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David W. E. Hone & Eric Buffetaut (Guest Editors)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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CONTENTS/INHALT

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer; design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

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A short history of pterosaur research

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1. Personal remarks

Talking about the history of pterosaur research, I feel somehow involved myself. So, if it may be permitted, I will begin with my personal story.

When I started my career at the Bavarian State Collection of Palaeontology and historical Geology in Munich, more than 40 years ago, my director, who had been also my professor, Richard DEHM, proposed that I should have a closer look at the Solnhofen pterosaurs. In my position as an Assistant Curator of Lower Vertebrates, I had no other choice as to change from my former special field of research completely, from invertebrate to vertebrate paleontology, from Jurassic bivalves to pterosaurs. At that time I could hardly imagine that this decision set the course not only for my further scientific and professional career, but also for my personal life. I have never regretted this change, and have always been very grateful to Professor DEHM, himself a specialist on Tertiary mammals, for his pushing me in this direction. In 1968 my very first publication on pterosaurs was a revision of the type specimen of *Pterodactylus kochi* (WAGNER 1837) from the lithographic limestone of Kelheim in Bavaria resulting in a revision of the systematics and taxonomy of the genus (WELLNHOFER 1968).

In fact, the conditions for this new start were very favourable at that time, in 1965. Despite the loss of fossil material during World War II, the Munich State Collections still had some unpublished Solnhofen pterosaur specimens, and numerous additional specimens were available in several private and public collections that were previously unknown. So, a revision of the Solnhofen pterosaurs seemed to be interesting, and was in fact badly needed, since the last paper had been published by Ferdinand BROILI in 1938, 27 years earlier (BROILI 1938). And the only publication on pterosaurs after WWII had appeared in 1964, on *Dsungaripterus* from the Lower Cretaceous of China, published by C.C. YOUNG – in, well, Chinese (YOUNG 1964).

My teacher, the late Professor DEHM (1907–1996), had been a student of Ferdinand BROILI (1874–1946) in Munich, who became professor of Palaeontology and director of the State Collections in 1919. He too had worked on Solnhofen pterosaurs and published almost a dozen papers between 1912 and 1938. BROILI himself was the student of Karl Alfred VON ZITTEL (1839–1904) who had also studied Solnhofen pterosaurs. Just remember the "Zittel wing" of *Rhamphorhynchus.* But also ZITTEL's predecessors on the Munich university chair of palaeontology, and directors of the Bavarian Palaeontological

Figure 1: Cosimo Alessandro COLLINI (1727–1806), keeper of the Mannheim Natural History Collections. In 1784 he published a description of the first known pterosaur, without, however, realizing the true nature of the animal as a flying reptile.

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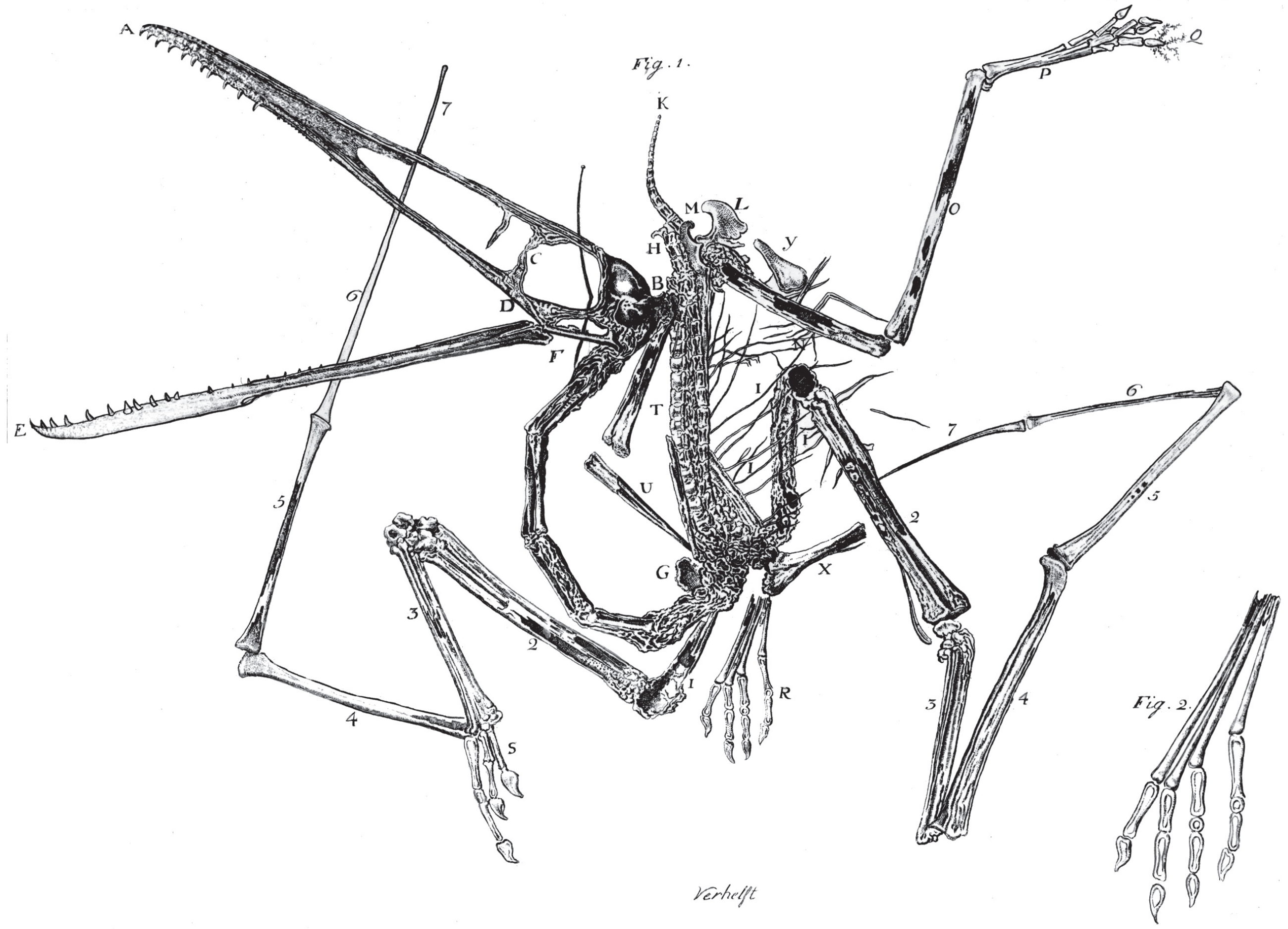

Figure 2: *Pterodactylus antiquus* (SOEMMERRING, 1812), holotype specimen, from the Late Jurassic Solnhofen lithographic limestone of Eichstätt, was the first fossil record of pterosaurs. The original copper engraving of the specimen, as it was published by Cosimo Alessandro COLLINI in 1784. Bavarian State Collection of Palaeontology and Geology Munich (BSPG), AS I 739.

