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A taxonomic revision of *Noripterus complicidens* and Asian members of the Dsungaripteridae

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Abstract: After being inaccessible for a number of years, the holotype and other specimens of the dsungaripterid pterodactyloid pterosaur *Noripterus complicidens* are again available for study. Numerous taxa assigned to the Dsungaripteridae have been described since the erection of *Noripterus*, but with limited comparisons to this genus. Based on the information from Young's original material here we revise the taxonomic identity of *N. complicidens* and that of other Asian dsungaripterids. We conclude that *N. complicidens* is likely to be distinct from the material recovered from Mongolia and this latter material should be placed in a separate genus.

The dsungaripterid pterosaurs are a group of derived pterodactyloids that are characterized by having toothless jaw tips (Kellner 2003; Unwin 2003). A number of taxa also show expansions of the bone around the tooth alveoli such that the jaw is swollen at the bases of the teeth, or the teeth may even be covered with bone entirely (e.g. see Martill *et al.* 2000). Dsungaripterids also have characteristically thick bone cortices, such that their long bones are more dense than those of similar-sized pterosaurs (Fastnacht 2005).

Described by C.C. Young (1964), the dsungaripterids remain a clade with few taxa assigned to them (see Lü *et al.* 2009*a*). The more inclusive clade Dsungaripteroidea may or may not include the somewhat problematic *Germanodactylus cristatus* from the Late Jurassic of the Solnhofen limestones of Germany. This species has been recovered as both a basal dsungaripteroid (e.g. Unwin 2003; Lü *et al.* 2009*a*) or close to the Ctenochasmatidae (e.g. Kellner 2003). Currently its affinities remain uncertain, but the recent rediscovery of the missing counterplate to the *G. cristatus* holotype in Dublin, Ireland (Hone 2010) may yet help solve this issue. Here, we follow Lü *et al.* (2009*a*, *b*) in considering this species a dsungaripteroid and also follow their definition of the clade (see also Unwin 2003; Witton 2013, p. 201, and for an alternative definition see Kellner 2003).

Dsungaripteroids have a wide distribution (Witton 2013, p. 203) but the dsungaripterids are known primarily from the Cretaceous of Asia with *Dsungaripterus*, *Noripterus* and *Longchognathosaurus* all being found in the Junggar Basin of western China (Lü *et al.* 2009*b*) and further material coming from Mongolia (Bakhurina 1986; Lü *et al.* 2009*b*). Other specimens referred to the Dsungaripteroidea herald from South America (e.g. Martill *et al.* 2000) and Europe (in the form of *Germanodactylus*), although the identification of a number of these as dsungaripteroid is questionable and many are fragmentary.

The holotype and referred material of *Noripterus* that was discovered and described by Young has not featured in the literature to our knowledge since the original description (Young 1973), despite the description of new material referred to this genus (Lü *et al.* 2009*b*). While reasonably well illustrated, much of Young's original paper was devoted to new material of *Dsungaripterus*, written in Chinese and not easy to obtain. Indeed the holotype of *Noripterus* has not been available for at least a decade and was thought lost for a time. Part of the holotype and two referred specimens have, however, now returned to the IVPP and this material is now available for study. The referral of new material to *Noripterus* (Lü *et al.*, 2009*b*) and putative synonymies of some dsungaripterid taxa (Maisch *et al.* 2004) make this material important for pterosaurian taxonomy. Here we present a revision of the taxonomy of this genus and other Asian dsungaripterids.

Institutional abbreviations

BSPG, Bavarian State Collection of Palaeontology, Munich, Germany.

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

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Specimens

Identification of specimens

Multiple specimens referred to *Noripterus complicidens* are housed at the IVPP following their collection by Young. In his description, Young (1973) suggests that he collected elements of approximately eight individuals. However, not all of them were given different field numbers or museum accession numbers, and only a few were illustrated or measured in the description. This makes it difficult at this point to refer each element correctly to Young's (1973) identifications. Furthermore, examination of the *Noripterus* specimens currently at the IVPP reveals the holotype to be incomplete but also that the specimen numbers and field numbers do not match across specimens. This suggests some confusion in assignment of material to formal IVPP collection numbers.

The holotype IVPP V 4062 bears the field number 64045. Young (1973) considered two specimens with field numbers 64041-7 and 64043-3 to be paratypes and a fourth specimen was unnumbered.

