POTENTIAL FOR INTRACRANIAL MOVEMENTS IN PTEROSAURS

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ABSTRACT

Based on comparative anatomical, morphological and phylogenetic considerations the potential of pterosaurs for cranial kinesis is assessed. Our investigation shows that whereas skeletally mature derived pterodactyloids have completely fused, rigid, doubtlessly akinetic skull, the skulls of more basal pterosaurs and skeletally immature derived pterodactyloids possess key morphological correlatesfeatures in the morphology of their otic and basal joints that are suggestive of cranial kinesis, namely streptostyly. In addition there seems to be a continuous transition in the ossification degree of the skull being low in most non-pterodactyloids, intermediate in *Rhamphorhynchus* and Archaeopterodactyloidea, and high in derived pterodactyloids. Incomplete fusion state could also indicate loose connection between skull elements. On the other handAt the same time, the fact that other anatomical requirements such as permissive kinematic linkages, which are also prerequisites of all types of cranial kinesis, are absent refers to an akinetic skull. Thus, the presence of the morphological attributes indicative of intracranial movements in some pterosaurs can either be of mechanical and ontogenetic importance or, alternatively, considered as the remnant of a real, kinetic skull of the predecessor of pterosaurs, or both.

Key words: cranial kinesis, pterosaur, streptostyly

Formázott: Betűtípus: Dőlt

Formázott: Balra zárt

INTRODUCTION

Kinesis and pterosaurs — The occurrence of cranial kinesis among a variety of tetrapods have long been recognized (see Frazzetta, 1962 for references), but the conceptual definition was first provided by Versluys (1910, 1912) who defined a kinetic skull as allowing any intracranial movements between the elements excluded that of the lower jaw. Cranial kinesis as a phenomenon, being present in the earliest tetrapods (movable palatoquadrates and palatal and facial elements; Iordansky, 1989) and in some extant teleosts and amphibians (Rieppel, 1978; Summers and Wake, 2005), is generally considered a plesiomorphic character (Iordansky, 1990) and is thought to be most prominent within archosaurs and lepidosaurs (Herrel et al. 1999). However, clear evidence of true cranial kinesis, which should be distinguished from slight movements occurring at many patent sutures and allowing dissipation of mechanical stresses, exists unambiguously only in some squamates and birds among amniotes (Holliday and Witmer, 2008). Nevertheless, some forms of cranial kinesis have been and probably will be suggested for numerous extinct vertebrates, including mainly dinosaurs. In contrast to dinosaurs, the notion of intracranial movements in another archosauromorph group, the pterosaurs is not so common. Except for the work of two authors, Arthaber (1919) and Wild (1978, 1984), who regarded the Early Jurassic *Dorygnathus banthensis* and the Upper Triassic *Eudimorphodon ranzii*, respectively, as having streptostylic quadrate, and Bennett (1996a~~b~~) who used the term "metakinetic skull" as a streptostylic character suggestive of archosauromorph nature of pterosaurs in his phylogenetic analysis, thus accepting Wild's (1978, 1984) concept for *Eudimorphodon,* this issue has largely been ignored. Hence, streptostyly, which refers to the anteroposterior rotation of the quadrate about the otic joint (for further information see suppl.), was the only form of kinesis ever suggested for pterosaurs. Most pterosaurologists have regarded the pterosaurian skull as universally akinetic (e.g. Wellnhofer, 1978; Buffetaut et al. 2002; Fastnacht, 2005). In the light of the dominance of more derived pterosaurs with firmly fused skull bones in the fossil record, this attitude is easy to understand. On the other hand, based on the apparent close affinities of pterosaurs to dinosaurs (Hone and Benton, 2008, and see Fig. 1 for the position of Pterosauria in a broader phylogenetic context), for which cranial kinesis has been proposed on several occasions (e.g. Colbert and Russell, 1969; Galton, 1974; Norman, 1984; Norman and Weishampel, 1985; Chiappe et al. 1998; Mazzetta et al. 1998, see suppl.), and on certain morphological attributes of some pterosaurian skulls it seems reasonable to pay more attention to the potential of intracranial movements in pterosaurs. For the acquirement of the

necessary theoretical background a supplementary epitome is provided which contains detailed information on basic concepts such as the different forms, morphological correlates, functional significance, occurrence, origin, and evolution of cranial kinesis in other diapsid reptiles. In this supplement the extremely kinetic skull of Serpentes is not regarded.

Osteological aspects of kinesis in extant and extinct taxa — To reveal features that are suggestive of cranial kinesis sSeveral methods have been in use mainly in extant taxa (Frazzetta, 1962, 1983; Smith and Hylander, 1985; Patchell and Shine, 1986; Condon, 1987; Herring and Teng, 2000; Metzger, 2002; see suppl.). Among the most important features is the presence of morphological correlates which include the co-operating muscle, connective and skeletal tissues assuring the proper functioning of the involved joint systems and –which can be assigned to certain types of kinesis (Bahl, 1937; Bühler, 1981; Rieppel and Gronowski, 1981; Zusi, 1984; Rieppel, 1993; Arnold, 1998; Metzger, 2002; see suppl.). Nevertheless it must be remembered that the absence of Tthese morphological correlates can allow the exclusion of cranial kinesis but the presence of them can only indicate the potential for movement and cannot definitively prove its presence *in vivo*, thus they must be viewed with a measure of caution (Throckmorton, 1976; Herrel and De Vree, 1999; Metzger, 2002; Holliday and Witmer, 2008). When it comes to extinct vertebrates, significant amount of information is lost due to the incompleteness or lack of preservation of soft tissues that must have had important role in intracranial movements. The only available data in most cases are the osteological features which, however, are not always reliable indicators of cranial kinesis, as already mentioned above (Throckmorton, 1976; Herrel and De Vree, 1999; Metzger, 2002; Holliday and Witmer, 2008). Holliday and Witmer (2008) have defined four criteria or morphological correlates that are indispensible concerning inferences of powered cranial kinesis in fossil taxa. The first two criteria regard the detectable presence of mobile joints in the otic (quadrato-squamosal) and basal (basipterygo-pterygoid) regions of the skull (Holliday and Witmer, 2008). They stated that the mobile joint type in these regions must be synovial. "Synovial joint", the presence of which is often referred to as one of the most important criteria in kinetic bony connections, implies a non-interdigitate, finished, smooth joint with synovial capsule (Holliday and Witmer, 2008). The osteological correlates of synovial joints are 1) the presence of convex and complementary concave joining surfaces of the participating elements; 2) the smooth articular surface indicative of hyaline cartilage covering; 3) rough, parallel striated zone and occasionally large pits distal to the smooth surface revealing the presence of the joint capsule and ligament attachments, respectively (Holliday and Witmer, 2008). However, skull elements which are to form a mobile joint (mobility at

least to the extent over which it can be referred to as kinetic joint), can also be connected in different ways, for instance via ligament (e.g. quadrato-pterygoid ligament), or in some special cases movement can occur even in a smooth/slightly interdigitating fibrous joint (e.g. frontal-parietal joint in mesokinesis of geckoes, see suppl.). Furthermore flexibility can be ensured via inbuilt flexion zones formed by thin bony lamellae (e.g. craniofacial hinge in prokinesis of birds, see suppl.). If one of these features is present, similarly to synovial joints, it can assure mobility in the critical otic and basal regions of the skull. The third criterion Additional morphological correlates necessary for inferences of powered cranial kinesis which hasve been cited by Holliday and Witmer (2008) as another morphological correlate of cranial kinesis are is the state of development of the protractor muscles in the skull and the permissive kinematic linkages. They considered the presence of well-developed preotic and levator pendants as osteological indicators of protractor muscles (e.g. m. protractor pterygoideus) which could have operated powered intracranial movements (Holliday and Witmer, 2008). The presence, reconstructed size and attachment areas of most muscles in fossil groups are, however, obscure at best, and the functional significance of the protractor muscle group in extant taxa is sometimes also inconclusive (Gussekloo and Bout, 2005). The fourth criterion is referred to as Ppermissive kinematic linkage which includes those taxon-specific features that permit observable intracranial movements in extant taxa possessing true kinetic skull. These are in general related to elimination or mobility-modification of the surrounding bony elements surrounding the movement centers that would otherwise hinder the referred intracranial movements. Furthermore Holliday and Witmer (2008) defined three categories of inferred kinetic state, of which, obviously, only the first two criteria can be applied to extinct forms:

1. *partially kinetically competent*: the skull possesses key synovial joints and protractor muscles, but lacks bony gaps permitting movement
2. *fully kinetically competent*: the skull possesses key synovial joints and protractor muscles as well as permissive bony linkages, but lacking demonstrable movement *in vivo*
3. *kinetic*: the skull possesses key synovial joints, protractor muscles and permissive bony linkages as well as demonstrable movement *in vivo*

Thus, extinct taxa, such as dinosaurs or pterosaurs may at most be fully kinetically competent. In extant diapsids true cranial kinesis only occurs along with the reduction of certain cranial elements (lower temporal bar in lepidosaurs but also the postorbital bar in gekkotans and varanids; the supratemporal, postorbital and lacrimal bar in birds, see suppl.), so it seems

parsimonious to conclude (although not laid down) that some form of reduction of bones might also be necessary to acquire a kinetic diapsid skull.

