continues to be problematic; several problems need to be considered independently. The first question is stance – quadrupedal or bipedal – and the second is gait – sprawling or parasagittal. The humerus could not have protracted and retracted much unless it were almost fully extended. The bony stops on the anterior and posterior sides of the glenoid fossa would have prevented a fore and aft motion of more than about 60 degrees, less further constraint by soft tissues. Thus, the fore and aft motion would have been about the length of the humerus, which is a short step of about half the length of the torso. Hence the forelimb could not have powered locomotion, but only gone along for the ride. And in forward locomotion, the forearm can only follow what the humerus does.

The Crayssac tracks testify that some pterosaurs could walk on four legs. They do not tell us that all or most did. We know the trackmakers were slowly moving pterosaurs because their forelimbs are so far outside the midline of the body, beyond the hindlimbs. This also tells us something interesting about the gait of the hindlimbs, which are close to the body midline. The hip is a ball-and-socket joint, and this is where nearly all the variability in lateral movement comes from in the hindlimb. The knee is a hinge with no possibility of significant rotation: the fibula is much smaller than the tibia and fused to it, so the distal portions of these bones plus the fused proximal tarsals cannot support rotation. The ankle and phalangeal joints are all hinges. The head of the femur is round and offset from the shaft by an angled neck, much as in humans and some birds and other dinosaurs. In all these animals, some rotation is possible but

it is limited, so the most efficient hindlimb motion would have been parasagittal; indeed it is difficult to imagine any other gait. The Crayssac hindfoot tracks show that pterosaurs did not sprawl, but maintained a parasagittal gait close to the body midline. There is also no trace of a uropatagium or of any influence of its presence. This may have been variable in pterosaurs, but clearly was not essential to all.

The Crayssac tracks reflect animals moving slowly, perhaps foraging for food. They do not suggest that much of the weight was normally borne by the forelimbs; this animal was leaning forward. When it began to run, it is difficult to see how support from the forelimbs would have been necessary or even useful. In a basal, non-pterodactyloid pterosaur, the body must be hunched even farther forward to touch the ground, and the forelimbs would have been of even less use in locomotion than in pterodactyloids. Skeletal proportions strongly imply that pterosaurs came from bipedal animals, and that only some were facultatively quadrupedal.

Clark et al. found comparatively limited movement at the metatarso-phalangeal joint of the Mexican specimen of *Dimorphodon*, and inferred from this that pterosaurs were flat-footed instead of digitigrade. This seems consistent with the tracks assigned to pterosaurs, which show clear impressions of the metatarsals; although in incompetent substrates the metatarsals are frequently impressed even by digitigrade animals, especially "low-angled" ones, as Gatesy has shown. However, the Yale specimens of *Dimorphodon* show some variation in MP joint latitudes. More intriguing, though, is the phylogenetic context of the observation by Clark et al. A variety of basal ornithodiran metatarso-phalangeal joints, including those of early dinosaurs and lagosuchians, are similarly limited. We reconstruct these basal ornithodirans unquestionably as digitigrade, and the tracks of even early dinosaurs show that they normally were digitigrade. If the pterosaur's foot motion is to be restricted by this joint, why do we not also assert it for these other ornithodirans? The joint may have been less restricted than we suppose; or, more motion was contributed at the ankle and the phalangeal joints.

The Crayssac tracks must be pterosaurian, for reasons noted above. However, other tracks, beginning with those originally called *Pteraichnus* by Stokes in the 1950s, as well as many examples referred to this form by Lockley, Wright, Unwin, and their colleagues, are quite different from the Crayssac tracks. Those that have the manus nearly as close to the midline as the pes cannot be pterosaur tracks, because the small digits could not have been oriented in that position if the forelimbs are brought toward the midline. In none of the fossil trackways referred to pterosaurs has it been possible to reconstruct a phalangeal formula. In most, it is impossible to tell exactly how many phalanges there are, especially in the manus, and proponents of the pterosaurian identity of these tracks do not agree which ones are represented. This hypothesis would of course be falsified if adequately preserved tracks with diagnostic features of pterosaur feet were discovered. But for the present, we need to follow much stronger methodological criteria for paleoichnology before accepting poorly preserved and undiagnostic tracks as pterosaurian.

In sum, basal pterosaur limb segment proportions show that pterosaurs evolved from bipedal ancestors and were primarily bipedal and parasagittal in their gait; when pterodactyloids walked as facultative quadrupeds the forelimbs had little role in locomotion. Most trackways referred to pterosaurs were made by other kinds of animals, probably crocodiles. Isolated features should not be used to prescribe function and ecology in extinct animals; rather, such observations should be integrated with independent, testable lines of evidence from functional morphology, phylogeny, and ichnology.

THE FIRST PTEROSAUR REMAINS FROM THE LATEST CRETACEOUS PHOSPHATES OF MOROCCO

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During palaeontological field work in 2000, pterosaur remains were found by the "Office Chérifien des Phosphates" (OCP) in the Late Cretaceous phosphatic deposits of the Kingdom of Morocco. The pterosaur material comes from the eastern part of the Oulad Abdoun Basin, between the cities of Khouribga and Oued Zem. It was collected from the "site 1" of Sidi Daoui area, in the northern part of the Grand Daoui zone, an actively quarried area for phosphate. Stratigraphically, the pterosaur occurred in the upper part of the "bed 3" of the miners, which is Late Maastrichtian in age according to selachian data.

The pterosaur remains are enclosed in a block 98 cm long and 34 cm wide. The phosphatic matrix is grey to yellow-coloured, mottled with orange. Several fossils were found associated during the mechanic preparation of the specimen. They consist of fish vertebrae, and shark, ray, enchodontid, pycnodontid and mosasaurid teeth, as well as "coprolites" and nodules. Moreover, the "site 1" has also yielded abundant articulated remains of other actinopterygians, mosasaurids, elasmosaurids, and marine turtles. This fauna indicate a marine depositional environment.

