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

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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

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Restudy of *Liaoxipterus* (Istiodactylidae: Pterosauria), with comments on the Chinese istiodactylid pterosaurs

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Abstract

Two Chinese istiodactylid pterosaurs *Liaoxipterus* and *Longchengpterus* are re-described in detail. The hyoid apparatus of *Liaoxipterus* is also described. Based on the specimen (*Longchengpterus*), new characters of *Nurhachius* are added: a distinct ridge along the middle line on its ventral surface of the rostral portion of the skull, a distinct groove on the middle line of the dorsal surface of the mandibular symphysis, and a sharp, tooth-like process appears on the central portion of the tip of the lower jaw. Among the four reported Chinese istiodacylid pterosaurs, three of them: *Liaoxipterus*, *Istiodactylus sinensis* and *Nurhachius* are valid. *Longchengpterus* is the synonym of *Nurhachius*. *Haopterus* may be a primitive form of istiodactylid pterosaurs.

Key words: Chinese istiodactylid pterosaurs, Jiufotang Formation, western Liaoning

Zusammenfassung

Zwei chinesische Flugsaurier der Familie *Istiodactylidae*, *Liaoxipterus* und *Longchengpterus*, werden hier im Detail neu beschrieben. Zusätzlch wird der Hyoidbogen von *Liaoxipterus* beschrieben. Basierend auf diesen Individuen (*Longchengpterus*) werden neue Merkmale von *Nurhachius* hinzugefügt: eine deutliche Rippe entlang der Mittellinie auf der ventralen Fläche des Rostrums; eine ausgeprägte Furche in der Mitte der dorsalen Fläche der Mandibularsymphyse und ein scharfer, zahn-ähnlicher Fortsatz im zentralen Teil des vorderen Endes des Unterkiefers. Innerhalb dieser vier chinesischen istiondactylen Flugsaurier sind *Liaoxipterus*, *Istiodactylus sinensis* und *Nurhachius* valide. *Longchengpterus* ist das Synonym für *Nurhachius. Haopterus* könnte eine primitive Form eines istiodactylen Flugsauriers sein.

Schlüsselwörter: Chinesische istiodactyle Flugsaurier, Jiufotang Formation, West-Liaoning

摘要：本文详细地重新描述了产自中国的两件帆翼龙类标本：辽西翼龙和龙城翼龙，同时对辽西翼龙的舌骨器官也进行了记述。根据新的标本（龙城翼龙），补充了努尔哈赤翼龙的以下特征：头骨吻端腹面沿中线方向具有一明显的脊，下颌缝合部背面沿中线具有一明显的沟以及下颌吻端中部具有尖锐的牙齿状突起。在 4 件已报道的中国的帆翼龙中，其中 3 个属种：辽西翼龙、中国帆翼龙及努尔哈赤翼龙是有效的。龙城翼龙是努尔哈赤翼龙的同物异名。郝氏翼龙可能是帆翼龙的原始类群。

关键词：中国的帆翼龙，九佛堂组，辽西

1. Introduction

Liaoxipterus brachyognathus was the first istiodactylid pterosaur reported from China and it was initially assigned to the Ctenochasmatidae, based on the lower jaw and the tooth number, which is smaller than in typical ctenochasmatid pterosaurs (Dong & Lü 2005). However, further repairing of the specimen shows that the tooth and lower jaw morphologies of *Liaoxipterus* are similar to those of *Istiodactylus* (Howse et al. 2001), and the systematic analysis also supports that it belongs to istiodacylid pterosaurs, thus it is reassigned to Istiodactylidae (Lü et al. 2006). Before the discovery of Chinese istiodactylid pterosaurs, Istiodactylidae was a monospecific family containing only *Istiodactylus latidens* (Seeley 1901), known from the Early Cretaceous Vectis Formation of the Isle of Wight (Howse et al. 2001). Seeley (1901) named the holotype *Ornithodesmus latidens*, referring to a genus he had erected for a synsacrum from the Isle of Wight (Seeley 1887). Hooley (1913) later referred two specimens, BMNH R3877 and BMNH R3878, to O. latidens. Howse & Milner (1993) re-identified the material of the type species of *Ornithodesmus* as belonging to a theropod dinosaur. Later, Howse et al. (2001)

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erected the genus *Istiodactylus* and family Istiodactylidae for *'O.' latidens*. At present, four species and three genera of istiodactylid pterosaurs have been reported from the Jiufotang Formation (*Liaoxipterus brachyognathus* Dong & Lü, 2005; *Nurhachius ignaciobritoi* Wang et al., 2005; *Longchengpterus zhaoi* Wang Li et al., 2006; *Istiodactylus sinensis* Andres & Ji, 2006). *Liaoxipterus* is distinguished from *Nurhachius ignaciobritoi* and *Longchengpterus zhaoi* by the wide rostral end of the lower jaw, but it is difficult to compare it with that of *Istiodactylus sinensis*, whose lower jaw is exposed in lateral view, so that it is not known whether the rostral end of the lower jaw is broad or pointed. The lower jaw and tooth morphologies of *Nurhachius ignaciobritoi* and *Longchengpterus zhaoi* are identical, thus both are regarded as belonging to the same species. *Longchengpterus zhaoi* is a junior synonym of *Nurhachius ignaciobritoi*. *Liaoxipterus brachyognathus* (Dong & Lü 2005) and *Longchengpterus zhaoi* are restudied, all these provide more information on the study of the Chinese istiodactylid pterosaurs.

Abbreviations: BMNH, British Museum of Natural History; CAR: Jilin University; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; LPM: Liaoning Paleontological Museum at Western Liaoning Institute of Mesozoic Paleontology, Shenyang Normal University; NGMC, the National Geological Museum of China, Beijing, People's Republic of China.

2. Systematic Palaeontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Dsungaripteroidea Young, 1964
Istiodactylidae Howse, Milner & Martill, 2001

Liaoxipterus brachyognathus Dong & Lü, 2005

Emended Diagnosis: Rostral end of the lower jaw expanded, 26 lower jaw teeth, tooth bearing cingulum on the lingual surfaces, hyoid apparatus Y-shaped, ratio of the length of the mandibular symphysis to the lower jaw length is about 0.25.