According to Young's (1973) description of the holotype, IVPP V 4062 should consist of a partial lower jaw, several cervical vertebrae, several dorsal vertebrae, the distal part of a coracoid, the proximal part of a humerus, the distal part of an ulna, proximal wrist elements, a partial fourth metacarpal, a partial wing phalanx, the distal part of both femora and some further bone fragments. Of this material, only the fused partial dentaries (Fig. 1) can be identified and this does bear the field number 64045, but the other elements are missing and may now be lost. One large wing metacarpal (which appears far too large to be associated with the jaws) also bears the field number 640[numeral missing]5, but Young (1973) considered this too large to belong to the holotype and we agree with this assessment. However, this does imply that multiple individuals were collected under a single field number.

Fortunately although little of this material has been illustrated, Young (1973) did measure many of the elements described in his paper and thus the identity of a number of specimens can be determined by their published dimensions and occasional field numbers. Sorting of the available material reveals the presence of a minimum of five individuals that can currently be identified:

(1) The holotype IVPP V 4062 (field number 64045) – a pair of partial, fused dentaries.

(2) Unnumbered paratype specimen (field number 64043-3) – consisting of one near complete left wing: humerus, radius and ulna, wrist including partial pteroid, manus and two complete wing phalanges and a broken third. A second incomplete wing metacarpal and first wing phalanx are also present (presumably the right). A complete left hindlimb is also preserved. This specimen was figured in Young (1973, plate V), although it is incorrectly described as being field number 64041-7. This list of material matches the description of material given this field number in Young's description and thus this specimen appears to be complete as originally recovered. This specimen has now been given an IVPP designation and is hereafter referred to as IVPP RV 73001 (Fig. 2).

(3) IVPP V 4059 (field number 64041-7) – a partial skeleton consisting of two cranial pieces that are thought to be from the dentary rami, one near complete cervical, a second very partial cervical, two fused vertebral centra that based on their size are part of the notarium, a scapulacoracoid, a humerus, two proximal ulnae and one distal ulna (or radius), one partial wrist complex (proximal and distal syncarpals), the midshaft of metacarpal IV with parts of two other metacarpals attached, two manual phalanges of digits I–III, two proximal parts of the first wing phalanges

Fig. 1. The currently available holotype material of *Noripterus complicidens* (IVPP V 4062) – partial dentaries with some intact teeth. The teeth are widely spaced and show slight expansion of bone around the base of some towards the rear of the jaw. Scale bar is 20 mm.

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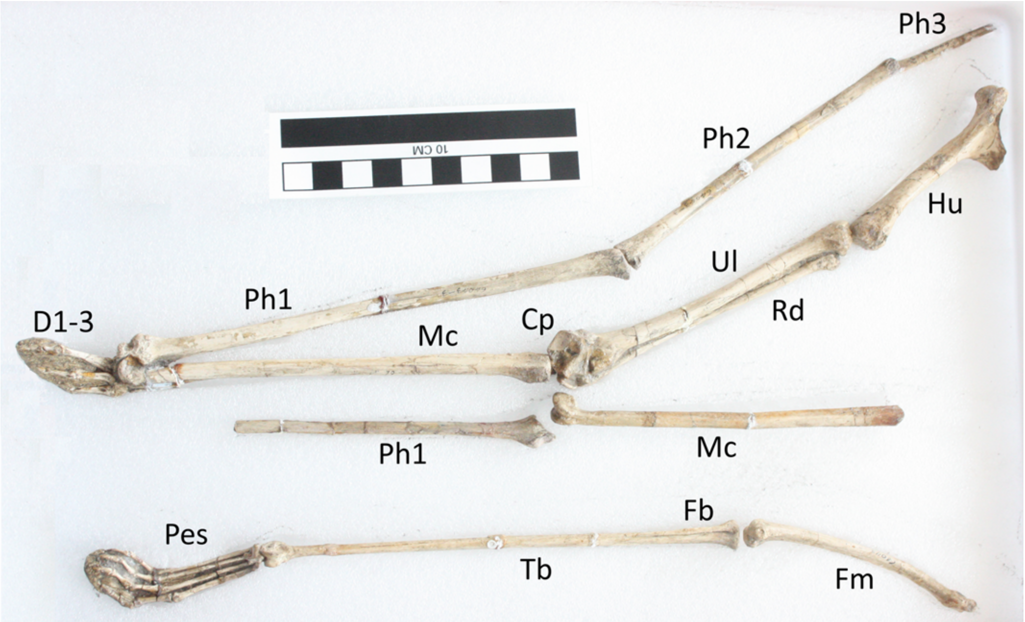