Skulls of pterosaurs in general — In order to discuss the issue of cranial kinesis in pterosaurs, a brief general description of pterosaurian skulls is inevitable. The skull of pterosaurs can generally be characterized as being lightly built (fenestrated) and elongated, and they always have complete lower temporal arch formed by mainly the jugal and partially the quadratojugal. ~~The basic "bauplan" of the skull of the two morphotypes is illustrated in Fig. 4.~~ There are two distinct morphological types of pterosaurs, the more basal non-pterodactyloid (generally referred to as "rhamphorhynchoid") and the more derived pterodactyloid constructions (not considering the "mixture"-like new find, *Darwinopterus* [Lü et al. 2009]) which have significant differences in their body as well as skull architecture (Fig. 24). Whereas ~~the "rhamphorhynchoid" constructions~~non-pterodactyloids (Fig. 24A) have an antorbital fenestra (2) and a naris (1) separated by a bony bar consisting of the conjunction of the maxillary process of the nasal and the nasal process of the maxilla, pterodactyloids (Fig. 24B) have usually more elongate rostrum with a confluent and very large nasoantorbital fenestra (1+2). In addition the confluence of certain palatal fenestrae (8+9) is also a characteristic of pterodactyloids (Ősi et al. 2010). The basic "bauplan" of the skull of the two morphotypes is illustrated in Fig. 2. Some pterodactyloids are edentulous, while all hitherto known non-pterodactyloid pterosaurs have numerous teeth and sometimes elaborate dentition. Although the genus *Rhamphorhynchus* has obviously given the name of the described morphotype (and earlier the subordo, too), the pronounced anterior inclination of the quadrate ~~two morphological attributes of its skull~~ found in this genus remarkably differs from ~~those~~ the condition demonstrated ~~of~~ by more basal non-pterodactyloids with nearly vertical quadrate (Ősi, in press), and more resembles the derived state ~~of~~found in pterodactyloids. ~~These are the high ossification degree of the skull (in contrast to the incomplete fusion state of more basal non-pterodactyloids, see below), and the pronounced anterior inclination of the quadrate (in contrast to the nearly vertical position of the quadrate in more basal non-pterodactyloids, Ősi, in prep)~~. Thus it is not surprising that most cladistic analyses, although differing in several points, generally agree on the derived nature of this genus. Note that the term "rhamphorhynchoid" is used here only in its morphotype-sense and does not imply real phylogenetic category, whereas pterodactyloids form a valid, monophyletic clade, thus can be applied both in phylogenetic and morphotype context. Interrelationships of pterosaur genera are shown in figure 3~~5~~.

In the following discussion pterosaurian skulls are investigated in the matter of morphological correlates of potential intracranial movements following mainly the evaluation strategy applied by Holliday and Witmer (2008) for dinosaurs and considered in the context of what we recently know about the phenomenon of intracranial movementscranial kinesis. Accordingly they can be assigned to the most parsimonious state concerning cranial kinesis.

Institutional abbreviations — **AMNH**, American Museum of Natural History, New York, USA; **BMNH**, British Museum of Natural History, London, England; **BNM**, Bündner Naturmuseum, Chur, Switzerland; **BSPG**, Bayerische Staatsammlung für Paläontologie und Geologie, München, Germany; **BXGM**, Benxi Geological Museum, Liaoning Province, China; **CD**, Desirée Collection of Rainer Alexander von Blittersdorff Rio de Janeiro, Brasil; **CM**, Carnegie Museum of Natural History, Pittsburgh, USA; **DNPM MCT**, Museu Ciencias da Terra, Setor de Paleontologia do Departamento Nacional de Producao Mineral, Rio de Janeiro, Brasil; **GMV**, Chinese Geological Museum, Beijing, China; **GPIUB**, Geologisch-Paläontologisches Institut, Universität Bonn; **IGO**, Instituto de Geología y Paleontología, La Habana, Cuba; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **KUVP**, Museum of Natural History, University of Kansas, Kansas, USA; **MCSNB**, Museo Civico di Scienze Naturali di Bergamo, Italy; **MPUM**, Dipartimento of Scienze della Terra dell'Università di Milano, Italy; **MSFN**, Museo Friulano di Storia Naturale, Udine, Italy; **NSM**, National Science Museum, Tokyo, Japan; **PIN**, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; **RGM**, Naturalis (Nationaal Natuurhistorisch Museum), Leiden, The Netherlands; **SMNF**, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany; **SMNK,** Staatliches Museum für Naturkunde, Karlsruhe, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Texas Memorial Museum, University of Texas, USA; **WDC**, Wyoming Dinosaur Center, Wyoming, USA; **YPM**, Peabody Museum of Natural History, Yale University, New haven, USA; **ZMNH**, Zhejiang Museum of Natural History, Zhejiang Province, China.

MATERIALS AND METHODS

In the present study pterosaurs are subjected for the first time to an investigation on their potential or incapacity for cranial kinesis. To infer the likelihood of cranial kinesis in pterosaurs in a phylogenetic context we applied Extant Phylogenetic Bracket (EPB) method (Witmer, 1995), since cranial kinesis involves unpreserved soft tissues to a high degree. Because of different interpretations of the phylogenetic position of pterosaurs, the two most widely accepted approaches have been used in the evaluation; 1) Pterosauria is the sister group to Dinosauria (Hone and Benton, 2008) being bracketed by birds and crocodiles (Fig. 1b); 2) Pterosauria is a basal Archosauromorpha (Bennett, 1996a) being bracketed by lepidosauromorhs and birds or by lepidosauromorhs and crocodiles (Fig. 1c,SM). The evaluation was based on the search for morphological correlates indicative of cranial kinesis ~~mentioned above~~ and was carried out in 26 different pterosaur genera most of which had either almost complete skull material or crucial skull elements of good preservation. Of the 27 investigated genera 13 can be assigned to non-pterodactyloids and 14 to pterodactyloids. Among the 71 ~~The~~ investigated ~~genera~~ specimens 45 were available for personal examination, and these are as follows: *Eudimorphodon ranzii* MCSNB 2888 (m); ~~*Carniadactylus rosenfeldi* MSFN 1797 (holotype);~~ *Carniadactylus* sp. MPUM 6009 (m) ('*Eudimorphodon ranzi' sensu* Wild, 1978~~9~~); *Caviramus filisurensis* ~~('*Raeticodactylus filisurensis' sensu* Stecher, 2008)~~ BNM 14524 (m) ('*Raeticodactylus filisurensis' sensu* Stecher, 2008); *Dimorphodon macronyx* BMNH 41212-13 (m), R 1035 (m); *Dorygnathus banthensis* BSPG 1938 I 49 (m), ~~WDC-CTG-001,~~ SMNS 18969 (m), 50164 (m), 50914 (m), 51827 (m), 55886 (m), ~~50914, 51827~~ WDC-CTG-001 (m); *Rhamphorhynchus muensteri* BSPG ~~G~~ AS VI 34 (m), 1867 II 2 (m), 1889 XI 1 (i), 1927 I 36 (m), 1929 I 69 (m), 1934 I 36 (i), 1938 I 503 (i), ~~1929 I 69,~~ 1955 I 28 (m), 1989 XI 1 (m), ~~1867 II 2,~~ SMNK PAL 6596 (?), SMNS 52338 (m), 56980 (m), ~~52338, ; CM 11434;~~ *Campylognathoides liasicus* SMNS 18879 (m), ~~SMNS~~ 50735 (m), *Campylognathoides zitteli* SMNS 9787 (m), ~~CM 11424~~; *Scaphognathus crassirostris* ~~GPIUB 1304 (holotype),~~ SMNS 59395 (i); *Austriadactylus cristatus* SMNS 56342 (m) (holotype); ~~*Cacibupteryx caribensis* IGO-V 208 (holotype); *Batrachognathus volans* PIN 52-2; *Dendrorhynchoides curvidentatus* GMV2128; *Anurognathus ammoni* (uncatalouged); *Jeholopterus ningchengensis* IVPP V12705;~~ *Pterodactylus antiquus* BSPG AS I 739 (m); *Pterodactylus kochi* (*P. antiquus sensu* Bennett, 1996b) BSPG AS V 29 (m), AS XIX 3 (m), 1878 VI 1 (i), 1883 XVI 1 (m), 1937 I 18 (m), SMNF R 4072 (m); *Pterodactylus micronyx* (*Gnathosaurus subulatus sensu* Bennett, 1996b) BSPG 1971 I 17 (i); *Pterodactylus* sp. BSPG 1936 I 50 (i), SMNF R 4074 (m); *Germanodactylus cristatus* BSPG 1892 IV 1 (m); ~~*Gegepterus changi* IVPP V 11981;~~ *Ctenochasma gracile* BSPG 1920 I 57 (m) (*C. elegans*