The pterosaur block includes five vertebrae and an indeterminate fragment of bone. All identifiable vertebrae come from the cervical region. They are disarticulated but could belong to the same individual. The vertebrae are crushed and relatively damaged. The centra are hollow and the thickness of the cortical bone is generally 1 mm. The outer surface of the bone has been chipped or is missing in places and there is evidence of sedimentary infilling by phosphate.

As typical in pterodactyloids, the cervical vertebrae show a disparity in length, the longest one (fifth?) measuring about 30 cm long. Three of the vertebrae are similar in form to the mid-cervicals of Azhdarchidae (e.g., very elongate centrum with a vestigial or absent neural spine). The two other ones display a different pattern as they are characterised by a prominent neural spine. These vertebrae are probably posterior cervicals. The Moroccan pterosaur is here provisionally referred to as Azhdarchidae indet. By comparison with other azhdarchids, the estimated wingspan is about 5-6 m, which represents a large pterosaur.

Up to now, azhdarchids have been reported in the African-Arabian Plate from the Early Cretaceous of Niger (undescribed), the mid-Cretaceous deposits of southern Morocco as well as the Late Cretaceous of Senegal, Jordan (*Arambourgiania philadelphia*) and possibly Negev. The cervical vertebrae described here represent the first record of this group in the latest Cretaceous of Morocco and northern Africa, and one of the youngest records of pterosaurs worldwide.

THE SECONDARY SEXUAL CHARACTERISTIC THEORY OF PTEROSAUR WING DEVELOPMENT

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Three theories have been proposed for the origin of pterosaur flight: the arboreal leaping theory, the arboreal parachute theory and the cursorial theory. The first proposes that pterosaurs grew wings and gained the power of flight in the course of leaping from tree to tree, as many primates do. The second proposes that pre-pterosaurs passively dropped from a height and spread a gliding membrane to cushion, direct and extend a fall, like gliding lizards do. The third proposes that pterosaurs and their immediate ancestors were bipeds that ran along the ground and at speed jumped into the air. All three were proposed at a time when pterosaurs were considered archosaurs or the sister group to dinosauiromorphs.

A recent cladistic analysis that redescribes the prolacertiforms *Cosesaurus*, *Sharovipteryx* and *Longisquama* as pterosaur sister taxa gives new insight into this problem. The analysis indicates that nearly all previously considered pterosaur apomorphies, except those of the wing, were already present in this nonvolant group. These are generalized here : 1) enlargement of the skull ; 2) reduction of the torso ; 3) four sacral vertebrae (bipedal indicator) ; 4) attenuation of the tail (cursorial indicator) ; 5) a sternal complex composed of an anteriorly expanded and keeled interclavicle fused to large overlapping clavicles wrapped around a median sternum (arboreal indicator?) ; 6) a dorsoposteriorly-oriented, narrow scapula ; 7) a tall coracoid provided with a narrow ventral articulation to the interclavicle ; 8) elongation of the digits of the manus (arboreal character) ; 9) elongation of the penultimate phalanges of the manus (arboreal indicator) ; 10) reduction of manual digit V ; 11) elongation of the anterior process of the ilium (bipedal indicator) ; 12) fusion of the pubis and ischium ; 13) elongation of the tibia greater than the femur (cursorial indicator) ; 14) reduction of the fibula to a splint (a narrow gait indicator) ; 15) reduction of the tarsal elements to five in the pattern of pterosaurs ; 16) a more symmetrical metatarsus (a narrow gait indicator) ; 17) a digitigrade pes in the pattern of the trackmaker of *Rotodactylus* ; 18) elongation of the proximal phalanx of pedal digit V ; 19) appearance of accessory dermal membranes ; 20) and there are others.

Characters in this list indicate that pterosaur sister taxa were digitigrade, occasionally bipedal, and arboreal, supporting aspects of all three previously proposed theories. The critical character in the new proposal is the 90° twist of metacarpal IV. This twist makes digit IV flex in the plane of the metacarpal. Thus whenever a hypothetical wingless pre-pterosaur would cling to a tree of any diameter, digit IV would move in an arc tangential to the circumference of the tree. No longer used for support and locomotion, digit IV became a signaling device capable of rapid flexion and extension similar to the extendable throat sack of an anole. The unused ungual disappeared. Originally digit IV could have been provided with a small but colorful dermal extension — originating distally rather than proximally, and supported by fibers. Under natural selection such an ornamentation would have had the potential to enlarge. Folding away an increasingly large advertisement would also have been important. The pectoral morphology necessary for flapping flight was already present in *Longisquama*, perhaps as an aid to adduction during clinging or as part of a display ritual. In addition, prolonged tree-clinging may have contributed to the development of the propatagium and pteroid as passive aids to help prevent elbow over-extension if the pre-pterosaur held its torso away from the tree trunk rather than embracing it closely. Of course, ultimately all of these characters would have contributed to the development of each other and to experimental leaping, gliding, and flapping excursions.

GLIDING DREPANOSAURIDS, A CASE HISTORY

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The Drepanosauridae are small to medium sized (10 –50 cm) diapsid reptiles known from the Late Triassic of Northern Italy and U.S. They show a rigid and barrel shaped trunk, a long, deep, laterally compressed “leaf”-like tail; relatively long limbs ending in very long, narrow and sharp claws. The genera *Drepanosaurus* Pinna, *Megalancosaurus* Calzavara, Muscio and Wild and *Dolabrosaurus* Berman and Reisz, have been ascribed to the Drepanosauridae (Renesto 2000 and ref. therein). Another undescribed genera from Northern Italy quoted as “*Vallesaurus*” (*nomen nudum*, cat. n. MCSNB 4571 of the Museo di Scienze Naturali “E. Caffi” Bergamo,) has been considered a possible drepanosaurid (Renesto, 2000). The Drepanosauridae are considered as basal archosauromorphs but their taxonomic position is still uncertain.

Functional morphology

Life style of the drepanosaurids has been debated *Megalancosaurus* was considered to be arboreal, *Drepanosaurus*, in a first time was considered a fossorial reptile and *Dolabrosaurus* was first considered as aquatic, but further studies demonstrated that in both genera skeletal correlates are more consistent with arboreal life (see Renesto 2000 and ref. therein). Re-analysis of all *Megalancosaurus* specimens indicated that this genus and drepanosaurids in general, are more specialized to arboreal life than previously suspected.

