

The first dsungaripterid pterosaur from the Kimmeridgian of Germany and the biomechanics of pterosaur long bones

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A partial vertebral column, pelvis and femora of a newly discovered pterosaur are described. The remains from the Upper Jurassic (Kimmeridgian) of Oker (northern Germany) can be identified as belonging to the Dsungaripteridae because the cross-sections of the bones have relatively thick walls. The close resemblance in morphology to the Lower Cretaceous *Dsungaripterus* allows identification of the specimen as the first and oldest record of dsungaripterids in Central Europe. Furthermore, it is the oldest certain record of a dsungaripterid pterosaur world wide. The biomechanical characteristics of the dsungaripterid long bone construction shows that it has less resistance against bending and torsion than in non-dsungaripteroid pterosaurs, but has greater strength against compression and local buckling. This supports former suggestions that dsungaripterids inhabited continental areas that required an active way of life including frequent take-off and landing phases. The reconstruction of the lever arms of the pelvic musculature and the mobility of the femur indicates a quadrupedal terrestrial locomotion.

Key words: Reptilia, Pterosauria, Dsungaripteridae, locomotion, biomechanics, Jurassic, Germany.

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Introduction

In recent years, the northern part of Germany has yielded an increasing number of Upper Jurassic/Lower Cretaceous archosaurian remains. One of the main fossiliferous localities is the Langenberg quarry (Rohstoffbetriebe Oker GmbH & Co.), situated about 80 km southeast of Hannover at the town of Oker (Fig. 1). Only recently, an exceptionally well preserved skull of a juvenile brachiosaurid dinosaur has been

described from this site (Laven 2001; Mateus et al. 2004; Sander et al. 2004). This and further dinosaur material has been collected by members of the “Verein zur Förderung der niedersächsischen Paläontologie e.V.”, who regularly collect fossils at the still active quarry. In August 2001, a well-preserved pterosaur specimen was found in the spoil pile at the base of the quarry, consisting of a part of the vertebral column, pelvis, and both femora. The purpose of this paper is the systematic assignment of the specimen and the description of its specific osteological features in relation to the locomotor options of the animal.

Institutional abbreviations.—DFMMh, Dino-Park Münchenhagen/Verein zur Förderung der niedersächsischen Paläontologie e.V., Germany, SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. Main, Germany.

Geological setting

During the early and middle Kimmeridgian, the Langenberg area (Lower Saxony, Germany) was part of a shallow-water basin (Lower Saxonian Basin). Because the mainland (“Mitteldeutsches Festland”) was situated very close to the southeast, the depositional environment of the Langenberg area can be characterized as a lagoon or bay (Delecat et al. 2001). Plant remains and the mollusc fauna indicate that fresh water was transported from the mainland into the basin. The light grey-coloured mudstones, in which the pterosaur specimen was found, are part of a mixed series of limestones,

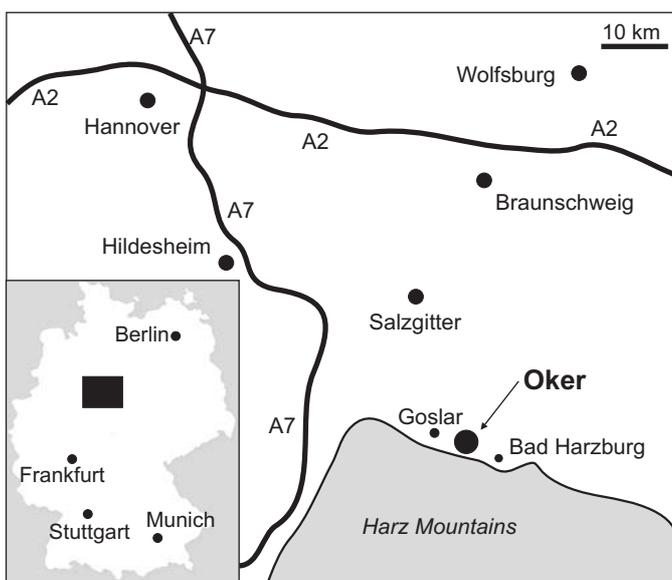


Fig. 1. Map of north-central Germany, showing the locality of Oker near Goslar, Lower Saxony, Germany, enclosed by the motorways A2 and A7.

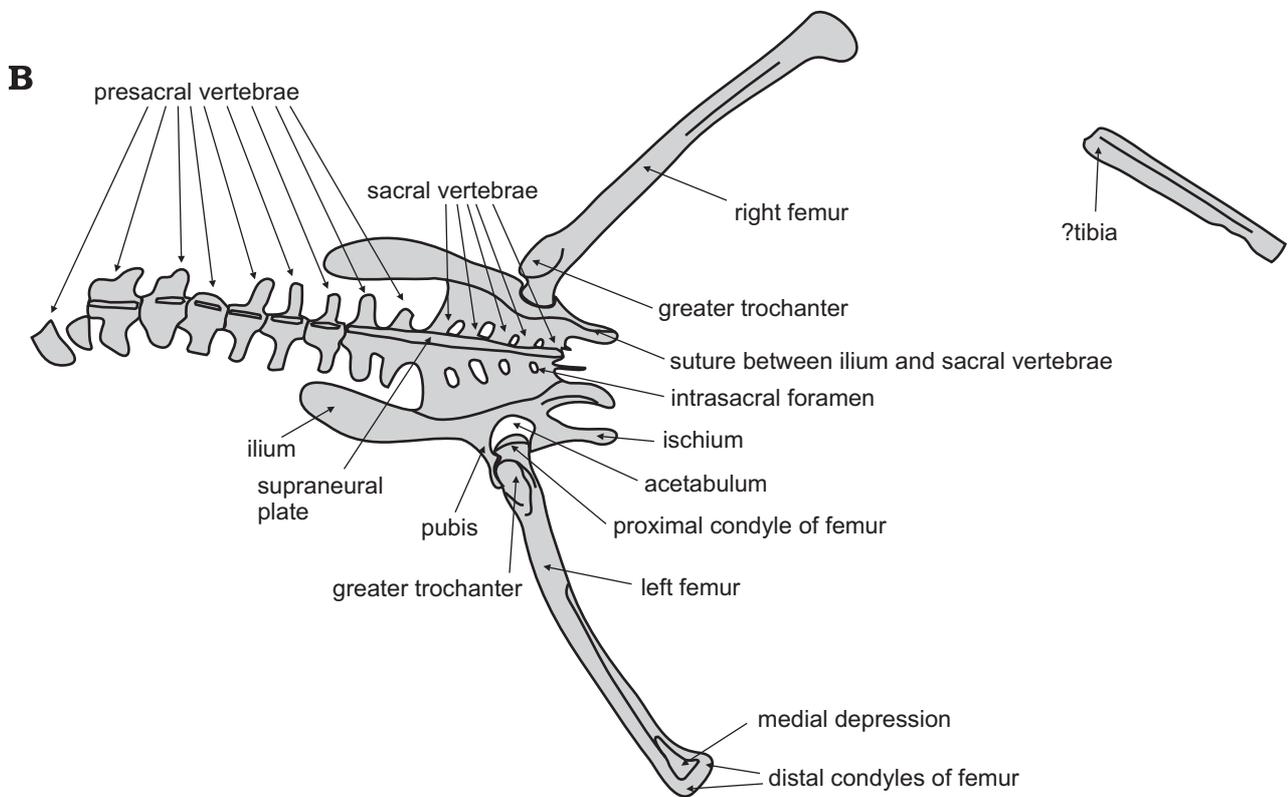
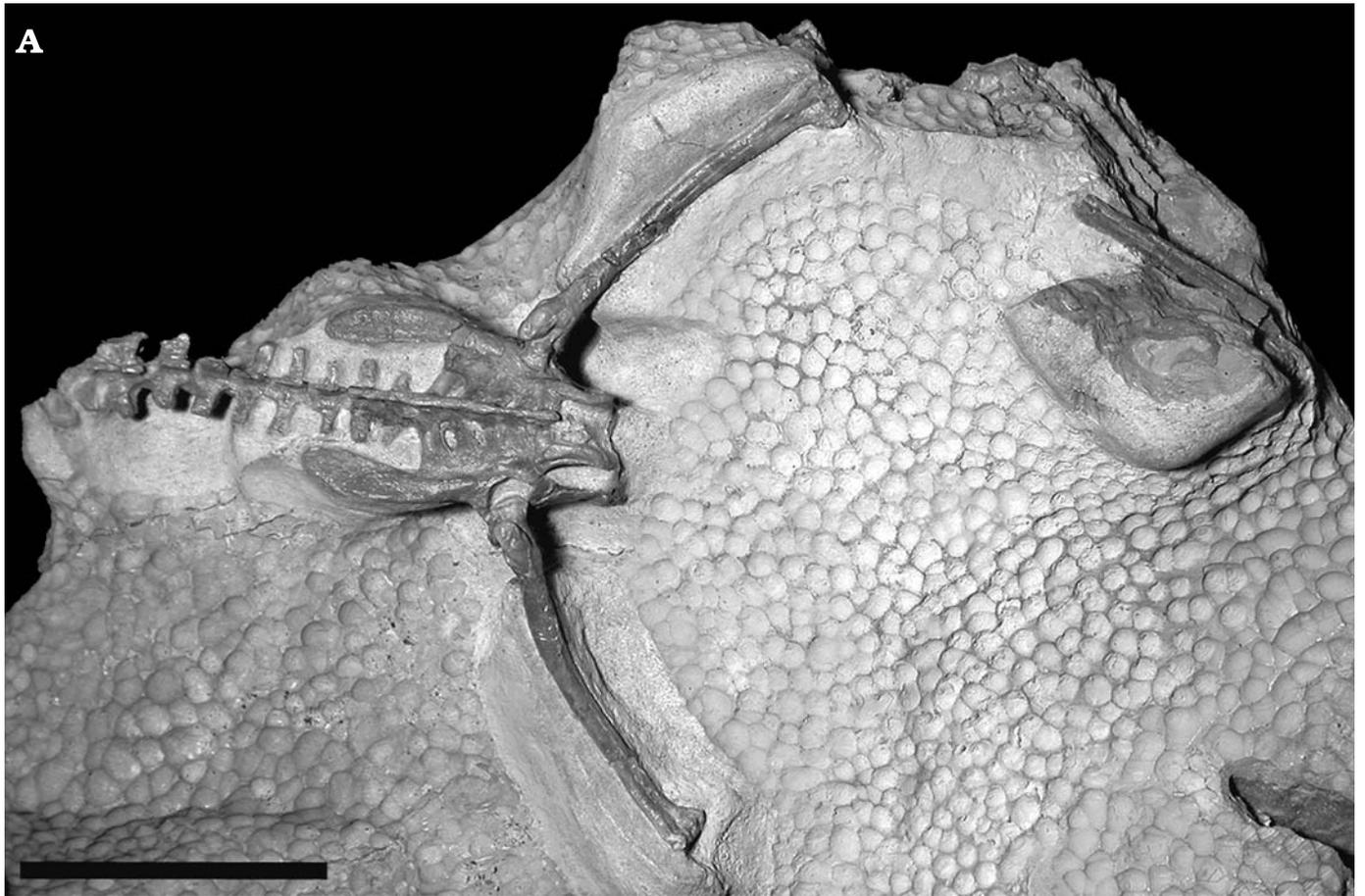


Fig. 2. *Dsungaripteridae* gen. et sp. indet., DFMMh/FV 500. A. Dorsal view of specimen. B. Interpretative drawing. Scale bar 100 mm.

dolomites, marls and claystones. In the area of the Langenberg quarry, these sediments were deposited in channels either formed in shallow-water or as part of a deltaic complex (Pape 1970; Fischer 1991).