sensu Bennett 2007); *Ctenochasma* sp. SMNS 81803 (m); ~~*Anhanguera bittersdorffi* holotype ()~~, *Anhanguera* sp. ~~MCT 1501-R,~~ SMNK uncatalogued (m); ~~*Anhanguera piscator* NSM-PV 19892;~~ *Araripesaurus santanae* BSP~~G~~ 1982. I. 90 (i) (holotype) ('~~*Anhanguera santanae*',~~ ~~*sensu* Wellnhofer, 1985;~~ '*Santanadactylus araripensis*', *sensu* Bennett, 1993; see Fig. 7C); ~~*Istiodactylus latidens* BMNH R 0176;~~ ~~*Istiodactylus sinensis* NGMC 99-07-011;~~ *Tapejara wellnhoferi* SMNK PAL 1137 (i)~~, MCT 1500-R, CD-R-080, AMNH 24440; *Sinopterus dongi* (IVPP) V13363; *Huaxiapterus benxiensis* BXGM V0011; *Pteranodon* sp. KUVP 976, 2212, YPM 1177; *Zhejiangopterus linhaiensis* ZMNH M1330; *Quetzalcoatlus* sp. TMM 41961-1, 41954-62~~. Where there was no possibility for the authors to examine the original specimens in person, the specimens were assessed based on the related literature, casts and published photos of high resolution. These 26 specimens were as follows: *Carniadactylus rosenfeldi* MSFN 1797 (m) (based on Dalla Vecchia, 2009); *Campylognathoides liasicus* CM 11424 (m) (based on Wellnhofer, 1974); *Scaphognathus crassirostris* GPIUB 1304 (m) (based on cast SMNS 80203); *Cacibupteryx caribensis* IGO-V 208 (m) (based on Gasparini et al. 2004); *Batrachognathus volans* PIN 52-2 (m) (Ryabinin, 1948 and Dalla Vecchia, 2002); *Dendrorhynchoides curvidentatus* GMV2128 (m) (based on Dalla Vecchia, 2002); *Anurognathus ammoni* (m) (uncatalouged, based on Bennett, 2007a and high resolution photos ~~provided by Helmut Tischlinger~~); *Rhamphorhynchus muensteri* CM 11434 (m) (based on high resolution photos); *Gegepterus changi* IVPP V 11981 (i) (based on Wang et al. 2007); *Anhanguera bittersdorffi* (m) (based on Campos and Kellner, 1985); *Anhanguera* sp. MCT 1501-R (i) (Kellner, 1996); *Anhanguera piscator* NSM-PV 19892 (i) (Kellner and Tomida, 2000); *Coloborhynchus spielbergi* RGM 41880 (m) (based on Veldmeijer et al. 2006); *Istiodactylus latidens* BMNH R 0176 (?) (based on Hooley, 1913); *Istiodactylus sinensis* NGMC 99-07-011 (m) (based on Andres and Ji, 2006); *Tapejara wellnhoferi* AMNH 24440 (?) (based on Wellnhofer and Kellner, 1991), CD-R-080 (i) (based on Kellner, 1989), MCT 1500-R (i) (based on Kellner, 1996); *Sinopterus dongi* IVPP V13363 (?) (based on Wang and Zhou, 2003); *Huaxiapterus benxiensis* BXGM V0011 (?) (based on Lü et al. 2007); *Pteranodon* sp. KUVP 976, 2212, YPM 1177 (m) (based on Bennett, 2001); *Zhejiangopterus linhaiensis* ZMNH M1330 (m) (based on Cai and Wei, 1994); *Quetzalcoatlus* sp. TMM 41961-1, 41954-62 (m) (based on Kellner and Langston, 1996). In brackets the generally accepted or feasible ontogenetic state of the referred specimens are indicated by 'i': immature (juvenile or subadult), 'm': mature (adult) and '?': uncertain. Where it was possible, all joints of the skull elements which might be relevant or might refer to any type of intracranial movements have been evaluated. Braincase, as expected to be fused in all adult specimens

and putative circumorbital elements are not considered ~~here~~in the joint-morphological investigation. Skeletally immature specimens ~~which certainly would have had completely fused skulls as adults (e.g. tapejarids, ornithocheirids),~~ have also been examined to allow for a possible change in the biomechanical behavior of the skull during ontogeny. ~~there was no possibility for the authors to examine in person, were assessed based on the related literature.~~

The phylogenetic tree of Dalla Vecchia (2009) and that of Andres and Ji (2008) was used in the evaluation of results in a phylogenetic context. However, it must be taken into account that the tree of Dalla Vecchia (2009) differs from the results of most other phylogenetic analyses in the position of anurognathids, which group is considered a derived clade by Dalla Vecchia (2009) and a basal non-pterodactyloid group by Bennett (1996a), Kellner (2003), and Unwin (2003).

RESULTS

EPB evaluation — Using the phylogenetic interpretation of Hone and Benton (2008) EPB gives a Level II inference (Witmer, 1995) of cranial kinesis in pterosaurs, since extant crocodiles possess akinetic skull, whereas birds exhibit a variety of intracranial movements. Applying Bennett's (1996a) approach the two ways of bracketing pterosaurs give different levels of inference. If the bracket is formed by lepidosauromorhs and birds, both of which have kinetic skulls, cranial kinesis in pterosaurs is Level I inference, whereas bracketing pterosaurs between lepidosauromorhs and crocodiles implies again Level II inference.

Morphological correlates — The morphological observations are subdivided into ~~two~~three main categories, namely joint morphology of skull elements, osteological correlates of protractor muscles and ossification degree of the skull as a unit.

Joint morphology. In pterosaurian skulls~~, based on apparent joint morphology which depends also on the stage of skeletal maturity,~~ two characteristic types of joints can occur: ~~overlapping joints, patent or interdigitating~~ fibrous joints and synovial joints ~~can be present~~ (see Fig. 4A-D, and E,F, respectively~~6~~). Thin portion of bony elements, which might be capable of flexion like the bending zones in birds, may also ~~occur~~be present.

Fibrous joint can further be subdivided into two categories based on the articular surface morphology of the connecting elements. The first and ~~The~~ most common fibrous

joint~~joint type~~ is formed by ~~alongside lying (Fig. 6A) or~~ overlapping ~~(Fig. 6B)~~ bony processes (Fig. 4A,B) of the participating, mostly viscerocranial elements (see table 1). This overlapping arrangement, which broadly speaking corresponds to the term scarf joint, mostly implies broad, often oblique contact areas between the bones that were most likely joined by fibrous connective tissue. Table 1 summarizes the connecting skull elements that show this joint morphology and the overlapping-overlain relations of them detected in almost all referred specimens where the preservation and incomplete fusion state allowed proper identification of joint morphology. The occurrence of overlapping fibrous joints between the referred skull elements is consistent and apparently universal among pterosaurs. The nature of connection between some palatal elements is ambiguous, because, apart from the few cases where significant information can be gained from palatally exposed or three dimensional specimens (see Ősi et al. 2010), the palatal construction of most pterosaurian skulls is hypothetical at best. However, based on its long, narrow wing-like processes, the pterygoid is expected to have connected to the ectopterygoid, palatine and maxilla via overlapping fibrous joint. This situation is found between the pterygoid and palatine in *Dorygnathus banthensis* SMNS 50702 and *Pterodactylus* sp. BSPG 1936 I 50. The same could have applied to the palatine-maxilla junction by virtue of the morphology of their contacting areas suggested by Ősi et al. (2010), and indeed seems to be the case in *Dorygnathus banthensis* BSPG 1938 I 49, SMNS 50914, WDC-CTG-001, *Rhamphorhynchus muensteri* SMNK PAL 6596, *Pterodactylus* sp. BSPG 1936 I 50. The ectopterygoid-maxilla junction is also overlapping in *Rhamphorhynchus muensteri* CM 11434. The second fibrous joint category is the patent or interdigitating suture where the articulating parts of the elements are much more robust and distinct, and do not become as thin as the overlapping bony processes (Fig. 4C,D). Patent (also referred to as open) suture (Fig. 4C) refers to an earlier developmental state of the interdigitating suture (Fig. 4D) and can be identified by the straight, non-interdigitating contact areas in skeletally immature specimens (Fig. 4C). These suture morphologies ~~-~~ were present between the counter-elements of the frontal and parietal bones, in the fronto-parietal suture, between the counterparts of the premaxillae, the premaxillae and nasals and between some palatal elements such as the quadrato-pterygoid joint. Patent sutures were present between the counterparts of the frontals in *Dorygnathus banthensis* SMNS 18969, 50164, WDC-CTG-001 (Fig. 4C), *Anurognathus ammoni* (uncatalouged), *Rhamphorhynchus muensteri* BSPG 1938 I 503, *Pterodactylus antiquus* BSPG AS I 739, *Pterodactylus kochi* BSPG 1878 VI 1, *Anhanguera piscator* NSM-PV 19892, between the counterparts of the parietals in *Dorygnathus banthensis* SMNS 50164, WDC-CTG-001 (Fig. 4C),

