

PRELIMINARY RESULTS OF A PHYLOGENETIC ANALYSIS OF THE PTEROSAURS FROM WESTERN LIAONING AND SURROUNDING AREAS

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Abstract: Many pterosaurs were found recently in western Liaoning and the surrounding areas. Of the 17 genera and 18 species named, only four genera can be assigned confidently to known families. Due to the incompleteness of pterosaur remains (some are represented by postcranial material, whereas others are known from skulls only), the phylogenetic relationships of these pterosaurs are unclear. Based on the modified character matrix of Kellner (80 characters), the relationships of Liaoning pterosaurs (56 taxa, including outgroups) are explored. Preliminary results show that: 1) *Dendrorhynchoides* and *Jeholopterus* belong to Anurognathidae; 2) the clade formed by *Boreopter* and *Feilongus* is basal to other omithocheirids; 3) *Liaoningopterus* is a primitive form of Anhangueridae; 4) *Beipiaopterus* is a possible basal ctenochasmatoid; 5) *Eosipterus* is basal to Germanodacylidae; 6) *Eoazhdarcho* and *Eopteranodon* may be early forms of Azhdarchoidea; 7) *Chaoyangopterus* and *Jidapterus* may belong to Azhdarchoidea, but they are more derived than *Eopteranodon* and *Eoazhdarcho*, and 8) three Chinese tapejarids form a monophyletic group.

Key words: Phylogenetic analysis, pterosaurs, Liaoning, China

INTRODUCTION

Pterosauria is generally divided into two groups: the long-tailed Rhamphorhynchoidea and the short-tailed Pterodactyloidea. Unlike other vertebrate groups, such as mammals and theropod dinosaurs, which have been subject to more intense study, pterosaurs, an important group of flying reptiles that existed throughout most of the Mesozoic, have been largely ignored (Unwin, 2003) due to their patchy fossil record. Originally, the relationships of pterosaurs were based mostly on overall skeletal similarities (Young, 1964; Kuhn, 1967; Wellnhofer, 1978; Wild, 1978), rather than shared derived characters. Howse (1986) was the first to publish a phylogenetic study of pterosaurs using cladistic techniques, although his results bear little taxonomic resolution and did not represent the most parsimonious solution (Kellner, 1995; Kellner and Langston, 1996). Bennett (1989) was the first to apply the program PAUP (Phylogenetic Analysis Using Parsimony) to analyze interrelationships of Cretaceous pterosaurs, and other phylogenetic studies have since been conducted for various purposes (Bennett, 1994; Unwin, 1992, 1995; Kellner, 2003, 2004; Unwin, 2003; Wang *et al.*, 2005) (Figs. 1-3).

Since the first pterosaur was discovered from western Liaoning and the surrounding areas (hereafter referred to as the Liaoning pterosaurs; Ji and Ji, 1997), 18 species of 17 genera, belonging to at least four families of both of the major clades of pterosaurs have been reported (Ji and Ji, 1997, 1998; Wang and Lü, 2001; Wang *et al.*, 2002; Wang and Zhou, 2003 a, b; Czerkas and Ji, 2002; Li *et al.*, 2003; Lü, 2003; Dong *et al.*, 2003; Lü and Ji, 2005a, b; Dong and Lü, 2005; Lü and Yuan, 2005; Lü and Zhang, 2005; Wang *et al.*, 2005). Only three of these genera (*Dendrorhynchoides*, Ji and Ji, 1998, Ji *et al.*, 1999; *Jeholopterus*, Wang *et al.*, 2002 and *Pterorhynchus*, Czerkas and Ji, 2002) belong to the Rhamphorhynchoidea, whereas only one of them, *Pterorhynchus*, has a long tail typical of rhamphorhynchid pterosaurs. The remaining genera belong to the Pterodactyloidea. Some pterosaur genera are known from skull material, whereas others have been named on the basis of postcranial material only. Specimens with skulls are more easi-

ly assigned to a specific family or genus, whereas those lacking skulls are difficult to assign at the family or genus level.