State Collections, Albert OPPEL (1831–1865) and Andreas WAGNER (1797–1861), had published a series of papers on pterosaurs beginning in 1837. And, most importantly, the first pterosaur ever discovered, *Pterodactylus antiquus*, the holotype specimen (Fig. 2), has been housed in the Munich collections since the beginning of the 19th Century, and here it was studied again by a Munich scholar, Samuel Thomas VON SOEMMERRING (1755–1839), who published several papers on Solnhofen pterodactyls between 1812 and 1820 (WELLNHOFER 1975). So I could resume this more than 150 years of Munich tradition of pterosaur research, and I always felt as part of this tradition. Indeed, here was the place were an important chapter of the early history of pterosaur research had been written.

2. Early discoveries

In tracing the history of pterosaur research in retrospect we inevitably arrive at the aforementioned *Pterodactylus antiquus* from the Upper Jurassic Solnhofen lithographic limestone of Eichstätt in Bavaria. The specimen was first described by Cosimo Alessandro COLLINI (1727–1806) in 1784, when it was kept in the Natural History Collections in Mannheim in the Palatinate. COLLINI (Fig. 1), a historian and naturalist, was the keeper of these collections in the castle of the Elector Karl Theodor. Like many 18th Century naturalists, COLLINI no longer believed that fossils were mineral formations or remains left behind by the Great Flood. In his early years COLLINI had been secretary to VOLTAIRE, and so was definitely a child of the Age of Enlightenment realizing that fossils are the petrified remnants of living animals from earlier epochs. Obviously he was an adherent of the French naturalist Leclerc DE BUFFON who proposed that fossil organisms, unknown in the present world, were exterminated periodically by geological catastrophes, or “revolutions”.

COLLINI provided an amazingly accurate illustration of the fossil skeleton, and he rightly recognized that the creature’s arms could be folded, and he even suspected that a membrane could have been attached to them. Although he found similarities to bats, he interpreted it as a marine vertebrate of unknown nature, since it was preserved in Solnhofen limestone along with fishes, crustaceans and other marine organisms (COLLINI 1784).

Only 17 years later, in 1801, the famous Georges CUVIER (Fig. 3) in Paris recognized the still unnamed Eichstätt fossil vertebrate as a reptile. He identified the long, slender bones at the forelimbs as the elongated phalanges of one finger to which a flight membrane must have been attached. Accordingly he concluded that the animal was a flying reptile of a group no longer existing in the present world. It was only in 1874, when the discovery of imprints of the actual wing membrane confirmed CUVIER'S conclusion. In 1809 CUVIER finally named the flying reptile from Eichstätt "*Ptero-Dactyle*", "wing finger", later to be changed into the generic name *Pterodactylus.* Finally, in his standard work "Recherches sur les Ossemens fossiles" CUVIER (1824) drew the conclusion that the animal was able to fly using a membrane supported by a single digit of the four-fingered hand. Moreover, the pterodactyl could hang from tree branches by its three small clawed digits. It could perhaps also crawl on the ground, but could not walk bipedally, and possibly only stand upright on the hindlimbs. It is remarkable that CUVIER had based his description and study of the fossil

Figure 3: Georges CUVIER (1769–1832), the prominent French vertebrate palaeontologist and founder of the method of comparative anatomy. He was the first to recognize the Eichstätt fossil vertebrate as a flying saurian, a pterosaur, which he called *Ptero-Dactyle*.

solely on COLLINI'S detailed illustration of 1784. He had never seen the original fossil himself (WELLNHOFER 1984).

In the meantime different interpretations of the animal were being proposed, such as the one by the Göttingen anatomist Johann Friedrich BLUMENBACH (1807) who argued that it was a bird, a waterfowl, or SOEMMERRING (1812) who was convinced that the animal was a mammal, a new kind of bat (Fig. 4). He determined its position as intermediate between bats and birds, naming it *Ornithocephalus*, "bird skull". He even suggested a "gradual sequence" of animals between flying mammals and birds, and may thus have been influenced by the evolutionary theories of Jean Babtiste DE LAMARCK. This alone brought him in conflict with CUVIER'S catastrophism.

Although SOEMMERRING, unlike CUVIER, had the advantage of being able to study the original fossil in Munich were it had been transferred to from Mannheim in 1802 (WELLNHOFER 1975), he misidentified the bones of the forelimb, taking the humeri as clavicles (which are absent in pterosaurs), the ulnae as humeri, and the metacarpus as the lower arm. However, he correctly recognized four digits of the hand including the elongated fourth finger for stretching a flight membrane. Independently of CUVIER he assumed that the animal fed on insects which it caught on the wing.

It was only in 1817 when a second pterosaur fossil was discovered from the lithographic limestone, a very small skeleton, which appeared even more bat-like to SOEMMERRING (1817), because of its short head. He compared it to the parti-coloured bat, *Vespertilio murinus*. With its wing span of only 25 cm this individual is still one of the smallest pterosaurs known so far. Today, we know that it is clearly a baby pterosaur, an juvenile individual of one of the larger species of *Pterodactylus.* Nevertheless, LYDEKKER (1888) established for this specimen a distinct genus, *Ptenodracon* on which HOOLEY (1913) based even a new subfamily, Ptenodraconinae.

Juvenile characters were not always recognized as such, and differences in size were taken as diagnostic at the species and generic levels. Consequently, this splitting led to an enormous increase in the number of taxa. In his great monograph on the Reptiles of the lithographic limestone the leading vertebrate palaeonologist in Germany, Hermann VON MEYER, described more than 40 Solnhofen pterosaur specimens, and assigned them to 20 different species (MEYER 1859–1860). Among those was also *Pterodactylus crassipes*, an incomplete skeleton from the Upper Jurassic limestone of Jachenhausen near Kelheim in Bavaria which, 110 years later, turned out to be actually an *Archaeopteryx* specimen, today called the "Haarlem specimen" (OSTROM 1970). Then, in 1970, it was the fourth specimen of the Solnhofen urvogel known, after the London, Berlin, and Maxberg specimens (WELLNHOFER 2008).

Around 1825 the great Bayreuth fossil collector and paleontologist, Georg Graf zu MÜNSTER, had in his collection of Solnhofen fossils an isolated skull and lower jaw. He sent the fossil to SOEMMERRING in Munich asking for his opinion. SOEMMERRING replied that (in translation): "the ornitholith seems to belong to a particular genus of waterfowl which could have been similar to a seagull or a diver". At that time it would have been the oldest bird from the fossil record, long before the discovery of the first *Archaeopteryx* specimen in 1861. Obviously, Graf MÜNSTER was not quite convinced, since he sent a cast of the skull also to August Georg GOLDFUSS, professor at Bonn university, who in contrast to SOEMMERRING identified it as the skull of a pterosaur, a new species which he named *Pterodactylus muensteri*. GOLDFUSS himself had in his collections a Solnhofen pterosaur skeleton lacking the tail, but with a similar skull that he described as *Pterodactylus crassirostris*, a species later to be assigned to a new genus, *Scaphognathus* by WAGNER (1861).

