

A new dsungaripteroid pterosaur from the Lower Cretaceous of the southern Junggar Basin, north-west China

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Abstract

A new dsungaripteroid pterosaur, *Lonchognathosaurus acutirostris* gen. et sp. nov., is erected for the anterior part of a skull from the Lower Cretaceous Lianmuxin Formation (Upper Tugulu Group) of Liuhonggou, near Urumqi, in the southern Junggar Basin (Xinjiang Uygur Autonomous Region, People's Republic of China). It is distinguished from other dsungaripteroids by its straight and delicate premaxillary rostrum, the presence of only eight teeth in each maxilla, of which the posteriormost is the smallest, and a tooth row that ends anterior to the fenestra nasopraeorbitalis. A phylogenetic analysis of the Dsungaripteroidea based on cranial characters indicates that *Lonchognathosaurus* is the sister taxon of *Dsungaripterus*. It is demonstrated that the Germanodactylidae is most probably a paraphyletic assemblage of basal, Jurassic dsungaripteroids. The genus *Germanodactylus* is probably paraphyletic as well.

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1. Introduction

In 2001, members of the Sino-German Cooperation Project on the Mesozoic Stratigraphy and Palaeontology of the Junggar Basin (SGP) discovered a highly fossiliferous locality in the lower part of the Lianmuxin Formation (Upper Tugulu Group, ?Aptian–Albian) of the Liuhonggou Valley, south-west of Urumqi, the capital of the Xinjiang Uygur Autonomous Region

in north-west China. Besides numerous bivalves, osteichthyans and turtles, well-preserved remains of pterosaurs were discovered. Unfortunately, nearly all the bones found, including all the pterosaur material, were completely disarticulated.

The pterosaur finds are significant because, with the exception of an isolated tibia and fibula originally described as a possible bird by Young (1964, see also Buffetaut, 1996), they are the first from the southern Junggar Basin. All other dsungaripteroid fossils from the Junggar Basin have been found in the upper part of the Tugulu Group in the vicinity of Wuerho (Urho), north of Karamay in the north-west of the basin

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(Young, 1964, 1973). The purpose of this paper is to describe the most important and diagnostic pterosaur find from Liuhonggou, an incomplete skull of a new genus and species of dsungaripteroid.

Institutional abbreviations. SGP, Sino-German Project collection, currently housed at the Institut und Museum für Geologie und Paläontologie, University of Tübingen, Germany. The collection remains the property of the People's Republic of China and will be transferred to a public Chinese collection after the scientific studies are finished. The final repository will be announced in an internationally accessible journal. BSPHG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany. MCZ, Museum of Comparative Zoology, Cambridge/Mass., USA.

2. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Dsungaripteroidea Young, 1964

Diagnosis. Pterodactyloid pterosaurs that share the following derived features: Tips of the jaws toothless (except for *Germanodactylus ramphastinus*); maxillary teeth nearly as broad as they are tall; largest teeth located towards the end of the tooth row; distal ends of the paroccipital process strongly expanded, forming a distinct bulge in the lateral profile of the occiput (see Unwin and Lü, 1997). To these can be added: at least a slight ring-like bony wall surrounds the alveoli (convergent in the Lonchodectidae); at least a low sagittal crest is present (convergent in the Ctenochasmatoidea); thick-walled limb bones; strongly bowed femora; wing phalanx I with strong anterior bowing. The Dsungaripteroidea (sensu Unwin and Lü, 1997 and Unwin, 2003) is here defined as the last common ancestor of *Germanodactylus cristatus*, *G. ramphastinus*, *Dsungaripterus weii* and all of its descendants.

Dsungaripteridae Young, 1964

Genus *Lonchognathosaurus* gen. nov.

Type species. *Lonchognathosaurus acutirostris* gen. et sp. nov.

Derivation of name. Greek, λόνχη, lance, γνάθος, jaw, σάυρος lizard.

Diagnosis. Large dsungaripterid, estimated skull length (assuming skull proportions similar to *Dsungaripterus* and “*Phobetor*”) probably around 400 mm. Alveolar margin of upper jaw completely straight. Premaxillary rostrum very delicate and slender, ending in a needle-like tip. Well-developed, striated and grooved sagittal crest with concave anterior margin. Only eight maxillary teeth. Tip of upper jaw edentulous. Tooth row starts far anterior to sagittal crest and ends anterior to nasopreorbital opening. Teeth widely spaced (distance between individual tooth positions always more than distomesial length of tooth). Alveoli not bulbously expanded but surrounded by a low ring of bone.

Lonchognathosaurus acutirostris gen. et sp. nov.

Derivation of name. Latin *acus*, needle, *rostrum*, snout.

Holotype. SGP 2001/19, anterior part of a skull (Figs. 1, 2).

Type locality and stratum. Liuhonggou, south-west of Urumqi, Xinjiang Uygur Autonomous Region, People's Republic of China, lower part of Lianmuxin Formation (?Aptian–Albian), Upper Tugulu Group.