Because the specimen described herein was found in the spoil pile at the base of the quarry, its exact stratigraphical level is not known. Based on sedimentological comparisons, however, it can be assigned to a certain sequence of middle Kimmeridgian mudstones (levels 100 to 119 of Fischer 1991). These middle Kimmeridgian sediments and their fauna in the Langenberg quarry indicate an environment with mixed salinity and possible terrestrial conditions as represented by mud cracks. Vertebrates are represented by sea turtles, “dwarf” crocodiles and sauropods (Laven 2001; Mateus et al. 2004; Sander et al. 2004). However, layers 100 to 119 (Fischer 1991) have not yielded any vertebrate remains so far.

Systematic palaeontology

Order Pterosauria Kaup, 1834

Suborder Pterodactyloidea Plieninger, 1901

Family Dsungaripteridae Young, 1964

Locality: Langenberg Quarry, Oker near Goslar, Lower Saxony, Germany.

Horizon and age: Lower Kimmeridgian mudstones (Werner Fricke personal communication, Goslar, Germany 2004).

Material.—DFMMh/FV 500, 10 thoracic vertebrae, complete pelvis and sacrum, left and right femur, ?part of right tibia.

Description.—The specimen was prepared mechanically, revealing most of the dorsal and lateral surfaces of the bones with the rest of the specimen still embedded in the matrix (Fig. 2). The bones are uncrushed and preserved three-dimensionally. The vertebrae, sacrum, and pelvis are fully articulated. The right femur is articulated in its acetabulum, whereas the left femur is slightly displaced out of its acetabulum, but still is in contact with it. The possible remains of the right tibia are situated 37 cm posterior to the right femur and orientated in an anterolateral-posteromedial direction.

Presacral vertebrae.—There are nine presacral vertebrae preserved, still in full articulation with each other and with the sacrum (Fig. 2). The left transverse process of the most anterior, tenth presacral vertebra is visible at the erosional edge where the specimen is broken off. The total length of the presacral vertebral column is 45 mm with each vertebra measuring about 5 mm in length and 12 to 14 mm in width across the transverse process. The length-height ratio of the vertebrae is 1:1, with the spinous process measuring about 50% of the total height. The spinous processes are rectangular in lateral view. The posteriorly elongated dorsal crista of the penultimate presacral vertebra is fused with the anteriorly elongated dorsal crista of the last presacral vertebra forming the supraneural plate. The spinous process and the post-

zygapophyses of the last presacral vertebra are fused with the first sacral vertebra, but here a suture still is visible. The transverse processes of the last six vertebrae are slender (roughly 1:2 ratio of width to length) and rectangular. The transverse processes of the anterior three vertebrae (including the isolated left transverse process) are bent posteriorly and are more obtuse (1:1 ratio of width to length). Due to the nature of preservation, the articulation of pre- and post-zygapophyses are not clearly visible.

Sacral vertebrae.—The sacrum comprises five completely fused sacral vertebrae (Figs. 2, 3). The size of the vertebrae decreases posteriorly, from 20 mm, 18 mm, 14 mm, 10 mm, to 8 mm in width across the transverse processes. The height of the vertebrae cannot be determined, because the ventral part of the vertebral column is still embedded in the matrix. The supraneural plate of the fused spinous processes is slightly thickened laterally. Irregular longitudinal striations are visible on the surface of this expansion. The transverse processes of the vertebrae, especially of the first sacral vertebra face posterolaterally and are fused with a distinctive suture to the ilium. They are distally expanded in anterior-posterior direction and fused with each other, thus enclosing the spaces between the processes. Like the vertebrae, these intersacral foramina also decrease in size from anterior to posterior.

Pelvic girdle.—The elements of the pelvic girdle are completely preserved with the exception of the ventral parts of the right pubis which are missing (Figs. 2, 3, 8A). The bones are co-ossified, so that sutures between individual bones are barely detectable. Although the ventral side of the pelvic girdle is still embedded in matrix, it can be assumed from the visible parts and the diverging angle relative to each other, that the pelvis is ventrally open and not fused (Fig. 4). There is no evidence of distortion or disarticulation on the dorsal side of the pelvis or at the fused articulation with the sacral vertebra. Nor are there any signs of any dorsomedially projecting processes of the pelvic bones which continue into the matrix. Unfortunately, no further preparation is possible at this side to clarify this unambiguously.

Ilium.—The ilium is relatively long (47 mm) with the preacetabular process measuring about 3/5 of the total length and extending anteriorly to the level of the articulation between the sixth and seventh preserved presacral vertebrae. The process is curved anteromedially and expanded laterally with the greatest width at the level of the second last presacral vertebra. The ilium forms the dorsal border of the acetabulum, enclosing the upper half of this excavation. A prominent postacetabular process is developed posterodorsal to the acetabulum and rises above the level of the preacetabular process. This process is orientated more or less horizontally and is slightly concave in dorsal view. The ventral margin of the process is upwardly concave and lies just at the level of the dorsal margin of the acetabulum. The right and left processes are roughly parallel. In about half of the height of the process, a horizontally orientated depression

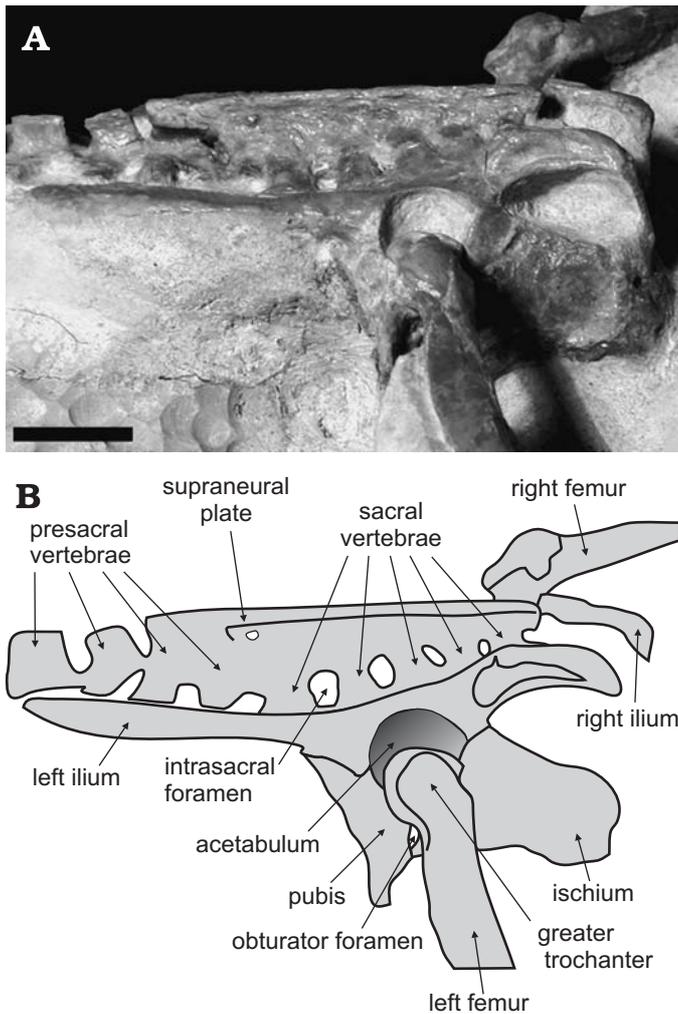


Fig. 3. *Dsungaripteridae* gen. et sp. indet., DFMMh/FV 500. **A.** Left lateral view of pelvis. **B.** Interpretative drawing. Scale bar 10 mm.

which is deepest anteriorly is visible at about mid-height of the process.

Pubis.—The pubis is rectangular in lateral view, and taller than long. It forms the anteroventral quarter of the border of the acetabulum. On the left side of the pelvis, the anterior margin of the pubis is bent laterally. Whether this is the natural morphology of the pubis or if the bone was deformed post-mortem cannot be determined, because the anterior margin of the right pubis is mostly embedded in matrix. The anterodorsal process of the pubis extends to the level of the suture between the ilium and ischium.

The suture between the pubis and ischium is barely visible. Together, the bones surround the obturator foramen, which has a diameter of about 3 mm. The pubis and ischium are connected by a 3 mm long suture ventral to the obturator foramen.

Ischium.—The ischium is plate-like with two processes. The main process is orientated almost vertically and extends posteriorly to the level of the posterior end of the postacetabular process. At its end, the process is about 6.5 mm in height and

12 mm long. The second process extends posteroventrally from the posteroventral border of the obturator foramen. It is about 6 mm long and about 3 mm high.

The ischium forms the posteroventral quarter of the border of the acetabulum. Both the ischium and pubis enclose the obturator foramen (see description of pubis).