Campylognathoides liasicus SMNS 18879, *Anurognathus ammoni* (uncatalouged), and in the fronto-parietal joint in *Dorygnathus banthensis* SMNS 18969, WDC-CTG-001 (Fig. 4C), *Anurognathus ammoni* (uncatalouged), *Rhamphorhynchus muensteri* BSPG 1938 I 503, *Campylognathoides zitteli* SMNS 9787, *Campylognathoides liasicus* SMNS 18879, *Scaphognathus crassirostris* GPIUB 1304, *Pterodactylus kochi* BSPG 1878 VI 1. The fronto-parietal suture is often marked by a well developed transversal ridge even in skeletally immature specimens with patent suture (e.g. *Dorygnathus banthensis*, WDC-CTG-001, Fig. 4C). Other specimens where the preservation and incomplete fusion state allowed the recognition of fibrous joints between the referred skull elements showed interdigitating sutures often with very faint suture lines (e.g. fronto-parietal joint in *Rhamphorhynchus muensteri* 1934 I 36, *Campylognathoides liasicus* SMNS 50735, *Scaphognathus crassirostris* SMNS 59395, *Pterodactylus kochi* SMNF R 4074, *Araripesaurus santanae* BSPG 1982 I 90, etc.). Different fusion state on the dorsal and ventral side of the same elements also occurred; e.g in *Dorygnathus banthensis* WDC-CTG-001 on the dorsal surface the fronto-parietal suture is apparently still open (Fig. 4C), whereas on the ventral surface it already shows an interdigitating appearance (Fig. 4D). In the very same specimen the suture between the premaxillae is still visible on the dorsal surface but there is no sign of it on the ventral surface. This might suggest an earlier fusion of the ventral or medial sides of the skull elements. ~~this joint type strongly resembles those of certain dinosaurs for which a so called "sliding" motion has been proposed (see suppl.).~~ Distinguishing overlapping and interdigitating suture morphology has proven to be difficult if the joint is completely fused.

Synovial joints are not frequently found in the skull of pterosaurs; however, there are some taxa and/or ontogenetic stages in which there is a seemingly synovial connection between the quadrate and squamosal (Fig. 4F, 5) and the basipterygoid and pterygoid bones (Fig. 4E, 6A). ~~Examples for~~Among the investigated specimens ~~suggestive of synovial quadrate-squamosal joint are~~ the non-pterodactyloids *Eudimorphodon ranzii* MCSNB 2888, *Austriadactylus cristatus* SMNS 56342, *Carniadactylus rosenfeldi* MSFN 1797, *Carniadactylus* sp. MPUM 6009 ~~('Eudimorphodon ranzi' sensu Wild, 1979)~~, *Caviramus filisurensis* ~~('Raeticodactylus filisurensis' sensu Stecher, 2008)~~, BNM 14524; *Dimorphodon macronyx* BMNH 41212-13 (Fig. 5E); *Dorygnathus banthensis*, WDC-CTG-001 (Fig. 7F), SMNS 18969, ~~SMNS~~ 50164, ~~SMNS~~ 55886, *Campylognathoides liasicus* SMNS 18879, *Campylognathoides zitteli* SMNS 9787 (Fig. 5A, B), ~~SMNS type specimen,~~ *Scaphognathus crassirostris* ~~holotype~~ GPIUB 1304, *Rhamphorhyynchus muensteri* BSPG 1938 I 503, and pterodactyloids *Araripesaurus santanae*, ~~holotype,~~ BSPG 1982. I. 90 ('*Anhanguera*

santanae', sensu Wellnhofer, 1985; *'Santanadactylus araripensis', sensu* Bennett, 1993; see (Fig. 57C), *Anhanguera piscator* NSM-PV 19892, -*Tapejara wellnhoferi* SMNK PAL 1137 (Fig. 57D), AMNH 24440 most likely have had synovial quadrate-squamosal, i.e. otic joint. In these specimens the quadrate has a distinct, well developed *condylus cephalicus* on its ascending process (Fig. 57) which fits in the corresponding cotylus on the ventral side of the squamosal (fig 57B). The surface texture of condylus cephalicus is superbly preserved in *Dorygnathus banthensis* WDC-CTG-001 and undoubtedly indicative of hyaline cartilage covering (Fig. 57F). The nature of the ~~pterygoid-~~basipterygoid-~~quadrate~~pterygoid, i.e. basal joint is ~~miscellaneous. Whereas there is an ~~ostensibly synovial ~~joint between the pterygoid and basipterygoid~~ in *Eudimorphodon ranzii* MCSNB 2888, *Carniadactylus rosenfeldi* MSFN 1797, *Cacibupteryx caribensis* IGO-V 208, *Dorygnathus banthensis* SMNS 18969, 50702, 51827 (Fig. 4E), *Scaphognathus crassirostris* GPIUB 1304, ~~e.g.~~ *Rhamphorhynchus muensteri* BSPG 1989 XI 1, SMNK PAL 6596, CM 11434 (Fig. 6A)~~, the medial process of the quadrate seems to be fused to the pterygoid in the same specimen (Fig. 7A). In addition this arrangement is likely to apply to *Dorygnathus banthensis* SMNS 18969, SMNS 50164, SMNS 51827, *Campylognathoides liasicus* SMNS 50735 (Fig. 7B) and probably to all other non-pterodactyloids, as well~~. In these specimens the basipterygoid processes have distinct, blunt ending which articulate with the corresponding convex facet of the pterygoid (Fig. 6A). The expected rough surface structure distal to the presumably synovial articular surfaces (on the quadrate and basipterygoid) which would be suggestive of the presence of a synovial capsule is hardly discernible in any of the specimens either due to bad preservation or preparational artifacts. Acidic preparation for instance can result in destruction or modification of the original bone surface (e.g. *Dorygnathus banthensis* WDC-CTG-001), whereas transparent coating used in order to protect the fossils from chemical or mechanical effects might disguise important morphological attributes (e.g. *Campylognathoides liasicus* SMNS 18879, *Dorygnathus banthensis* SMNS 18969). Nevertheless, both the basal and otic joints are apparently synovial fulfilling two of the defined morphological criteria of cranial kinesis (Holliday and Witmer 2008)

As for possible "bending zones", almost all viscerocranial elements of the pterosaurian skulls are considerably thin and many of them are even lamella-like~~the nasal, jugal, maxilla, quadrate, palatine and the pterygoid might have thin lamella-like regions in some taxa~~. However, on the medial surface they are always reinforced mechanically by a bracing system of thickened bony spars. For instance in *Dorygnathus banthensis* WDC-CTG-001~~The nasal, is on the whole a thin element which can become even thinner close to the midline where it~~

contacts the posterodorsal process of the premaxilla. The jugal is also thin but on the medial surface of the jugalit is mechanically reinforced strengthened by a tetraradiate bracing system of thickened bony spars that run along the long axis of the four processes. whereas the maxilla is supported medially by a vertical lamina that enhances both the lateral nasal process and the ventral palatal plate (Ősi et al. 2010(based on *Dorygnathus banthensis* WDC-CTG-001).