Although many pterosaur species have been found in Liaoning, their interrelationships have not been investigated. The aim of this paper is to explore the interrelationships of most Liaoning pterosaurs using a cladistic approach. This study differs from Wang *et al.* (2005)'s analysis, which included only four genera of Liaoning pterosaurs.

Institutional Abbreviations - BPV, Beijing Natural History Museum, Beijing, China; CAD, CAR, Jilin University, Changchun, China; CDM, Changzhou China Dinosaur Park, Changzhou, China; GMN, Geological

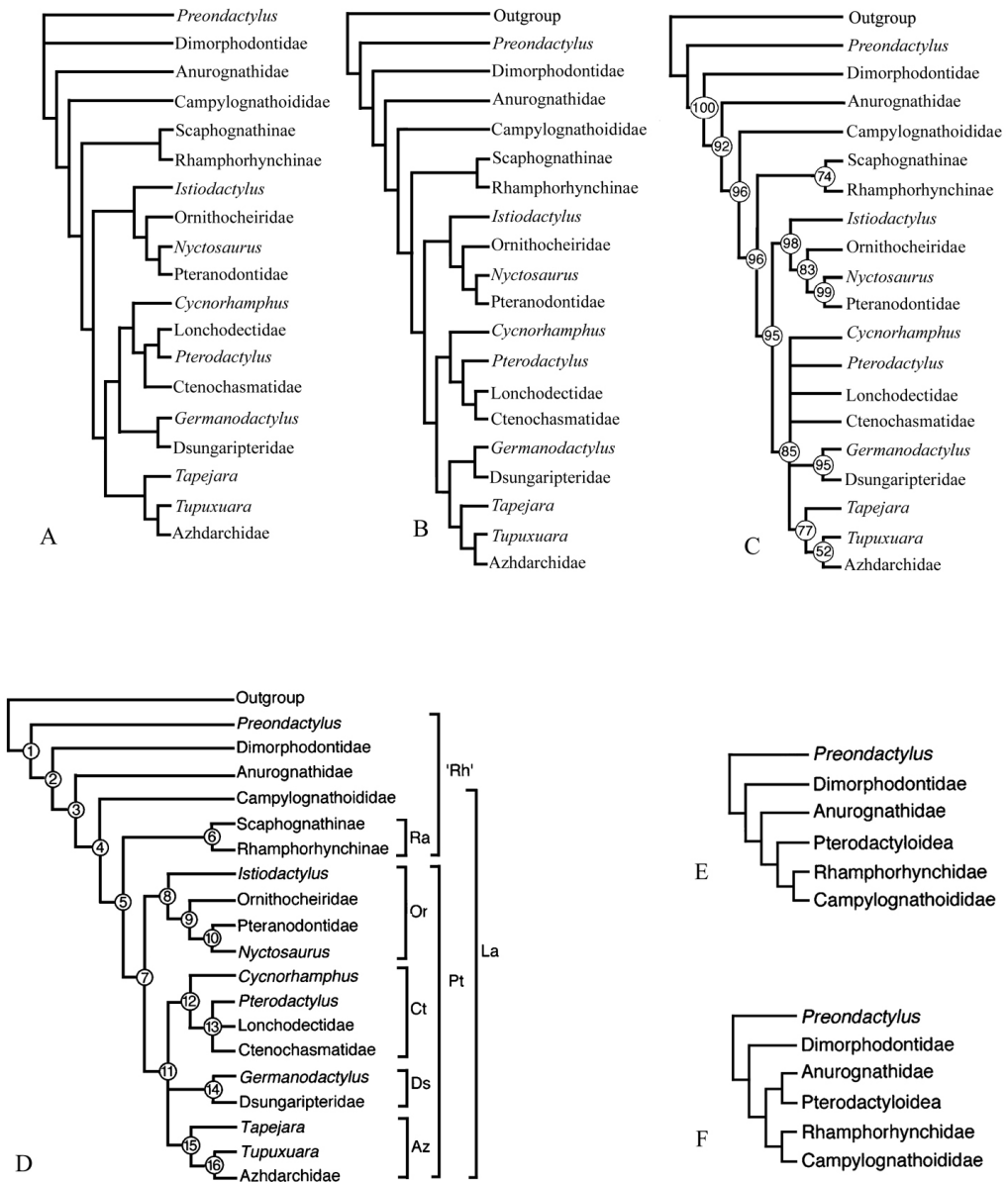


Fig. 1. Cladograms (A-F) of pterosaur relationships proposed by Unwin (2003), further interpretations see Figs. 6 and 7 of Unwin (2003).