The very large eyes and inflated parietal region may be indicative of good, vision, useful for locomotion and precise prey location among tree twigs and possibly good limb coordination. The neck of *Megalancosaurus* was very flexible only on the vertical plane, but torsion was eliminated by the “hypapophyses” and lateral mobility was limited by the buffer-like zygapophyses of the cervical vertebrae. The presence of hypapophyses in the cervicals and of very high neural spines in the anterior dorsal vertebrae suggest that robust muscles or tendons may have been originated from these structures permitting the neck to be held upright, retracted and suddenly projected forward. The notarium-like structure formed by the anterior dorsal vertebrae, may have served to articulate the free end of the scapula and is also the area for the insertion of a very powerful *latissimus dorsi*, a retractor and elevator of the humerus which plays an important role in raising the humerus backwards above the glenoid level. The clavicles rendered the pectoral girdle stiff and, if the very high scapula was connected to the supraneural plate as in pterosaurs, the shoulder formed a solid “ring” like in birds and pterosaurs.

gliding by shifting posteriorly the center of weight. In gliding phalangeriids the tail is long and it acts as a rudder, but it is flattened *dorsoventrally*, providing further lift during gliding, while the *laterally* flattened tail of drepanosaurids could not provide any lift. As a possible solution the tail could have been kept raised at some extent during gliding shifting forward the center of gravity, and the long neck may have helped in this task acting as counterbalance. The lack of a claw on the allux in some specimens may suggest that this latter was embedded in the membrane as in the gliding phalangeriid *Acrobates*. This may explain why the stoutness of the proximal phalanx of the allux which served to keep the patagium stretched. The gliding bauplan for *Megalancosaurus* cannot be considered as a plausible model for the morphology of a putative ancestor of birds (contra Ruben, 1998) because drepanosaurids were eventually skelobranchial gliders (Fig 1 B - C) with a patagium extending between anterior and posterior limbs, consequently excluding the possibility of a bipedal gait, and bipedality is considered to have developed prior to the attainment of gliding/flying abilities in pre-birds (Fig 1 A), both by supporters of the cursorial and of the arboreal theory for the origin of bird flight.

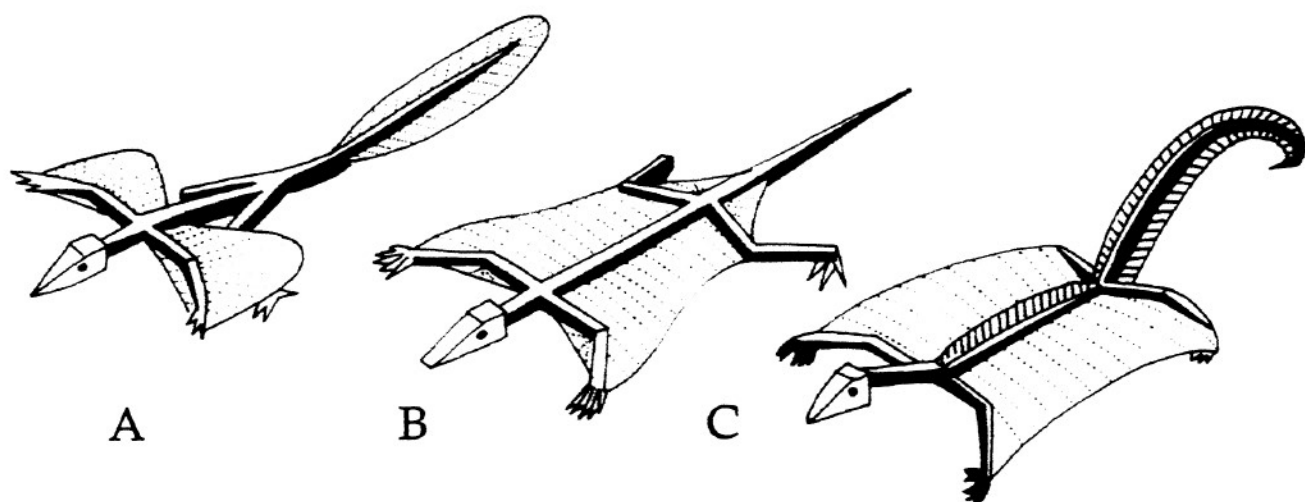


Fig. 1 - Gliding bauplan of a pre bird (A), of a generalized skelobranchial glider (B) and of an hypothetical gliding drepanosaurid (C).

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PTEROSAUR TRACKS FROM THE LATE CRETACEOUS OF NORTHERN MEXICO : PALEOECOLOGICAL AND ANATOMICAL IMPLICATIONS

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The pterosaurian record in Mexico includes to the moment, an uncrushed skeleton of a rhamphoryncoid pterosaur from the Middle Jurassic La Boca Formation, some unarticulated remains similar to *Nyctosaurus* from the Albian Tlay'a Formation, and an isolated wing phalanx from the Late Campanian El Gallo Formation, in the States of Tamaulipas, Puebla and Baja California respectively. Among the vertebrates found in the sedimentary sequence of the Cerro del Pueblo Formation, of Latest Campanian age, in southeastern Coahuila, pterosaurs are known through very fragmentary remains; however, an isolated bone fragment suggests the presence of the Family Ornithocheiridae.

In relatively recent times pterosaur tracks were discovered at the El Pelillal Tracksite in the Municipio de Ramos Arizpe, southeastern Coahuila. The site is an outcrop of a redish to light-brown, fine-grained, intensely bioturbated and ripple-marked sandstone. It is located stratigraphically higher within the Cerro del Pueblo sequence. At the moment, besides the tracks of pterosaurs, those of turtles, crocodiles, and one of a small theropod dinosaur are known, additionally, an isolated track similar to those of the Ichnogenus *Brasilichnium* has been collected. Among those of pterosaurs two different morphotypes are distinguished.