Protractor muscles. Following the criterion on the presence and development of protractor musculature defined by Holliday and Witmer (2008), the orbitotemporal part of the braincase has been investigated to search for possible attachment areas of musculus levator pterygoidei (mLPt) and musculus protractor pterygoidei (mPPt). These two muscle groups are generally considered as being of crucial importance in active kinesis: mLPt and mPPt are constrictor dorsalis muscles and play role in protraction of the kinetic system (the quadrate in the streptostylic movement), whereas the adductor musculature, m. adductor mandibulae externus and m. pterygoideus retract it (Herrel et al. 1999, Metzger, 2002, Holliday and Witmer 2007, 2008). Although the attachment areas can vary among different extant taxa, by and large mLPt originates on the ventral side of the parietal or on the fused laterosphenoid-prootic complex and inserts on the dorsal surface of the pterygoids; mPPt originates on the basisphenoid and/or prootic and inserts on the dorso-medial side of the pterygoid (Herrel et al. 1999, Metzger, 2002, Holliday and Witmer 2007, 2008).

The morphology of the pterygoid is well known in different pterosaurian taxa (for morphological description see Ősi et al, 2010). The corpus of this tetraradiate element is generally thin compared to its processes in non-pterodactyloids (e.g. *Dorygnathus banthensis* SMNS 50164, *Campylognathoides liasicus* SMNS 50735, *Rhamphorhynchus muensteri* CM 11434), but might be more robust in pterodactyloids (e.g. in *Anhanguera* sp. SMNK uncatalogued) without lateral process (see Ősi et al. 2010). In case protractor muscles were to attach on its surface, they probably would have inserted on the dorsal side of its corpus or near its posterior end which was more robust and connected to the basipterygoid and quadrate.

The orbitotemporal region of the pterosaurian skulls, however, is poorly known since the bones surrounding the endocranial cavity are pneumatic, thus badly crushed in most cases (Bennett, 2001). In this respect there are only handful examinable specimens, which bear reliable information for the adequate reconstruction of this skull region. These mostly three dimensional, well-prepared specimens (*Tapejara wellnhoferi* MCT 1500-R, AMNH 24440, *Anhanguera* sp. MCT 1501-R, *Pteranodon* sp. KUVP 976, 2212, YPM 1177, *Coloborhynchus spielbergi* RGM 401880) were not accessible for the authors of the recent

paper, thus the relevant braincase elements namely the basisphenoid, laterosphenoid and prootic have been evaluated based exclusively on literature data (Kellner, 1996; Wellnhofer and Kellner, 1991, Bennett, 2001; Veldmeijer, 2006). Detailed photos and explanatory figures of this region are found in Kellner 1996, Wellnhofer and Kellner 1991 and Bennett 2001.

The basisphenoid in pterosaurs is mostly elongated and anteroventrally directed in basal non-pterodactyloids as well as in the more derived pterodactyloids (Kellner, 1996). Posteriorly it contacts the basioccipital to which it is firmly fused with very faint or obliterated suture line, whereas anteriorly it forms the basipterygoid processes which articulate with the pterygoids. It borders the cranioquadrate opening medially, and its anterior end forms the posterior margin of the interpterygoid vacuity (Bennett, 2001). In *Tapejara wellnhoferi* MCT 1500-R the dorsal part of the basisphenoid is expanded but ventrally becomes thin. Anteriorly it is connected to the interorbital septum by numerous bony struts but its base is free of these trabeculae (Kellner, 1996); the same condition that was found in *Pteranodon* (Bennett, 2001). In AMNH 24440 the basisphenoid-parasphenoid complex is an expanded, somewhat concave bony plate (Wellnhofer and Kellner, 1991). The basisphenoid of *Pteranodon* is an elongate element extending anteroventrally to contact the pterygoids via short but slightly expanded basipterygoid processes (Bennett, 2001). In *Coloborhynchus spielbergi* RGM 401880 the basisphenoid narrows posteriorly where it contacts the basioccipital.

The sutures of the laterosphenoid with the surrounding elements are mostly unclear, thus there are different interpretations concerning its extent in pterosaurs. Bennett (2001) considered it the element forming the interorbital septum, whereas Kellner (1996) regarded the interorbital septum as a separate element (pseudomesethmoid). Due to these (and probably also interspecific) differences the contacts of the laterosphenoid are not alike in the two interpretations. According to Bennett (2001) in *Pteranodon* it has a Y-shaped cross section dorsally where it contacts the frontals, and ventrally it develops into a strut-meshwork reaching down to the basisphenoid. Anteriorly its dorsal margin extends into the median pneumatic space. It has also lateral processes that extend from the anterodorsal corner and contact the lacrimals. The processes are not fused to the lacrimals but have blunt terminations. Posteriorly the laterosphenoid may overlap the prootic and opisthotic. In contrast Kellner (1996) described the laterosphenoid as being connected anteriorly to the frontal and via a medially directed process to the "pseudomesethmoid", and posteriorly to the parietal and prootic in *Tapejara wellnhoferi* MCT 1500-R. In *Anhanguera* sp. MCT 1501-R the

laterosphenoid is expanded under the ventrolateral surface of the parietal, and contacts the prootic posteroventrally (Kellner, 1996).

The prootic along with the opisthotic and basioccipital form the walls and floor of the endocranial cavity. In *Pteranodon* the prootic and opisthotic together form the otic capsule (Bennett, 2001). The prootic has a complex morphology in *Tapejara wellnhoferi* MCT 1500-R, and lies between the laterosphenoid, parietal and opisthotic in *Anhanguera* sp. MCT 1501-R.

All three braincase elements are pierced by foramina forming the passages of different cranial nerves. Elevated areas at the base of the laterosphenoid-prootic complex identified as the attachment areas for mLPt and mPPt in dinosaurs (Holliday and Witmer, 2008) or muscle scars are not reported in any of the referred specimens, nor there is any other detailed study investigating skull musculature other than those which manipulate the mandible (Fastnacht, 2005; Ősi, in press). Owing to the extensive free surface on the braincase and pterygoids, however, there are still remaining areas for potential protractor muscles to attach.

Degree of skull ossification. ——In the evaluation of fusion state of the skull skeletally mature and immature specimens must be distinguished and ideally only mature specimens should be taken into account. Our investigation implies pointed out that , in addition to the aforementioned differences in the skull architecture, the two morphotypes most non-pterodactyloids and derived pterodactyloids (equivalent to Dsungaripteroidea [Kellner 2003]) seem to be consistently distinct in this regard (Fig. 7) with the derived non-pterodactyloid genus *Rhamphorhynchus* and basal pterodactyloids (equivalent to Archaeopterodactyloidea [Kellner, 2003]) occupying a fusion state somewhere between the two extremities regarding ossification degree of the skull (Fig. 9). Completely ossified skull elements without any trace of suture lines can hardly be found among more basal non-pterodactyloid pterosaurs (Fig. 9B). In fact, mMost cranial elements of those non-pterodactyloid pterosaur specimens that are generally considered adults these pterosaurs are distinct (*Eudimorphodon ranzii* MCSNB 2888, *Campylognathoides liasicus* CM 11424, *Carniadactylus* sp. MPUM 6009, *Caviramus filisurensis* BNM 14524, *Dimorphodon macronyx* BMNH 41212-13, *Dorygnathus banthensis* SMNS 50702, 51827, 55886 [Fig. 7B], *Austriadactylus cristatus* SMNS 56342, *Anurognathus ammoni*, uncatalouged), very often disarticulated or even scattered (*Batrachognathus volans* PIN 52-2, *Dendrorhynchoides curvidentatus* GMV2128, *Dimorphodon macronyx* BMNH R 1035, *Dorygnathus banthensis* SMNS 18969, 50164, 50914, BSPG 1938 I 49, WDC-CTG-001, *Campylognathoides liasicus* SMNS 18879, 50735, *Campylognathoides zitteli* SMNS

9787). ~~even in otherwise complete specimens that are considered adults~~ (~~probably in terms of reaching sexual maturity, e.g. *Dorygnathus banthensis* SMNS 18969, SMNS 50164, SMNS 50914, SMNS 55886 [Fig. 9B] *Eudimorphodon ranzii* MCSNB 2888, *Campylognathoides liasicus* SMNS 50735; SMNS 18875, *Dimorphodon macronyx* BMNH 41212-13.~~ In contrast, those specimens of derived pterodactyloids which are considered adults have completely ossified skulls with very faint or no suture lines (*Anhanguera bittersdorffi* uncatalouged holotype, *Anhanguera* sp. SMNK uncatalogued [Fig 7A], *Pteranodon* sp. KUVP 976, 2212, YPM 1177, *Tapejara wellnhoferi* CD-R-080, *Zhejiangopterus linhaiensis* ZMNH M1330; *Huaxiapterus benxiensis* BXGM V0011 *Quetzalcoatlus* sp. TMM 41961-1, 41954-62,) (Fig. 9A). An intermediate degree of skull ossification seems to be exhibited in almost all specimens of the derived non-pterodactyloid *Rhamphorhynchus muensteri* (BSPG AS VI 34, 1867 II 2, 1927 I 36, 1929 I 69, 1934 I 36, 1955 I 28, 1989 XI 1, CM 11434, SMNK PAL 6596) and in archaeopterodactyloids (*Pterodactylus antiquus* BSPG AS I 739, *Pterodactylus kochi* BSPG AS XIX 3, 1937 I 18, SMNF R 4072, R 4074, *Germanodactylus cristatus* BSPG 1892 IV 1, *Ctenochasma gracile* BSPG 1920 I 57, *Ctenochasma* sp. SMNS 81803).