Fig. 2. The near complete fore and hindlimbs of IVPP RV 73001. Elements still bear Young's (1973) original field number for the specimen – 64043-3. Abbreviations are as follows: Cp, carpal block; D, manual digits; Fb, fibula; Fm, femur; Hu, humerus; Mc, metacarpals; Pes, foot (including tarsals); Ph, wing phalanges; Rd, radius; Tb, tibia; Ul, ulna.

and parts of three other wing phalanges, a near complete pelvis and sacrum (with three proximal caudal centra in association), two femoral heads and two distal femoral ends, two tibial shafts and two distal tibial ends, a number of isolated metatarsals and pedal phalanges and a small block of matrix of numerous pedal elements. These pieces were mounted on a board in their approximate anatomical positions and it is clear that many of the now fragmentary long bones were originally complete based on marks in the underlying dust where the shafts are now absent (Fig. 3). The pelvis and hindlimbs are those illustrated as the specimen on the left side of Young (1973, plate IV).

(4) Unnumbered specimens consisting of a distal wing metacarpal, a large carpal (assuming this wrist element belongs with the metacarpal). The larger metacarpal is the one with the field number of the holotype but that is here considered a separate individual.

Originally Young (1973) mentions a number of other elements but without illustrations or any measurements, and as not all elements described above have field numbers they cannot be positively referred to his description. The fact that Young gave them separate field numbers does suggest that the specimens came from different localities. Some field numbers in Young's paper include suffixes (e.g. 64041-10 as opposed to 64041) and are presumed to refer to different specimens recovered at a single locality, although none of the numbers written on specimens contain the suffix values even when they were used in the paper and so cannot necessarily be aligned to a specific specimen. These specimens are: 64041, distal part of the wing metacarpal; 64041-10, a humerus; and 64044, a fragment of cervical vertebra (this might now be included with IVPP V 4059).

Almost all of the material is in good condition and despite breaks and damage appears to have undergone little or no distortion and has also suffered little erosion. Measurements and subtle anatomical features can therefore be treated as correct. Fusion of various elements (e.g. fusion of the scapula to the coracoid, fusion of the extensor tendon process to the first wing phalanx, fusion of the pelvic elements) across several specimens suggests that most, if not all, of these animals were close to osteological maturity. Although there is variation in the sizes of various elements that occur in multiple specimens (e.g. the humeri, femoral heads), the apparently smaller specimens still show the above fused elements and thus the whole collection is tentatively treated as being of similar osteological maturity.

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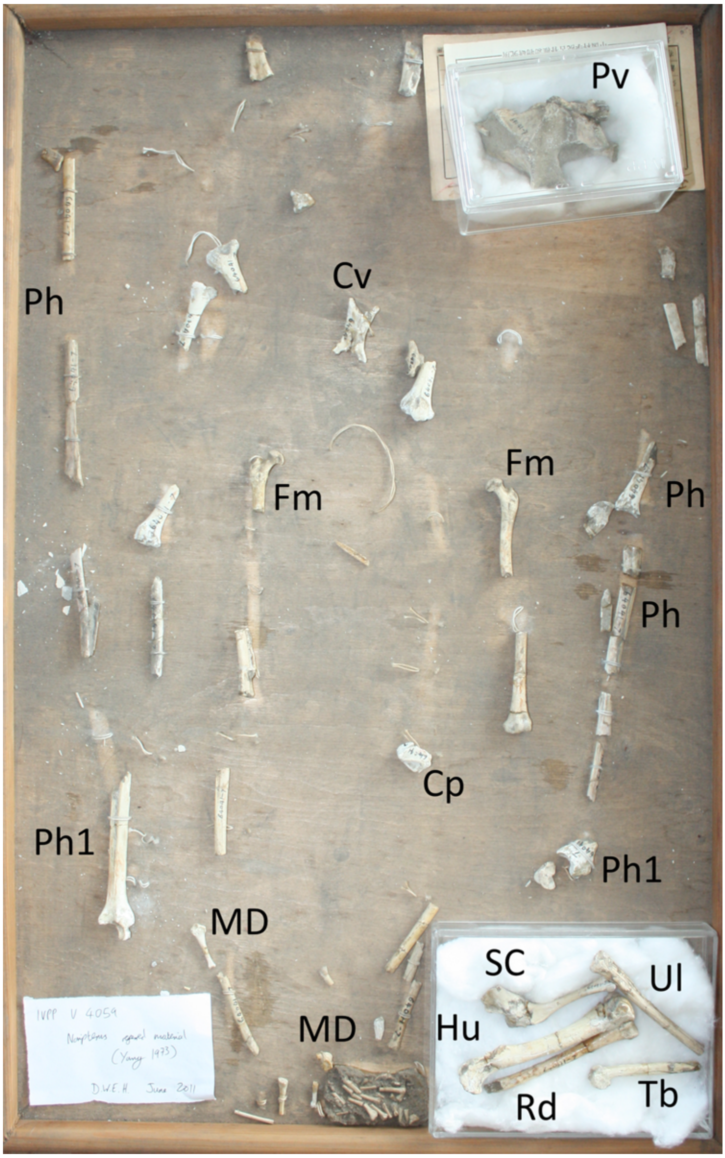