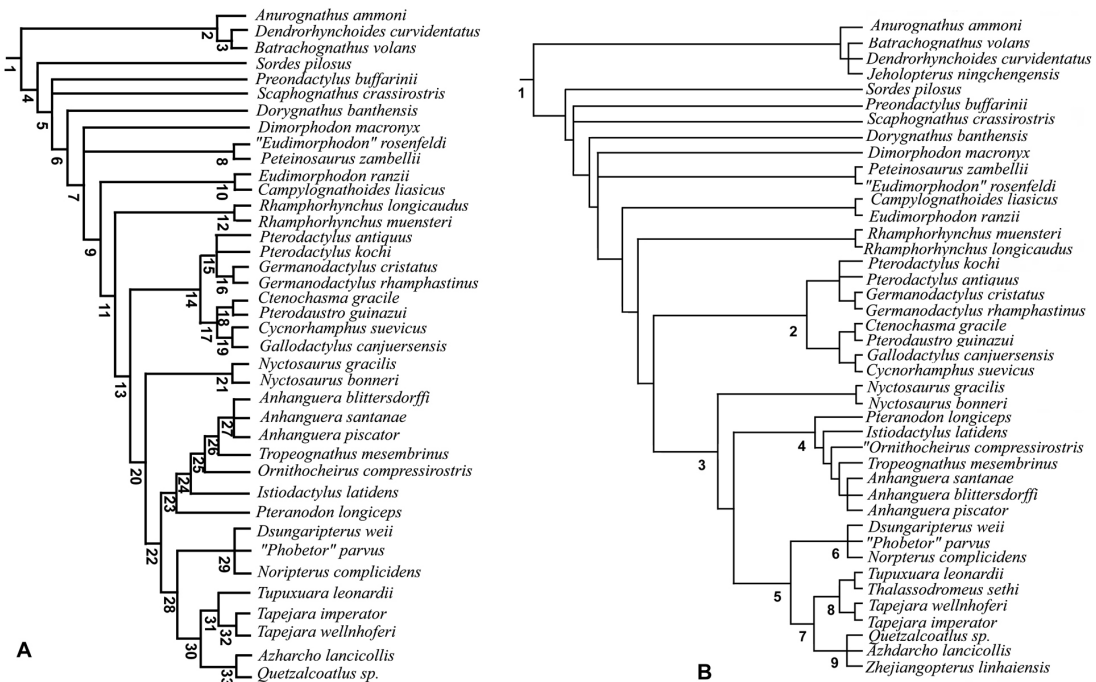


Fig. 2. Cladograms (strict consensus trees) of pterosaurs. A is from Kellner (2003); B is from Kellner (2004).

Museum of Nanjing, Nanjing, China; GMV, National Geological Museum of China, Beijing, China; JZMP, Jinzhou Museum of Paleontology, Jinzhou, China; LPM, Liaoning Paleontological Museum at Institute of Mesozoic Paleontology of Western Liaoning Paleontology in Shenyang Normal University, Shenyang, China.