2.1 Redescription of *Liaoxipterus* (CAR-0018)

Most of the lower jaw is relatively well preserved, but the distal portions of both branches and most teeth are missing (Fig. 1A; Tab. 1). In dorsal view, the distal end of the lower jaw is expanded, similar to that of *Istiodactylus latidens* (Seeley 1901; Howse et al. 2001), but differs from that of *Nurhachius ignaciobritoi* (Wang et al. 2005) and *Longchengpterus zhaoi* (Wang Li et al. 2006), in which the distal end of the lower jaw is pointed (Fig. 2). Inferred from the shapes and sizes of the anterior teeth on the tip of the lower jaw, which pointed anterolaterally, all the teeth are the same in sizes and shapes. Four nearly complete teeth are preserved on the left side. Other teeth are preserved either as tooth impressions or tooth roots or just tooth sockets. The tooth number on the left side of the jaw is 13. It is uncertain on the right side due to the poor preservation. But it is probably the same as on the left side. Thus the total tooth number for the lower jaw is about 26. All the teeth are rhombic. The length of the tooth root is longer than that of the crown. Four tooth roots are preserved in the rostral end. Among the preserved teeth, the maximum width of the tooth is 3.52 mm, and the tooth root length is 5.02 mm. The teeth are labiolingually compressed, similar to those of *Nurhachius ignaciobritoi* (Wang et al. 2005). The tooth roots of the anterior teeth are longer than those of the posterior teeth. The lingual surface of the teeth is smooth with a distinct boundary between the root and the crown. The boundary is delimited by a cingulum (Fig. 3A). The cross-section of the crown base is sub-oval. The interdental spaces between the anterior teeth are small, however, from the space between the seventh and eighth teeth, it becomes larger, and is largest between the two posteriormost teeth (Tab. 2). All the teeth extend laterodorsally. A nearly complete hyoid apparatus is well-preserved between the mandibular branches, and it seems to be preserved in situ. The hyoid apparatus is a Y-shaped group of small bones. The length of the corpus including the hypohyal or lingual process is 26.3 mm, and the diameter of the corpus is 1.27 mm. The whole length of the hyoid apparatus (from the tip of the lingual process to the distal end of the ceratobranchial II) is 107.85 mm. The divarication of the ceratobranchial II is 21°. The highly elongated lingual process of the hyoid apparatus in *Liaoxipterus* is similar to that of *Chameleon* (Kardong 1998), which has a lingual feeding behavior, while the elongated ceratobranchial II is similar to that of *Vipera*. The similar structure of the hyoid between *Liaoxipterus* and *Chameleon* may indicate that *Liaoxipterus* may also have had a lingual feeding behavior and may have been an insect-eating pterosaur.

Table 1: Measurements of the lower jaw of *Liaoxipterus* (in cm)

Elements	
Jaw length	15.7(preserved); 18.2(estimated)
Mandibular symphysis length	4.5
Rostral end width	1.7 (preserved); 18 (estimated)
Angle formed by two branches	28°
Maximum width of both branches	4.8
Hyoid diameter	0.127
Fused portion length	2.63
Hyoid whole length	10.79
Length of each branch	8.18
Angle formed by two branches	21°

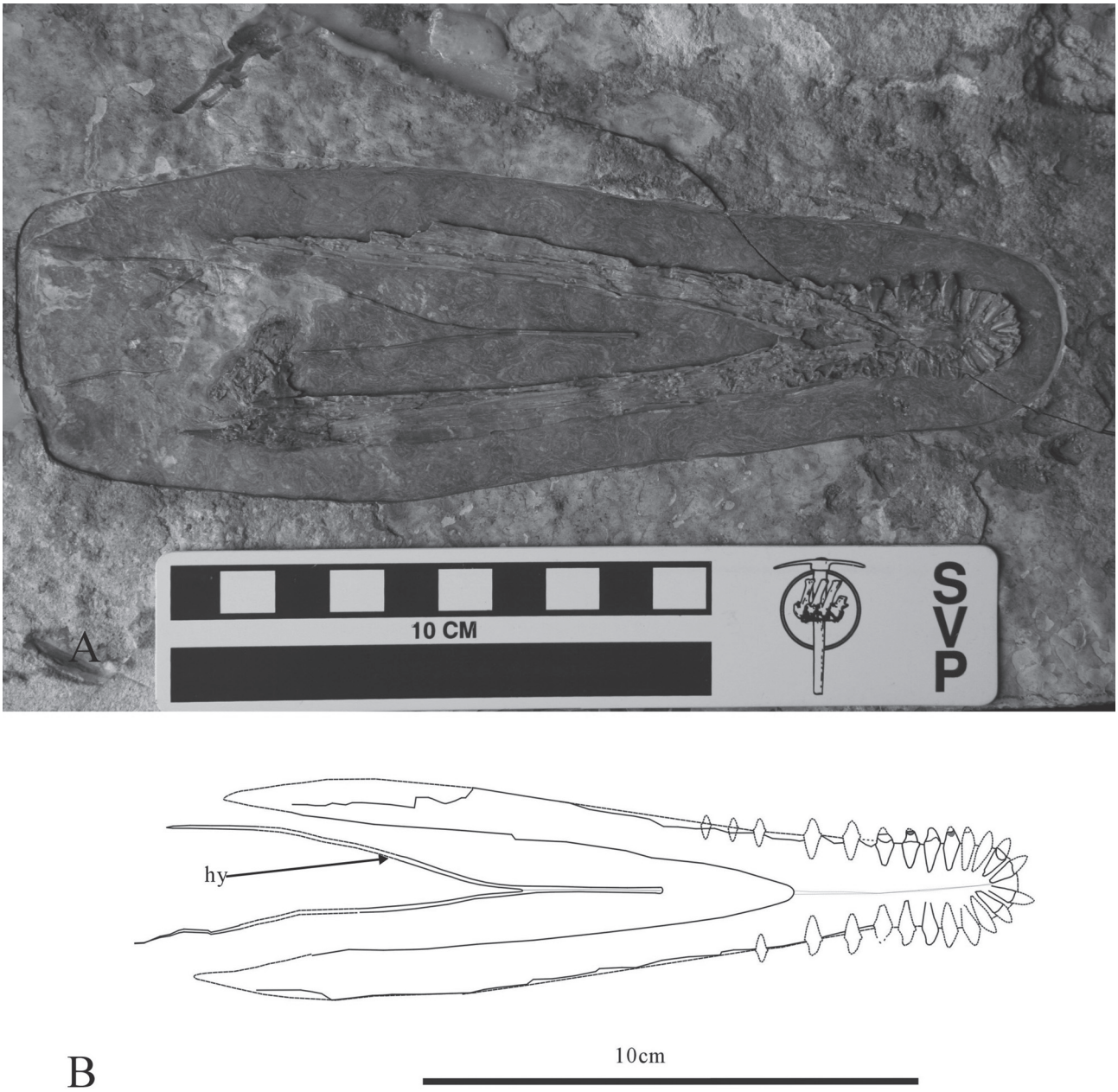

Figure 1: Photograph (A) and line drawings of *Liaoxipterus brachyognathus*. Abbreviation: hy, hyoid.