Fig. 3. The material belonging to specimen IVPP V 4059 of *Noripterus* (field number 64041-7) as found in the collections with material mounted on a wooden board – note that in many cases long bones are broken and parts are missing but their original position and size can often be identified based on the cleaner parts of the board. Abbreviations as in Figure 2 with the following additions: Cv, cervical vertebra; MD, manual and/or pedal elements; Pv, pelvis; SC, scapulocoracoid. Not all elements are identified or labelled here.

The material collected by Young came from four different localities but all of them were close together (most quarries were less than 10 km apart; Dong 1973) and there is little reason to think that these were not comparable localities of the same or similar horizons. The fact that multiple specimens are all a close match in size, shape, morphology and preservational condition/colour where they overlap is weak but supporting evidence that all of the material is of one taxon. Here we therefore follow Young (1973) in considering all of this material to belong to *N. complicidens*, despite the current lack of overlap between the holotype and other material. The material is also consistently

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different from that referred to *Dsungaripterus* (e.g. the ratios of the limbs – see below) while consistent between specimens again, also suggesting that all of this material represents a single taxon, although identification of the original quarries and a specimen with a skull would greatly help strengthen this case.

Systematic palaeontology

Diagnosis of Noripterus

Young's (1973) original diagnosis is largely redundant in the context of modern taxonomic characteristics. He listed the following characteristics to distinguish *Noripterus complicidens* from other pterosaurs/*Dsungaripterus*: (1) it is smaller than two-thirds of the size of *Dsungaripterus weii*; (2) it has teeth on the anterior tips of the mandible, unlike the toothless tip in *Dsungaripterus weii*; (3) it has narrow and elongated cervical vertebrae; (4) the angle formed by scapula and coracoid is not large, and the distal part of coracoid may not connect with sternum directly; (5) the diaphysis of humerus is straight, without a hatchet-like deltopectoral crest; (6) the proximal carpals form a triangle, and the ratio of ulna to metacarpal IV is 69%; and (7) the forelimbs and hind limbs are thin, the formula of phalanges are 2, 3, 4, 4, 0, and the formula of pes phalanges is 2, 4, 4, 5, 0.

Of these, characteristics (1), (3) and (4) are vague and thus not diagnostic as they cannot therefore be easily compared with other pterosaurs. For characteristic (6), the ratio of the ulna to the wing metacarpal is 74% in at least one specimen Young collected, making the value for this ratio of 69% questionable. The description of the proximal carpals as triangular in general form is correct but the shape is unknown in *Dsungaripterus*. The description of the limbs as 'thin' in characteristic (7) is vague and the phalangeal formulae of the manus and pes is the same for all pterodactyloid pterosaurs and thus not diagnostic.

Characteristics (2) and (5) are not immediately problematic, but comparisons of the specimens with other pterosaurs reveal issues with them. Although the description of the teeth as reaching the tips of the mandible is unclear since the rostral end is missing and thus it is not clear if the teeth actually did extend to the tips of the jaws. However, they certainly do appear to be closer to the tip of the jaw than in *Dsungaripterus* and so this does suggest a potential difference between them. The shaft of the humerus is straight in *Noripterus*, but this is also the case in many other pterodactyloid pterosaurs and is therefore not diagnostic. It is not clear how the non-hatchet-like deltopectoral crest is supposed to be diagnostic and so this remains unclear. Collectively therefore this definition is problematic and difficult to justify as a diagnosis that is currently valid (although this in itself does not invalidate the taxon). More recently, Lü *et al.* (2009*b*) provided a new diagnosis for *Noripterus* based on newly recovered material from Mongolia.