Figure 8~~10~~ represents the summary of results, where the distribution of different morphological correlates, which might suggest potential for intracranial movements in pterosaurian skulls, is indicated in a phylogenetic context.

DISCUSSION

Among the morphological features of pterosaurian skulls assessed in this study there are some which seem to indicate intracranial movements, and others which apparently do not allow any mobility between the referred elements.

Joint morphology and mobility —The most common joint type, the overlapping ~~(Fig. 6B)~~ joint (Fig. 4A,B) ~~can~~ strongly resembles those found in dinosaurian skulls ~~also be found in dinosaurs~~ and has been considered by several authors to be capable of sliding motion (see suppl.). However, as Holliday and Witmer (2008) pointed out, there is no extant equivalent of such moveable joints; in fact this joint arrangement must have prevented any

kind of motion between the joining elements. Nevertheless, there are synovial joints in which the participating elements do not show a typical convex condyle — concave cotyle morphology but rather both articular ends are straight, well defined and robust structures with smooth surfaces that can slide alongside each other ~~For them to be capable of the proposed sliding movement, the overlapping bones must have formed a real synovial joint~~ (like e.g. in the basipterygoid-pterygoid joint in the palate of birds~~;~~ (Zusi, 1993) or *Varanus*, (pers. obs.). The overlapping joints with elongated, tapering bony processes found in the pterosaurian and dinosaurian skulls, however, ~~which they obviously have not, since they do not~~ exhibit the morphological correlates of neither typical nor sliding synovial joints (see above). ~~-~~The morphology and structural arrangement of the overlapping joints in the pterosaurian skulls are rather indicative of fibrous joint; something similar to the rigid scarf joints found in crocodiles (Ősi et al. 2010). In addition, the proposed sliding motion would have also been hampered by the immobility of adjacent bones. Thus ~~I~~in agreement with Holliday and Witmer (2008) here we reject the variety of intracranial movements via such "sliding" joints supposed for dinosaurs; thus the joints in the pterosaurian skulls in which the participating elements uniformly show this arrangement are regarded as being incapable of any significant movement. Hence, ~~based on specimens in which the respective suture lines could still be distinguished, several~~ all the joints listed in table 1 have been excluded from having potential for kinesis in pterosaurs~~(see table 1)~~.

Patent (Fig. 46C) or ~~slightly~~ interdigitating fibrous joints (Fig. 46D) which are mostly completely fused without any traceable suture line in skeletally mature specimens indicate complete immobility ~~in this skull region~~between the connecting elements. ~~The ridge indicating the frontal-parietal suture, which would be of crucial importance for mesokinetic movements (see suppl.), would have obviously prevented dorsoventral rotation of the frontal along this suture as it happens in a mesokinetic skull.~~ For instance ~~I~~in *Dorygnathus banthensis* SMNS 50164 the parietals are fused to the frontals but the contralateral elements are not, which implies that these two elements fuse earlier during ontogeny than either the contralateral frontals or parietals to each other (in case there was a determinate order of fusion of cranial elements). This refers to the immobile nature of the front~~oal~~-parietal joint already in earlier ontogenetic stage. However, in *Campylognathoides liasicus* SMNS 50735 the frontoparietal suture seems to be still open, whereas the contralateral elements are already fused without suture impression. Thus, either there is interspecific variation in the order of fusion of cranial elements or there is no determinate fusion order whatever.~~, thus precluding the potential of the pterosaurian skull for mesokinesis~~. In any case the transversal ridge

indicating the frontoparietal suture in every ontogenetic stage would have prevented the mesokinetic dorsoventral rotation of the frontal along this suture, thus precluding the potential of the pterosaurian skull for mesokinesis (see suppl.). Based on their phylogenetic position of pterosaurs within Archosauromorpha (Fig. 1B,3C; Hone and Benton, 2008), the absence of mesokinetic movements at the frontoal-parietal joint in pterosaurs is to be expected. Fibrous joints found in other areas of the skull are also rigid and immobile.

The quadrate-squamosal joint with distinct *condylus cephalicus* (Fig. 7) on the quadrate (Fig. 5) that has a surface texture characteristic for hyaline cartilage covering (Fig. 57F) and with corresponding cotyle on the squamosal (Fig. 5B) suggests the presence of a synovial otic joint between the quadrate and squamosal. The articular morphology found between the basipterygoid and pterygoid indicates the presence of synovial joint, too. With respect to function All synovial joints have inherent potential for movement, thus it might seems obvious to presume that with such synovial morphology the quadrate must have been capable of anteroposterior rotation (streptostyly)ie along with the pro- and retraction of the basal unit via synovial basipterygoid-pterygoid joint. However, there are twois a serious problem main uncertainty factors inwith this assertion. This problem is related to other morphological constraints with which all concerned skull elements must be in accordance for the animal to achieve streptostyly. The animal either has to reduce some bony elements lateral and medial to the distal end of the quadrate or its connections to these bones must be significantly mobile (e.g. synovial or ligamentous connection) for it to be capable of anteroposterior rotation. In addition, if the basal joint was to be functional, too (pro- and retraction of the muzzle coupled with quadrate movement), the basal unit as well as the skull roof must have contained flexible regions. No reduction or mobility modification can be observed in the adjacent bones and skull regions in pterosaurs. The bones lateral to the quadrate form typical overlapping joints (quadratojugal overlaps the quadrate and is overlain by the jugal, see table 1), and these bones are connected to all surrounding elements via overlapping joint, thus the position of them can be considered fixed. Hence they form a most probably immobile, rigid lower temporal arch which, along with the fused quadrate-pterygoid joint, would not allow the anteroposterior movement of the quadrate. In addition to that, the squamosal has a ventral process that overlaps the ascending process of the quadrate laterally which further fixes the position of the quadrate. Accordingly streptostyly can almost certainly be ruled out even in taxa such as *Eudimorphodon ranzii*, *Dorygnathus banthensis*, *Tapejara wellnhoferi* (juvenile), etc. where the form and construction of the quadrate-squamosal and basipterygoid-pterygoid regions are indicative of kinesis (contra Wild 1978, Ősi in press). In

spite of their synovial morphology, the basal and otic joints were not to form movable joints, and this quasi-contradiction must be resolved. The term "synovial" is a structural joint category which implies the morphology of the connecting elements but does not necessarily refer to a mobile (diarthrodial) joint (Holliday and Witmer, 2008). First, the morphology of the quadrate-squamosal joint can be explained otherwise, as well. Since lot of cranial elements, including the quadrate, ossify endrochondrally i.e. cartilage is present during the ossification process (Dixon, 1997), this articular surface structure can simply imply that these elements were connected by presence of fibro- or hyaline cartilage thus forming a cartilaginous rather than synovial joint. Cartilaginous joints typically form the growth regions of immature long bones during earlier ontogenetic stages ensuring longitudinal growth or the intervertebral discs (REF). In primary cartilaginous joints or synchondroses the bones are connected by hyaline or fibrocartilage and may ossify with age, whereas in secondary cartilaginous joints or symphyses the articulating bones are covered with hyaline cartilage and have thick pad of fibrocartilage between them. Although the condyle-cotyle morphology is not usually found in cartilaginous joints (REF), initially both of these types could have accounted for the described morphology in the basal and otic joints of pterosaurs,. of the bone as it has already been suggested for the cranial bones of dinosaurs by Holliday and Witmer (2009). Nevertheless, if cartilage was present in these regions only to facilitate bone growth during earlier ontogenetic stages this as it has already been suggested for the cranial bones of dinosaurs (Holliday and Witmer 2008)was the case, traces of the cartilagethis morphology would only be present in skeletally immature specimens., yYet some non-pterodactyloid specimens which show this feature are considered adults, thus skeletally mature (e.g. *Eudimorphodon ranzii* MCSNB 2888, *Scaphognathus crassirostris* GPIUB 1304, *Campylognathoides liasicus* SMNS 18879, *Dorygnathus banthensis* SMNS 50702, etc., see above). Hence, either the ontogenetic age of these specimens has to be re-defined in these cases or the cephalic condyle with cartilaginous covering, which adults also possessed, had a role other than simply providing places of bone growth. This leads us further to the problem of identifying ontogenetic stages in fossils and is discussed below.