The first morphotype, which is called here robust morphotype, is represented by several manus prints and two pes prints. The manus prints are tridactyl, with a strong asymmetry, and shows the typical pterosaurian configuration. It shows morphological similarities with *Pteraichnus stokesi* Lockley et al., 1995. In regard to this morphotype, the best pes print preserved is a left print preserved as convex hyporelief. It bears four digits, a rounded and well defined heel pad and a posterior projection. There is a slab bearing a second impression of this projection.

The second morphotype is represented by manus prints of what represents a new *Pteraichnus* ichnospecies. It is characterized by *Pteraichnus*-like manus prints with a homogeneous slenderness along the digit impressions and a great angle of divarication between digits I and II, thus forming an obtuse angle. These features clearly differ from those present in the known *Pteraichnus* ichnospecies. This morphotype is some times found as thinner prints in which the digits are observed even as lines.

The whole ichnofaunal composition plus the geological observations at the El Pelillal Tracksite suggest a shallow freshwater environment. This agrees with the interpretation that Cretaceous pterosaurs, and particularly *Pteraichnus* tracks, are more frequently associated to deposits that represent freshwater and/or lacustrine environments.

The El Pelillal Tracksite is a manus dominated *Pteraichnus* assemblage, that bears several hand prints against two pes prints. A remarkable feature of the first morphotype is the presence of pes prints bearing a projection posterior to the heel pad. This projection, not found in the known species of *Pteraichnus*, suggests that at least some pterosaurs were digitigrades. Thus, this projection represents a true structure and must be a metatarsal impression. This rises an image of a pterosaur in a pose similar to some aquatic birds (e.g., a cormorant) resting on their metatarsals.

ANATOMY, FUNCTIONAL MORPHOLOGY AND SYSTEMATICS OF *DIMORPHODON*

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Dimorphodon macronyx is an early Jurassic rhamphorhynchoid pterosaur originating from localities around Lyme Regis, Dorset and Aust Cliff, Gloucester in the marine Blue Lias shale. The holotype (BMNH R.1034) was originally described by William Buckland (1835) who gave it the generic name '*Pterodactylus*'. It wasn't until further specimens were unearthed, complete with cranial material, that Richard Owen re-christened this genus *Dimorphodon* in reference to the two distinct types of dentition exhibited in the upper and lower jaws. The type specimens (BMNH R.1034, BMNH R.1035, BMNH 41212 and BMNH 41346) are housed in the Natural History Museum in London and have been much neglected since Owen wrote his monograph in 1870.

Dimorphodon is a fairly large rhamphorhynchoid with a wingspan of just under 1.5m. It is diagnosed by a proportionally massive skull (20cm long) comprised of narrow bony struts, which define huge nasal, antorbital, orbital and temporal fenestrae. The teeth exhibit two types of morphology – long anterior 'laniaries' (Owen 1870) and more posteriorly placed minute 'lancets'. It is the primary purpose of this research to re-describe this unusual animal in the light of modern theories and recent preparation work, which has revealed previously obscured areas of the braincase and joint surfaces. Following on from this, a detailed analysis of pterosaur hind limb functional morphology will be attempted. The mode of terrestrial locomotion of pterosaurs is still the centre of much debate with ideas ranging between cursorial bipedal motion, sprawling quadrupedal gait and adaptations towards leaping or underwater swimming. Fortunately the London specimens are in excellent condition enabling a re-analysis of *Dimorphodon*'s hind limb and pelvis such that a muscle reconstruction and estimation of range of motion can be attempted. A combination of this with centre of mass calculations using Donald M. Henderson's mathematical-computational modelling technique for bilaterally symmetrical animals (Palaeobiology, 1999), and comparison of leg-trunk measurements with birds and various ornithopods and theropods may shed some new light on the matter of pterosaur locomotion.

The second objective of this research is to perform a cladistic analysis on the Order Pterosauria using PAUP, selecting outgroups from amongst the basal archosaurs. It is hoped that the results of this analysis will either support or redefine the relationships between and within the established clades, as well as provide the basis for the construction of a phylogenetic tree using Andrew B. Smith's method of range extension through utilising stratigraphic data ("Systematics and the Fossil Record", 1994).

COMMENTS ON PTEROSAUR BONE HISTOLOGY

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Thin sections of pterosaur bones have not been extensively studied so far. Until now mainly isolated bones were the subject of this type of analysis. The first known section of pterosaur bone consists of a humerus illustration of an unknown pterosaur from 1849. Fifty years later Seitz observed the presence of secondary osteons in phalanxes of *Pteranodon*. The most complete study was performed by de Ricqlès and colleagues. They analyzed the variation on the histology between the same bones in different pterosaur taxa, and discussed pterosaur ontogeny, mechanical function, and mechanical construction of the tissues. In South American pterosaurs this kind of analysis began a few years ago with sections of an Anhaguerid pterosaur from Santana Formation, Brazil. Here we present some results of the histological analysis of a partial skeleton of an Anhaguerid pterosaur, from the Romualdo Member (Aptian-Albian), Santana Formation and a proximal end of an ulna from Argentina. The first specimen (MN 4809-V; Museu Nacional) comprises both wings (from humerus to third phalanx - F3D4) and one hind limb (left tibia, left femur and right foot). All bones are extremely well preserved, showing no evidence of compaction. Thin sections of the diaphyseal portion of each bone were observed in cross and longitudinal view and the histological structures were compared. Among the preserved features we could observe the presence of a developed Haversian system, with the canaliculi and numerous osteocyte lacunae. The external surface is formed by lamellar periosteal bone, suggesting that this specimen represents an adult individual. Among the observed features, we identified two lines of arrested growth (LAG) in F3D4. In the Mc IV, the LAG is positioned closer to the lamellar periosteal bone while in the ulna the LAG is positioned in the middle of the cortex. Some bones, such as the femur, do not exhibit LAGs. This variation of the position and presence of the LAGs is not fully understood, but might represent differential growth rates in the different bones of the same individual. In the second specimen the histological structures are very different from the first. In this pterosaur the cross-section of diaphysis shows a well vascularized, rapidly growing fibrolamellar bone, very similar to that observed in living birds.