The definition of Lü *et al.* (2009*b*) is as follows:

> Skull with a developed saggital crest, which begins above the interval between the 7th and the 8th tooth position (from anterior to posterior) of the upper jaw, extending posteriorly along the midline of the skull and terminating above at the level of the middle of the dorsal rim of the orbit; Anterior toothless parts of both jaws straight; Ratio of the length of the mandibular symphysis to that of the lower jaw approximately 0.54; Deep groove on the midline of the dorsal surface of the dentition [sic] part of the mandibular symphysis; Teeth laterally compressed with sharp tips; Thirty teeth on the upper jaw and 20 teeth on the lower jaw; Six teeth on upper jaw below the margin of the nasoantorbital opening; The alveoli are not expanded into protuberances; The dentition in the upper jaw extends about one-third further posteriorly than that of lower jaw; Ratio of tibia to femur length is approximately 1.7.

Although this is a significant improvement on the original diagnosis of Young, this is also problematic. Assuming that this material does relate to *Noripterus complicidens* (see below), only three of the characteristics of Lü *et al.* (2009*b*) can be seen in the holotype of *Noripterus*, and two of these are not apomorphic. Among dsungaripterids, the characteristic 'anterior toothless parts of both jaws straight' is also true of the holotypes of *G. cristatus* (BSPG 1982 IV 1) and *Longchoganthosaurus* (Maisch *et al.*, 2004 – although see the discussion below on the validity of this genus). The characteristic 'alveoli are not expanded into protuberances' is also present in *G. cristatus* and may be present here, despite some damage to the base of the teeth – at least one tooth in the holotype jaw of *Noripterus* has a slight expansion of bone around the alveolus in the holotype and more may be present (Figs 1 & 4). The third characteristic, 'teeth laterally compressed with sharp tips', can be partly inferred in the holotype by the shape of the alveoli being laterally compressed, and the sole tooth present, while damaged, is sharp tipped. However, again this is also true of *G. cristatus*, which appears to have rather laterally compressed teeth and these are certainly pointed. Thus under Lü *et al.*'s (2009*b*) revised diagnosis, the holotype of Young (1973) is not necessarily a specimen of *Noripterus*, and a revised diagnosis is therefore provided below.

Pterosauria (Kaup, 1834)
Pterodactyloidea (Plieninger, 1901)
Dsungaripteridae (Young, 1964)
Noripterus complicidens (Young, 1973)

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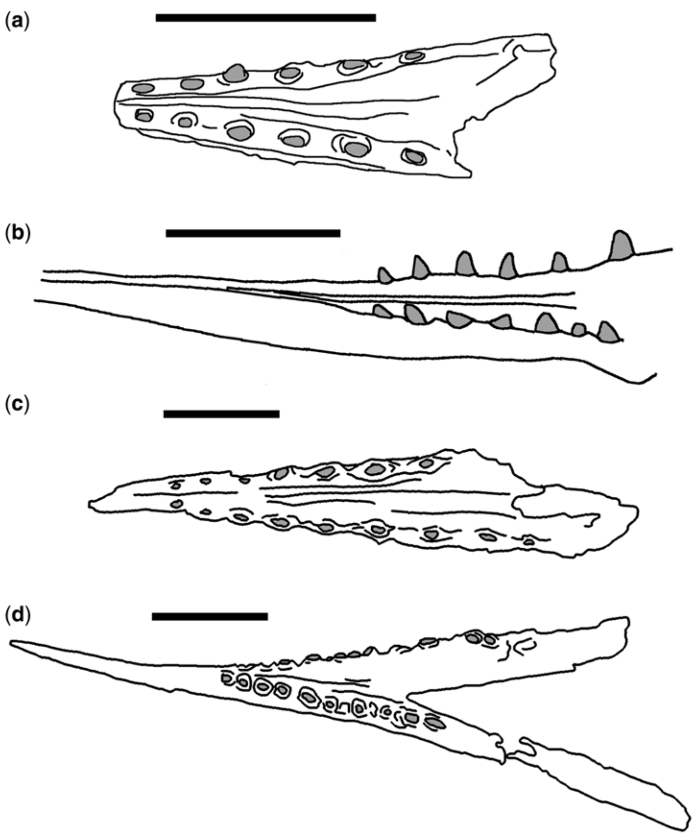