However, at that time GOLDFUSS could not know that both specimens actually belonged to a new, distinct group of pterosaurs with long vertebral tails. This became apparent only in 1839, when Graf MÜNSTER received a complete skeleton

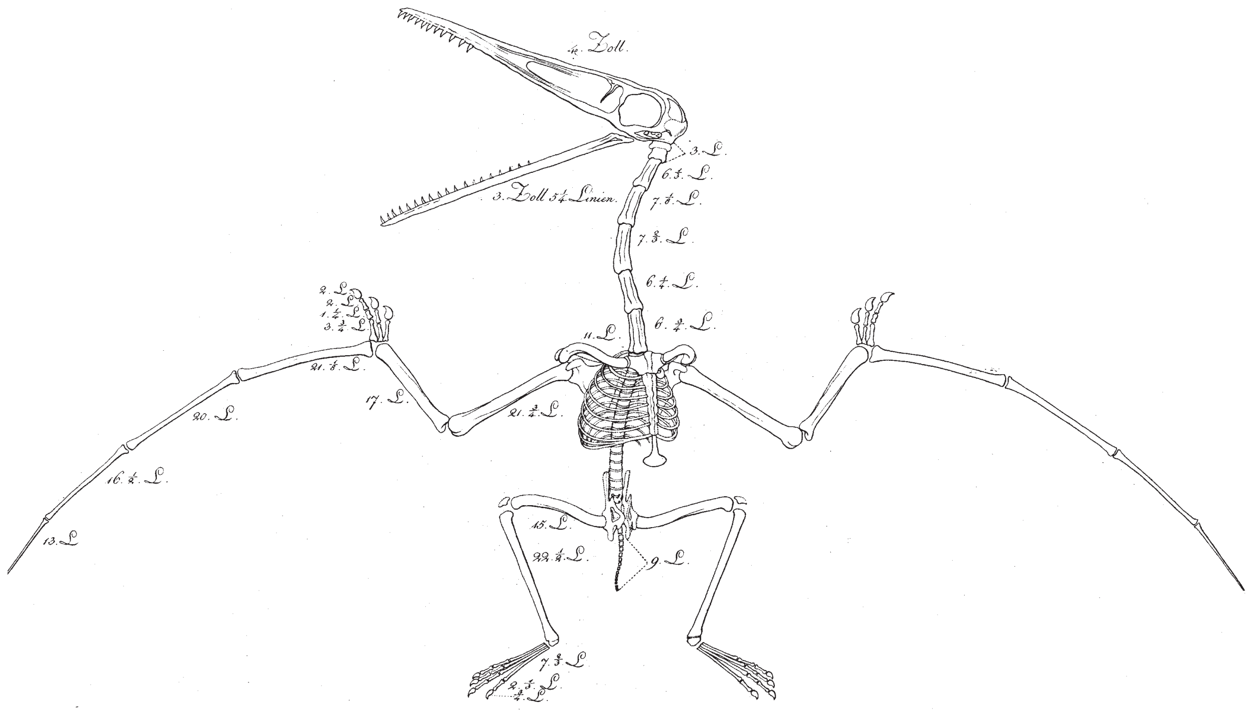

Figure 4: This first skeletal reconstruction of a pterosaur was published by the Munich anatomist von Soemmerring in 1812. In the interpretation of the bones of the forelimbs he was, however, mistaken.

from Solnhofen showing a long, slender tail. Consequently, Hermann von Meyer introduced a subdivision in long-tailed and short-tailed pterosaurs, formally established by Plieninger (1901) as two suborders of the order Pterosauria: Rhamphorhynchoidea and Pterodactyloidea. Already in 1834 the flying reptiles had been called Pterosauri by Johann Jacob Kaup, and in 1842 Richard Owen introduced the name Pterosauria, a taxon designated as an order of the class Reptilia.

The early history of pterosaur research shows clearly the cautious attempt to understand the true nature of these unusual, for most even fascinating, animals of a distant past. It would not be fair, even arrogant, if we would smile over some of the erroneous ideas and strange looking life restorations our predecessors have produced. Indeed, they had to rely on a very sparse fossil documentation of pterosaur fossils, and we must not forget that at the beginning of the 19th century only a handful of fossil reptiles were known. Besides *Pterodactylus* these were, *Protorosaurus* from the Permian Kupferschiefer of Eisenach, an ichthyosaur from the Lias of Bad Boll in Württemberg, a crocodile from the Lias of Whitby in Yorkshire, and a *Mosasaurus* from Maastricht in the Netherlands.

3. First pterosaurs from the Lias

Until 1828 pterosaurs were only known from the Solnhofen lithographic limestone. But in 1829 William Buckland, one of the "fathers of British geology", described skeletal remains of a pterosaur from the Blue Lias outcrops at the Dorset coast in Southern England (Buckland 1829). He assigned it to a new species as *"Pterodactylus" macronyx,* after the strong claws on the digits, but in 1859 Richard Owen established a separate genus, *Dimorphodon*, after the double shape of its teeth. At the same time Liassic pterosaurs were discovered also in Germany, from Franconia and Württemberg. In 1830 Carl von Theodori reported on isolated pterosaur bones from Upper Liassic rocks near the former monastery of Banz in the upper Main valley in Franconia. For this species, *"Pterodactylus" banthensis*, Andreas Wagner introduced a new genus, *Dorygnathus,* in 1860. It was only in 1856, when Albert Oppel reported on the first pterosaur specimen, a single lower jaw, from the Liassic *Posidonia* shales of Holzmaden and Bad Boll in Württemberg. The Liassic *Posidonia* shales of Holzmaden have produced a series of excellent specimens since, represented by two genera, *Dorygnathus* and *Campylognathoides*, with at least three species.

In Württemberg a second locality, the Kimmeridgian lithographic limestone of Nusplingen, has yielded pterosaurs, too: *Pterodactylus suevicus*, described by August Quenstedt in 1855, and *Rhamphorhynchus kokeni* by Felix Plieninger in 1907. Also from the lithographic limestone of Cerin in France skeletal remains of pterosaurs came to light around the middle of the 19th century (Meyer 1859–1860).