2.2 Redescription of *Longchengpterus (Nurhachius)*

Longchengpterus (LPM0003)(=*Nurhachius* (IVPP V-13288)) was briefly described by Wang Li et al. (2006), and the detailed description is as follows: The skeleton is almost complete with both skull and lower jaw preserved (Fig. 4; Tab. 3). The posterior part of the skull is exposed on the right side and its anterior portion is exposed ventrolaterally (Fig. 2B). The nasoantorbital opening is large and triangular in lateral view. The rostrum is low with a straight dorsal outline.

The quadrate is obliquely orientated and is inclined about 150° backwards relative to the ventral margin of the skull. The position of the articulation between the skull and mandible is under the anteroventral corner of the orbit. The orbit is pear-shaped, and the position of the orbit relatively to the nasoantorbital fenestra is nearly the same level. The right tooth row is exposed, however, the number of tooth sockets is not clear due to the lack of the anterior part of the upper jaw. The preserved part of the rostral portion of the skull indicates that there is a distinct ridge along the middle line on its ventral surface.

The lower jaw is almost completely preserved. The retroarticular process is long. The jaw does not have a helical jaw joint. The dorsal margin of the lower jaw is nearly straight in lateral view, and there is no coracoid eminence. There are nine teeth on each side of the lower jaw. All the teeth are located anterior to the posterior margin of the mandibular symphysis. A distinct groove appears on the middle line of the dorsal surface of the mandibular symphysis. A sharp, tooth-like process appears on the middle part of the tip of the lower jaw and this process is located between the two anteriormost teeth. The two anteriormost teeth extend anterodorsally. The third tooth are ori-

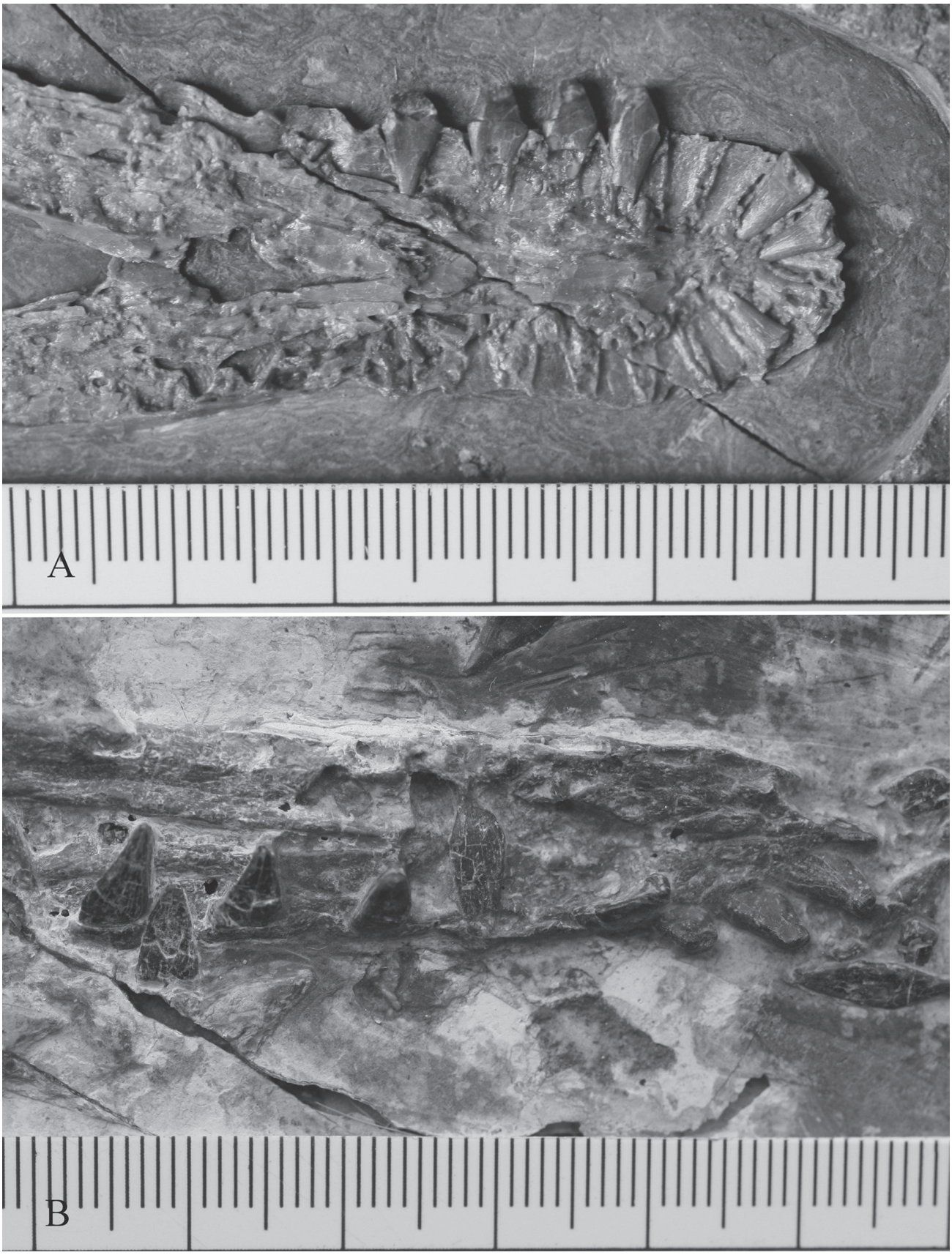

Figure 2: Rostral end comparisons of the lower jaws of *Liaoxipterus brachyognathus* (A), and *Longchengpterus zhaoi* (B). Scale bars are in centimeters.