These results show that histological features can vary among the bones of the same individual, limiting the information that can be obtained of such studies based solely on isolated elements.

PTEROSAUR BONE HISTOLOGY : A RE-EXAMINATION OF SOME OF THE EARLIEST HISTOLOGICAL SECTIONS

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In 1855, John Quekett of the Hunterian Museum in London published a catalogue of the thin section specimens contained in that institution. Among the many thin sections of fossil specimens were 15 histological sections of pterosaur bones. These transverse and longitudinal sections had been cut from eight different bones, found in the Lower Chalk of Kent, the Wealden of Sussex and the Stonesfield Slate of Oxfordshire, UK. These are believed to be the earliest thin sections and descriptions of pterosaur bone histology, previous descriptions having been based on fractured surfaces.

Six of these pterosaur bone thin sections were among the specimens that survived the bombing of London during WWII, although the original bones from which they were cut were destroyed. Previous reports that the surviving histological sections were in poor condition are unfounded. A re-examination in early 2001 found them in excellent condition and suitable for histological analysis. The sections have now been photographed in plane and crossed polarised light for the first time.

Five of the sections are histologically typical pterosaurian bone, composed of fibro-lamellar cellular bone and containing a reticular arrangement of primary canals. However, one transverse thin section (numbered Bb69) is histologically distinct (see Figure). This section of bone is oval and measures 3 mm x 2 mm. It contains a central lumen, measuring 0.5 mm x 1 mm, which is incompletely lined by an endosteal lamella (a). The periosteal bone comprises two distinct tissues that are separated by a reversal line (r). The innermost periosteal tissue is strongly Haversian with large secondary osteons (b). The outer periosteal tissue is highly vascularised by numerous longitudinal primary osteons (c). These primary osteons become more abundant as the periosteal surface of the bone is approached.

The original specimen from which it was made was described as "a small, tapering bone, probably of Pterodactyle, from the Stonesfield Slate" (Quekett, 1855, p. 125). Its slender appearance led Quekett to identify it as a small pterosaur bone. However, the Stonesfield Slate is well known for other Bathonian (Middle Jurassic) vertebrates, including sharks, bony fishes, chelonians, dinosaurs and mammals. Only one other pterosaur bone from this area has been studied in thin section (Seitz 1907).

PTEROSAUR SOFT TISSUES : EVIDENCE, ANATOMY AND PALAEOBIOLOGICAL SIGNIFICANCE

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The ubiquity and rapidity of decay processes coupled with the vagaries of fossilisation mean that most of what we know about pterosaurs is based on their bones and teeth. These structures have provided important insights into pterosaur palaeobiology but, without information regarding soft tissue anatomy, the range and depth of such understanding is likely to remain rather limited. The Extant Phylogenetic Bracket approach could yield some general information regarding pterosaur soft tissues, but is handicapped at present by the uncertainty regarding the relationships of pterosaurs to other diapsids (Unwin 1999). In any case, this approach cannot discover structures (e.g. « hair ») that, within Diapsida, are unique to pterosaurs.

Bone morphology is a more important source of indirect evidence for soft tissues, but rarely yields precise information regarding the size or anatomy of particular structures. A notable exception is the brain case which, together with cranial endocasts, has yielded some details of the morphology of the brain and the arrangement of the cranial nerves (Wellnhofer 1991, Kellner 1996). Other nerves, one or two blood vessels, pneumatic diverticulae and various muscles, most notably from the pectoral, pelvic and forelimb regions, have also been inferred on the basis of osteological features (Wellnhofer 1991, Bennett 2001).

Direct fossil evidence for pterosaur soft tissues (see Table 1), while rare, is the most important source of information for these structures and has provided vital insights into pterosaur anatomy, locomotory abilities, ecology and physiology. The evidence is usually in the form of impressions (e.g. wing membranes of *Rhamphorhynchus* and *Pterodactylus* [Wellnhofer 1970, 1975] and some foot prints), but is occasionally represented by mineralised structures (e.g. Sordes [Unwin & Bakhurina 1994]). Caution is necessary when interpreting such evidence, however, because even well preserved fossil remains must have been modified to some degree by taphonomic processes. Comparison of the same structures in different individuals, or even different taxa, and identification of the same structures preserved in different ways can both help to pinpoint true anatomical details and exclude artefacts of preservation.

Wing-membrane fibres (aktinofibrils), for example, occur in at least ten different pterosaur genera and are preserved in three different ways, yet exhibit a remarkable uniformity in their anatomy and organisation. This observation strongly supports arguments that they are not folds, but true fibre-like structures (Padian & Rayner 1993), and has thrown much light on their construction, distribution and function.

In many cases, the fossilised soft tissues, or their impressions, provide anatomical information that cannot be inferred from bone morphology or phylogenetic relationships. Critically, exceptional preservation in a range of taxa shows that the flight surface was composed of a thin membrane (almost certainly derived from the integument) and, perhaps most importantly of all, that the flight membranes linked together the fore and hind limbs in the flight apparatus (Unwin & Bakhurina 1994). This arrangement has fundamental implications for the terrestrial and aerial abilities of pterosaurs, the origin of pterosaur flight and the evolutionary history of the group (Unwin 1999).

Soft part impressions in a few specimens of *Rhamphorhynchus* and *Pterodactylus* (Wellnhofer 1970, 1975) and fragments of fossilised integument in several individuals of *Sordes* (Sharov 1971), have yielded another unique insight into pterosaur anatomy. These fossils indicate that parts of the head and body were covered by short, slender, 'hair'-like structures that formed a fine pelt (Wellnhofer 1991, Frey & Martill 1998) whose primary function is likely to have been temperature control. This is consistent with other evidence from histological studies and theoretical considerations of energetic requirements for flight, which suggest that the basal metabolism of pterosaurs was more like that of extant mammals and birds than extant reptiles (Wellnhofer 1991).