Acetabulum.—The acetabulum extends from the level of the anterior margin of the transverse process of the third sacral vertebra to the level of the anterior margin of the transverse process of the fifth sacral vertebra. The cross-section is circular with a diameter of about 6 mm. The degree of perforation cannot be observed, because most of the acetabulum is filled by matrix. The dorsal border of the acetabulum is formed by the ilium, the anteroventral quarter by the pubis and the posteroventral quarter by the ischium.

Femur.—Both femora are slender and distinctly curved in anterior direction and also exhibit a pronounced inward bowing (Figs. 5, 6). The neck of the femur is orientated dorsomedially with an angle of 130 degree relative to the diaphysis. It bears a distinctive head with a basal diameter of about 5 mm. A ridge separates the smooth-surfaced head from the neck, giving it a somewhat mushroom-like shape. The greater trochanter is de-

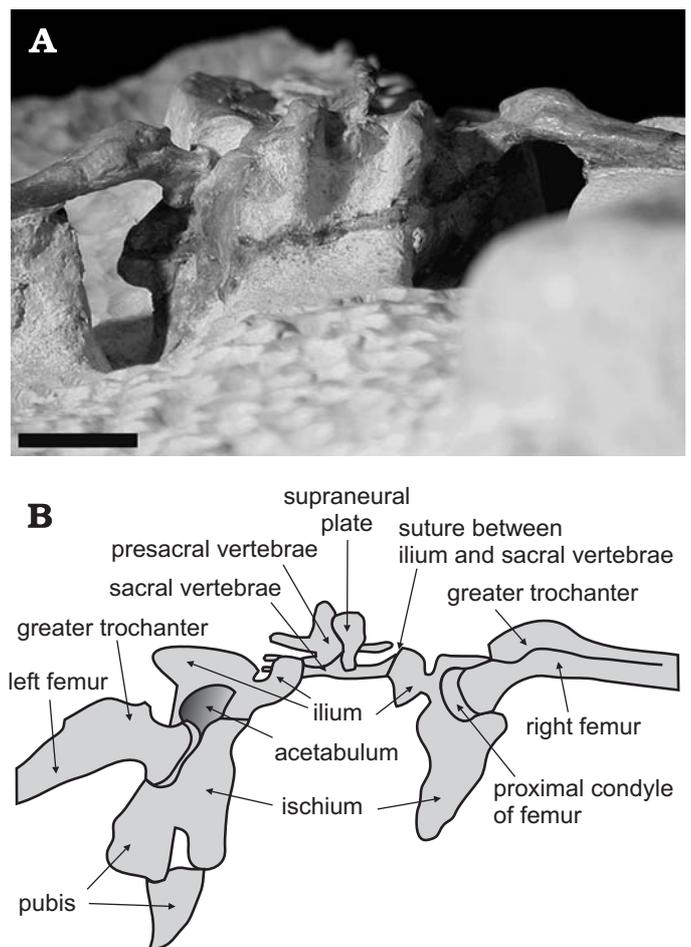


Fig. 4. *Dsungaripteridae* gen. et sp. indet., DFMMh/FV 500, posterior view of pelvis. For anatomical explanations see text and Fig. 2. Scale bar 10 mm.

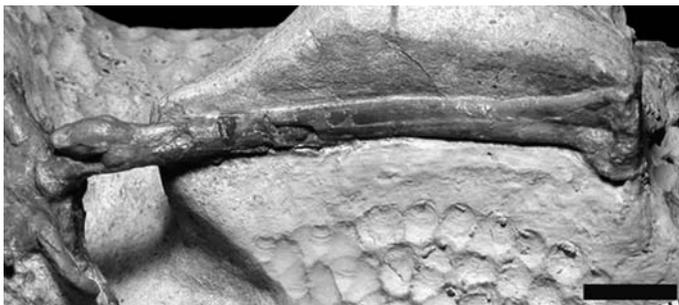


Fig. 5. Dsungaripteridae gen. et sp. indet., DFMMh/FV 500, dorsal view of right femur. For anatomical explanations see text and Fig. 2. Scale bar 10 mm.

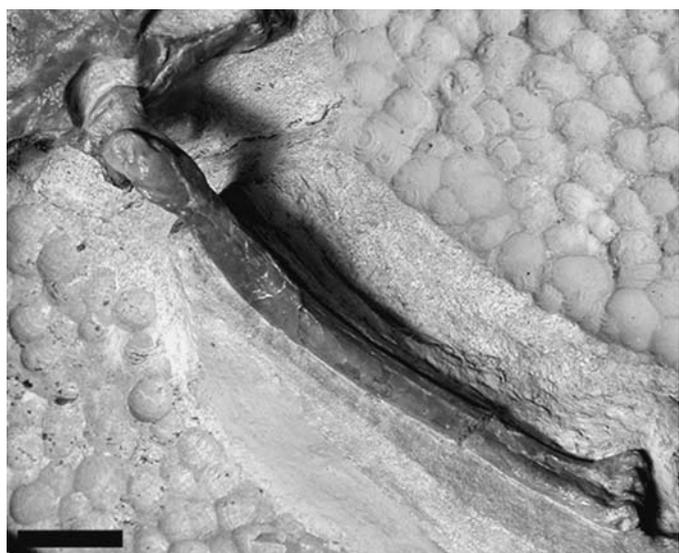


Fig. 6. Dsungaripteridae gen. et sp. indet., DFMMh/FV 500, dorsal view of left femur. For anatomical explanations see text and Fig. 2. Scale bar 10 mm.

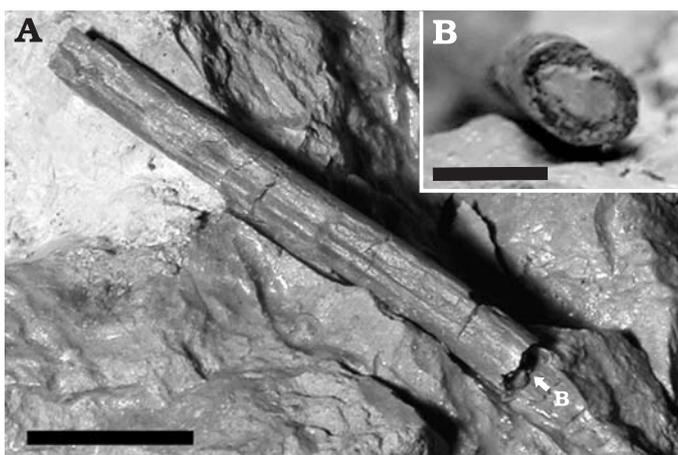


Fig. 7. Dsungaripteridae gen. et sp. indet., DFMMh/FV 500. A. Fragment of ?tibia. B. Cross-section of ?tibia. Scale bars 10 mm. Note exceptionally thick cortex and consequent constricted lumen in the diaphysis.

veloped ventrolateral to the head and neck. It measures about half of the diameter of the femur at this level. A deep fossa can be seen on the dorsolateral side of the trochanter. Distal to the

greater trochanter the femur narrows in the anterior-posterior direction, thus giving the diaphysis an elliptical cross-section. At the distal end, the femur is expanded laterally and medially so that the width of the epiphysis is about twice that of the diaphysis. Two condyles are visible, separated by a medial groove. This groove merges proximally in a medial triangular depression on the posterior surface of the femur. The depression flattens proximally and has about the same length as the width of the distal epiphysis.

Possible tibia.—The fragment of a long bone is situated about 36 mm posterior to the right femur (Fig. 7A). Its long axis is orientated in an anterolateral-posteromedial direction. The fragment is broken perpendicular to its long axis, thus revealing an elliptical cross-section with a central cavity (Fig. 7B). The thickness of the cortex (= bone wall) measures roughly one quarter of its total diameter for the major axis and one third for the minor axis. From the dorsal view a longitudinal groove is visible.

By comparison with other pterosaurs and because of its position and size, this isolated bone most likely represents part of the right tibia.

Discussion

Systematic discussion

The three-dimensional, uncrushed preservation of the specimen allows for comparison with the postcranial skeleton of other pterodactyloid pterosaurs. Although the presacral vertebral column is rather undiagnostic, the morphology of the pelvis and femur can be used for a systematic assignment. Moreover, the sacrum with five sacral vertebrae is typical for a number of pterodactyloid pterosaurs but excludes the Pteranodontidae (Wellnhofer 1978). The long-tailed Rhamphorhynchoidea possess only three sacral vertebrae.

Pelvis.—Comparisons with the pelves of other known Jurassic pterosaurs reveal no significant similarities between them and the present specimen. Either the shape of the ilium is different or the ischium is plate-like and not divided into two distinct processes (Fig. 8). Among other Jurassic taxa, only *Pterodactylus* has a “raised” postacetabular process on the ilium, similar to the specimen reported herein, but it differs in the morphology of its ischium (Fig. 8B).

The pelvis of the present specimen is clearly distinguished from the Cretaceous “ornithocheirid” type of pelvis, however, it shares a prominent postacetabular process (Fig. 8C), but in ornithocheirids, the ischium and pubis are fused to form a broad ischiadic plate. Closer affinities are suggested by the “Queensland” pelvis described by Molnar (1987: fig. 1), which was also assigned to the Ornithocheiridae (Fig. 8D). Molnar’s specimen, however, is only fragmentary and the restoration may be debatable. Furthermore, the position and size of the obturator foramen of the “Queensland specimen” is unlike the specimen described here.