ented laterodorsally and slightly anteriorly, and the posterior teeth extend dorsomedially. The mandibular rami are nearly at the same level with the symphysis. The tooth sockets are rectangular, small and elongated. The teeth are labiolingually compressed with a sharp tip, and the alveolar margin of the lower jaw is slightly bent upward, which is similar to the con-

Table 2. Measurements of the spaces between teeth of *Liaoxipterus* (in mm)

Tooth No.	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12
Distance	0.37	0.37	0.37	0.37	0.37	0.37	1.78	3.2	5.1	5.5	7.40

dition in the holotype of *Nurhachius ignaciobritoi*. The medial surface of the teeth is flat and their lateral surface is slightly convex without a ridge, unlike the case in *Istiodactylus sinesis* (Andres & Ji 2006).

There are five cervical vertebrae preserved. The atlantoaxis is fused and exposed on its right side. Its anterior articular end is concave and there is no pleurocoel on the lateral surface.

The scapula and coracoid are fused into a scapulocoracoid. The distal ends of the scapula and coracoid are slightly expanded. The shaft of the scapula is straight. There is a broad tubercle on the ventroposterior margin of the coracoid. The distal end of the humerus is wider than its proximal end. There is no pneumatic opening on the proximal end of the humerus. The shaft of the humerus is expanded distally. Both ulna and radius are straight and the same length. The ulna is much wider than the radius. The ratio of the diameter of ulna to radius is 2.5. The proximal end of the ulna is slightly expanded. The distal end of the radius is much more expanded than its proximal end. The wing metacarpal is straight and relatively short. The proximal end of the wing metacarpal is slightly expanded. Three wing phalanges are preserved. The fourth wing phalanx is missing. The olecranon-like extensor tendon process is fused with the

Table 3: Measurements of *Longchengpterus* (= *Nurhachius*) (mm)

	Length	Width
Skull	263.9	-
Nasoantorbital opening	91.8	25.3 (height: posterior margin)
Lower jaw	226.9	-
Mandibular symphysis	77.2	-
Isolated upper jaw tooth	14.7	-
Complete upper jaw teeth 1,2,3	13.3, 11.1,11.2	3.8,3.9,3.8
atlantoaxis	17.9	-
Third cervical vertebra	26.5	
Fourth cervical vertebra	28.3	
Fifth cervical vertebra	28.2	12.6
Scapula	44.5	6.5 (shaft)
Coracoid	56.3	9.3 (shaft)
Humerus	88.3	19.6 (shaft)
Ulna	156	15
Radius	156	6
Pteroid	12	-
Metacarpal IV	101	11
Wph1	188	12.5
Wph2	157	9
Wph3	120	6
Femur	100	8

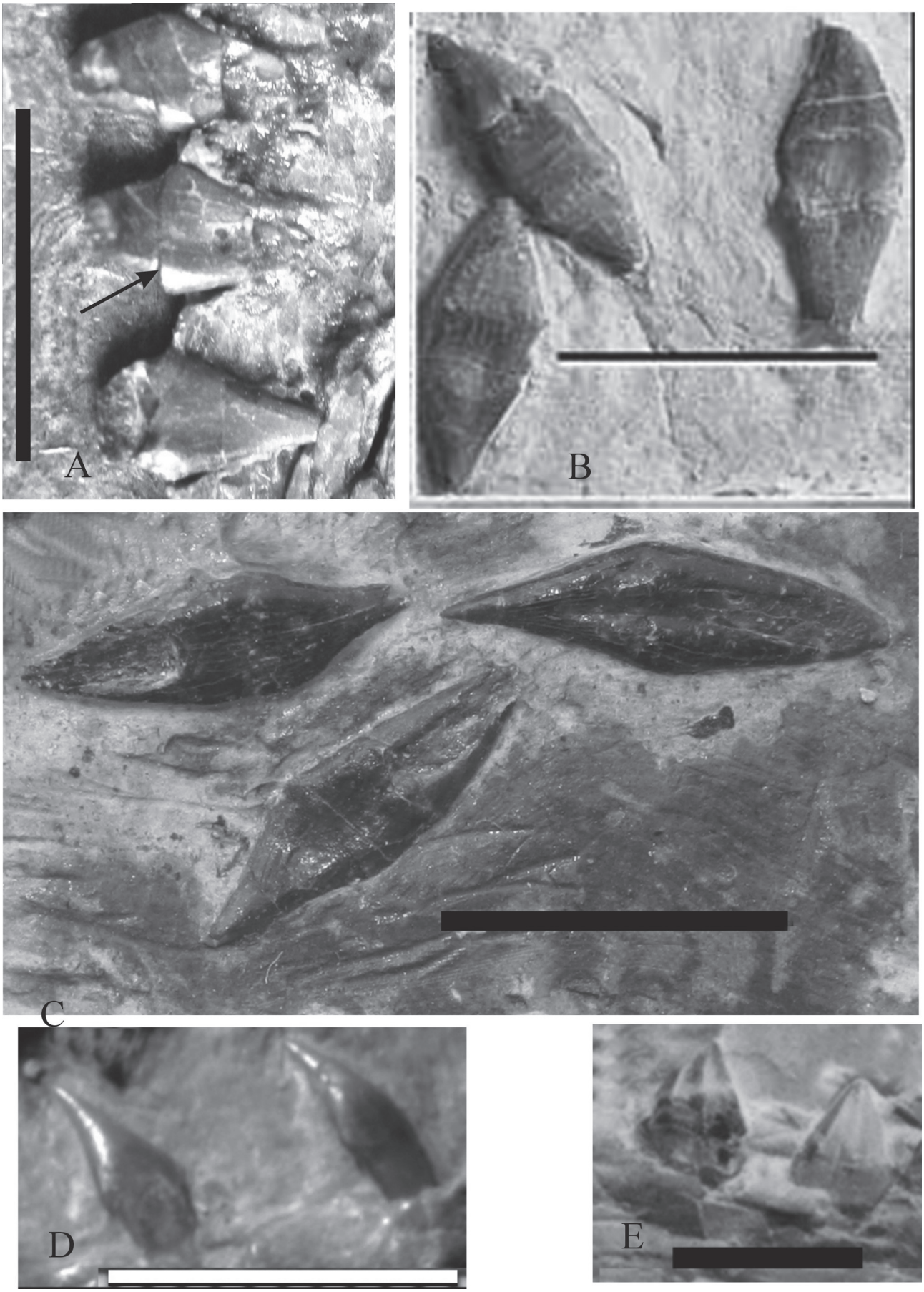

Figure 3: Comparison of the teeth of Chinese istiodactylid pterosaurs, A: *Liaoxipterus brachyognathus*, showing a cingulum on the tooth (arrow points); B: *Nurhachius ignaciobritoi* (from Wang et al. 2005); C: *Longchengpterus zhaoi*; D: *Haopterus gracilis*; E: *Istiodactylus sinensis*. Scale bars = 1 cm.