The study of pterosaur soft tissues is still in its infancy. Nevertheless, it has already contributed much to our understanding of pterosaur anatomy, in particular integumentary structures, and has yielded some critical insights into the basic nature of pterosaurs, most notably the construction of the flight apparatus (Unwin 1999). The challenge for future studies will be to integrate more fully our growing knowledge of soft tissues with other aspects of pterosaur palaeobiology such as growth, locomotion, physiology and phylogeny, so that we can develop a more comprehensive understanding of these extraordinary animals.

jaw sheaths	<i>Rhamphorhynchus, Pterodactylus, Tapejara</i>
'bristles' fringing jaws	<i>Batrachognathus</i>
throat sacs	<i>Rhamphorhynchus, Pterodactylus</i>
cranial crests	<i>Rhamphorhynchus, Pterodactylus, Tapejara</i>
?trachea	<i>Pterodactylus</i>
sections of the ?gut	<i>Rhamphorhynchus</i>
?muscles	<i>Pterodactylus</i>
integument including 'hair'	<i>Sordes, ?Dorygnathus, Rhamphorhynchus, Pterodactylus, Crato azhdarchid</i> (Frey & Tischlinger 2000)
tail-flap	<i>Sordes, Rhamphorhynchus</i>
wing membranes	<i>Anurognathus, Batrachognathus, Eudimorphodon, Sordes, ?Scaphognathus, Dorygnathus, Rhamphorhynchus, Pterodactylus, ?Eosipterus, Santana pterodactyloid</i> (DGM 1475-R), <i>Crato azhdarchid, Zhejiangopterus</i>
webs between manus digits I-III	<i>Crato azhdarchid</i>
webs between pedal digits I-IV	<i>Sordes, Rhamphorhynchus, Pterodactylus, Crato azhdarchid</i>
claw sheaths	<i>Batrachognathus, Sordes, Rhamphorhynchus, Pterodactylus, Crato azhdarchid</i>

Table 1 - Soft part structures identified on the basis of impressions or fossilised soft tissues

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TWO ISOLATED TEETH OF PTEROSAURS FROM THE UPPER JURASSIC (LOWER KIMMERIDGIAN) OF LA ROCHELLE (CHARENTE-MARITIME, WESTERN FRANCE)

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Since the 19th century, the Upper Jurassic of Western France, and more precisely the Lower Kimmeridgian of the La Rochelle region, has yielded numerous but isolated remains of marine vertebrates, such as selacians, holosteans and metriorhynchid or teleosaurid crocodilians (VIGNAUD *et al.*, 1994).

A few years ago, two isolated teeth of pterosaurs (R. VULLO's collection) were found by private collectors in two different localities. The biostratigraphy established thanks to the ammonite fauna allows an accurate datation of these fossils. The first tooth comes from "La Pointe du Chay" (Cymodoce zone, Pseudolictor horizon), near the village of Angoulins. The second one has been collected in a slightly more recent level, in "Les Boucholeurs" (Cymodoce zone, Chatellailonensis horizon), near Châtelaillon (Fig. 1). "La Pointe du Chay" deposits correspond to a reef barrier and a proximal neritic environment, whereas they indicate deeper water in "Les Boucholeurs" (HANTZPERGUE, 1989).

The tooth coming from "La Pointe du Chay" (specimen VR24, fig. 2a-d) is 19 mm high. It is quite robust, with a broad base. However, it is strongly labio-lingually compressed and shows a flattened cross-section. Very slight mesio-distally and labio-lingually curvatures can be observed. A carina is developed on both anterior and posterior edges. The enamel covers the tip of the crown, is extended toward the tooth base along the two edges, and is reduced more distally on the lingual side than on the labial one. This enamel coating is totally smooth, excepted the presence on the lingual face of a few irregular and short ridges close to the middle part of the posterior edge. The basal part of the crown shows a smooth dentine. From the base to the apex, there are numerous but very faintly parallel growth rings.

The second specimen (specimen VR25, fig. 2e-h), discovered in "Les Boucholeurs", is very similar to the first one, in its general morphology as well as in its enamel pattern. It differs only by its larger size (23 mm high) and by its shape more robust.

Same tooth morphology is observed in Ornithocheiridae tooth (see WELLNHOFER & BUFFETAUT, 1999 : morphotype III, p. 139, fig. 8). If the attribution of the teeth from the Kimmeridgian of La Rochelle to this family was confirmed, it would be the oldest occurrence of those pterosaurs, known up to now from the Berriasian to the Cenomanian. (WELLNHOFER & BUFFETAUT, 1999 and KNOLL, 2000). Nevertheless, a comparison with the teeth, slenderer but reminiscent, of the largest species of *Rhamphorhynchus* (WELLNHOFER, 1975), like *R. longiceps*, is necessary in order to precise the affinities of the form found in La Rochelle.

These two teeth reveal the presence of large pterosaurs in Western France during Lower Kimmeridgian. Such specimens, whose wingspan should have reach 3 metres, must have represent the largest forms among the Jurassic pterosaur fauna. Note also that one century ago, remains of an unidentified pterodactyloid have been described from the Upper Kimmeridgian (Autissiodorensis zone) of Fumel (Lot-et-Garonne) (SAUVAGE, 1900, 1902). Unfortunately, teeth are unknown in this locality.

The fossil record of pterosaurs in France is rather sparse. Thus, although the material described here consists only of two isolated teeth, this new occurrence increases our knowledge of the pterosaur fauna from the Upper Jurassic of the Aquitaine Basin.

Stage	Zone	Serie	Horizon	"Formation"	Locality
Lower Kimmeridgian	Cymodoce		Chatelaillonensis	Châtelailon Marls	Les Boucholeurs (specimen VR25)
			Pseudolictor	Coral beds	La Pointe du Chay (specimen VR24)
	Rupellense				

Figure 1 – Stratigraphic position of the two teeth from the Lower Kimmeridgian of the region of La Rochelle.