Fig. 4. Tracings of the jaws of Asian dsungaripterid pterosaurs to show tooth size and spacing (teeth or alveoli are in grey). (**a**) The holotype dentaries of *Noripterus*; (**b**) the dentaries of the Mongolian material referred to '*Phobetor*' by Lü *et al.* (2009*b*) (modified from their fig. 4e); (**c**) the holotype maxillae of *Longchognathosaurus* (the premaxillae are known but not drawn here); and (**d**) unnumbered IVPP specimen of *Dsungaripterus*. Scales bars A, B and C, 20 mm; D, 50 mm.

Definition and diagnosis

Dsungaripterid pterosaur that can be diagnosed by the presence the following characteristics: only mild expansion of bone around the base of the alveoli; and possesses a relatively short wing metacarpal (ratio to first wing phalanx close to 0.8). It can be further diagnosed by the following combination of characteristics: straight jaw-tips with a deep midline groove on the dentary symphysis.

Discussion

Dsungaripterid taxonomy

Noripterus has been repeatedly assigned to the Dsungaripteridae or recovered as a part of this group in phylogenetic analyses (e.g. Wellnhofer 1978; Kellner 2003; Unwin 2003; Maisch *et al.* 2004) based on Young's material and description. However, none of the diagnostic characteristics listed by Unwin (2003) to define the dsungaripterids can be seen in the remaining material of the holotype of *N. complicidens*. However, Unwin's (2003) characteristics of limb bones with relatively thick walls and a strongly bowed femur are both clearly present in the other material collected by Young that are referred to this taxon. A number of long bone elements are broken and the cortex thickness can be measures, and these are between 0.75 and 1.25 mm, for elements that are 5.4 and 4.3 mm in diameter (ulna and tibia respectively). These are close to those ratios reported considered diagnostic for the Dsungaripteridae (Fastnacht, 2005) and are above the values recorded for most other pterosaurs.

One characteristic from Kellner (2003) diagnoses the other available material as belonging to the Tapejaroidea (i.e. the dsungaripterids + azhdarchoids): a massive medial crest on the

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humerus with a developed proximal ridge. However the presence of teeth therefore supports this taxon as a dsungaripterid alone as all azhdarchoids are toothless. A second characteristic of Kellner (2003) – teeth with proximal oval base – is also seen here in the holotype dentaries and supports the referral to Dsungaripteridea (*sensu* Kellner, 2003). Witton (2013, pp. 2–8) also notes that the humeri of dsungaripterids lack pneumatopores and also have a large deflected deltopectoral crest as seen here in Young's material (Fig. 2).

Noripterus is then a dsungaripteroid pterosaur and also can be assigned to the Dsungaripteridae. The straight tips to the mandible and the presence of only very mild expansion of the bone around the base of the teeth clearly separate *Noripterus* from *Dsungaripterus* (Young, 1964) and its overall size at osteological maturity is considerably smaller than that of specimens of *Dsungaripterus*. Thus, despite the fact that much of the holotype of *Noripterus* cannot be accounted for, what remains is diagnostic and the taxon is valid. The additional material representing the paratypes and other specimens helps further separate *Noripterus* from *Dsungaripterus*. Although in some details (e.g. the pelvis and wing phalanx morphology) the two are very similar, there are differences. *Dsungaripterus* has a proportionally much shorter humerus (or longer femur) compared with *Noripterus* (humerus to femur ratio of 0.57, based on IVPP V 2776 from Elgin (2014) compared with 0.81 in IVPP RV 73001).

As the second named dsungaripterid, *Noripterus* must then be considered a valid taxon. The question remains, however, as to whether or not other more recently described taxa are synonymous with *N. complicidens*.

As part of the revision of the genus and description of new material, Lü *et al.* (2009*b*) synonymized '*Phobetor*' (Bakhurina, 1986 – the name is preoccupied and thus required replacement; Bakhurina & Unwin, 1995) with *Noripterus*. Much material has been assigned to '*Phobetor*' (Bakhurina & Unwin, 1995); this is a small, straight-jawed dsungaripterid known from Mongolia (Bakhurina 1986) and thus clearly bears at least some resemblance to *Noripterus.*

As described above, the new and largely complete specimen described by Lü *et al.* (2009*b*) was shown to be a very close match for that described as '*Phobetor*' by Bakhurina (1986; Bakhurina & Unwin 1995) and some of the details also match the holotype and referred material presented here. A detailed description of the remains of '*Phobetor*' has yet to be produced by either group, so detailed comparisons between this and the *Noripterus* material cannot be made; however, there are some notable differences between the two taxa.