The thin lamella-like elements, indeed, might have been relatively flexible and bending could have been structurally possibleindeed. However, considering these elements and their surroundings one by one, it becomes clear that even if the internal construction of the element itself had allowed bending had been structurally possible in the thinner zones (e.g. the nasal does not have stiffening system), the internal construction and the arrangement of adjacent bones would not have allowed any bending movement. For instanceConsidering the

nasal first, if there was any movement allowed along the thin region of the nasal, it would be a laterodorsal rotation of the nasals relative to the dorsal process of the premaxilla. However, this motion must have been impeded by the adjacent but surely fixed bones (maxilla, lacrimal, frontal) to which it was connected via fibrous, immobile joints. Thus the exceptionally thin bone walls, which are so characteristic of the whole skeleton of pterosaurs, must have contributed to the lightness of the skull as well as postcranium rather than ensured structural flexibility.

Protractor muscles and mobility — The reconstruction of muscles in extinct animals is ambiguous at best. Reconstructions inferred from the presence of muscle scars, extensive bony surfaces, tubercles etc. and/or from muscle arrangement found in the closest extant relatives (EPB) can be misleading for more reasons. First, not all muscles leave muscle scars on their attachment areas. Muscle scars are to be expected in those muscles which connect to the bone via collagenous tendon, whereas muscles with flashy attachment on the bone leave no traces of their origination or insertion areas (REF). Even if the muscle most probably have had tendinous contact to the bone (concluded from EPB), the state of preservation, preparational artifact or the relatively hidden position of the bone (e.g. laterosphenoid, prootic) can all prevent the detection of muscle scars. Second, the attachment areas need not be very extensive or distinct in any other way. In fact, free surface area on the bone, be it ever so limited, might provide places of attachment for smaller muscles. Third, inferring from closest living relatives might be inherently dangerous in two ways. In the case of pterosaurs depending on the interpretion of their phylogenetic position (see for different phylogenies in Bennett 1996a, Hone and Benton, 2008), the bracketing taxa in EPB might well be crocodiles, birds or lepidosauromorphs. These clades are very distinct morphologically as well as functionally bearing relatively few common features and sometimes homology-relations in their skeleton and musculature are still not clear (REF). In addition, interspecific differences in the musculoskeletal system might be very high. For instance, regarding the skull of birds, some taxa exhibit passive cranial kinesis without any protractor muscle activity (rhynchokinesis in palaeognathous birds, Gusseklo and Bout, 2005, see suppl.), while others (e.g.toucan) have completely akinetic skulls (for reference see Zusi, 1993). Moreover, in the lepidosaur *Sphenodon* there is even intraspecific variance in the presence of the pro- and retractor muscles of the pterygoids, despite that they have completely akinetic skull (Metzger, 2002). In sum, the probability that pterosaurs possessed the protractor muscle system necessary for streptostyly cannot be estimated; their role in cranial kinesis, however, based on the evaluation of joint morphology, can be excluded.

Degree of ossification and mobility — The apparent incomplete ossification of the skull ~~of~~ in ~~basal~~ most non-pterodactyloid pterosaurs such as *Eudimorphodon*, *Dorygnathus*, *Campylognathoides*, etc. and the intermediate fusion state found in *Rhamphorhynchus* and archaeopterodactyloids like *Pterodactylus* or *Ctenochasma*, seem to occur irrespective of ontogenetic age and suggest~~s~~ loose connection between the~~ir~~ cranial elements. However, concerning fossil vertebrates, the terms *adult*, *juvenile*, *skeletally mature* or *immature* often lead to confusion either because there is no consensus in their use or we do not know enough of the ontogeny of the extinct organism to define exactly what is meant by which~~are not completely consequent~~ (see Bennett, 1995, 1996~~b~~a for a review). The small number of known specimens in most taxa further prevents the establishment of a more systematic terminology. ~~makes things even more ambiguous~~. Although it seems to be true that most known non-pterodactyloid pterosaurs and archeopterodactyloids have incompletely ossified skull with at least distinct sutures, it still might be possible that all of these hitherto known specimens are skeletally immature. The continuous debate on whether the establishment of a new species is reasonable or the specimen only represents a different ontogenetic status of an already described species also illustrates this quandary. (see Bennett, 1996, 2007b, Dalla Vecchia, 2002, 2009). Those cases where the rest of the skeleton seems to be mature and only the skull indicates immaturity (e.g. *Dorygnathus banthensis* WDC-CTG-001, with fused syncarpals, but isolated skull bones), ~~This would suggest~~ raise an issue on whether there is a~~a~~ determined sequence of ossification process among different skeletal elements with the skull ~~bones fusing~~ ossifying ~~to each other~~ last. On the other hand the differences in the ossification degree of the skull and sometimes of other skeletal elements (e.g. carpals, scapulocoracoids) as well could refer to different ontogenetic strategies along the diverse evolutionary lineages of pterosaurs~~in the two morphotypes~~: whereas non-pterodactyloid and archaeopterodactyloid pterosaurs could have grown a lifetime long with an accelerated development ~~before~~ until reaching sexual maturity and ~~then,~~ after that ~~reaching adulthood,~~ a much more decelerated but still continuous growth (like modern crocodiles), derived pterodactyloids could have had determinate growth strategy. In this case continuous growth would suggest the presence of open sutures a lifetime long, whereas derived pterodactyloids with determinate growth would have completely fused bones after reaching final body size. Bennett (1993) came to a very similar conclusion by suggesting indeterminate growth strategy for non-pterodactyloid and more basal pterodactyloid pterosaurs after discussing characters that refer to different ontogenetic stages in pterosaurs. However, this interpretation contradicts to the results of the histological investigations on pterosaur bones which suggest that pterosaurs, even the more basal ones,

had relatively fast and deterministic growth (de Ricqlès et al. 2000; Padian et al. 2004; Chinsamy et al. 2009; Steel, 2009). Another idea which might give an explanation for the differences includes biomechanical considerations. Stress-strain distribution and forces acting on a skull during feeding can be quite different when comparing a rigid, united skull (derived pterodactyloids) with an incompletely fused and thus structurally more elastic skull (basal pterosaurs). In his biomechanical investigation Fastnacht (2005) demonstrated that "butt-ended sutures resist compression but will fail in tension; scarf joints with oblique articulating surfaces accommodate tensile and compressive forces in all directions with usually only minor movement (Rafferty & Herring, 1999); interdigitating contacts resist compressive and tensile forces and prevent slipping between adjacent bones". (pp!!!) He furthermore stated that whereas most derived pterosaurs have fused skull with no sutural impression, which he referred to as 'single unit skull', in Upper Triassic and Lower Jurassic pterosaurs the skull consists of a cluster of bones that disarticulate post mortem, thus it is a composite rather than a single unit skull. He also suggested that in brevirostrine taxa (e.g. anurognathids) the incomplete fusion of the skull elements may be a direct mechanical consequence of the high strains present in relatively short skulls (Fastnacht, 2005, pp. 185). In this context the issue of feeding strategy is of crucial importance: there could have been a principal difference in feeding behavior between basal and derived pterosaurs which was responsible for this alteration in ossification degree. Nevertheless, this field also abounds in uncertainties; hence it is not the most useful aspect to settle this question. Still, due to the aforementioned morphological features, the incomplete skull ossification of the considered specimens, regardless of whether they were adults or juveniles, skeletally mature or immature, could not have resulted in cranial kinesis. Thus, if there indeed was a significant difference in the ossification degree and hereby in the mechanical behavior of the skull between these groups two morphotypes, this difference certainly did not lie in the potential of the more basal pterosaurs for cranial kinesis. On the other hand the incomplete fusion state of the skull could have been an ancestral heritage: although we know almost nothing about the origin of pterosaurs, it is almost certain that the ancestor must be envisioned as a small, arboreal, lizard-like diapsid reptile (Bennett, 1997) which was most probably insectivorous (Ősi, in press.). Since insectivory has been related to the evolution of cranial kinesis in amniotes (Bout and Zweers, 2001), it is conceivable that the predecessors of pterosaurs indeed had kinetic skulls, thus the unfused nature and other morphological features indicative of intracranial movements in the skull of basal pterosaurs can be considered as a residuum of a real kinetic skull which is already out of order. In this case we might face the phenomenon

called transfer exaptation which refers to the loss of original function of a certain feature (Arnold, 1994).