Description. The specimen consists of the anterior portion of a skull, extending slightly posterior to the anterior margin of the nasopreorbital opening. It has suffered somewhat from lateral compression.

The premaxilla is toothless. It forms a very slender, pointed and straight, laterally compressed rostrum, which is less than 1 mm in height at its anterior tip,



20 mm

Fig. 1. *Lonchognathosaurus acutirostris* gen. et sp. nov., left lateral view of holotype (SGP 2001/19) from the Lianmuxin Formation (Upper Tugulu Group) of Liuhonggou, Xinjiang, China.

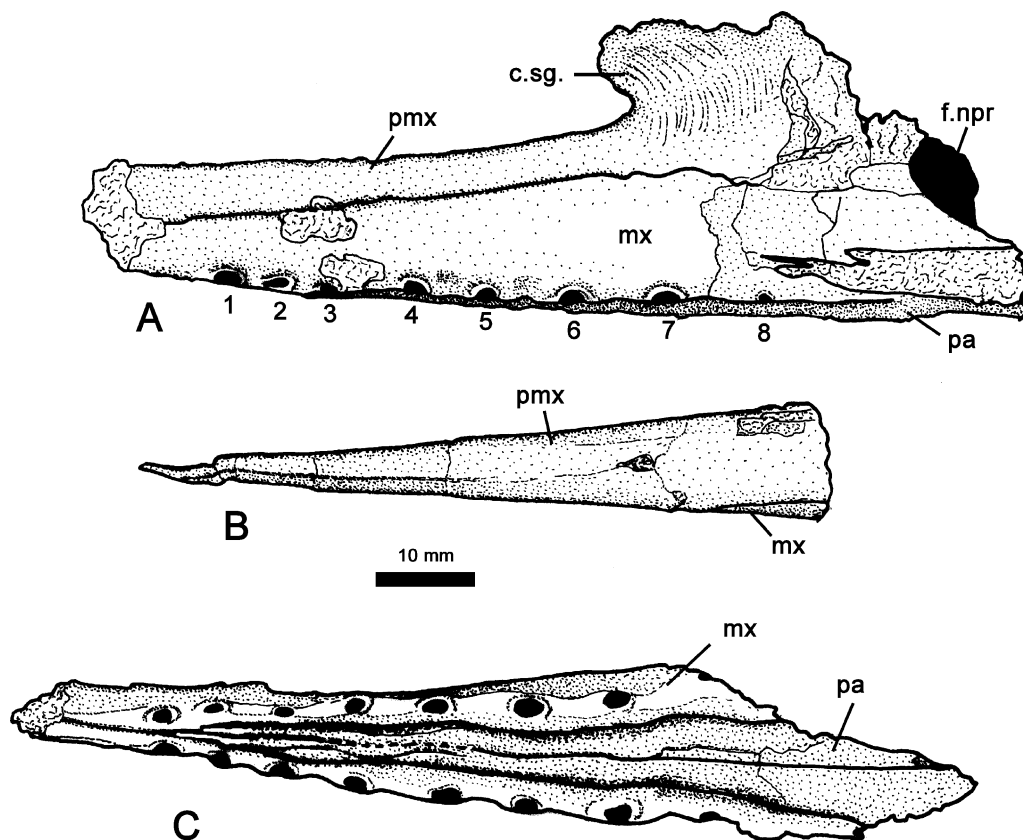


Fig. 2. *Lonchognathosaurus acutirostris* gen. et sp. nov., drawings of the holotype (SGP 2001/19). A, posterior portion of snout in left lateral view. B, anterior end of snout in left lateral view. C, posterior portion of snout in ventral view. Abbreviations: c. sg, crista sagittalis; f. np., fenestra nasopraeorbitalis; mx, maxilla; pa, palatine; pmx, premaxilla; 1–8 maxillary alveoli.

being needle-like in shape. From its anterior end, the dorsal outline of the premaxilla slowly and continuously ascends, whereas the ventral margin of the bone is straight. A shallow groove extends from close to the tip of the rostrum backwards on its lateral side for about 20 mm. In palatal view, the centre of the premaxillary rostrum is flat, whereas the lateral margins are raised into prominent ridges.

Between the level of the sixth and seventh maxillary tooth, about 28 mm anterior to the nasopreorbital fenestra, the premaxilla expands dorsally into a narrow, plate-like crista sagittalis. The dorsal margin of the crista is not preserved fully intact, but it is unlikely that much is missing. It has a preserved maximum height of about 10 mm. Its anterior margin is deeply concave. Its dorsal margin is more or less straight. The lateral surface is covered by strong, anteriorly concave striations. Directly in front of the nasopreorbital fenestra, the premaxilla-maxilla suture cannot be followed without uncertainty.