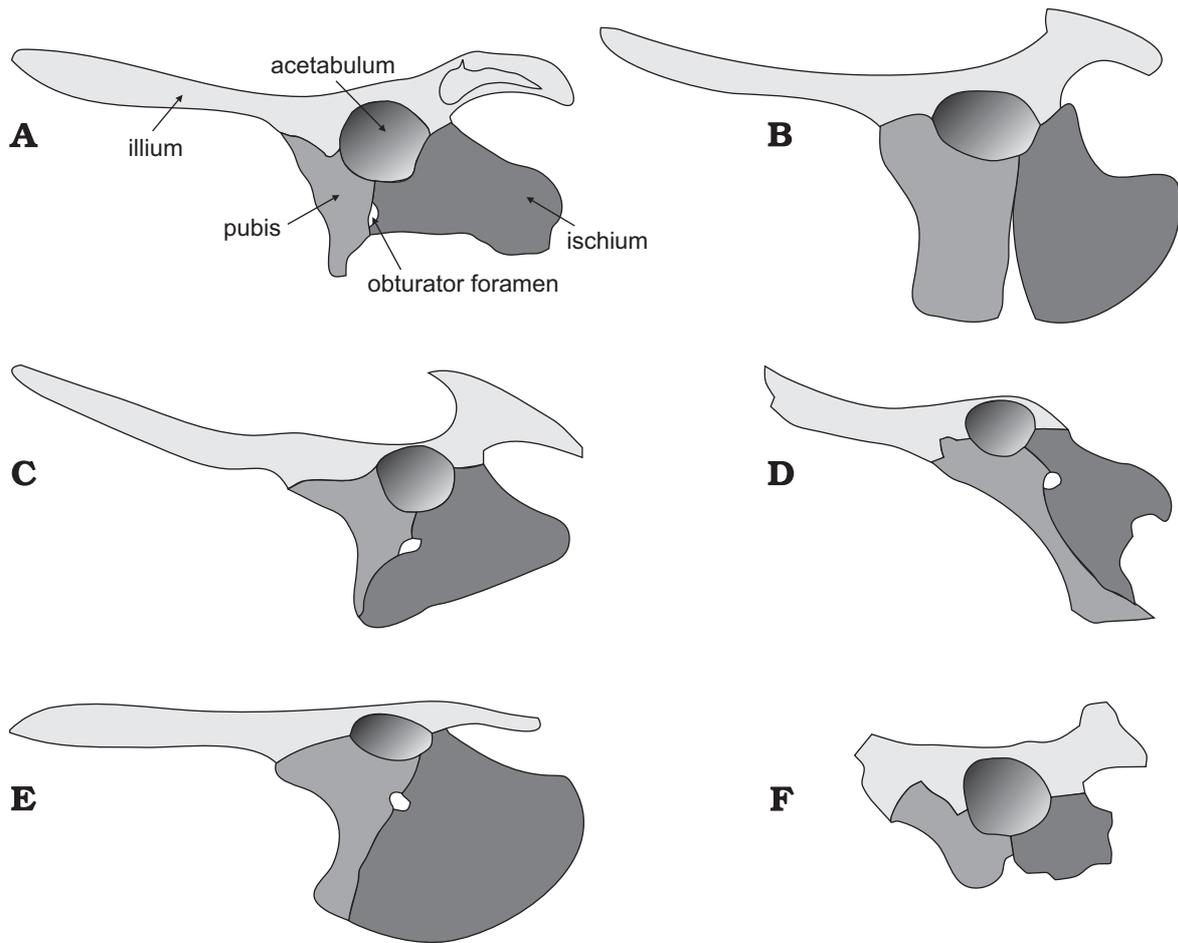


Fig. 8. Comparative reconstructions of pterosaurian pelvises. **A.** *Dsungaripteridae* gen. et sp. indet., DFMMh/FV 500. **B.** *Pterodactylus* sp. **C.** *Ornithocheirus* sp. **D.** "Queensland pterosaur". **E.** *Germanodactylus* sp. **F.** *Dsungaripterus weii*. All drawn to the same size.

A fragmentary pelvis (Fig. 8F) is known for the Lower Cretaceous pterosaur *Dsungaripterus weii* from China (Young 1964: figs. 3, 6). Only two pelvises are known from this taxon, both missing most of the distal parts of the pelvic bones. As in the studied specimen, the *Dsungaripterus* ilia also possess a prominent postacetabular process and a similar anterodorsal process of the pubis. Young (1964), however, mentions seven sacral vertebrae in *Dsungaripterus*, but based on his drawings, this statement is hard to verify (the feature is only visible in dorsal view).

Femur.—The femur of the present specimen differs from most other known pterosaurian femora by its distinct curvature in two directions (Figs. 5, 6). This feature is known elsewhere only in dsungaripteroids like e.g., *Germanodactylus*, *Noripterus*, or *Dsungaripterus*, whereas a number of pterosaurs like e.g., *Pteranodon* or *Pterodaustro* show only a lateral curvature if any (Unwin 2003). The femur of *Dsungaripterus* is nearly indistinguishable from the one described herein (Fig. 9). Both femora possess an identically bent shaft. As in the present specimen, the femur of *Dsungaripterus* is relatively long and slender, both condyles are only distally expanded and the greater trochanter has a lateral fossa.

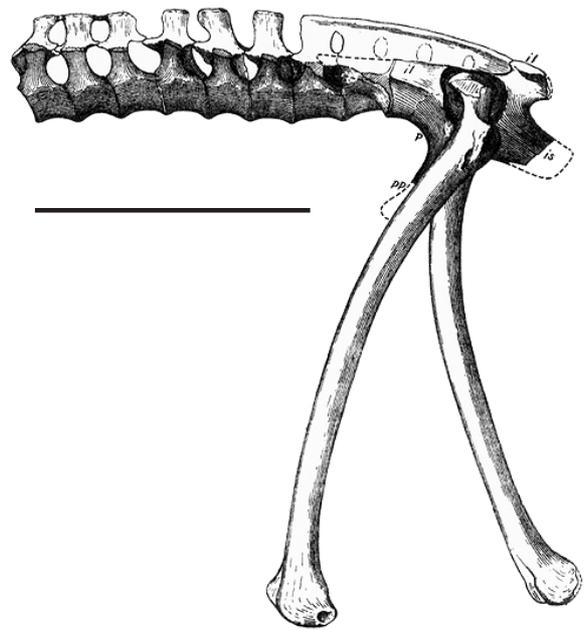


Fig. 9. Original drawings of *Dsungaripterus weii* by Young (1964). Note strong curvature of the diaphysis, reminiscent of the condition in the studied specimen. Scale bar 100 mm.

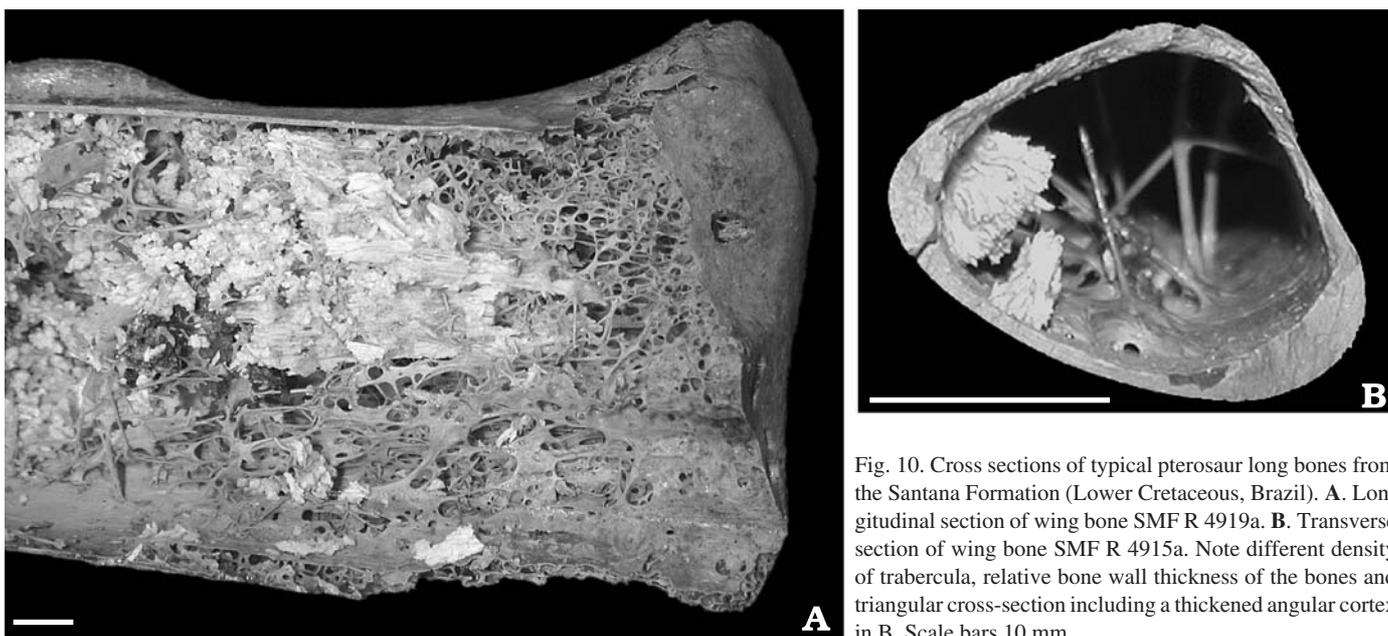


Fig. 10. Cross sections of typical pterosaur long bones from the Santana Formation (Lower Cretaceous, Brazil). **A.** Longitudinal section of wing bone SMF R 4919a. **B.** Transverse section of wing bone SMF R 4915a. Note different density of trabecula, relative bone wall thickness of the bones and triangular cross-section including a thickened angular cortex in B. Scale bars 10 mm.

Other systematic features.—Whereas the morphology of the possible tibia is systematically uninformative, its preservation allows determination of the cross-sectional area of this bone (Fig. 7B). It is an elliptical, hollow tube with a bone-wall thickness (t) of about one-third of the average diameter ($2 \times R$) of the shaft (R/t value after Currey 1984 of about 3.3 for the lesser diameter to 4.2 for the major axis). This value is rather uncommon in pterosaurs, where the long bone walls are extremely thin compared to the total diameter with typical R/t ratios of about 7 to 20. This is especially true for the long bones of azdhardchoids, ornithocheiroids and pteranodontoids which have very high ratios. Non-dsungaripteroid pterodactyls and rhamphorhynchoids have thicker bone walls than these groups but still significantly thinner than dsungaripteroids. This can be demonstrated by measuring broken bones, e.g., from Solnhofen or Santana specimens (Fig. 10).

According to Unwin (1995, 2003; Unwin et al. 1996), the relatively thick walls are unique to dsungaripteroids among pterosaurs. For these reasons I assign the present specimen to this group. The superfamily Dsungaripteroidea was proposed by Unwin (1995, 2003) by merging the families Dsungaripteridae and Germanodactylidae. The close relationship between these two families has earlier been proposed by Young (1964) and Wellnhofer (1978). The Germanodactylidae are represented by three genera, *Germanodactylus* from the lower Tithonian from Bavaria, Germany (Wellnhofer 1978), *Normannognathus* from the upper Kimmeridgian of Normandy, France (Buffetaut et al. 1998), and *Tendaguripterus* from the Kimmeridgian/Tithonian of Tanzania (Unwin and Heinrich 1999). Recently, Unwin and Heinrich (1999) also referred material from the Upper Jurassic of Tanzania to the Germanodactylidae, which Galton (1980) had previously described as dsungaripterid remains.