The sole diagnostic characteristic given by Bakhurina (1982) was the shape of the facets on the proximal tibia and these at least appear to be very similar to that of IVPP RV 73001 (although this is partially obscured by the proximal tarsals). Unwin & Bakhurina (2000) suggested that the limbs of the limited and fragmentary '*Phobetor*' holotype were indistinguishable from their counterparts in *Dsungaripterus* and *Noripterus* but that other material confirmed the validity of the Mongolian taxon. However, the femora of IVPP RV 73001 and V 4059 have a pronounced anterior–posterior curvature along the shaft – a characteristic shared by *Dsungaripterus* (Young, 1964); this does not appear to be present in the referred '*Phobetor*' material of Lü *et al.* (2009*b*) as the femur figured has instead a slight lateral curve. The condition of this referred specimen suggests that it has undergone little or no taphonomic distortion and thus this may yet be a significant difference between '*Phobetor*' and other taxa.

The ratio of the tibia to the femur is also distinct – it is very high (>1.8) in IVPP RV 73001 (Fig. 2), but only *c.* 1.7 in the material described by Lü *et al.* (2009*b*). Similarly the ratio of the length of the wing metacarpal to the first wing phalanx is 0.83 in *Noripterus* but 0.88 in the referred material. Given the similar sizes of these animals (humeral lengths of 77 and 84 mm respectively) and the fact that both are likely osteologically mature then these differences are quite marked. Other characteristics also potentially separate this material from *Noripterus*. For example, the humerus illustrated by Lü *et al.* (2009*b*, fig. 2) shows a deltopectoral crest that extends further from the shaft of the humerus but is less dorsoventrally tall compared with that of *Noripterus*.

The coding of Lü *et al.* (2009*a*) for a major phylogenetic analysis that covered numerous pterosaurs includes several differences between *Noripterus* (apparently coded from Young's material) and what they refer to as the 'Tatal pterosaur' (which we infer as their material that was referred to *Noripterus* by Lü *et al.* 2009*b*). Two characteristics refer to major proportions between long bone elements (ratio of humerus to ulna, and of metatarsal III to the tibia) and thus are additional differences to those we identify above. The third scored difference in the datamatrix gives the Tatal pterosaur laterally compressed teeth, but this is scored as absent in *Noripterus* (although, as noted above, we would also consider *Noripterus* to possess this trait). In short, the material of Lü *et al.* (2009*b*) may be synonymous with '*Phobetor*', but both sets of specimens (the '*Phobetor*' material, and in particular the Tatal material) have a number of notable differences with *Noripterus* and suggest that they are distinct taxa.

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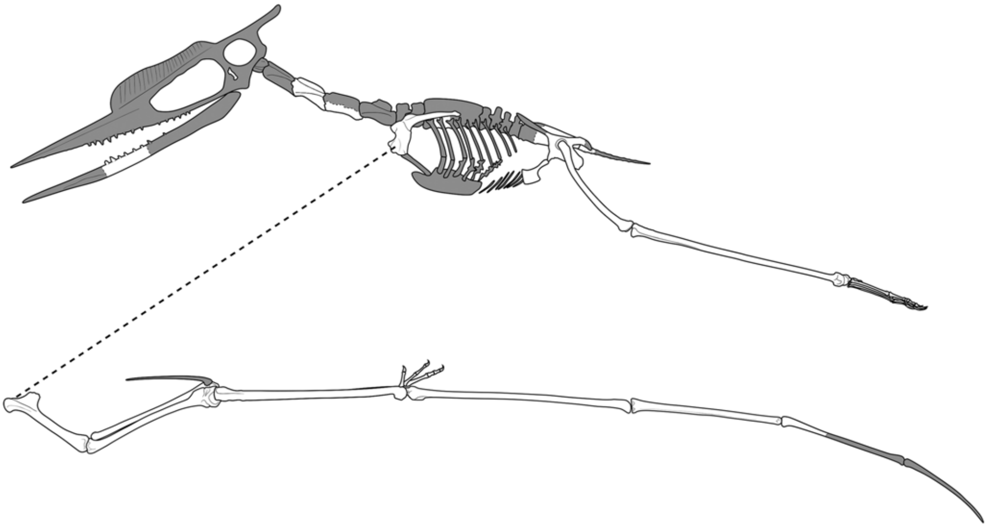

Fig. 5. Reconstruction of *Noripterus complicidens* based on the C.C. Young's material (image by Rebecca Gelernter). Elements known are in white; unknown elements are greyed out. Missing parts are restored based on Lü *et al.* (2009*b*) and Witton (2013, p. 207).