The anteriormost 20 mm of the alveolar margin of the maxilla are edentulous. Further posteriorly, a row of eight alveoli is preserved on either side. The anteriormost seven alveoli increase slightly in size posteriorly, whereas the last is very small. There is no indication on

the more completely preserved right side of the specimen (Fig. 1C) that the tooth row continues further posteriorly.

The alveoli all have slightly raised margins, but they are not bulbously expanded to the degree seen in some other dsungaripteroids. The entire alveolar margin of the maxilla is almost completely straight, with only a slight convexity. Behind the last alveolus, the maxilla forms the anterior and anteroventral margin of the nasopreorbital fenestra. The tooth row thus clearly ends anterior to that opening.

In ventral view (Fig. 1C) the anterior portions of the palatines are visible between the raised alveolar margins of the maxillae. The ventral surface of each palatine is markedly convex anteriorly, so that a furrow is formed between the two elements. Further to the posterior, the ventral palatine surfaces become flat. The palatines end anteriorly at the level of the first pair of maxillary teeth with a lanceolate and slightly serrated suture towards the maxillae.

Nothing is preserved of the dentition. The individual alveoli are slightly elongated anteroposteriorly, which might in part be due to lateral compression. The distance between individual alveoli is always larger than their anteroposterior length. The spacing of the alveoli

increases markedly posteriorly, with the exception of the seventh and eighth alveoli. The measurements for the distances between the better preserved right row of alveoli are approximately: 2.5–3.5–4.5–5–5.5–7.5–6 mm. As noted above, the size of the alveoli also increases slightly posteriorly. The possibility of considerable lateral compression makes measurements somewhat ambiguous, however.

Comparison. The specimen can be identified as a dsungaripteroid by the following features (according to Unwin and Lü, 1997): The jaw tips are toothless (at least in the upper jaw), and the largest teeth are located towards the end of the tooth row. The shape of the teeth and the morphology of the paroccipital processes cannot be assessed in the type of *Lonchognathosaurus*. The striated sagittal crest of *Lonchognathosaurus* is also a general feature of the Dsungaripteroidea, and probably an even more inclusive group (see Unwin and Lü, 1997). The morphology of the crest is especially similar to that of the South American dsungaripterid *Domeykodactylus* (E. Frey, pers. comm., 2002) and the Central Asian genera *Dsungaripterus* (Young, 1973) and “*Phobator*” (Wellnhofer, 1991).

The Dsungaripteroidea consists of two families: the more plesiomorphic (and, as noted by Unwin and Heinrich, 1999, possibly paraphyletic) Germanodactylidae, which is exclusively Late Jurassic in age and known from Western Europe and East Africa; and the Dsungaripteridae, which is exclusively Lower Cretaceous and known from Central and East Asia, South America and, possibly, eastern Europe. Material from the Upper Jurassic of Germany that might pertain to this family has yet to be described.

Within the Dsungaripteroidea, *Lonchognathosaurus* is somewhat difficult to assign. It does not show the bulbously expanded alveoli, which have been noted as autapomorphic for Dsungaripteridae by Martill et al. (2000); the possible relationships of *Lonchognathosaurus* to the germanodactylids must, therefore, be discussed, although the reduced number of teeth and edentulous snout tip clearly do not suggest germanodactylid relationships.

The Germanodactylidae is currently represented by three genera: *Germanodactylus*, *Normannognathus* and *Tendaguripterus* (Unwin and Heinrich, 1999). *Germanodactylus* (Wagner, 1851; Wiman, 1925; Wellnhofer, 1970, 1978, 1991), which is by far the best known of these, is easily distinguishable. Its upper dentition comes close to the tip of the snout (*G. cristatus*) or even reaches it (*G. rhamphastinus*). There are, thus, toothed premaxillae and many more upper teeth in *Germanodactylus* than in *Lonchognathosaurus*. The sagittal crest of *Germanodactylus* is low and lacks a concave anterior margin. The rostrum is straight, as in *Lonchognathosaurus*, but not as delicate.

Normannognathus (Buffetaut et al., 1998), known exclusively from a single snout, is also distinguished from *Lonchognathosaurus* by its complete upper dentition. The rostrum is slightly curved dorsally, as in *Dsungaripterus*, and less delicate than in *Lonchognathosaurus*. It has a sagittal crest with a concave anterior margin, as do *Lonchognathosaurus* and *Dsungaripterus*, but it was much higher. The morphology of *Normannognathus* generally indicates that it is a much more basal dsungaripteroid than *Lonchognathosaurus*.

Tendaguripterus (Unwin and Heinrich, 1999) is based on a single lower jaw fragment and, therefore, not directly comparable to *Lonchognathosaurus*. The enormous geographic (Tanzania vs. north-west China) and stratigraphic (upper Upper Jurassic vs. upper Lower Cretaceous) discrepancy between the two finds, however, renders it close to impossible that the two taxa could be identical. In addition, *Tendaguripterus* lacks the diagnostic characters of the Dsungaripteridae that are clearly present in *Lonchognathosaurus*.