However, the specimen described here differs from the known germanodactylid postcranial material in the morphology of the pelvis and femur (Fig. 8E). In consideration of its strong affinities to the holotype of *Dsungaripterus weii*, in having a similar pelvis, a similar curved femur and thick long bone walls, the here described specimen has to be assigned to the Dsungaripteridae. Due to the absence of more diagnostic features, however, it seems best to refer the specimen to Dsungaripteridae gen. et sp. indet.

Occurrence and distribution of dsungaripterids

So far, dsungaripterids are only known from the Lower Cretaceous and mainly reported from Asia. Two species, *Dsungaripterus weii* (Young 1964) and *Noripterus complicidens* (Young 1973), were found in the Lower Cretaceous of Sinkiang, China. Another presumed dsungaripterid, *D. parvus* (Bakhurina 1982) from the basal Lower Cretaceous of west-

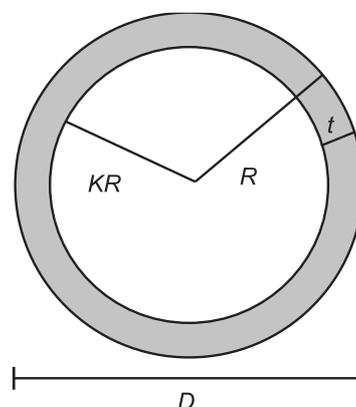


Fig. 11. Geometric parameters in a hollow circular cross-section. D , diameter; KR , inner radius; R , outer radius; t , wall thickness. After Currey and Alexander (1985).

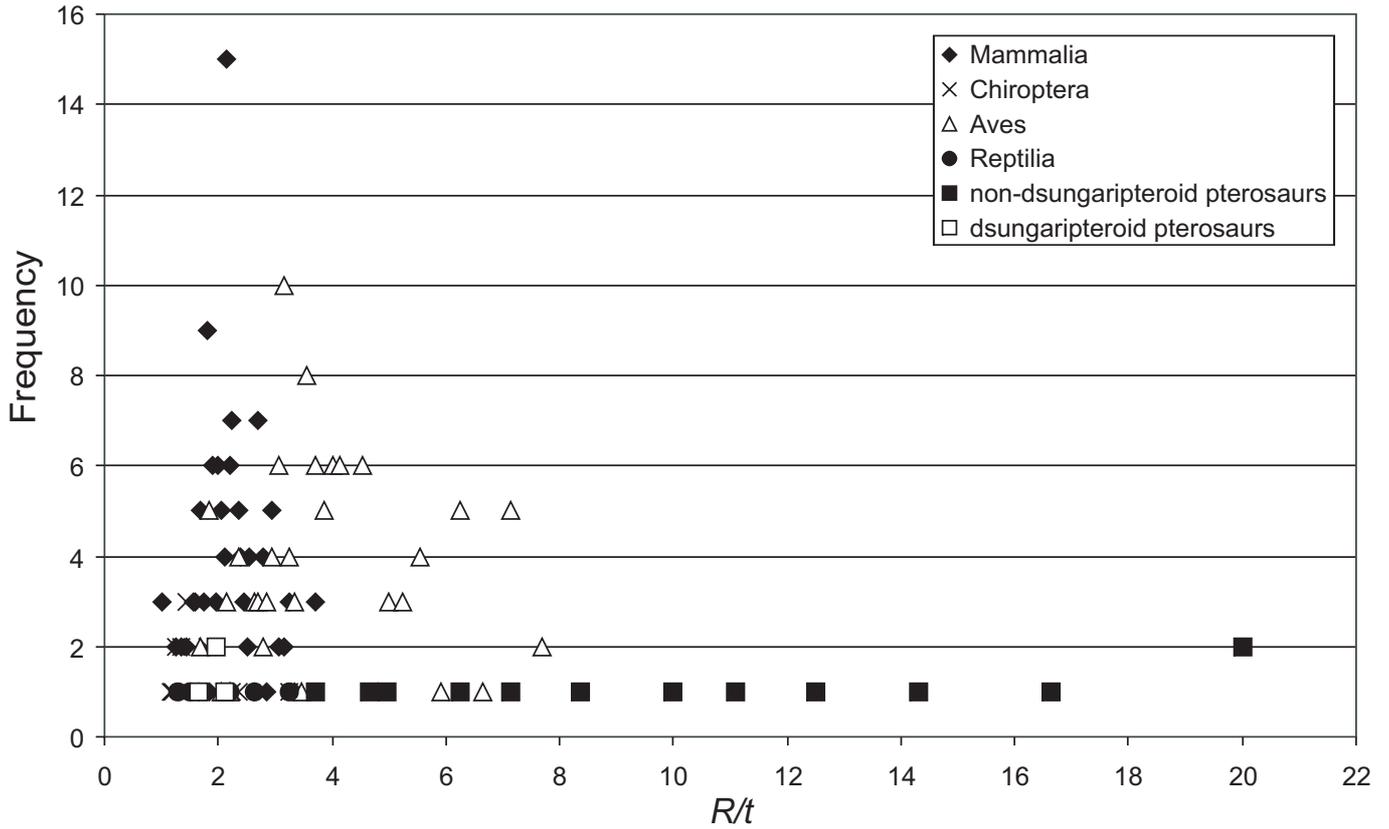


Fig. 12. Frequency of R/t -values in samples of different tetrapod groups, based on data from Currey and Alexander (1985), and my own data.

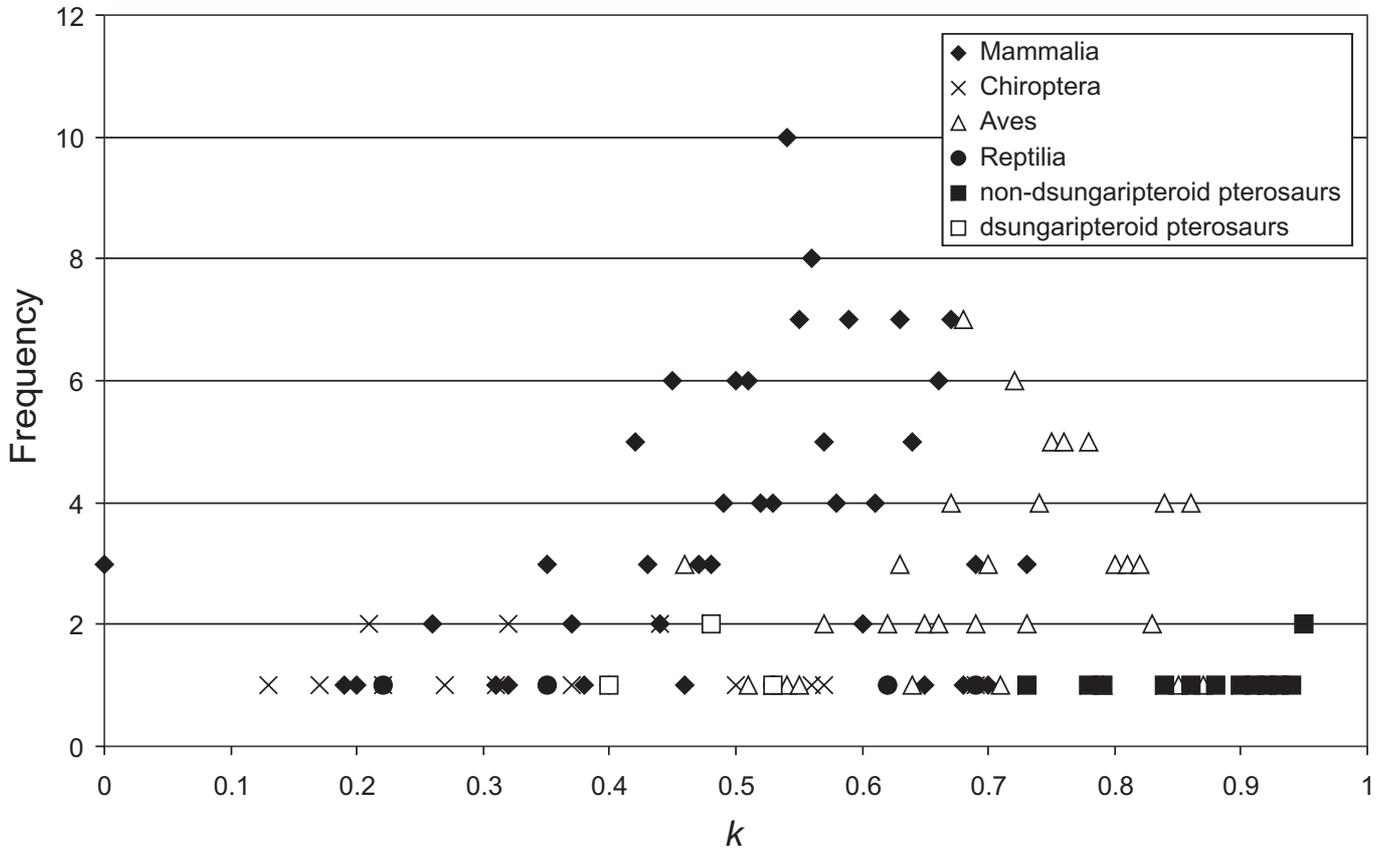


Fig.13. Frequency of K -values in samples of different tetrapod groups, based on data from Currey and Alexander (1985), and my own data.

ern Mongolia, was later assigned to the new genus “*Phobetor*” (Bakhurina 1986), a name which is preoccupied (Unwin and Bakhurina 2000). Another locality, Tatal, in western Mongolia recently has yielded more remains from this species from at least 45 individuals, including juveniles (Bakhurina and Unwin 1995; Unwin and Bakhurina 2000).

Unwin et al. (1996) described an incomplete proximal wing-phalanx from the Hauterivian/Barremian Amagodani Formation of Japan, which they referred to the Dsungaripteridae because of its unusually thick-walled bone.