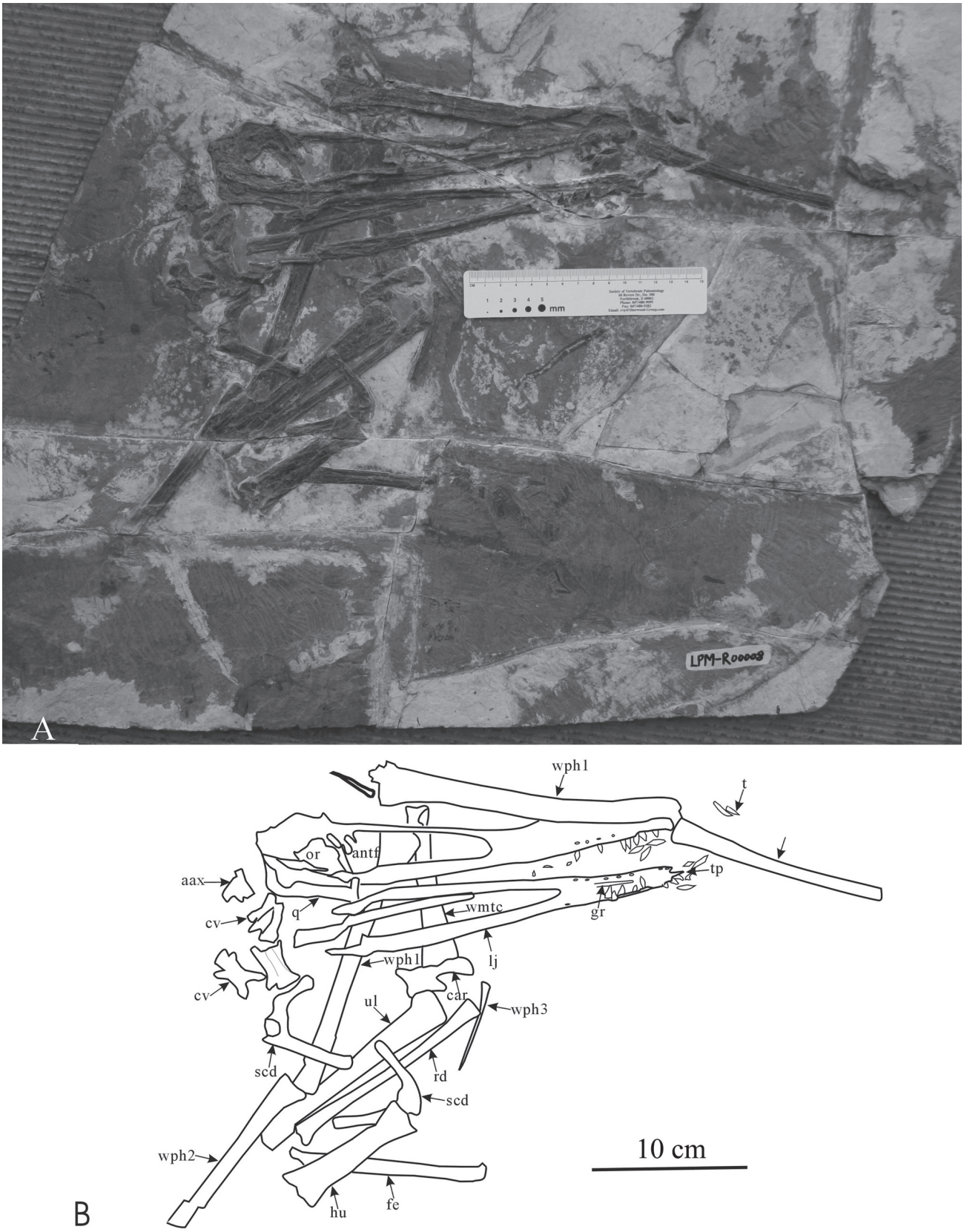

Figure 4: Photograph (A) and outline drawings (B) of *Longchengpterus zhaoi* (= *Nurhachius ignaciobritoi*). Abbreviations: aax, atlantoaxis; antf, nasoantorbital fenestra; car, carpals; cv, cervical vertebrae; fe, femur; gr, groove; hu, huerus; lj, lower jaw; or, orbit; q, quadrate; rd, radius; scd, scapulocoracoid; t, teeth; tp, tooth-like process; ul, ulna; wmtc, wing metacarpal; wph1–3, wing phalanges 1–3.

proximal end of the first wing phalanx, indicating that it is an adult individual. A distinct pneumatic opening is present on the extensor tendon process. Both the first and second wing phalanges are slightly curved posteriorly. A short displaced metacarpal indicates that the metacarpals do not reach the proximal carpals. The manual claw is large. The distal carpals are fused into a rectangular unit. The femur is completely preserved, however its distal end is covered by the humerus. The femoral head is ball-shaped with a distinct neck. The angle formed by the neck and the femoral shaft is about 25°.

3. Discussion

Among the toothed pterosaurs found in western Liaoning and its surrounding areas, *Haopterus* Wang & Lü, 2001 is the only one whose posterior tooth morphologies are close to those of istiodactylid pterosaurs, although their tips are much sharper than in the typical istiodactylid pterosaurs (Fig. 3). The phylogenetic analysis also shows that *Haopterus* is basal to istiodactylid pterosaurs (see Lü et al. 2006: fig. 4.9). *Haopterus* may be a primitive istiodactylid pterosaur.