Within the Dsungaripteridae, *Lonchognathosaurus* is distinguished from the type genus of the family, *Dsungaripterus*, by a number of features. In *Dsungaripterus* (Young, 1964, 1973), the tips of both upper and lower jaw curve distinctly upwards, whereas the tip of the upper jaw in *Lonchognathosaurus* is completely straight. The tip of the snout of *Lonchognathosaurus* is extremely gracile and needle-like, and clearly less robust than that of *Dsungaripterus*. *Lonchognathosaurus* has only eight maxillary tooth positions, whereas *Dsungaripterus* has 12. The dentition of *Dsungaripterus* extends just distal to the anterior margin of the sagittal crest, whereas in *Lonchognathosaurus* the teeth are largely anterior to the sagittal crest. The expansion of the alveolar margins is much greater in *Dsungaripterus* than in *Lonchognathosaurus*. These features certainly distinguish the two forms on a generic level.

Domeykodactylus (Martill et al., 2000) is again difficult to compare to *Lonchognathosaurus*, as it is largely based on mandibular material. The mandibular alveoli of *Domeykodactylus* are very similar to those of *Dsungaripterus*, however, and it appears highly likely that the alveoli of the upper jaw had a similar morphology. *Domeykodactylus* possesses numerous small, closely spaced, mandibular teeth. It would be surprising to find an upper dentition similar to that of *Lonchognathosaurus*, i.e., few, widely spaced, moderately large teeth combined with such a mandibular dentition. These features allow *Domeykodactylus* and *Lonchognathosaurus* to be distinguished on a generic level.

“*Phobator*”, i.e. *Dsungaripterus parvus* (Bakhurina, 1982, 1983, 1986), also known as the Tatal pterosaur (Bakhurina and Unwin, 1995) is, again, difficult to compare, as the well-preserved cranial material of this taxon is still not formally described. Good illustrations

were, however, published by Wellnhofer (1991) and it is on these that our comparison is mainly based. “*Phobator*” is distinguished from *Lonchognathosaurus* by its more robust anterior snout tip. However, in both genera the tip of the snout is straight, not dorsally curved as in *Dsungaripterus*. As in *Dsungaripterus*, the upper tooth row does not extend far beyond the anterior margin of the sagittal crest in “*Phobator*” but it extends posteriorly well below the nasopreorbital fenestra. The number of teeth clearly exceeds eight (compare Wellnhofer, 1991, p. 120). Bakhurina and Unwin (1995, p. 222) noted that “*Phobator*” has more teeth than *Dsungaripterus*, i.e. more than 12, in the upper jaw. The sagittal crest of “*Phobator*” has a convex anterior margin. In *Lonchognathosaurus* and *Dsungaripterus*, the anterior margin of the sagittal crest is clearly concave.

The skull of *Noripterus* is very incompletely known (Young, 1973). Contrary to some previous statements (e.g., Wellnhofer, 1978, 1980, 1991), the only skull fragment figured and described by Young is the anterior end of a lower jaw, not an upper one (compare Young, 1973, where this is explicitly stated, as also noted by Buffetaut et al., 1998). It is unclear why Wellnhofer (1978, 1980, 1991) stated that the anterior end of the jaw is toothless in *Noripterus*. Young (1973) did not mention this, as the anterior tip of the lower jaw is not preserved. What he really said was that the anterior end of the lower jaw, which is missing, might have contained one or two additional pairs of teeth. Judging from the single preserved mandibular fragment, Young (1973) was probably correct. Certainly, as also explicitly stated by Buffetaut et al. (1998), the lower jaw symphysis of *Noripterus* was almost completely toothed. This makes *Noripterus* quite similar to “germanodactylids” like *Normannognathus* (Buffetaut et al., 1998) whereas it is very different from *Dsungaripterus* and “*Phobator*” (making Bakhurina’s 1982 assertion that *Noripterus* is the same as *Dsungaripterus* exceedingly unlikely). It is therefore considered highly improbable that the skull of *Lonchognathosaurus*, which shows the most extreme tooth reduction of all dsungaripteroids, could fit into the almost completely toothed anterior end of the mandible of *Noripterus*. The arrangement of the teeth of the lower jaw is similar in both taxa, but widely spaced alveoli are a general character of most dsungaripteroids and not indicative of a close relationship. It should also be noted that from Young’s (1973) description and figures, there is little evidence for the claim that *Noripterus* had the bulbously expanded alveoli seen in *Dsungaripterus*, and it must therefore, in our opinion, remain uncertain whether *Noripterus* is correctly assigned to the family Dsungaripteridae as envisaged by Martill et al. (2000).

Other putative dsungaripteroids, such as *Puntanipterus globosus* (Galton, 1981), *Herbstosaurus pigmaeus* (Unwin, 1996) or “*Santanadactylus*” *spixi* (Bennett, 1989, 1994) and *Kepodactylus insperatus* (Harris and

Carpenter, 1996; but see Carpenter et al., 2003) are as yet not definitely regarded as members of the group. They need further study before their systematic placement can be definitely determined.