The fact that dsungaripteroids were well established in the Upper Jurassic of Laurasia was demonstrated by Unwin and Heinrich (1999). Only two other records document the existence of dsungaripterids outside Asia, both from South America. Bonaparte and Sánchez (1975) described the tibia and fibula of a pterosaur from the Lower Cretaceous of Patagonia and named it *Puntanapterus globosus*. Galton (1980) referred this specimen to the Dsungaripteridae because of its similarities to the specimens from Tendaguru. Recently, Martill et al. (2000) reported a new dsungaripterid taxon, *Domeykodactylus* from the Upper Jurassic/Lower Cretaceous of Chile. It consists of an incomplete mandible and a referred fragment of the premaxilla. The presence of the dsungaripterid from the Langenberg therefore is the first record of this family in Europe and possibly one of the oldest dsungaripterid fossils known so far.

Biomechanical characteristics of pterosaur bones

According to Unwin (2003, see also Unwin et al. 1996), typical dsungaripteroid bones show relatively thick bone walls compared to the non-dsungaripteroid pterosaur bone type (see Fig. 7B). The latter are thin-walled with a typical cortical thickness of about 1 mm (Fig. 10). Modelling the cross-section of a bone as a hollow circle (Fig. 11), the relationship between bone wall thickness and the diameter of the bone can be described by the R/t -ratio (radius/thickness of the cortex) or alternatively by the parameter K (see Fig. 11 and Appendix 1 for definition) (Currey and Alexander 1985). For non-symmetrical cross-sections like the present long bone fragment (Fig. 7B) or the wing phalanges of pterosaurs (Fig. 10B), the R/t -ratio is not a constant value but spans a range of values.

Typical values for pterosaur long bones range from 7 to 20 (R/t -ratio, Fig. 12) and 0.73 to 0.95 (K -value, Fig. 13), indicating that pterosaurs have relatively thin bone walls in comparison to other vertebrates, which have much lower values. Also, other flying vertebrates like birds and bats possess significantly lower values than pterosaurs (Figs. 12, 13). Moreover, gas-filled long bones of birds have thinner walls than marrow-filled bones. The bones of most flightless birds have thicker bone walls than volant birds (Cubo and Casinos 2000). In bats, only the stylo- and zeugopodial bones have relatively high R/t -ratios, whereas the values for the phalanges are similar in thickness to the typical mammalian distribution (Fig. 12).

Although the phenomenon of thin-walled, hollow bones has often been cited as a way to make a skeleton lighter, this is only true in terms of total mass (Currey and Alexander 1985). If the ratio between bone and muscle is considered, birds have higher ratios than mammals (Cubo and Casinos 1994; Currey 2002). This means that in birds the reduction of the mass of the soft tissue portion is more significant than the mass-saving effect of having hollow bones.

Besides total weight reduction, reduced cortical thickness affects the mechanics of the bones. This can be demonstrated by modelling a pterosaur long bone as a hollow tube. Compared to a solid cylinder, a hollow tube of the same mass has larger axial (I_x/I_y) and polar (I_p) moments of inertia (Nachtigall 2000). Hence, a hollow cylinder also has increased bending and torsional strength (see Appendix 1). Bending and torsional loads are the most important loads during flight. This was demonstrated by Swartz et al. (1992) who measured high torsional and bending stresses in the wing bones of bats. Biewener and Dial (1995) also showed that in the humerus of pigeons the torsional strength is the most critical design feature.

For a non-circular cross-section the effects are similar to that of hollow sections. In this case, however, the values of the axial and polar moment are not constant in every direction but distributed unevenly. This is caused by variation of the R -value which has to be defined as the particular distance of the centroid to the outer wall (Fig. 10B). Additionally, the bone wall thickness may vary too (Fig. 10B). Therefore, the bending and torsional strength show local maxima and minima in certain directions.

The relationship of cross-sectional area and its mechanical consequences for birds has been studied by Cubo and Casinos (1998a, b, 2000; Casinos and Cubo 2001) who demonstrated that resistance against torsion is one of the key features in explaining the cross-sectional shape of long bones

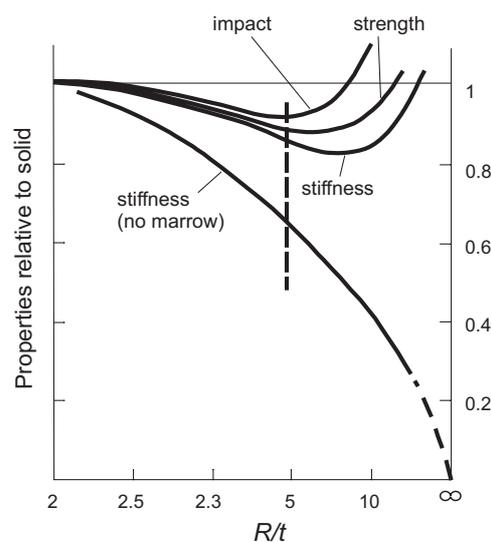


Fig. 14. Mechanical properties in bending by variation of R/t . Solid bone with R/t -value of 1 is defined as 1. Level of dsungaripterid R/t -value dashed. After Currey (1984).

from the wing extremity and leg. In their studies, marrow-filled bones were shown to have relatively thicker cortical walls and higher bending strengths than pneumatized bones with relatively thinner bone walls (Fig. 14). This may have also been true for the hollow pterosaur bones, which were not filled by marrow but were pneumatized instead.

The higher the R/t -ratio of a hollow tube, the more likely local buckling of the structure will be (see Appendix 1) due to the forces acting in the direction of the long axis of the cylinder. Pterosaur bones would tend to buckle more easily than bird bones based on the relatively thinner bone walls of pterosaurs. The studies of the loading regimes of recent bats (Swartz et al. 1992) demonstrated that compressive forces in the direction of the longitudinal axis of the wing bones are unlikely to occur in this group. The wing construction of pterosaurs, however, differs from this group and compressive forces may have been substantial (James R. Cunningham, personal communication 2004), but may not have reached the critical values for failure of the bones.

The long bones of dsungaripteroid pterosaurs are different from the typical pterosaur bones described above. The relatively thick-walled dsungaripteroid long bones have R/t -ratios from 1.6 to 2.1 and K -values from 0.4 to 0.53. Dsungaripteroids plot close to the main distribution of typical mammal bones and the marrow-filled bones of birds (Figs. 12–14). Expressed in mechanical terms, dsungaripteroid bones have lower values of area and polar moment of inertia and therefore reduced bending and torsional strengths as compared to non-dsungaripteroid pterosaur bones (see Appendix 1). This is independent of whether circular or non-circular cross-sections are considered. As mentioned previously, the infilling of bird bones by marrow has the effect of reducing bending stresses (Cubo and Casinos 2000). The cross-sectional areas of the dsungaripteroid long bones of wings and legs fall well within the range of marrow-filled bones, with a relatively high resistance to impact loading and high strength and stiffness (Fig. 14). Therefore, marrow may have also been present in dsungaripterid bones too. Consistent with this suggestion is that no pneumatic foramina have been observed in dsungaripteroid long bones.

Dsungaripteroid bones are less likely to fail under compressive forces along the long axis of the bone because of their thick bone walls (see Appendix 1). The occurrence of these compressive forces is indicated by the noticeably bent femur in dsungaripterids, a feature which is diagnostic for this group within the Pterosauria. At first glance, this pre-bending would seem to weaken the bone under compression. This apparent design paradox is also observed in mammals and birds (Bertram and Biewener 1988; Cubo et al. 1999). Two reasons could account for this (Cubo et al. 1999): firstly, the curvature could serve as a system for allocating and packing muscle bellies; secondly, the loading direction and theoretical failure direction is predetermined by the curvature. Variation in cross-section or bone wall thickness may play a role here, too. In the second case, the expected buckling

would be prevented by the counter-action of the leg muscles (Bertram and Biewener 1988).

Further evidence for the importance of compressive forces in dsungaripteroid long bones is indicated by the expanded articular surfaces in the long bones, another feature characteristic of dsungaripteroids (Unwin et al. 1996). Besides allowing a greater mobility between the articulating bones in case of simple convex articulations, the forces transmitted between bones are distributed over a larger area. This helps to reduce compressive stress in the underlying bone (Currey 2002).

Therefore, resistance against compressive forces and local buckling seem to be an important feature in the dsungaripteroid long bone construction. These loading states are not, however, typical for forces produced during flight if birds and bats are used as analogues (Swartz et al. 1992; Biewener and Dial 1995). In these animals, compressive forces are mainly produced during the take-off and landing phases of flight and terrestrial locomotion. Lacking contradicting fossil evidence, the same has to be assumed for pterosaurs as long as further information on the mechanical properties of the wing membrane and their influence on the loading regimes of the bones are available. So far, numerical analyses of wing bones with an attached wing membrane mostly give evidence only for bending and tensile stresses (Eberhard Frey, personal communication 2003).

Most pterosaurs are viewed to be behavioural analogues to extant marine birds, spending most of their life airborne, gliding above the sea. Compressive loading conditions in the wing and leg long bones, would, therefore, have been relatively uncommon. On the other hand, a more continental habitat would put different demands on the animal since this would involve a more frequent succession of take-offs and landings, as well as increased reliance on terrestrial locomotion. Because dsungaripteroids are mainly known from continental deposits, the typical dsungaripteroid bone construction is consistent with an active way of life in this environment.