Liaoxipterus, Nurhachius, Istiodactylus sinensis, and *Longchengpterus* are assigned to Istiodactylidae, based on the following characters: skull elongated, but with short snout region anterior to nostrils, extensive nasoantorbital fenestra occupying much of the snout (*Nurhachius, Istiodactylus sinensis*, and *Longchengpterus*), mandible with an abbreviated symphysis, all teeth labiolingually compressed with sharply pointed crowns and truncated triangular roots shorter than crowns (Howse et al. 2001). All the Chinese istiodactylid pterosaurs are smaller than *Istiodactylus latidens*. Among the four reported Chinese istiodactylid pterosaurs, *Liaoxipterus* is easy to separate from *Nurhachius ignaciobritoi* (Wang et al. 2005), and *Longchengpterus zhaoi* (Wang Li et al. 2006), based on their lower jaw morphologies (Fig. 2); but it is difficult to separate from *Istiodactylus sinensis*, because the tip of the lower jaw of *Istiodactylus sinensis* is preserved lateromedially, and it is not clear whether the tip of the lower jaw is expanded or pointed.

Nurhachius ignaciobritoi was the second istiodactylid pterosaur found from China (Wang et al. 2005). The tooth morphology and lower jaw tooth number of *Nurhachius* (Wang et al. 2005: fig. 2b) are similar to those of *Liaoxipterus*. However, *Nurhachius* differs from *Liaoxipterus* in that there are two tiny anteriorly projecting teeth on the tip of the lower jaw (Wang et al. 2005), the anterior teeth on the tip of the lower jaw are the same in size and shape and project anterolaterally in *Liaoxipterus*. The teeth of *Liaoxipterus* bear a distinct cingulum, which separates the crown from the root (Fig. 3A), whilst the teeth of *Nurhachius (Longchengpterus)* do not bear a cingulum (Fig. 3B,C). The tiny anteriorly projecting teeth on the tip of the lower jaw indicate that the tip of the lower jaw is pointed rather than expanded, similar to that of *Longchengpterus zhaoi* (Wang Li et al. 2006). According to the size of the lower jaw, *Nurhachius* is larger than *Liaoxipterus*. Except for the difference of the tip of the lower jaw, other characters of the lower jaws (tooth number, and labiolingually compressed teeth with a cingulum) of the two pterosaurs are identical. If the shape of the tip of the lower jaw (pointed or expanded) is not caused by sexual dimorphism, they may represent different genera of Istiodactylidae, otherwise, they belong to the same genus. If they belong to the same genus, *Nurhachius* is a junior synonym of *Liaoxipterus*.

Istiodactylus sinensis (NGMC 99-07-011) is the third istiodactylid pterosaur reported from China (Andres & Ji 2006). According to the size of the skull, it is the largest Chinese istiodactylid pterosaur hitherto reported. The tooth number of *Istiodactylus sinensis* is the highest among the Chinese istiodactylid pterosaurs. The tooth morphologies are slightly different from those of *Liaoxipterus*, *Nurhachius* and *Longchengpterus* in that they are relatively wider and shorter and some teeth have a slight medial carina in *Istiodactylus sinensis* (Andres & Ji 2006).

Longchengpterus zhaoi is the fourth reported Chinese istiodactylid specimen. Because the skull shape and tooth morphology of *Nurhachius ignaciobritoi* (Wang et al. 2005) and *Longchengpterus zhaoi* (Wang Li et al. 2006) are identical (Fig. 2B,C), they belong to the same species. Therefore, *Longchengpterus* is a junior synonym of *Nurhachius*. Based on the new specimen *(Longchengpterus)*, the new added characters of *Nurhachius* are: a distinct ridge along the middle line on the ventral surface of the rostral portion of the skull, a distinct groove on the middle line of the dorsal surface of the mandibular symphysis, and a sharp, tooth-like process on the central portion of the tip of the lower jaw.

The phylogenetic positions of Chinese istiodactylid pterosaurs: In order to determine the phylogenetic positions of Chinese istiodactylid pterosaurs within the pterodactyloid pterosaurs, the characters were scored based on the modified data/matrix of Kellner (2004) (see Lü et al. 2006). The character descriptions and data/matrix are listed in Appendix 1. The 50% majority-rule tree of 34000 most parsimonious trees (Fig. 5) shows that *Haopterus* is basal to the istiodactylid pterosaurs, and it may be a primitive istiodactylid pterosaur; *Longchengpterus zhaoi* and *Istiodactylus sinensis* form a sister group, which indicates that they may belong to same species.

4. Conclusions

Among the four reported Chinese istiodactylid pterosaurs, *Liaoxipterus brachyognathus*, *Istiodactylus sinensis* and *Nurhachius ignaciobritoi* are valid names. *Longchengpterus zhaoi* is a junior synonym of *Nurhachius ignaciobritoi*. *Haopterus gracilis* may be a primitive form of istiodactylid pterosaur. The different shapes of the tip of the lower jaw of *Liaoxipterus* (expanded) and *Nurhachius* (pointed) may be caused by sexual dimorphism. However, further confirmation of this needs more specimens. At present, *Nurhachius* is temporarily regarded as a valid genus.

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Figure 5: The cladogram of pterodactylid pterosaurs, based on the 50% majority-rule of 34000 most parsimonious trees, employed 45 taxa (ingroups) and 80 characters.

by the DFG to Lü JC. Thanks to K. Moser for the translation of the abstract into German.

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Appendix 1

The character descriptions and date/matrix are used for phylogenetic analysis (Lü et al. 2006; most of them are chosen from Kellner 2004): 0 = plesiomorphic character state; 1~7 = derived character states; ? = missing data; – = character not applicable.