4. Discoveries of Cretaceous pterosaurs

The first remains of pterosaurs from the Cretaceous were in fact discovered as early as 1827. They were collected by Gideon Mantell from the Wealden of Tilgate Forest in Sus-

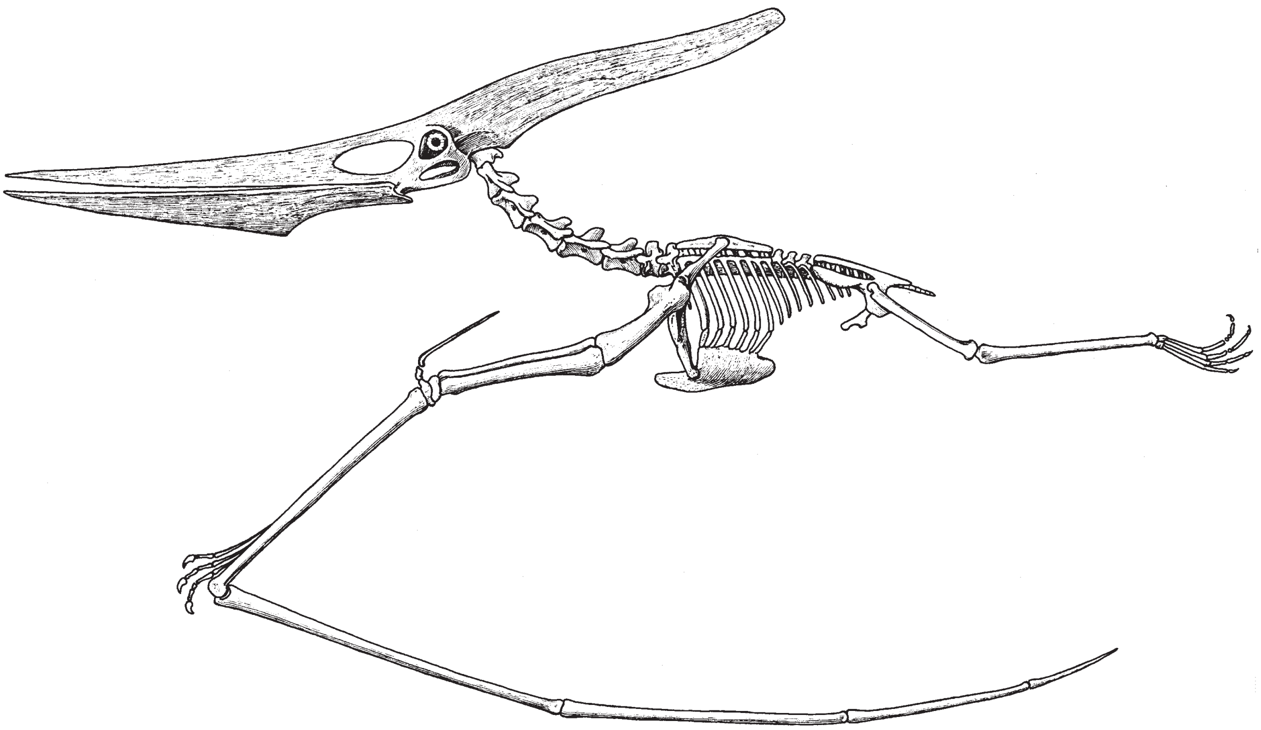

Figure 5: George F. Eaton published a monograph on The Osteology of *Pteranodon* in 1910, on the basis of the material from the upper Cretaceous Niobrara Chalk of West Kansas, USA in the Yale Peabody Museum in New Haven, CT, USA. His skeletal restoration of this pterosaur with a wingspan of about 7 meters was the standard for decades.

sex. First he had taken them as hollow "bones of birds", but later on were recognized as pterosaurian (Mantell 1827). In England it was Richard Owen (1804–1892), superintendent of the British Museum of Natural History in London, who worked intensely on pterosaurs, between 1846 and 1879. His material came from the Liassic and the Cretaceous of several localities in southern England. Based on osteological analysis Owen identified pterosaurs as true reptiles, and in keeping with his concept of archetypes considered them as cold-blooded animals. Therefore, he believed that the size of pterosaurs was limited from the outset. However, the discovery of pterosaurs of large size, such as *Ornithocheirus* from the Chalk of Kent, forced Owen to concede that: "these pterosaurs must have been able to raise a larger mass into the air, than could have been done by the warm-blooded mammal … and that the manifestation of creative power in past time surpass the calculations that are founded upon actual nature." (Owen 1870).

The other prominent palaeontologist in the second half of 19th Century England working on pterosaurs was Harry Govier Seeley (1839–1909), professor of Geology at King's College in London. He collected and studied especially the abundant bone material from the Cambridge Greensand. Between Owen and Seeley developed a violent controversy (Seeley 1870). Seeley believed that pterosaurs, by analogy to birds, must have been warm-blooded. This, in his view, justified a separation from the class of reptiles, somewhere in between reptiles and birds. In 1901, in his popular book *Dragons of the Air*, Seeley summarized his previous work on the osteology, life style and classification of all pterosaurs, his *Ornithosauria*, known at that time (Seeley 1901). While Owen had classified pterosaurs as true reptiles with a reptilian physiology, was Seeley convinced that they had a high metabolic level, and a bird-like physiology, as far as the lungs, the heart, and the brain structure are concerned. This also included the mode of locomotion on the ground, namely bird-like. The debate between Owen, as the leading opponent to Darwin's theory, and Seeley was of course not just about the nature of the pterosaurs, but it was one on the validity of species transformations and evolutionary progress.

5. American discoveries

Until the middle of the 19th Century research on pterosaurs was carried out mainly on the basis of fossils from Bavaria, Württemberg, and England. It was not before 1870 when pterosaur fossils were discovered also in North America, from the Late Cretaceous Niobrara Chalk in West Kansas. In their collecting and study of this material the two famous rivals, Edward Drinker Cope (1840–1897) and Othniel Charles Marsh (1831–1899) inevitably got involved. In the summer of that year Marsh and his field crew discovered long, hollow, thin-walled bones, which reminded him of the English pterodactyls. However, these creatures must have been much larger. Subsequent collecting of additional material led to a publication by Marsh on *Pterodactylus ingens* and *Pterodactylus occidentalis* in 1872, only five days before his rival, Cope, published on *Two new Ornithosaurians,* also from the Niobrara Chalk. It was the first fossil record of truly gigantic flying animals, but also the first evidence that there were toothless forms that were not known before. In addition, the American pterosaurs had a peculiar cranial bony crest. In 1876 Marsh established the name *Pteranodon,* thus separating it from the European genera. He also identified a second, smaller genus from the Niobrara Chalk, *Nyctosaurus.* How productive the fossil sites in West Kansas really were, was documented by George F. EATON of Yale Peabody Museum in his 1910 monograph on the osteology of *Pteranodon,* listing a collection of pterosaur bones from a total of 465 individuals (EATON 1910). For a long time all what was known of *Pteranodon,* and about large pterosaurs in general, was based on EATON's fundamental work (Fig. 5). It was not until 90 years later, Chris BENNETT, on the basis of additional material including 1100 specimens, presented a modern monographic revision of the osteology and an analysis of functional morphology of *Pteranodon* (BENNETT 2001).

More than 100 years after the *Pteranodon* discoveries by COPE and MARSH the largest pterosaur ever was discovered by Douglas LAWSON in Maastrichtian terrestrial deposits of West Texas, subsequently described as *Quetzalcoatlus northropi,* in 1975. Later, detailed studies and restorations have been carried out by Wann Langston, Austin, Texas. The wingspan of this giant was calculated at 11 to 12 meters, raising the question, how these large pterosaurs may have gotten off the ground and flown. But even an actively flying model of this pterosaur built by aeronautical engineer Alan MCCREADY in 1985 could not solve this problem.