Discussion. If *Lonchognathosaurus* is compared to the other genera from Xinjiang, i.e., *Dsungaripterus* and *Noripterus*, it is evident that it retains some quite plesiomorphic features. In particular, it lacks the strong, bulbous expansion of the alveoli characteristic of some other dsungaripterids. Instead, it rather resembles Jurassic forms like *Germanodactylus* or *Tendaguripterus* with regard to this character. Other characteristics of *Lonchognathosaurus*, such as the well-developed sagittal crest with a concave anterior margin, are found both in dsungaripterids (*Dsungaripterus*) and Jurassic “germanodactylids” (*Normannognathus*). The strong reduction of the anterior dentition, resulting in a completely edentulous premaxilla is, however, a derived feature that *Lonchognathosaurus* shares with dsungaripterids. In fact it displays the most extensive reduction of the upper dentition known in the entire Dsungaripteroidea, with only eight pairs of maxillary teeth. In this context it must be noted that the shortness of the tooth row in *Lonchognathosaurus* is not only a result of reduction of the anterior teeth but also of the posterior teeth. This is evidenced by the fact that the tooth row of *Lonchognathosaurus* ends anterior to the nasopreorbital fenestra, unlike that of any other dsungaripteroid. The very small size of the eighth pair of maxillary teeth is also noteworthy in this context.

The combination of features of the skull and dentition enumerated above make it possible to assign *Lonchognathosaurus* definitely to the Dsungaripteroidea. In order to assess its phylogenetic position within that group, a cladistic analysis was carried out. This was considered necessary because even the most inclusive recent phylogenies of pterosaurs (Kellner, 2003; Unwin, 2003) only considered a limited number of dsungaripteroid taxa (*Germanodactylus*, *Dsungaripterus*, “*Phobator*” and *Noripterus* in the case of Kellner; *Germanodactylus* and the family Dsungaripteridae in the case of Unwin). The analysis presented here suffers from two shortcomings. First, those dsungaripteroid taxa for which not enough of the cranial skeleton is known to allow for a meaningful comparison to *Lonchognathosaurus* were excluded. These are *Noripterus complicidens* and *Tendaguripterus recki*, as well as the putative dsungaripteroids *Herbstosaurus*, *Puntanipterus*, *Kepodactylus* and “*Santanadactylus*” *spixi*. Whereas *T. recki* is only based on a minor jaw fragment, *Noripterus* is represented by well-preserved, associated postcranial remains. Unfortunately, for a large number of dsungaripteroids, including *Domeykodactylus*, *Normannognathus*, *Tendaguripterus* and *Lonchognathosaurus*, the postcranium is not known. If more information on the postcranial osteology of

dsungaripteroids becomes available, the phylogenetic hypotheses presented here will certainly be put to a severe test. This leads to the second problem with the present analysis, namely that it is restricted to cranial characters.

Nevertheless the results are largely in accordance with phylogenetic ideas proposed by previous authors in less explicit terms, and the resulting cladogram shows a very good agreement with the stratigraphic record. *Eudimorphodon ranzii* (data based on Wild, 1978) and *Pterodactylus kochi* (data based on Wellnhofer, 1970 and pers. obs.) were used as outgroups. Data for the ingroup taxa were taken from the existing descriptions, extended by personal observation in the case of *Dsungaripterus weii*. The analysis was based on ten characters of the cranium and dentition, which are listed and discussed below.

Character 1. Tip of the lower jaw toothed (0), toothless (1). It was decided to keep the presence or absence of teeth in the mandible and upper jaw as separate characters in our analysis because they must not be correlated. In the outgroup taxa, *Eudimorphodon* and *Pterodactylus*, the tip of the mandible is always toothed. This plesiomorphic condition is definitely retained only in *Normannognathus* and *Germanodactylus rhamphastinus* within the ingroup. It might also have been present in *Noripterus complicidens*. All other dsungaripteroids in which the mandible is known show a toothless tip to the lower jaw. The state of the character is unknown only in *Lonchognathosaurus* among the ingroup taxa.

Character 2. Tip of the upper jaw toothed (0), toothless (1). The plesiomorphic condition is found in the outgroup. It is retained by *Normannognathus* and *G. rhamphastinus*. All other adequately known dsungaripteroids show the derived condition. In *Domeykodactylus*, the tip of the upper jaw remains unknown.