Skull

1. Dorsal margin of the skull: Straight or curved downwards (0), concave (1), wave like (2) (modified).
2. Lower jaw: lateral compressed (0), comparatively broad (1), (modified).
3. Rostral part of the skull anterior to the external nares: reduced (0), elongated (less than half of skull length) (1), extremely elongated (more than half of skull length) (2).
4. Rostral end of premaxillae/maxillae downturned: absent (0), present (1).
5. Posterior margin of nasoantorbital fenestra: straight (0), concave (1) (from Unwin, 2003).
6. Position of the external naris: above the premaxillary tooth row (0), displaced posterior to the premaxillary tooth row (1).
7. Orbit: smaller than the antorbital opening (0), larger than the antorbital opening (1) (from Unwin, 2003).
8. Naris and antorbital fenstra: separated (0), confluent, short than 45% of the skull length (1), confluent, longer than 45% of the skull length (2).
9. Orbit comparatively small and positioned very high in the skull absent (0), present (1).
10. Orbit pear-shaped: absent (0), present (1).
11. Position of the orbit relatively to the nasoantorbital fenestra (naris+antorbital fenestra): same level or higher (0), orbit lower than the dorsal rim of the nasoantorbital fenestra (1).
12. The tip of the lower jaw: pointed (0), expanded (1).
13. Premaxillary sagittal crest: absent (0), confined to the anterior portion of the skull (1), high, displaced backwards, near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit, and extending backwards (2), low, displaced backwards near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit but not extending backwards (3), starting at the anterior portion of the skull and extended posteriorly above the occipital region (4), starting at the posterior half of the nasoantorbital fenestra (5), low, positioned in the middle portion of the rostrum not reaching the nasoantorbital fenestra (6), low, positioned in the middle portion of the rostrum extending until the middle part of the nasoantorbital fenestra (7).
14. Tip of the premaxilla expanded: absent (0), present, wih premaxillary end high (1), present, with premaxillary end dorsoventrally flattened (2).
15. Posterior ventral expansion of the maxilla: absent (0), present (1).
16. Rostrum: high, with convex outline (0), low with straight or concave dorsal outline (1), anterior region of rostrum low, but antorbital region expanded dorsally (2), anterior region of rostrum high, but antorbital region flat (3) (modified from Unwin, 2003).
17. Foramen on nasal process: absent (0), present (1).
18. Caudal end of mandible with distinct dorsal 'coronoid' eminence: present (0), absent (1) (from Unwin, 2003).
19. Bony frontal crest: absent (0), low and blunt (1), low and elongated (2), high and expanded posteriorly (3).
20. Bony parietal crest: absent (0), present, blunt (1), present, laterally compressed and posteriorly expanded, with a rounded posterior margin (2), present, consisting the base of the posterior portion of the cranial crest (3).
21. Posterior region of the skull rounded with the squamosal displaced ventrally: absent (0), present (1).
22. Position of the quadrate relative to the ventral margin of the skull: vertical or subvertical (0), inclined about 120° backwards (1), inclined about 150° backwards (2).
23. Position of the articulation between the skull and mandible: under the posterior half of the orbit or further backwards (0), under the middle part of the orbit (1), under the anterior half of the orbit (2).
24. Helical jaw joint: absent (0), present (1).
25. Supraoccipital: does not extend backwards (0), extends backwards (1).
26. Foramen pneumaticum piercing the supraoccipital: absent (0), present (1).
27. Expanded distal ends of the paroccipital processes: absent (0), present (1).
28. Nasal process of maxilla: vertical-subvertical (0), inclined backwards (1) (from Unwin, 2003).
29. Palatal ridge: absent (0), present (1) (modified).
30. Maxilla-nasal contact: narrow (0), broad (1), absent (2) (modified from Unwin, 2003).
31. Mandubular rami: at the same level (0), elevated well above symphysis (1) (from Unwin, 2003).
32. Mandibular symphysis: absent or very short (0), present, at least 30% of mandibular length (1).
33. Anterior tip of the dentary downturned: absent (0), present (1).
34. Ventral margin of skull: straight or slightly convex (0), curved downwards (1) (modified from Unwin, 2003).
35. Dentary bony sagittal crest: absent (0), blade-like and shallow (1), massive and deep (2) (modified).
36. Position and present of teeth: teeth present, evenly distributed along the jaws (0), teeth absent from the anterior portion of the jaws (1), teeth confined to the anterior part of the jaws (2), jaw toothless (3).
37. Location of largest teeth: rostral half of dentition (0), caudal half (1) (from Unwin, 2003).
38. Variation in the size of the anterior teeth in the upper and lower: absent (0), present (1) (modified).
39. Teeth with a broad and oval base (dsungaripterid-like tooth): absent (0), present (1) (modified).
40. Multicusped teeth: absent (0), present (1).
41. Peg-like teeth: absent (0), present, 15 or less on each side of the jaws (1), present, more than 15 on each side of the jaws (2).
42. Long slender teeth (Ctenochasma-like tooth): absent (0), present (1) (modified).
43. Laterally compressed and triangular teeth: absent (0), present (1).

Axial skeleton

44. Notarium: absent (0), present (1).
45. Atlas and axis: unfused (0), fused (1).
46. Postexapophyses on cervical vertebrae: absent (0), present (1).
47. Lateral pneumatic foramen on the centrum of the cervical vertebrae: absent (0), present (1).
48. Mid-cervical vertebrae: short, subequal in length (0), elongated (1) (modified).
49. Cervical ribs on mid-cervical vertebrae: present (0), absent (1).
50. Neural arch of the mid-cervical vertebrae: high with high neural spine (0), low with low neural spine or the spine absent (1) (modified from Unwin, 2003).
51. Number of caudal vertebrae: more than 15 (0), 15 or less (1).

Pectoral girdle

52. Length of the scapula: subequal or longer than coracoid (0), scapula shorter than coracoid (1>sca/cor>0.8) (1), substantially shorter than coracoid (sca/cor<0.8) (2).
53. Proximal surface of scapula: elongated (0), sub-oval (1).
54. Shape of scapula: elongated (0), stout, with constructed shaft (1).
55. Coracoidal contact surface with sternum: no developed articulation surface (0), articulation surface flattened, lacking posterior expansion (1), articulation surface oval, with posterior expansion (2).
56. Deep coracoidal flange: absent (0), present (1).
57. Broad tubercle on ventroposterior margin of coracoid: absent (0), present (1).
58. Cristospine: absent (0), shallow and elongated (1), deep or short (2).