6. Triassic Pterosaurs

So far, I have dealt with Jurassic and Cretaceous pterosaurs, but what about Triassic pterosaurs? Already in 1886 a small fossil reptile from Middle Triassic strata of Besano in the Italian Lombardy was described as a pterosaur by the Italian geologist Francesco BASSANI. After its tricuspid teeth he named it *Tribelesodon longobardicus*. In 1922 the Hungarian geologist and specialist in fossil reptiles, Franz Baron NOPCSA, published a detailed analysis and reconstruction of this putative Triassic pterosaur which was taken as the oldest from the fossil record. But in 1929 the Swiss paleontologist Bernhard PEYER discovered a small skeleton with extremely elongated neck vertebrae in Middle Triassic shales of the Monte San Giorgio in Ticino, Switzerland, equivalent in age to the strata of Besano. It was a juvenile individual of the prolacertilian reptile *Tanystropheus* which too had tricuspid teeth. By comparison, PEYER realized that *Tribelesodon* and *Tanystropheus* are in fact the same taxon. The long bones of *Tribelesodon* that had been taken for the long phalanges of the wing finger of a pterosaur, turned out to be the elongated cervicals of a juvenile *Tanystropheus*. And all of a sudden there were no longer any Triassic pterosaurs.

However, more than 50 years later, in 1973, the Italian geologist Rocco ZAMBELLI reported on the first unquestionable pterosaur from Upper Triassic (Norian) limestones near Bergamo in northern Italy, in the southern Calcareous Alps. It was an almost complete skeleton, and he named it *Eudimorphodon ranzii* (ZAMBELLI 1973), described in detail by WILD (1978). Meanwhile several specimens of Norian age have been discovered, not only in the southern but also in the northern Calcareous Alps, as in Tyrolia and Switzerland, and from several other localities in the United States and East Greenland, representing several distinct taxonomic units. It was quite unexpected that among the oldest pterosaurs in the fossil record there was not a single primitive or basic form, a pterosaurian *Archaeopteryx*, a "missing link". In contrast, however, at their earliest occurrence in the fossil documentation pterosaurs appeared as fully evolved and highly diverse, thus indicating that they had already passed an evolutionary history of some time, prior to the Late Triassic, a history that we have no evidence of, whatsoever. The very origin of pterosaurs is still an unresolved problem.

7. Early life restorations

Ideas, how pterosaurs may have looked like in life have been published as early as 1830, when the Munich zoologist Georg WAGLER depicted *Pterodactylus* swimming, using its wings like long penguin flippers, because he believed that pterosaurs and other marine reptiles belonged to a separate class of vertebrates which he named "Gryphi". Another peculiar life restoration was proposed by the English zoologist Edward NEWMAN who, in 1843, classified pterosaurs as carnivorous flying, warm-blooded marsupials with nice little ears and covered by a coat of fur (Fig. 6).

August GOLDFUSS, in 1831, however, showed them as flying reptiles climbing rock walls and cliffs, taken over by William BUCKLAND in his 1836 contribution to the "Bridgewater Treatises on the Power Wisdom and Goodness of God as manifested in the Creation" (Fig. 7). In Thomas HAWKINS *Book of the great Sea Dragons* of 1840 pterodactyls are shown with almost bat-like wings, scavenging on a carcass of an ichthyosaur, while other marine reptiles are locked in mortal combat. At Richard OWENS instructions, the English artist Benjamin Waterhouse HAWKINS produced two large pterodactyl sculptures for the Great Exhibition of 1851 in London's Hyde Park. They were exhibited in the largest iron-framed glass building of its time, the Crystal Palace, later to be transferred to the park of Sydenham in South London, where they can be viewed still today. These models were the first attempt at three-dimensional life restorations.

One of the earliest restorations of *Rhamphorhynchus* walking quadrupedally (Fig. 8) is the one by RIOU, an illustration contained in the popular book "La Terre avant le Déluge" by Louis Figuier, Paris 1863. This interpretation was inspired by fossil trackways found in the Solnhofen limestone which seemed to show foot and tail imprints of long-tailed pterosaurs. Only in 1940 it could be demonstrated that the real trackmakers were limulids, horseshoe crabs, sometimes still lying at the end of their death march tracks (CASTER 1940).

8. Flight biomechanics

The flight of pterosaurs became the focus of scientific interest already around the early years of the 20th century. Obviously stimulated by the development of man made aircraft, and by the growing interest in the aerodynamics of flight in birds, as for example shown by the experiments of Otto LILIENTHAL in Berlin, and the WRIGHT brothers in America, the flight of pterosaurs gained interest too. Typically, one of the

Figure 6: This rather strange life restoration of pterodactyls was published by Edward NEWMAN in 1843. He thought that pterosaurs were warm-blooded marsupial bats covered by a coat of fur.

first studies on this subject was published in the official organ of the Aeronautical Society of Great Britain, The Aeronautical Journal, in 1914. The article "On the flight of Pterodactyls" was coauthored by E. H. HANKIN, an aeronautical engineer, and the distinguished vertebrate paleontologist D. M. S. WATSON. Based on EATON's monograph of 1910 they used *Pteranodon*, but also uncrushed English material from the Cambridge Greensand. They concluded that the higher pterodactyls performed soaring rather than flapping flight. The pterosaur "with a body little larger than that of a cat had a wing span of 21 feet or more. The weakness of the flapping muscles, makes it highly probable that their habitual mode of flight was by soaring rather than flapping."(HANKIN & WATSON 1914). This first biomechanical study on the flight of large pterosaurs is considered a classical work, and for a long time was almost the only one on the topic.

Much later BRAMWELL & WHITFIELD (1974), in their work "Biomechanics of *Pteranodon*" investigated its flying abilities again. They calculated the weight of an individual with seven meters wingspan at about 16 kgs, and concluded that *Pteranodon* could fly at the extremely low minimum speeds of 6.7 m/sec. This made a gentle landing and take off from the