Character 3. Bony sagittal crest extending from the nasopreorbital fenestra backwards (0), present but low (1), present but high (2). In the chosen outgroup taxa, a bony sagittal crest is not present. Nevertheless it is found in a variety of other pterosaurs, including the basal Triassic taxon *Austriadactylus cristatus* (Dalla Vecchia et al., 2002), so the presence of a sagittal crest is homoplastic within Pterosauria. Nevertheless, in *Austriadactylus* it extends much farther forward, right to the anterior tip of the skull. It is, therefore, evidently not homologous to the sagittal crest displayed in the *Dsungaripteroidea* and other lophocratian pterosaurs (see Unwin, 2003). In *Germanodactylus cristatus* and *G. rhamphastinus*, a low sagittal crest extends from the anterior margin of the nasopreorbital opening backwards. It is longer in *G. rhamphastinus*, where it extends almost to the occiput, whereas in *G. cristatus* it only

reaches the posterior half of the orbit. In the other dsungaripteroids, including *Normannognathus*, a high, well-developed sagittal crest is present. Similar sagittal crests are also known in some other pterosaur groups, such as the Pteranodontidae (Eaton, 1910), and the presence of such sagittal crests has been considered as diagnostic of a much more inclusive group of pterodactyloid pterosaurs, named Lophocratia by Unwin (2003).

Character 4. Anterior margin of sagittal crest absent (0), convex or straight (1), concave (2). The plesiomorphic state of this character is found in the outgroup. Within the ingroup, *Germanodactylus cristatus*, *G. rhamphastinus*, and “*Phobetor*” *parvus* have sagittal crests with a convex or straight (i.e., posterodorsally ascending) anterior margin. In *Lonchognathosaurus*, *Dsungaripterus* and *Normannognathus*, the anterior margin of the sagittal crest is concave. In *Dsungaripterus weii*, for which several skull specimens are known (Young, 1973), the shape of the sagittal crest shows little variation.

Character 5. Tip of the jaws straight (0), curved upwards (1). In most pterosaurs, including the outgroup and the majority of ingroup taxa, the tips of the upper and lower jaws are straight. In *Normannognathus* and *Dsungaripterus*, however, they are distinctly curved upwards. Although this is probably a convergence, as indicated by the topology of the cladogram resulting from the present analysis, this conspicuous character had to be included. That it may be convergent rather than homologous in *Normannognathus* and *Dsungaripterus* is additionally indicated by the fact that upward-curving snouts are also known in other pterosaurs, such as some specimens of *Rhamphorhynchus* (Wellnhofer, 1975).

Character 6. Number of tooth pairs in the upper jaw more than 12 (0), 12 or less (1). In the outgroup and most of the ingroup taxa, the number of tooth pairs in the upper jaw always exceeds 12. Only in *Lonchognathosaurus* and *Dsungaripterus* is the dentition more strongly reduced. Whereas *Dsungaripterus* retains 12 tooth pairs in the upper jaw, *Lonchognathosaurus* has only eight. It is evident that there is a tendency towards tooth reduction in the phylogeny of the *Dsungaripteroidea*, which begins with fully toothed forms such as *Normannognathus* and *Germanodactylus rhamphastinus* in the Jurassic, and culminates in the late Early Cretaceous forms such as *Dsungaripterus* and, most extremely, *Lonchognathosaurus*.

Character 7. Number of tooth pairs in lower jaw more than 12 (0), 12 or less (1). In the outgroup and the majority of ingroup taxa the number of mandibular

tooth pairs always exceeds 12. In *Dsungaripterus* there are, however, only 11 pairs of mandibular teeth, and in “*Phobator*” there seem to be only nine or ten (see, e.g., Bakhurina and Unwin, 1995). In *Lonchognathosaurus* the lower jaw is unknown, but it probably had as few, or even fewer, mandibular teeth as these two genera, judging from the amount of tooth reduction it displays in the upper jaw.

Character 8. Anterior end of jaws not or moderately (0), extremely (1) pointed. The anterior tips of the jaws are not pointed at all but blunt in *Eudimorphodon*. In *Pterodactylus* and *Normannognathus* they are also quite bluntly rounded. In *Germanodactylus rhamphastinus* the jaws are fairly pointed, even though this taxon retains teeth in the tips of the jaws. This trend is carried further in the other dsungaripteroids. A culmination is again reached in *Lonchognathosaurus* where at least the tip of the upper jaw is modified into an exceedingly delicate and needle-like rostrum.

Character 9. Alveoli normal (0), with ring-like wall (1), at least some bulbously expanded (2). In the outgroup the alveoli of the teeth in both upper and lower jaw are comparable to those of other archosaurs. In the ingroup, there is always at least a low, ring-like bony wall around the alveoli. In three genera (*Domeykodactylus*, “*Phobator*” and, most conspicuously, *Dsungaripterus*) these bony walls are expanded into rounded, bulbous outgrowths of the jaw bones that surround much of the teeth.

Character 10. Largest teeth at the tip or in the middle of the jaws (0), towards the posterior end of the jaws (1). This is another general dsungaripteroid character first pointed out by Unwin and Lü (1997). It is not, however, present in *Germanodactylus rhamphastinus* and *G. cristatus*, where the largest teeth are instead situated at about middle jaw length, and certainly not at the posterior end of the jaws.