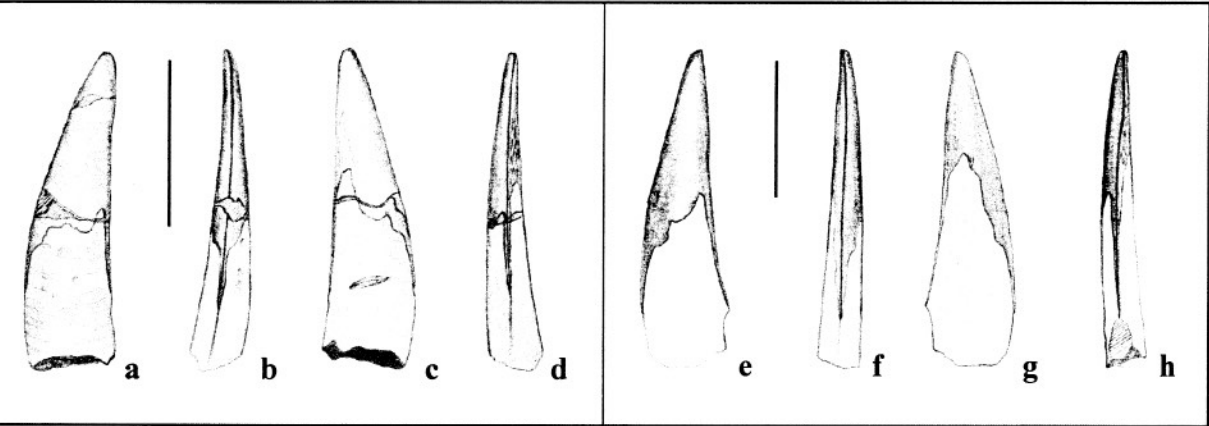


Figure 2 – Isolated pterosaur teeth from the Lower Kimmeridgian of “La Pointe du Chay” (VR24, fig. 2a-d) and of “Les Boucholeurs” (VR25, fig. 2e-h), in labial (a, e), anterior (b, f), lingual (c, g) and posterior (d, h) views. Scale bars equal 10 mm.

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A LATE TRIASSIC PTEROSAUR FROM THE NORTHERN CALCAREOUS ALPS

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Fossils of Late Triassic pterosaurs are still the oldest known evidence of these archosauromorph flying reptiles of the Mesozoic. Although exceptionally rare in the fossil record, several skeletal remains of diverse pterosaurian taxa have been discovered from Late Triassic deposits of Northern Italy, Luxembourg, France, Switzerland, England, Texas, and East Greenland, so far. This record documents global distribution as well as high diversity of the Pterosauria already at the time of their earliest evolutionary history.

Here, the discovery of disarticulated skeletal remains of an eudimorphodontid pterosaur from the Late Triassic of the Karwendel Mountains in Tyrolia, Austria, is reported. Besides a still unpublished pterosaur from the same horizon and area (Dalla Vecchia et al. in press) it is only the second record of Triassic pterosaurs from the Northern Calcareous Alps, after the discoveries in the Southern Calcareous Alps of Northern Italy, since 1973 up to the present. The fossil material, isolated jaws, bones and fragmentary skeletal parts of one individual have been collected from the Norian Seefeld Beds (also called "Bitumenmergel" or "Seefelder Fischechiefer") near Seefeld in Tirol, Austria. The fossiliferous formation of largely bituminous and calcareous layers originated on top of an extended marine carbonate platform, as an equivalent to the nearly contemporaneous limestones and dolomites in the Southern Calcareous Alps, as exposed in the Bergamo and Friuli area in Italy, that had produced pterosaur fossils, previously. Based on the stratigraphic significance of conodont index fossils the Seefeld Beds can be dated as Late Norian, most likely Sevatian.

Sufficiently well preserved skeletal elements include a jugal, isolated teeth, both mandibular rami with a dentition of uni-, tri- and pentacuspids teeth, cervical, dorsal and caudal vertebrae, ribs, sternum, scapulocoracoids, humerus, first phalanx of the fourth (wing) finger, pelvis, and tibia/fibula. There are morphological characters that support a subadult stage of the individual with an estimated wing span of 70 to 80 centimeters. The dentition is comparable with *Eudimorphodon ranzii* ZAMBELLI, 1973, from the Norian Calcare di Zorzino of Cene near Bergamo, Northern Italy. Some skeletal proportions and osteological features, however, are distinctive from this taxon, as well as from a second species, *Eudimorphodon rosenfeldi* DALLA VECCHIA, 1995, from the Norian Dolomia di Forni of Friuli, Northern Italy. The meaning of

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these differences in the Seefeld specimen, in particular the relatively long tibia and short wing phalanx 1, is discussed.

Of special interest is the unusual osteology of the caudal vertebrae. The zygapophyses and chevrons are not elongated into rod-like bony extensions, the so-called « ossified tendons ». The lack of this character, usually taken to be significant for all rhamphorhynchoid pterosaurs, functioning as structures stiffening the long tail, might be evaluated as a primitive trait for these basal pterosaurs. However, whether this character was typical for the genus *Eudimorphodon* can not be tested on the basis of the fossil material available.

The unique dentition, however, permits the assignment of the Seefeld pterosaur to the genus *Eudimorphodon*. The fragmentary state of the skeleton, certain skeletal proportions and osteological features, which might merely reflect ontogenic changes, most closely relate the specimen to the type species, *E. ranzii*. It is here preferred to use open nomenclature and refer it to as *Eudimorphodon* cf. *ranzii* ZAMBELLI 1973.