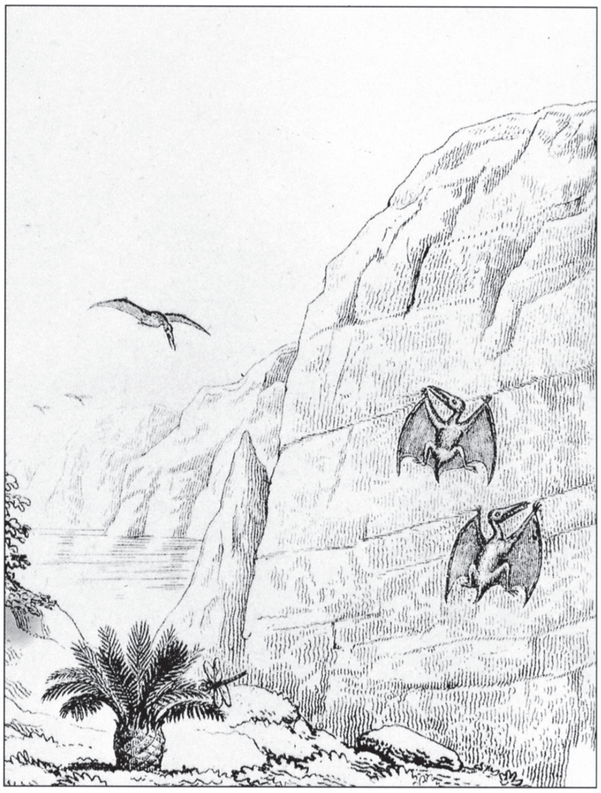

Figure 7: William Buckland, one of the "fathers of British Geology", regarded pterosaurs as animals of bat-like appearance living on cliffs by the Jurassic Sea. This illustration, almost a copy of a life restoration by Goldfuss (1831), was published in the "Bridgewater Treatises on the Power Wisdom and Goodness of God" (Buckland 1836).

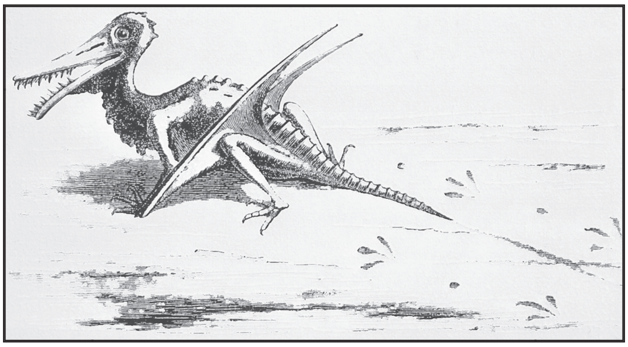

Figure 8: One of the earliest restorations of the long-tailed *Rhamphorhynchus* was the one by Riou and reproduced in Luis Figuier's "La Terre avant le Déluge" of 1863. This interpretation was inspired by fossil trackways found in the Solnhofen limestone which seemed to show the imprints of both, feet and tail. The real trackmaker, however, was *Mesolimulus*, the horseshoe crab.

ground possible, but may also have been the reason for their extinction, if due to climatic changes the average wind speed increased at the end of the Cretaceous. Heptonstall (1971), Stein (1975), Brower (1980, 1983), and others came to different conclusions, however. In his 2001 monograph Chris Bennett arrived at the conclusion that all past reconstructions of *Pteranodon* were incorrect, and that all those calculations of its flight performance were based on inaccurate data and required revision. Since the 1980s several studies on flight biomechanics of smaller pterosaurs have been published as those by Frey & Riess (1981), Pennycuick (1988), Padian (1979, 1983), and others (this volume). It is not possible here to review all these detailed studies.

9. The problem of terrestrial locomotion

It may be somewhat surprising that the problem of terrestrial locomotion of pterosaurs, otherwise animals extremely well adapted to flight, has caused so much interest and controversies. In one of David Unwins papers he condensed it into the question, whether pterosaurs were "joggers or waddlers". By several authors arguments have been put forward supporting quadrupedal versus bipedal locomotion. This was often coupled with a bat-like versus a bird-like stance and gait. The debate has actually started with Soemmerring (1812) and Goldfuss (1831), who were advocates of a bat-like, quadrupedal locomotion, as well as Abel (1925), who compared the pterodactyl's movement on the ground to that of a crawling bat. Hankin and Watson, in their 1914 aerodynamic study, imagined pterosaurs as completely helpless on the ground, pushing themselves along, after the manner of penguins. A bipedal model, however, was supported by Quenstedt (1855), and later by Harry Govier Seeley, who saw pterosaurs on the ground as walking bipeds, because he considered them closely related to birds (Fig. 9). In 1983 and in subsequent years Kevin Padian favoured the bipedal model of pterosaurs on the basis of osteological analyses of *Dimorphodon* (Padian 1983). In addition to cladistic analyses resulting in a sistergroup relationship of pterosaurs and dinosaurs, it was argued that their common ancestor could hardly have been an arboreal quadruped, but was a cursorial biped. The debate resembled somehow the controversy about the origin of avian flight "from the trees down or from the ground up".

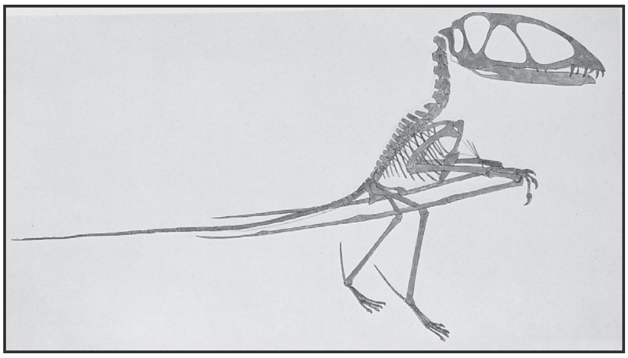

Figure 9: Restoration of the skeleton of the Early Liassic *Dimorphodon*, in a bipedal walking position as advocated by Harry Govier Seeley, according to his view of a bird-like physiology of pterosaurs (Seeley 1901).

The three-dimensionally preserved pterosaur bones from the very productive Lower Cretaceous Santana formation of Brazil (Fig. 10) made it possible to directly manipulate with the pelvis and femur at the hip joint in order to check the actual degree of movements in life (Wellnhofer 1988). In this situation one would expect a solution of the problem by