Hip construction and implications for terrestrial locomotion

Based on the idea that dsungaripterids inhabited a predominantly continental environment, it can be assumed that they also spent more time about moving on land than most pterosaurs, whose remains are derived from marine deposits. For years, the mode of terrestrial locomotion of pterosaurs has been subject of an intensive debate. Whereas some authors proposed a bipedal, running mode of locomotion at for all pterosaurs (e.g., Padian 1983a, b; Paul 1987) or at least only for large pterodactyloids (Bennett 1990, 1997a, b, 2001), others favoured a quadrupedal posture (e.g., Unwin 1987, 1988; Wellnhofer 1988, 1991a, b; Henderson and Unwin 1999, 2001a, b; Unwin and Henderson 1999; Chatterjee and Templin 2004). The morphology of the pelvis and the femur has played an especially important role in this discussion

(Padian 1983a, b; Wellnhofer 1988; Bennett 1990, 2001; Henderson and Unwin 1999; Unwin and Henderson 1999). In the present specimen the pelvis and femur are preserved three-dimensional and articulated, so it is possible to reconstruct some locomotor options by biomechanical means. The typical thick-walled dsungaripteroid long bone construction is non-informative in this debate, because it would permit both types of locomotion. Owing, however, to the exceptional preservation of the present specimen, it is possible to determine the range of motion of the femur. This range is heavily constrained by the orientation of the acetabulum. As described above, the acetabulum faces dorsolaterally rather than laterally as in typical bipedal animals (Padian 1983a, b). Assuming a subhorizontal posture of the sacrum as proposed by Wellnhofer (1988) and Bennett (1997a) for *Pterodactylus*, the femur of the present specimen can only be lowered about 40 degrees from the horizontal plane without disarticulation, whereas it can be elevated to the horizontal (Fig. 15). These limitations do not allow a proper bipedal gait since the femur can not be brought into a parasagittal position without a partial displacement of the femoral head out of the acetabulum. Although Bennett (2001: 133) alluded to the capability of muscles and ligaments to accommodate this, a stable mechanical state is not achieved when displacement is the condition of the femoral head during locomotion. With such a posture, the hinge-like knee-joint would not be orientated horizontally but inclined (Fig. 15).

A similar condition can be seen in other pterosaurs (Bennett 1990). Bennett (1990, 1997a, 2001), therefore, suggested for large pterodactyloids a more erect posture with the sacrum held about 60 degrees above the horizontal. The femur then would be buttressed against the well-developed anterior wall of the acetabulum. This allows the femur to swing in a parasagittal plane and according to his reconstruction (Bennett 1990: fig. 3) thus gives way to a bipedal upright stance and gait. Although a similar steeply inclined vertebral column was adopted by other authors (Chatterjee and Templin 2004; Henderson and Unwin 1999, 2001a, b; Unwin and Henderson 1999), it was demonstrated that such an orientation also permits a quadrupedal gait. Unwin and Henderson (1999) argued that only a steeply inclined pelvis is consistent with all constraints which act on a quadrupedal walking pterosaur construction. A bipedal gait would be unstable for such a construction because of the position of the center of mass which is situated close to the center of lift. For these reasons, Chatterjee and Templin (2004) argued that a bipedal stance was only used for short bursts during takeoff and landing phases. Following previous arguments (Padian 1983; Bennett 1997), they create a scenario in which the sacrum is kept in the same inclined position as during quadrupedal locomotion and in which the animal is stabilised by the folded wings. However, they fail to describe a full sequence beginning from quadrupedal locomotion to an airborne condition based on a biomechanical-static investigation. Unfortunately, such a description is also missing from a solely quadrupedal locomotion scheme.

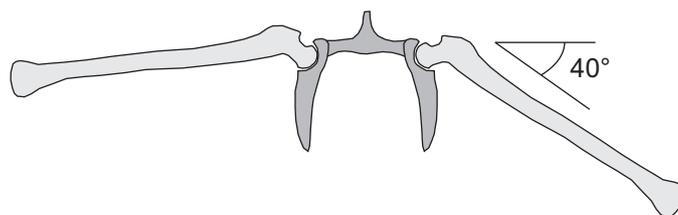


Fig. 15. Range of motion in transverse plane of the femur in a model of DFMMh/FV 500.

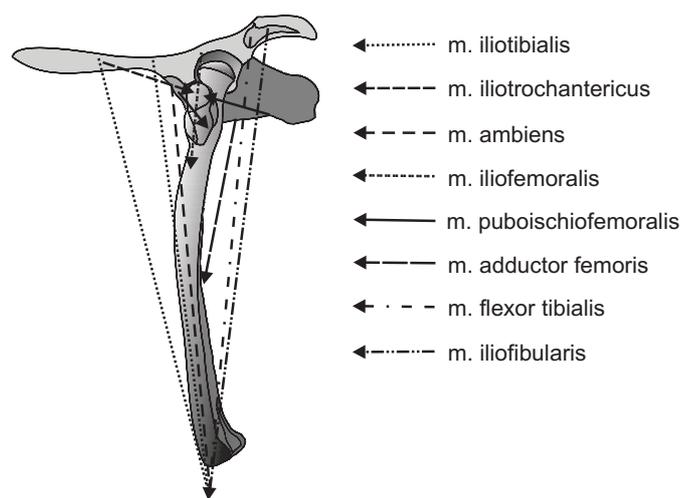


Fig. 16. Reconstruction of hip muscles in DFMMh/FV 500.

An important factor in all these studies is the biomechanics of the pelvis and femoral musculature, which has only been reconstructed tentatively. Using the extant phylogenetic bracket (Witmer 1997), and comparisons with other reconstructions in archosaurs (Wellnhofer 1978; Hutchinson 2001), the muscle attachment areas can be identified in the studied specimen (Fig. 16). On this basis, the alternative hypotheses can be tested for their biomechanical consequences.

Wellnhofer (1988) assumed that in a quadrupedal gait, the pelvis would have been held horizontally to upwardly inclined anteriorly. In this case, most of the femoral adductors and abductors attach at relatively large angles, representing effective lever arms in all phases of a hypothetical step-cycle (Fig. 17). The elongated anterior and posterior processes of the ilium contribute to the mechanical advantage by increasing the attachment angle and by increasing the cross-sections of the muscles if non-pennate muscles are assumed.

A different picture appears if an inclined hip posture is assumed. Here, the ilium is oriented at a large angle to the horizontal plane. Consequently, most muscle groups possess “poor” lever arms (Fig. 18) relative to the horizontal scenario. In every phase of a hypothetical step-cycle, certain muscle groups contribute only marginally to locomotion because of their mechanical ineffectiveness. In this case the enlargement of the ilium does not contribute much to the effectiveness of the lever arm systems for terrestrial locomotion.

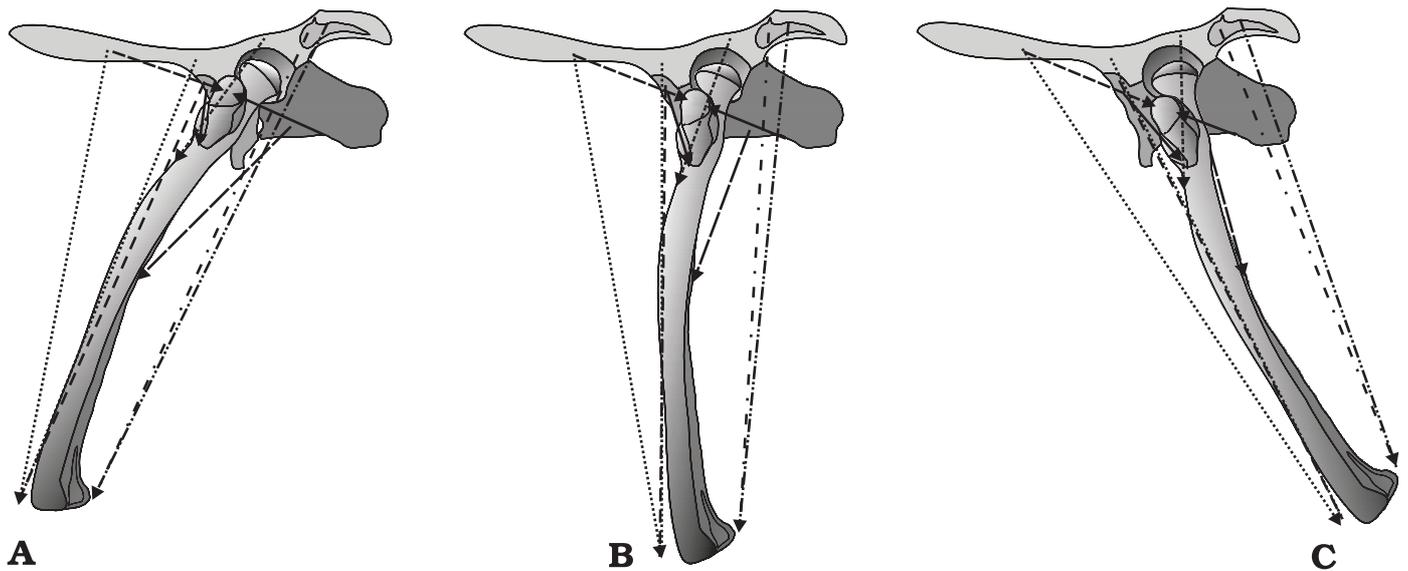


Fig. 17. Three hypothetical step cycles in quadrupedal locomotion of DFMMh/FV 500. Lines of action of the major hip muscles shown in start of retraction phase (A), intermediate (B), and start of protraction phase (C). Note vertical position of the pelvis and relatively good mechanical advantage of the muscle lever arms through all stages.