Forelimb

59. Proportional length of the humerus relative to the metacarpal IV (hu/mcIV): hu/mcIV>2.50 (0), 1.5<hu/mcIV<2.5 (1), 0.4<hu/mcIV<1.5 (2), hu/mcIV<0.40 (3).
60. Proportional length of the humerus relative to the femur (hu/fe): hu/fe≤0.8 (0), 1.4>hu/fe>0.8 (1), hu/fe>1.40 (2) (modified).
61. Proportional length of the humerus + ulna relative to the femur + tibia (hu+ul/fe+ti): humerus plus ulna about 80% or less of femur plus tibia length (hu+ul/fe+ti<0.8) (0), humerus plus ulna larger than 80% of femur plus tibia length (hu+ul/fe+ti>0.8) (1).
62. Pneumatic foramen on the proximal part of the humerus: absent (0), present on ventral side (1) (modified).
63. Pneumatic foramen on the proximal part of the first wing phalange: absent (0), present (1).
64. Deltopectoral crest of humerus with elongate rectangular profile: absent (0), present (1) (from Unwin, 2003).
65. Metacarpals I-III: disparate lengths (0), the same length (1) (from Unwin, 2003).
66. Distal end of the humerus: oval or D-shaped (0), subtriangular (1).
67. Proportional length of the ulna relative to the metacarpal IV (ul/mcIV): ulna 3.6 times longer than metacarpal IV (ul/mcIV>3.6) (0), length of ulna between four and two times the length of metacarpal IV (3.6>ul/mcIV>2) (1), ulna less than two times the length of metacarpal IV (ul/mcIV<2) (2).
68. Diameter of radius and ulna: subequal (0), diameter of the radius about half that of the ulna (1), diameter of the radius less than half that of the ulna (2).
69. Distal syncarpals: unfused (0), fused in a rectangular unit (1), fused in a triangular unit (2).
70. Pteroid: absent (0), present, shorter than half the length of the ulna (1), present, longer than half the length of the ulna (2).
71. Metacarpals I-III: articulating with carpus (0), metacarpal III articulates with carpus, metacarpals I and II reduced (1), not articulating with carpus (2).
72. Proportional length of the first phalanx of manual digit IV relative to the metacarpal IV (ph1d4/mcIV): both small and reduced (0), both enlarged with ph1d4 over twice the length of mcIV (1), both enlarged with ph1d4 less than twice the length of mcIV (2).
73. Proportional length of the first phalanx of manual digit IV relative to the tibiotarsus (ph1d4/ti): ph1d4 reduced (0), ph1d4 elongated and less than twice the length of ti (ph1d4/ti smaller than 2.00) (1), ph1d4 elongated about or longer than twice the length of ti (ph1d4/ti subequal /larger than 2.00) (2).
74. Proportional length of the second phalanx of manual digit IV relative to the first phalanx of manual digit IV (ph2d4/ph1d4): both short or absent (0), elongated with the second phalanx about the same size or longer than first (ph2d4/ph1d4 larger than 1.0) (1), elongated with the second phalanx up to 30% shorter than first (ph2d4/ph1d4 between 0.7 and 1.0) (2), elongated with the second phalanx more than 30% shorter than first (ph2d4/ph1d4 smaller than 0.7) (3).
75. Deltopectoral crest of humerus tonge-shaped, with necked base: absent (0), present (1) (from Unwin, 2003).
76. Unguals of manus and pes: simialr in size (0), manual unguals twice the size, or more, of the pedal unguals (1) (from Unwin, 2003).

Hindlimb

77. Proportional length of the femur relative to the metacarpal IV (fe/mcIV): femur about twice or longer than metacarpal IV (fe/mcIV>2.0) (0), femur longer but less than twice the length of metacarpal IV (1.0<fe/mcIV<2.0) (1), femur about the same length or shorter than metacarpal IV (fe/mcIV<1.0) (2).
78. Length of metatarsal III: more than 30% of the tibia length (0), less than 30% of the tibia length (1).
79. Fifth pedal digit: with four phalanges (0), with two phalanges (1), with 1 or no phalanx (extremely reduced) (2).
80. Last phalanx of pedal digit V: reduced or absent (0), elongated, straight (1), elongated, curved (2), elongated, very curved (boomerang-shaped) (3).

Pterodactylus kochi
001001-10000000101001 21?0?0-02010000000020000001111000100121100110 21?20212012020

Pterodactylus antiquus
001001-10000000101001 21?0?0-02010000000020000001111000100121100110 21?10212012020

Germanodactylus cristatus
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Germanodactylus rhamphastimus
001001-10000300101001 21?0??-?20?000000002000???11???001???211??11021???21?002???

Ctenochasma gracile
102001-10?0000010100121?0?0-?20100000000010??00111??001???211??11?21???212?02020

Pterodaustro guinazui
102001-10000000101001 21?0?0-?20100000000010???01111?001???211??1102?1??212002020

Gallodactylus canjuersensis
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Cycnorhamphus suevicus
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Nyctosaurus gracilis
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Nyctosaurus bonneri
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Pteranodon longiceps
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Istiodactylus latidens
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Anhanguera santanae
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Anhanguera blittersdorffi
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Anhanguera piscator
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00222111100122?1120012120

Dsungaripterus weii
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10?2200??110211?0212002120

Phobetor parvus
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Noripterus complicidens
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001?110211??212?02120

Tupuxuarara leonardii
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Thalassodromeus sethi
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Tapejara wellnhoferi
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Tapejara imperator
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Quetzalcoathus sp.
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Azhdarcho lancicollis
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?101?0?????????????

Beipiaopterus chenianus
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Boreopterus cuiae
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??2111????21?1?212?12120

Zhejiangopterus linhaiensis
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Sinopterus dongi
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02010110?2001?212002120

Sinopterus gui
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211??1??2001?21?0?2???

Jidapterus edentus
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Haopterus gracilis
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12????01022110?201??20

Chaoyangopterus zhangi
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00?1???2??222130?2120

Liaoningopterus gui
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Liaoxipterus brachyognathus
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Huaxiapterus jii
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201111002102121200 21??

Eopteranodon lii
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11??1??2102?2120?21??

Feilongus youngi
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Nurhachius ignaciobritoi
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Eosipterus yangi
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Huaxiapterus quingyangensis
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211??11?21??0212??2120

Huanxiapterus corallus
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10?111?21?122130?21??

Gegepterus changi
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0???????????0?0?0?????????

Istiodactylus sinensis
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11?21?010??22??22?20?2???

Longchengpterus zhaoi
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????????01?1??-???????