The diagnosis of another dsungaripterid from the Early Cretaceous Tugulu group, *Longchognathosaurus* (Maisch *et al.*, 2004), features characteristics of the cranium which cannot be observed in the *Noripterus* holotype (or currently available material). Only two characteristics can be compared with *Noripterus* and one of these is present in the holotype and thus cannot be considered an apomorphy of *Longchognathosaurus*.

Maisch *et al.*'s (2004) characteristic of 'alveoli not bulbously expanded but surrounded by a low ring of bone' can be seen in at least one alveolus of the *Noripterus* holotype and is thus not diagnostic for *Longchognathosaurus*. This feature also varies within specimens, as can be seen with the anterior most alveoli in the holotype of *Longchognathosaurus* that lack any kind of bone expansion around them (Fig. 4c), but those alveoli that are more posteriorly located do show some bony expansions. This change may represent a continuum along the tooth row from the anterior to posterior teeth and may point to differential use of the jaws in biting. A stronger bite is typically possible at the rear of the jaws and therefore it would make sense that durophagus animals might develop more robust dentition or support for their teeth in this part of the jaw. It is notable that, although badly damaged, the jaw of *Noripterus* also seems to show variation in the degree of bony expansions at the alveoli and thus caution should be used with characteristics based on bone expansions in these taxa.

The second of Maisch *et al.*'s (2004) characteristics is 'Teeth widely spaced (distance between individual tooth positions always more than distomesial length of tooth)', which is also true of *Noripterus*. Although the two taxa have different parts preserved (dentary v. maxilla), the teeth in dsungaripterids are similar in size, shape or spacing between the upper and lowers jaws, so these should be broadly comparable here. *Noripterus* has a range of 1.6–2.4 tooth lengths to spaces between adjoining teeth and this is near identical in *Longchognathosaurus*, being 1.7–2.4 tooth lengths. These both lie in sharp contrast to *Dsungaripterus* that has teeth larger than their successive spaces. The referred '*Phobetor*' material cannot be easily measured from the figures of Lü *et al.* (2009*a*), but they do appear to have relatively large spaces that are comparable with *Noripterus* (Fig. 4).

The proportional length to width of the teeth in these taxa is also very similar, measuring between 1.4 and 1.6 in *Noripterus* and between 1.6 and 1.8 in *Longchognathosaurus* (cf. *Dsungaripterus* mandible measures on an unnumbered IVPP specimens as 1.2–1.5). Although *Longchognathosaurus* is based on maxillae, and the part of *Noripterus* preserving teeth is dentaries, this does leave *Longchognathosaurus* with nothing to distinguish it from *Noripterus*. As a result, this taxon is here suggested to be potentially synonymous with *Noripterus*.

Thus a more detailed and comprehensive comparison is required between the holotypes of *Noripterus*, *Longchognathosaurus* and '*Phobetor*' as well as the undescribed material of '*Phobetor*' and the new material recently referred to *Noripterus*. Provisionally we suggest that '*Phobetor*' is indeed a valid

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genus that is distinct from *Noripterus* (assuming that Bakhurina's Tatal material is the same taxon as that of Lü *et al.*) based on the very different limb proportions, and that *Longchognathosaurus* is likely to be synonymous with *Noripterus* (although Andres *et al.*, 2010 have also suggested it may be synonymous with *Dsungaripterus*, which seems unlikely given the differences in tooth morphology and spacing, and the straight tips of the premaxillae). However, we refrain from making formal revisions here while much of the *Noripterus* holotype remains missing, and the original material of '*Phobetor*' awaits detailed description.

Although a number of specimens of the Dsungaripteridae have been recovered from Asia, few have been described or even illustrated in any detail to date, making comparisons between specimens and putative taxa difficult. However, the renewed access to C.C. Young's material of *Noripterus complicidens* reveals important characteristic information that helps resolve some issues in the taxonomy of the members of this group, and gives a much improved understanding of this intriguing taxon (Fig. 5).

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