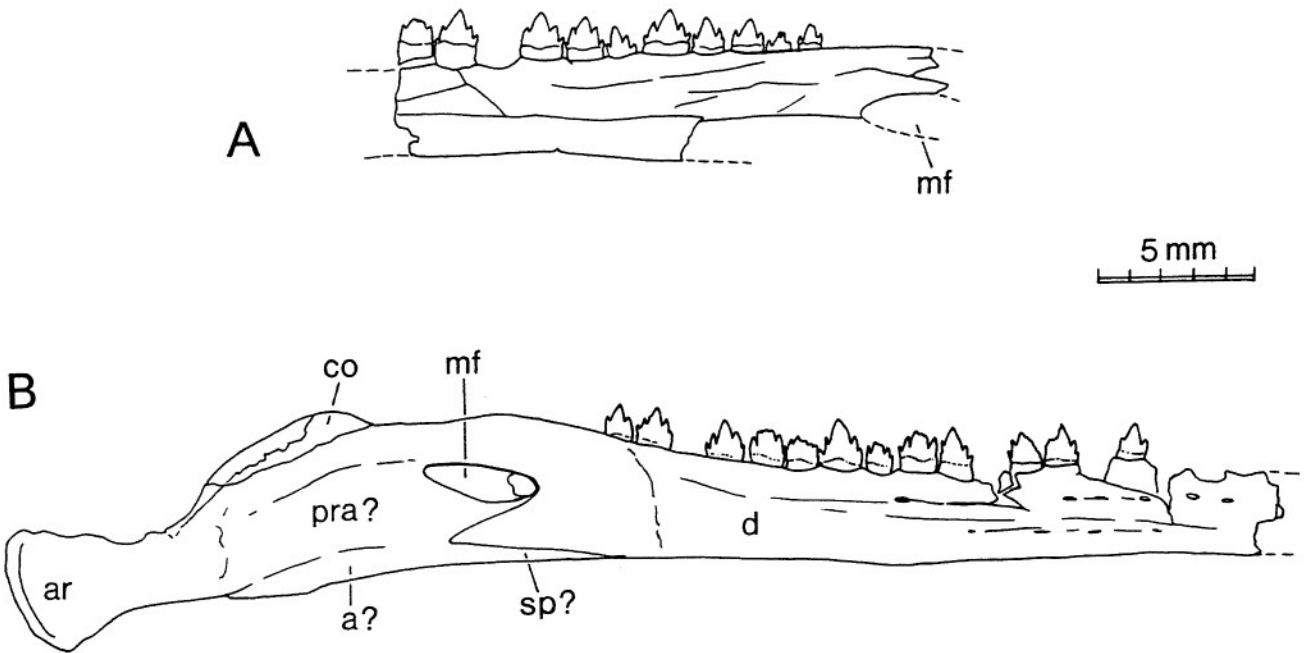


Figure caption

Eudimorphodon cf. *ranzii* ZAMBELLI, Late Norian, Seefeld Beds, Karwendel Mountains, Seefeld i. Tirol, Austria. Mandibles with multicuspoid teeth as preserved in lingual view. A, fragment of right mandible, middle segment ; B, left mandible with the anterior portion missing. Bayerische Staatssammlung für Paläontologie und Geologie, Munich, coll. nr. BSP 1994I 51. Abbreviations : a angular, ar articular, co coronoid, d dentary, mf fenestra meckeli (fossa adductoria), pra prearticular, sp splenial.

THE PTEROSAUR BRAIN

Debbie WHARTON

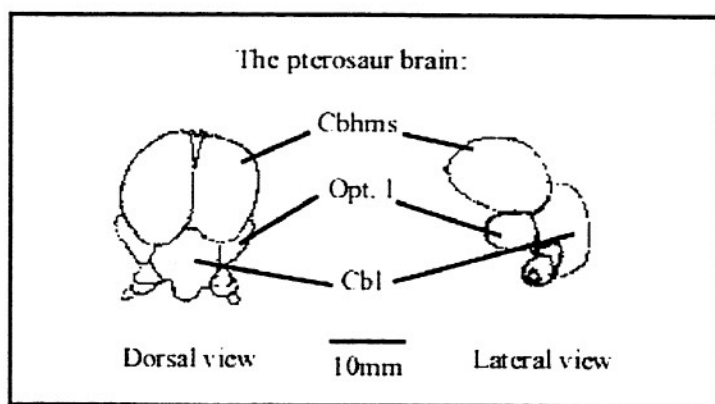
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Detailed analysis of the brain of the Pterosauria, and comparison with those of extant and other extinct Archosauria show that the pterosaurian endocranial nervous system is very similar to that of birds in terms of both size and morphology. The brain appears to have undergone the same changes; volumetrically, topographically and structurally, during its evolution from the primitive archosaurian state as that of birds.

Results show that the encephalisation quotients of some non-avian theropods may have surpassed those of some modern birds and that some pterosaurs may have had brains as developed as those of modern birds.

However, it is difficult to map out the trends of pterosaurian evolution as the phylogenetic framework upon which to base the analysis is not yet fully resolved. Fossil data linking derived pterosaurs with more primitive archosaurs remains insufficient to elucidate exact sequence and timing of the evolutionary patterns.

Hypotheses are presented concerning the exact relationship between the onset of the modifications in the brain and particular ecological, physiological and locomotory adaptations in the pterosaurs, non-avian theropods and early birds. Factors such as size, feeding habits, bipedality, nocturnality and flight, amongst others, and their positive feedback mechanisms are explored as possible explanations for some of the observed developments.



Key - cbhms : cerebral hemispheres ; Cbl : cerebellum ; Opt. 1 : optic lobe

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GLIDING PERFORMANCE OF LOWER CRETACEOUS PTEROSAURS

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The study of pterosaur flight has in the past been hampered by the paucity of suitable fossils, which are rarely complete and are almost invariably crushed flat. However, the Santana formation in Brazil has recently yielded several exceptional specimens that are preserved in full three-dimensional detail. Most are members of the "ornithocheiroid" group, which flourished in the early Cretaceous period and ranged in size from about 2m to over 9m in wingspan. A reconstruction of a typical individual, belonging to the genus *Anhanguera*, was carried out using twelve skeletons. The mass was estimated using a method of 3D mathematical slicing, and the spatial orientation and range of movement of the wing bones were found by manipulating the joints. For an animal with a wingspan of 4.5m, the mean estimated mass was 9kg and the corresponding wing loading was 66Nm^{-2} . Wind tunnel tests were undertaken on model wings to determine their lift and drag characteristics at various airspeeds. Unusually high lift coefficients were obtained (exceeding two in some cases), and control over the magnitude of developed lift was provided by flexion of the forewing, supported by the pteroid bone. The minimum gliding speed was found to be 8.5ms^{-1} , and the minimum sinking speed 1ms^{-1} . The envelope of gliding performance is presented.