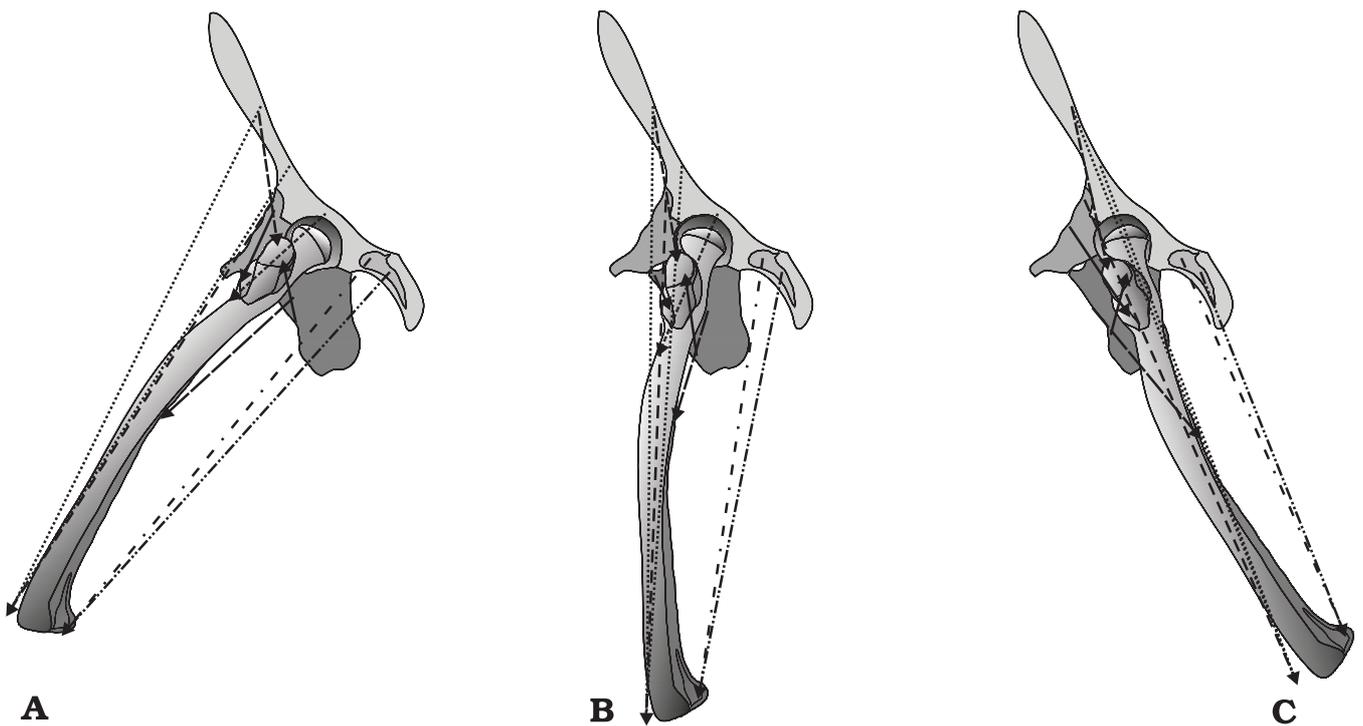


Fig. 18. Three hypothetical step cycles in bipedal locomotion of DFMMh/FV 500. Lines of action of the major hip muscles shown in start of retraction phase (A), intermediate (B), and start of protraction phase (C). Note inclined position of the pelvis reconstructed after Bennett (1990) and relatively poor mechanical advantage of the muscle lever arms through all stages.

As can be deduced from recent quadrupeds (e.g., Kummer 1959), such a construction may be well within the mechanical limits. It is, however, questionable whether the reconstructed muscular configuration for this specimen would allow an effective, fast run as proposed by the supporters of the

bipedal theory. In addition, comparison with the condition seen in other bipedal archosaurs (Hutchinson and Gatesy 2000; Hutchinson 2004a, b) shows that in these groups the hip and musculature configuration as well as the proportions of the hindlimbs are different from those of pterosaurs.

So far, there is no direct evidence in the way of pterosaur tracks to support either mode of locomotion for dsungaripterids. The known trackways of pterosaurs furnish only evidence of a quadrupedal gait (Mazin et al. 2001, 2003), where the femur is oriented more ventrolaterally than fully parasagittally. These tracks are much broader than for typical bipedal gaits in which the tracks from the feet of both sides overlap along the midline (Wade 1989). As deduced from the tracks, even higher speeds were achieved using a quadrupedal gait (Mazin et al. 2003).

I conclude from these reconstructions, that a quadrupedal terrestrial stance and gait is much more plausible in dsungaripterids than bipedal locomotion. The idea of habitual bipedal locomotion in dsungaripterid pterosaurs is rejected, although such a posture may be within the optional operational range of the pterosaur construction (as it is in other typical quadrupeds). The mobility of the femur indicates an inclined posture of the hip. Whether a change of this posture was dependant on the speed as proposed by Mazin et al. (2003) cannot be evaluated.

Conclusions

- The new specimen from Langenberg here described can be identified as the oldest dsungaripterid pterosaur and the first dsungaripterid from Central Europe.
- The typical dsungaripterid bone construction showing an increased cortical thickness relative to non-dsungaripterid pterosaurs has a greater strength against axially orientated compressive forces. In birds and bats these stresses are associated mainly with take-off and landing phases. Considering these latter groups as analogues, the strong bones are in accordance with theories that dsungaripterids populated continental habitats as suggested by their taphonomy.
- The hip construction (the arrangement of muscles and the mobility of the femur) indicate that dsungaripterids had the same quadrupedal stance and gait as inferred for other pterosaurs.

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Appendix 1

The following calculations are based on the model of a long bone as a hollow, circular tube (Fig. 11) with D = diameter, R = radius and t = wall thickness. All cross-sections are hollow with a constant wall-thickness, and not filled by marrow. For any non-circular cross-sections or sections with non-constant wall thickness, similar equations can be given or calculated by using special software. As mentioned in the text, ranges of values with maxima and minima of the values for certain directions will result from such cross-sections depending in the local values of R and t .

Area moment of inertia (I_x)

The area moment of inertia is defined as:

$$I_x = \frac{\pi}{4}((R)^4 - (R - t)^4) \quad (1)$$

Mean values based on data from Alexander and Currey (1985) and my own data for calibrated cross-sections (D set to 1) are:

Mammalia (without Chiroptera)	$3.5\text{--}4.9 \times 10^{-10}$
Chiroptera	$3.9\text{--}4.5 \times 10^{-10}$
Reptilia	$3.8\text{--}4.9 \times 10^{-10}$
Aves	$2.2\text{--}4.8 \times 10^{-10}$
Non-dsungaripteroid pterosaurs	$0.9\text{--}3.5 \times 10^{-10}$
Dsungaripteroid pterosaurs	$4.6\text{--}4.8 \times 10^{-10}$
(cross-sections scaled to the same size)	

Following beam theory, I_x helps to define the bending strength of a structure.

$$M = \sigma \times R / I_x \quad (2)$$

where M = bending strength, σ = ultimate stress in bending and R = radius. The structure fails if the working stress in bending reaches the ultimate stress in bending.

Based on the values of I_x above and assuming a similar σ , the typical Non-Dsungaripteroid Pterosaur Long Bone Construction (NDBC) would possess much lower bending strength than other long bone constructions and the Dsungaripteroid Bone Construction (DBC). However, all these constructions have different masses/cortical areas and therefore cannot be compared directly to one other. Such comparison can be achieved, however, by a simple calibration of bones of same mass/cortical area, NDBC and DBC.

If the density of bone is ρ , the mass per unit length of tubular bone is

$$m = \pi R^2 \rho (1 - K^2) \quad (3)$$

where m = mass per unit length of tubular bone, R = radius, ρ = density of bone and $K = (R-t)/R$.

Assuming an identical mass, a mean value for DBC of $R_1 = 0.5$ (ρ scaled to 1), $K_1 = 0.48$, $t = 0.26$ and $K_2 = 0.78$ for NDBC it follows:

$$\pi R_1^2 \rho (1 - K_1^2) = \pi R_2^2 \rho (1 - K_2^2) \quad (4)$$

$$\sqrt{\frac{R_1^2 (1 - K_1^2)}{(1 - K_2^2)}} = R_2 \quad (5)$$

$$\sqrt{\frac{0.5^2 (1 - 0.48^2)}{(1 - 0.78^2)}} = R_2 \quad (5a)$$

A NDBC of the same mass would have, $R_2 = 0.70$ and $t = 0.15$. Whereas after (1) I_x in DBC is 4.6×10^{-10} , I_x in NDBC is 14.7×10^{-10} . The bending strength in NDBC is about 2.3 times higher than in DBC, assuming an identical σ .

In terms of keeping the bending strength constant (1), (2), and (3) leads in the same way to the result, that if R increases, t decreases and the mass can also be reduced. This latter case is especially important for flying animals. It also applies to mass reduction in animals that exhibit a non-constant varying R and non-constant varying t .

Polar moment of inertia (I_p)

The polar moment of inertia is defined as:

$$I_p = \frac{\pi}{2}((R)^4 - (R - t)^4) \quad (6)$$

Mean values based on data by Alexander and Curry (1985) and my own data for calibrated cross-sections (D set to 1) are:

Mammalia (without Chiroptera)	$7.0\text{--}9.8 \times 10^{-10}$
Chiroptera	$7.0\text{--}9.8 \times 10^{-10}$
Reptilia	$7.6\text{--}9.8 \times 10^{-10}$
Aves	$4.5\text{--}9.5 \times 10^{-10}$
Non-dsungaripteroid pterosaurs	$1.8\text{--}6.1 \times 10^{-10}$
Dsungaripteroid pterosaurs	$9.0\text{--}9.6 \times 10^{-10}$

I_p helps to define the torque of a structure.

$$T = \tau \times R / I_p \quad (7)$$

where T = torque and τ = ultimate shear stress.

Based on the values of I_p above and assuming a similar τ , the NDBC would possess much lower torsional strength than other long bone constructions and the DBC. Based on the values and results from (5), (5a), and (6), I_p for DBC is 9.2×10^{-10} , for NDBC 29.42×10^{-10} . Assuming an identical τ , the torque in NDBC is about 2.3 times higher than in DBC.

As described above, by keeping the torque constant, R increases, t decreases and the total mass is reduced.

Failure by compression or buckling

Bone will fail by compression, if

$$F = s \times A \quad (8)$$

where F = force, s = compressive strength and A = cross-sectional area.

For a hollow circular cross-section of constant wall thickness:

$$A = \pi(R^2 - (R - t)^2) \quad (9)$$

It will fail by Euler buckling, if

$$F = \pi^2 EI_x / L^2 \quad (10)$$

where E = Young's modulus and L = length of the cylinder.

The cross-sectional area to prevent local buckling is

$$\propto (R/t)^{1/3} \quad (11)$$

If a bone is loaded in compression, it will theoretically fail by Euler buckling, when (8) > (10). In real bones, however, local buckling is more likely to occur than Euler buckling. The actual strength in bone is always less than the lower of the two theoretical strengths (Currey 2002). For more infor-

mation of failing of bones due to compressional forces see Currey (1984, 2002).

Given the above values, the DBC will fail by compression at a force about three times higher than in NDBC if s is constant. However, it will fail by Euler buckling at forces three times lower than in NDBC if L is constant. The more slender the construction, the more likely Euler buckling becomes. On the other hand, NDBC is susceptible to local buckling because of their thin walls. If some unknown compensation devices e.g., like the influence of soft-tissue or hydraulic stiffening are neglected this can only be compensated for by increasing the mass of the bone (e.g., by introducing trabecular struts), which is counter to the tendency to reduce mass in flying vertebrates.