The data matrix (Table 1) resulting from this set of characters was subjected to a parsimony analysis with

the aid of the computer program Paup* 4.0b10 (Swofford, 2003). A heuristic search with 1,000,000 replicates was carried out. All characters were treated as unordered and given equal weight. The usual default settings were in effect otherwise, and characters were not optimized.

The analysis yielded a single most parsimonious tree (Fig. 3) with a length of 18 steps. The consistency index is 0.72, the retention index 0.77. The outgroup taxa, *Eudimorphodon* and *Pterodactylus*, form a polytomy with the Dsungaripteroidea at the base of the tree. The most basal dsungaripteroid is *Normannognathus wellnhoferi*. As it is Kimmeridgian in age and thus, with the possible exception of *Tendaguripterus recki*, the most ancient dsungaripteroid, this is not surprising. The Early Tithonian taxa *Germanodactylus rhamphastinus* and *G. cristatus* occupy the next two positions. Therefore, neither the family Germanodactylidae as envisaged, e.g., by Unwin and Heinrich (1999), nor the genus *Germanodactylus* Young, 1964 were found to be monophyletic. This agrees with the recent more inclusive pterosaur phylogeny put forward by Unwin (2003, p. 180) whereas Kellner (2003) suggested a monophyletic *Germanodactylus*. The only synapomorphy he cites is, however, the presence of a sagittal crest. This feature can only be regarded as a synapomorphy if one does not accept monophyly of the Dsungaripteroidea sensu Unwin (2003). As we agree with the phylogeny put forward by Unwin, we also agree with him (Unwin, 2003, p. 180) that there is as yet no unequivocal evidence for monophyly of the genus *Germanodactylus* and that it should best be treated as a metataxon at the moment. Generally, the so-called “germanodactylids” appear as a successive set of Jurassic sister taxa to the higher dsungaripteroids. Unwin and Heinrich (1999) have already indicated that the Germanodactylidae was probably paraphyletic, but said this had to be demonstrated first by a phylogenetic analysis. This has now been done here, and it is therefore considered best to abandon the family-group taxon Germanodactylidae as long as there is no compelling evidence for its monophyly.

Table 1
Data matrix for the phylogenetic analysis of dsungaripteroid interrelationships

	1	2	3	4	5	6	7	8	9	10
<i>Eudimorphodon ranzii</i> Zambelli, 1973	0	0	0	0	0	0	0	0	0	0
<i>Pterodactylus kochi</i> (Wagner, 1837)	0	0	0	0	0	0	0	0	0	0
<i>Daitingopterus rhamphastinus</i> (Wagner, 1851)	0	0	1	1	0	0	0	1	1	0
<i>Germanodactylus cristatus</i> (Wiman, 1925)	1	1	1	1	0	0	0	1	1	0
<i>Normannognathus wellnhoferi</i> (Buffetaut et al., 1998)	0	0	2	2	1	0	0	0	1	1
<i>Domeykodactylus ceciliae</i> (Martill et al., 2000)	1	?	2	?	0	?	0	?	2	1
<i>Lonchognathosaurus acutirostris</i> gen et sp. nov.	?	1	2	2	0	1	?	1	1	1
“ <i>Phobator</i> ” <i>parvus</i> (Bakhurina, 1982)	1	1	2	1	0	0	1	1	2	1
<i>Dsungaripterus weii</i> Young, 1964	1	1	2	2	1	1	1	1	2	1

See text for a discussion of the characters.

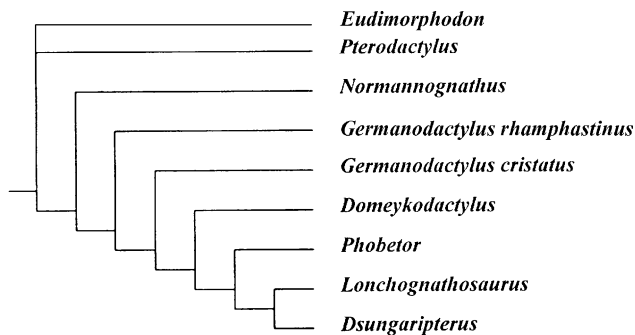


Fig. 3. Cladogram depicting the relationships of dsungaripteroid pterosaurs. See Table 1 for the data matrix. Tree length 18 steps, CI = 0.72, RI = 0.77.