CONCLUSIONS

Our investigation shows that, based on morphological, comparative anatomical, phylogenetic and ontogenetic considerations, the skull of most "adult" ~~basal~~ non-pterodactyloid pterosaurs (e.g. *Eudimorphodon ranzii*, *Dorygnathus banthensis,* etc.) and "juvenile" pterodactyloid specimens (e.g. *Tapejara wellnhoferi* SMNK PAL 1137) is *partially kinetically competent* at most. Accordingly their skull possessed key synovial joints and probably the necessary protractor muscles, as well, but lacked bony gaps or additional mobile regions which would have permitted intracranial movement. Thus, despite appearances, the skull of ~~basal~~ non-pterordactyloid pterosaurs as well as that of the skeletally immature individuals of derived pterodactyloids was virtually akinetic.

The presence of synovial joints and unfused sutures in the cranium of ~~basal~~ non-pterodactyloid pterosaurs and archaeopterodactyloids has most probably phylogenetic roots. Among diapsids there is a strong evidence of the plesiomorph nature of streptostyly, which secondarily became restricted to an immobile quadrate-squamosal joint in most archosaur clades. Currently only birds have demonstrably streptostylic quadrate among archosaurs but this is almost certainly a secondarily regained trait rather than a retained plesiomorphic character. The vestige of the streptostylic arrangement in other archosaurs, including non-pterodactyloid and skeletally immature pterodactyloid pterosaurs, might well have represented cartilaginous regions that permitted and facilitated cranial growth during ontogeny and/or ensured that the skull could bear relatively high stress and strain loads. Thus the morphological features indicative of cranial kinesis in some pterosaurian taxa might well be related to the phenomenon called transfer exaptation. Equally possible is the assumption that these characters represent a functionless residuum of a real kinetic skull possessed by the hitherto unknown diapsid ancestor of pterosaurs.

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TABLES

Overlying element	pmx	j	n	l	po	qj	pl	sq
Overlain element	n, f	mx, po, qj	l, mx	j	f, sq	q	mx	p

Table 1. Skull elements forming overlapping joints with one another in the pterosaurian skull. Abbreviations: **f**, frontal; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **p**, parietal; **pmx**, premaxilla; **po**, postorbital; **pt**,pterygoid; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal.

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FIGURE LEGENDS

Figure 1. Three levels (A, B, C) of diapsid phylogeny gradually focusing on the archosaurian clades (C). **A**, Interrelation of the major diapsid clades (after Lee, 2001); **B**, division of archosauriformes (after Sereno, 1991); **C**, two possible outcomes for the phylogenetic relationships among archosaurian clades focusing on the conspicuously different position of Pterosauria in the two cases (**WST**, Weighted Supertree; **SM**, Supermatrix Tree). Groups of special significance for the EPB evaluation of the present study are boldfaced.

Figure 2. Line drawing of the two skull-morphotypes based on the genera **A**, *Rhamphorhynchus* and **B**, *Gnathosaurus* representing the rhamphorhynchoid and pterodactyloid morphotype, respectively. Note the length of the rostrum, the state of the naris (**1**) and antorbital fenestra (**2**), and the state of two palatal fenestrae (**8**, **9**) as main differences between the two basic „bauplans". Abbreviations: **bpt**, basipterygoid; **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **p**, parietal; **pl**, palatine; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal; **1**, naris; **2**, antorbital fenestra; **3**, orbit; **4**, supratemporal fenestra; **5**, lateral temporal fenestra; **6**, choana; **7**, suborbital fenestra; **8**, pterygo-ectopterygoid fenestra; **9**, subtemporal fenestra; **10**, interpterygoid vacuity; **11**, cranioquadrate opening.

Figure 3. Pterosaur phylogeny based on the latest cladistical analyses. **A**, Interrelationships of non-pterodactyloid pterosaur species with indication of their relation to the more derived Pterodactyloidea (modified from Dalla Vecchia, 2009); **B**, interrelationships of the monophyletic Pterodactyloidea on family and generic level (modified from Andres and Ji, 2008).

Figure 4. Forms of joints occurring in the pterosaurian skull represented here by *Dorygnathus banthensis* SMNS 55886 (**A**, **B**), WDC-CTG-001 (**C**, **D**, **F**) and SMNS 51827 (**E**) specimens without considering complete fusion of elements. **A**, overlapping fibrous joint demonstrated by the postorbital-jugal connection in which the ascending processes of jugal overlaps the

descending process of postorbital; **B**, overlapping fibrous joint demonstrated by the lacrimal-jugal, jugal-maxilla and nasal-maxilla connections in which the processes of jugal, maxilla and nasal overlap the lacrimal, jugal and maxilla, respectively; **C**, patent suture preceding interdigitating fusion state demonstrated by the dorsal aspect of contralateral frontals, parietals and the frontoparietal connections (dorsal view); **D**, interdigitating suture preceding fibrous fusion of elements demonstrated by the ventral aspect of the frontal-parietal connections; **E** and **F**, apparently synovial joints demonstrated by the distinct articular surfaces of the basipterygoid processes (**E**) and the cephalic and mandibular condyles of the quadrate (**F**). Black arrows point to the articulating areas. Abbreviations: **bpt**, basipterygoid; **bs**, basisphenoid; **cc**, cephalic condyle; **f**, frontal; **fli**, impression of the frontal lobes of the brain; **ij**, unfused fibrous joint with interdigitating suture; **j**, jugal; **l**, lacrimal; **mc**, mandibular condyles; **mx**, maxilla; **n**, nasal; **oj**, overlapping fibrous joint; **p**, parietal; **pj**, unfused fibrous joint with patent suture; **pmx**, premaxilla; **po**, postorbital; **pt**,pterygoid; **q**, quadrate; **sj**, synovial joint. Scale bar: 1 cm.

Figure 5. Examples for quadrates having distinct cephalic condyle (**cc**) at the proximal end of the ascending shaft which is indicative of synovial quadrate-squamosal (otic) joint. **A**, *Campylognathoides zitteli* SMNS 9787; **B,** *Campylognathoides liassicus* SMNS 18879; **C**, *Araripesaurus santanae* BSP 1982. I. 90; **D**, *Tapejara wellnhoferi* SMNK PAL 1137; **E,** *Dimorphodon macronyx* BMNH 41212-13; **F**, close up of the proximal view of cephalic condyle in *Dorygnathus banthensis* WDC-CTG-001 where the fine texture of the surface indicative of hyaline cartilage covering becomes apparent. Scale bare of A, B, C, D: 1 cm; E: 0,5 cm.

Figure 6. Joint types of three articulating palatal bones, basipterygoid (**bpt**), pterygoid (**pt**) and quadrate (**q**). **A**, The superbly preserved *Rhamphorhynchus muensteri* CM 11434 ("Carnegie specimen") with in situ arrangement of these elements clearly shows that whereas the quadrate is fused to the pterygoid, the basipterygoid process forms an apparently synovial joint with the pterygoid (basal joint). **B**, Fused quadrate-pterygoid unit lying isolated on the slab of *Campylognathoides liasicus* SMNS 50735. Black and white arrows indicate the approximate or clear joining areas of the bones. Scale bar: 1 cm.

Figure 7. Comparison of the ossification degree of the skull of **A**, a derived pterodactyloid, *Anhanguera* sp. (SMNK uncatalogued) and **B**, a non-pterodactyloid, *Dorygnathus banthensis* (SMNS 55886). Note that whereas there are no visible suture lines between the skull elements of *Anhanguera* (**A**), the different skull elements of *Dorygnathus* (**B**) can easily be recognized due to the distinct suture lines (indicated by white arrows) that trace out the individual bone shapes.

Figure 8. The occurrence of different morphological correlates of potential cranial kinesis (see **A**, for symbol legend) in **B**, non-pterodactyloid pterosaurs represented at genus level and **C**, pterodactyloid pterosaurs represented at genus and family level demonstrated in a phylogenetic context (modified from **B**, Dalla Vecchia, 2009, and **C**, Andres and Ji, 2008). Those taxa which have been examined by the authors personally are marked by asterisks, while data for the remainder have been taken from related literature. Taxa without symbols have not been investigated here. Note that all non-pterodactyloids of well known skull morphology except for *Rhamphorhynchus* have a quadrate with distinct cephalic condyle and possess an incompletely fused skull as adult. Low ossification degree of the skull is also characteristic of basal pterodactyloids (Archaepterodactyloidea).