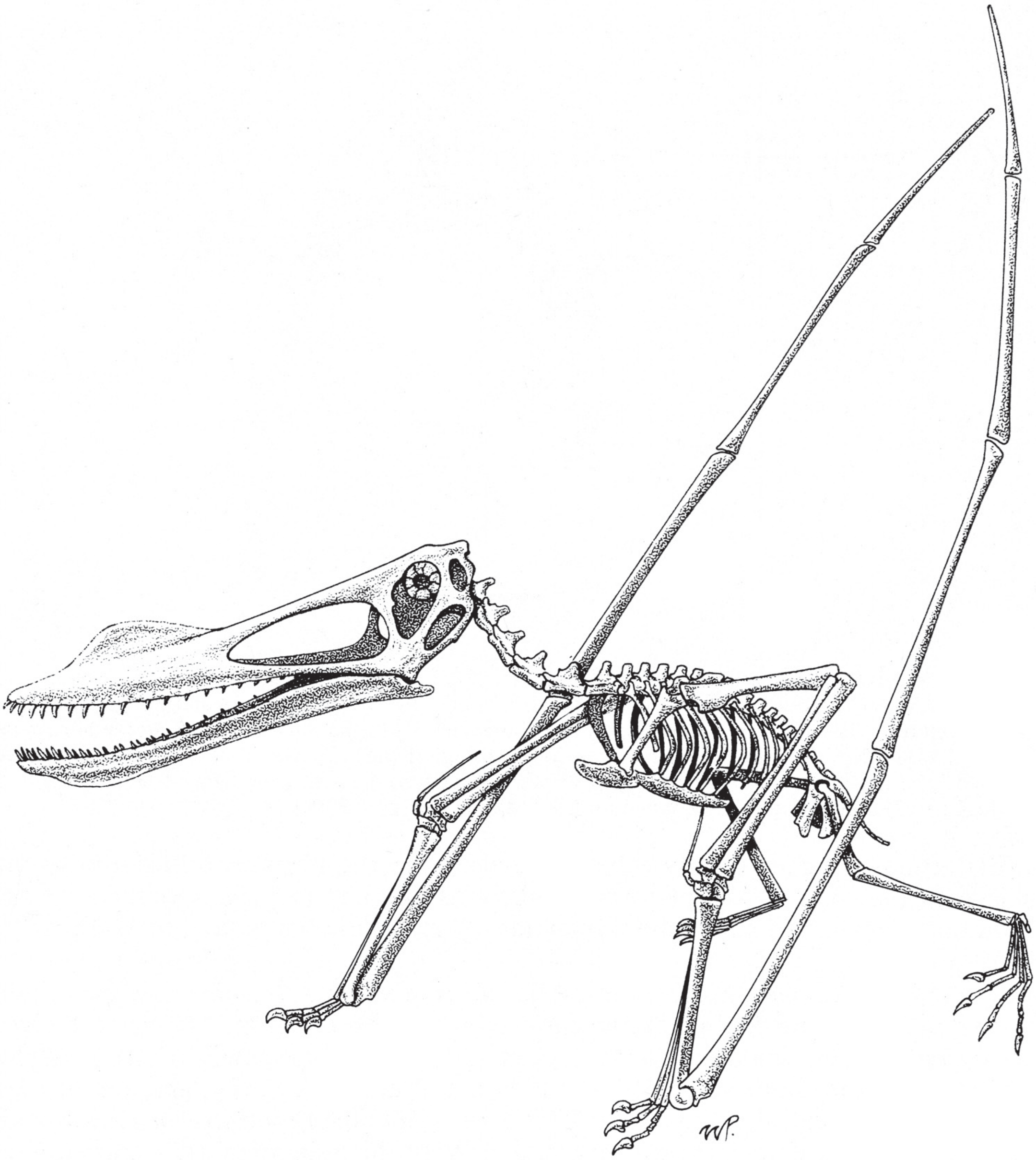

Figure 10: Skeletal restoration of *Anhanguera*, from the Lower Cretaceous Santana formation of Brazil, in a quadrupedal "semi-erect" and plantigrade stance and gait with the hind legs splayed out laterally (WELLNHOFER 1988).

pterosaurian trackways. Indeed, in 1957, STOKES described imprints from the Late Jurassic Morrison formation of Utah as pterosaurian, which he named *Pteraichnus saltwashensis*. These tracks were clearly produced by a quadrupedal animal (STOKES 1957). However, their pterosaurian nature was debated. But in 1995, Jean-Michel MAZIN and his colleagues announced the discovery of quadrupedal trackways in the Late Jurassic lithographic limestone at Crayssac in southern France, which they interpreted as pterosaurian. The evidence for their interpretation is quite convincing, as are the other trackways referred to as pterosaurian, and so the debate on the terrestrial locomotion of pterosaurs seems to be settled, after all (MAZIN et al. 1995).

10. The evidence of soft parts

Of course, the fossil preservation of soft parts as preserved especially well in the Solnhofen pterosaurs has played an important role in the evaluation of the physiology, and the reconstruction of pterosaur life models. In 1882 O.C. MARSH described a Solnhofen pterosaur, *Rhamphorhynchus phyllurus* (Fig. 11), with imprints of the wing membrane, and of an additional membrane at the tip of the long vertebral tail, a rhomboid terminal tail vane. He oriented it vertically, and interpreted it as a steering rudder (MARSH 1882).

By coincidence, in the same year Karl Alfred von ZITTEL in Munich published on an isolated *Rhamphorhynchus* wing with imprints of the membrane in a very detailed preservation. The specimen has since been called the "Zittel wing". Not only the size and shape of the wing, but also a peculiar internal strengthening system of fibres could be recognized. ZITTEL concluded from this that *Rhamphorhynchus* had very

Figure 11: *Rhamphorhynchus phyllurus* MARSH, 1882, from the Solnhofen lithographic limestone with well preserved imprints of the wing and tail membranes. In this illustration from the publication by MARSH (1882) a life restoration is added showing *Rhamphorhynchus* with wide wing membranes attached to the ankle, and a uropatagium between legs and tail.

narrow wings, and presented a life restoration (Fig. 12) quite in contrast to MARSH'S *Rhamphorhynchus* image with wide wings and the hind legs connected to an uropatagium (ZITTEL 1882). A particular controversy developed around the question of how the terminal tail vane was oriented – vertically or horizontally. MARSH oriented it vertically, as he correctly noticed a slight asymmetry in the outline. Others argued, for aerodynamic reasons, that it was held in a horizontal plane, for the purpose of pitch control. In 1957, in order to support this view, the German zoologist Erich VON HOLST built an actively flying model of *Rhamphorhynchus* flapping its wings, which could only fly with the vane in a horizontal position, and not in a vertical one (HOLST 1957). The asymmetry and osteological evidence from the caudal vertebrae, however, suggest that MARSH had been right, after all (WELLNHOFER 1991).

During the last few years new techniques of investigation under ultraviolet light has revealed details of soft tissue, especially the microstructure of the wing membrane with different layers, muscles, fibres and blood vessels. The pioneer of this fascinating technique is Helmut TISCHLINGER who, partly in cooperation with Eberhard FREY, published a series of papers with anatomical details of pterosaurs hitherto unknown (e.g. TISCHLINGER & FREY 2002). I may mention that in recognition of his pioneering work Helmut TISCHLINGER has been awarded the degree of a Doctor honoris causa (Dr. rer. nat. h.c.) of the University of Munich, in April 2007.