The Dsungaripteridae, which at the moment cannot be diagnosed by key synapomorphies but rather represent an advanced grade of dsungaripteroid evolution with a fair amount of homoplasy, contains the four genera *Domeykodactylus*, “*Phobetor*”, *Lonchognathosaurus* and *Dsungaripterus*. *Noriopteris* is also regarded as a member of that family in recent, more exclusive phylogenetic analyses (Kellner, 2003; Unwin, 2003) but could not be included in our analysis because its skull is too incompletely known. In the present analysis, *Domeykodactylus*, the sister taxon to the three Central Asian genera, is probably Early Cretaceous in age. The exact stratigraphic placement of the rocks in which it occurs is somewhat uncertain (Martill et al., 2000). It is certainly not younger, but rather older (as a late Jurassic age for the material cannot yet be definitely excluded) than the Central Asian forms. “*Phobetor*” from the Tsagan-Tsab Formation of western Outer Mongolia is probably also from the lower Lower Cretaceous (?Valanginian–Barremian). The two remaining genera, *Dsungaripterus* and *Lonchognathosaurus*, are both from the Lianmuxin Formation of the Tugulu Group in the north-western and southern Junggar Basin of Xinjiang respectively. They are, therefore, roughly coeval and it is not surprising that, in view of their close stratigraphic and geographic proximity, they are found to be sister taxa. The Lianmuxin Formation is generally considered to be late Early Cretaceous (Aptian–Albian) in age.

The almost exact correspondence between the, albeit patchy, fossil record of dsungaripteroids and the topology of the cladogram proposed here, which is admittedly based on a very restricted data set, is certainly noteworthy and yields some support to the phylogenetic arguments proposed here. Further material of several dsungaripteroid taxa is certainly needed before the data set presented can be expanded significantly and the proposed phylogeny tested.

A taxonomic result of the phylogenetic analysis is the paraphyletic status of the genus *Germanodactylus*. As phylogenetic taxonomy does not allow the use of

para- or polyphyletic taxa, it may become necessary to erect a new genus for *Germanodactylus rhamphastinus*, whereas the type species, *Pterodactylus cristatus* Wiman, 1925, can remain within the genus *Germanodactylus* Young, 1964. This is, however, beyond the scope of the present study, particularly as Bennett (1996, 2002) stated that the two species of *Germanodactylus* represent old adults of *Pterodactylus antiquus* and *P. kochi*, an interesting idea that has not yet been verified, however, by a proper taxonomic revision. Until this is done, the taxonomic assignment of *Germanodactylus cristatus* and *G. rhamphastinus* is debateable. It is, however, quite likely that they are generically different, whatever their affiliation to the various *Pterodactylus* species may be.

3. Conclusions

Lonchognathosaurus acutirostris is the third genus and species of dsungaripteroid pterosaur to have been recovered from the Junggar Basin. Young (1964, 1973) described *Dsungaripterus weii* and *Noriopteris complicidens*, based on well-preserved, articulated material from the Upper Tugulu Group of Wuerho (Urho) near Karamay in the north-west of the basin. *Lonchognathosaurus* occurs in a stratigraphically comparable level, being from the lower part of the Lianmuxin (Lianmuqin) Formation (the youngest of the four formations that constitute the Tugulu Group). Previously, only a posterior zeugopodium of a *Noriopteris*-like dsungaripterid was known from the southern Junggar Basin (Young, 1964; Buffetaut, 1996). It was found in an unspecified horizon of the Tugulu Group close to Changji, north-west of Urumqi. *Lonchognathosaurus* is, therefore, an important addition to our knowledge of the Early Cretaceous vertebrate faunas of the southern Junggar Basin. So far, the Early Cretaceous pterosaur fauna of the basin consists exclusively of dsungaripteroids. This is unusual, if it is compared to other Early Cretaceous pterosaur faunas. In western Mongolia, dsungaripteroids are also the only pterosaurs that have been discovered hitherto (Bakhurina, 1982, 1983; Bakhurina and Unwin, 1995). That this should be based only on a collecting bias seems unlikely in view of the excellent preservation and relatively common occurrence of pterosaurs at the main localities (Urho, Tatal, and also Liuhonggou) where these dsungaripteroids have been discovered. The reasons for the predominance of these particular pterosaurs in the Early Cretaceous deposits of the Junggar Basin and western Mongolia are, therefore, probably ecological but have not yet been investigated in detail. As the evolutionary history and anatomy of dsungaripteroids becomes better known, they should form the focus of interesting future research.

That the specimen from Liuhonggou represents a new genus and species fits with the other results reached by

the investigations of the SGP. The tetrapod fauna of the Tugulu Group in the southern Junggar Basin is very different from that of the north-western part, with respect to both its numerical and taxonomic composition. Whereas the Wuerho-Karamay region yields numerous dinosaur remains (Dong 1973), to date these animals are absent from the Lower Cretaceous of the southern Junggar Basin. Instead turtles are extremely common there at numerous stratigraphic levels in the Tugulu Group. The only other reptiles that occur are pterosaurs, which are, however, much less common than in the Wuerho-Karamay area. The turtles are currently being studied (see also Maisch et al., 2003; Matzke et al., 2004). So far all have been found to differ from those of the north-western part of the basin on a specific or even generic level.

The causes for the differences in faunal composition between the southern and north-western parts of the Junggar Basin, which parallels similar differences between the southern and north-eastern parts in the Middle and Upper Jurassic successions (see Maisch et al., 2001, 2003) also needs further investigation.

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