The preservation of soft parts and integumentary structures has also caused much speculation about the physiology of pterosaurs. Did they live on a reptilian or an avian physiology? Where they ectotherms or endotherms? As with the dinosaurs, the solution of a problem like this will always be difficult, and may be impossible. However, the discovery of a three-dimensionally preserved endocast of a pterosaur brain of *Parapsicephalus* from the Lias of Whitby (NEWTON 1888), and similar endocasts from Solnhofen and the Santana formation of Brazil revealed a more avian-type, rather than

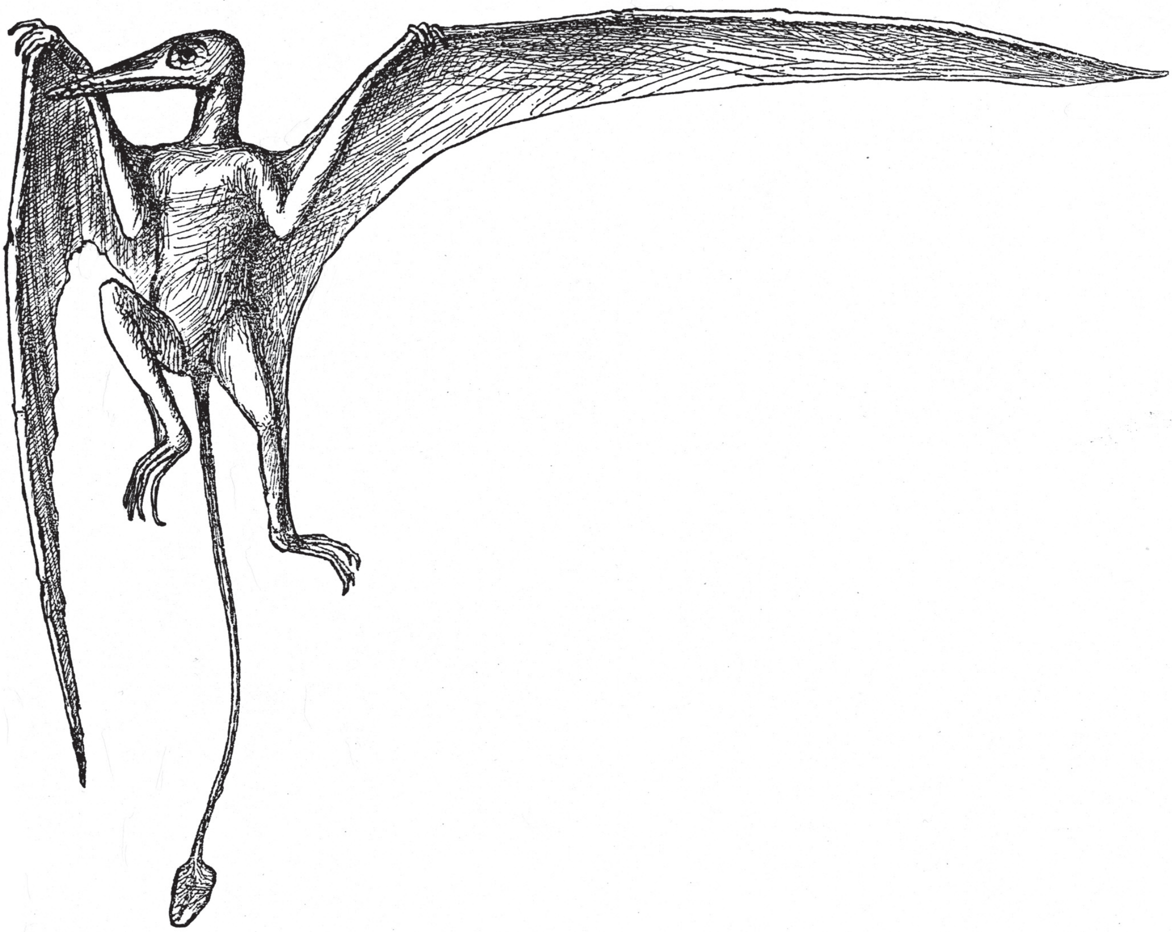

Figure 12: The life *Rhamphorhynchus* as reconstructed by Zittel (1882) on the basis of an isolated wing with the impressions of the membrane ("Zittel wing") has very narrow wings and no uropatagium.

reptilian brain morphology. Especially reports on a hair-like body covering in several pterosaur specimens from Holzmaden and Solnhofen, as already suggested by Goldfuss (1831) and described by Broili (1927), strongly supported the view of an advanced thermophysiology. The most spectacular specimens however, came to light in the Late Jurassic Karatau lake deposits of Kazakhstan described by Sharov (1971) as *Sordes pilosus.* However, Unwin & Bakhurina (1994) could show that most of the "hairs" preserved in those specimens are in fact internal strengthening fibres of the wing membranes, actinofibrills, not really hairs. But the authors maintained that integumentary filaments are present at other locations of the body. New Chinese pterosaurs might bring a solution to this problem (Wang et al. 2002).

11. Recent discoveries

During the last 30 years the Lower Cretaceous Santana and Crato formations of northeastern Brazil have become one of the most productive, and most important fossil lagerstätten for pterosaurs in the world. First reported by Price (1971), the fossiliferous nodules and flaggy limestones of these deposits have produced a great number of partly articulated, and three-dimensionally preserved skeletons. They are mostly large pterodactyloids in a considerable diversity, sometimes truly bizarre creatures with strange cranial crests, and even skinny sails on their heads. This material has added considerably to our understanding of pterosaur skeletal anatomy, taxonomy, systematics, and functional morphology.

Also from the Lower Cretaceous of South America, namely Argentina, a very strange pterosaur was discovered and first described by Bonaparte (1970): *Pterodaustro.* Documented by several skeletal remains it is a small pterodactyloid with an extremely derived dentition, forming a filter basket. Filter feeders had been known from Solnhofen before, as *Ctenochasma* and *Gnathosaurus*, but *Pterodaustro* with hundreds of long teeth in the elongated, curved lower jaw was far more specialized.

Also Early Cretaceous deposits in China have yielded pterosaurs, first described by C. C. YOUNG (1964) as *Dsungaripterus*. In recent years deposits of northeastern China have produced a series of new pterosaurs, especially from the Yixian formation in Liaoning, otherwise famous for its early birds and feathered dinosaurs. Here, for the first time, pterosaur eggs with embryos have been discovered, shedding light on reproduction and growth patterns of pterosaurs in general (WANG & ZHOU 2004).

12. Conclusions

It is impossible within this frame limit to stress all historical aspects of pterosaur research. Looking back two and a quarter of a century, fossil discoveries and scientific investigations have produced an overwhelming amount of material, information, data, and scientific results. There is evidence now for a worldwide distribution with fossil pterosaur records from all over Europe, East Greenland, Africa, the Middle East, Middle, Central and East Asia, North and South America, Australia, New Zealand, and even Antarctica. Today, pterosaurs are among the best studied fossil reptiles. Following the beginning of my own research in 1965, the number of publications on pterosaurs has increased tremendously, as has the number of taxa. In my 1978 volume "Pterosauria" of the *Handbook of Paleoherpetology* the bibliography listed a total of 327 references. Since then, during the last 30 years, almost 300 papers including some books on pterosaurs have been published. In popularity and importance pterosaurs as simply fascinating animals are certainly no longer "in the shadow of the dinosaurs".

This symposium here has demonstrated quite impressively that the number of students and younger pterosaur researchers has increased as well. What a hopeful signal for the future! New discoveries are being made, many promising projects are in preparation or have been carried out. But, there remain unresolved problems with regard to the origin, evolution and relationships, life style, and physiology of pterosaurs. There is plenty of work to be done for generations of vertebrate palaeontologists to come.

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