MATERIALS AND METHODS

The analysis of the interrelationships of the Liaoning pterosaurs was conducted by using the modified character matrix of Kellner (2004). Character description and character states were verified as much as possible from actual specimens (Plates I-II). Nearly all Liaoning pterosaurs are analyzed, including *Dendrorhynchoides curvidentatus* (Ji and Ji, 1998; Ji *et al.*, 1999; pers. observation), *Jeholopterus ningchengensis* (Wang *et al.*, 2002; pers. observation on the new specimens of Institute of Geology, Chinese Academy of Geological Sciences), *Beipiaopterus chenianus* (Lü, 2003), *Eosipterus yangi* (Ji and Ji, 1998; pers. observation), *Haopterus gracilis* (Wang and Lü, 2001), *Liaoningopterus gui* (Wang and Zhou, 2003a), *Chaoyangopterus zhangii* (Wang and Zhou, 2003a), *Sinopterus dongi* (Wang and Zhou, 2003b; pers. observation), *Sinopterus gui* (Li *et al.*, 2003), *Liaoxipterus brachyognathus* (Dong and Lü, 2005), *Boreopterus cuiiae* (Lü and Ji, 2005a), *Eoazhdarcho liaoxiensis* (Lü and Ji, 2005b), *Huaxiaopterus jii* (Lü and Yuan, 2005), *Eopteranodon lii* (Lü and Zhang, 2005), *Jidapterus edentus* (Dong *et al.*, 2003; pers. observation), *Feilongus youngi* (Wang *et al.*, 2005) and *Nurhachius ignaciobritoi* (Wang *et al.*, 2005; pers. observation on the new specimen at Shenyang Normal University: LPM 00023). Because this research focuses mainly of the relationships of Liaoning pterosaurs, four taxa (*Peteinosaurus zambellii*, *Eudimorphodon rosenfeldi*, *Ornoithocheirus compressirostris* and *Nyctosaurus bonneri*) were removed from Kellner's (2004) matrix. The matrix contains 80 characters and all characters are considered

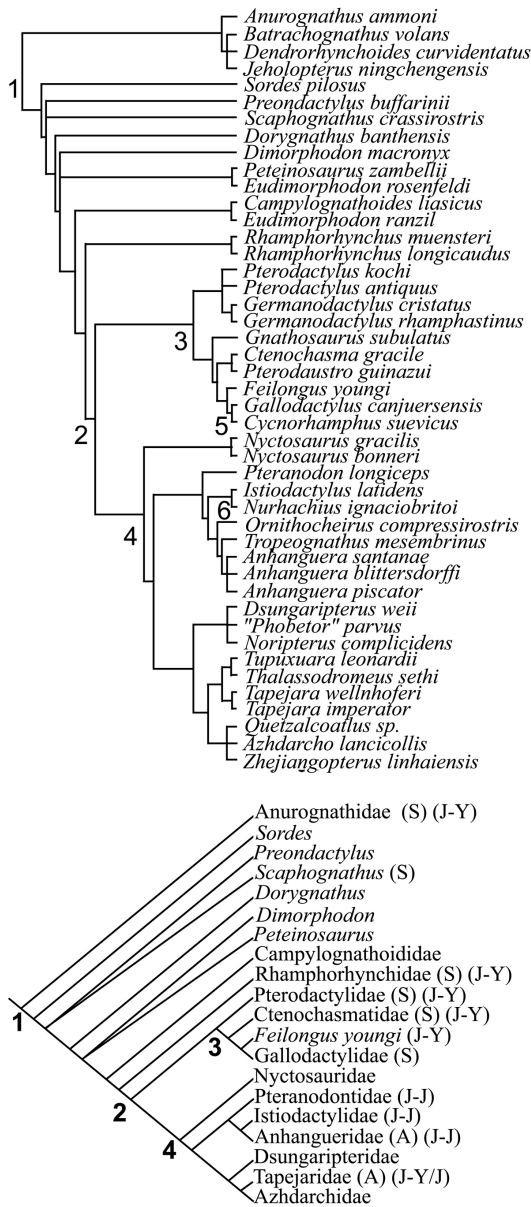


Fig. 3. Cladogram from Wang *et al.*, 2005.

un-ordered. The current analysis includes 56 taxa coded at the species level, with 3 outgroup and 53 in-group taxa. Modified characters from Kellner (2004) and new added characters are listed in Appendix 1. Unwin's (2003) taxonomy is applied to some of the pterosaurs.

PHYLOGENETIC ANALYSIS

The first analysis included all published Liaoning pterosaur species. Thirteen taxa were added to the matrices of Kellner (2004) and Wang *et al.* (2005). The phylogenetic analysis was performed using MacClade 4.04 (Maddison and Maddison, 1997) and PAUP 4.0b10 (Swofford, 1998). Due to the large data set (more than 20 taxa and many missing character states), a Heuristic Search was used (Swofford

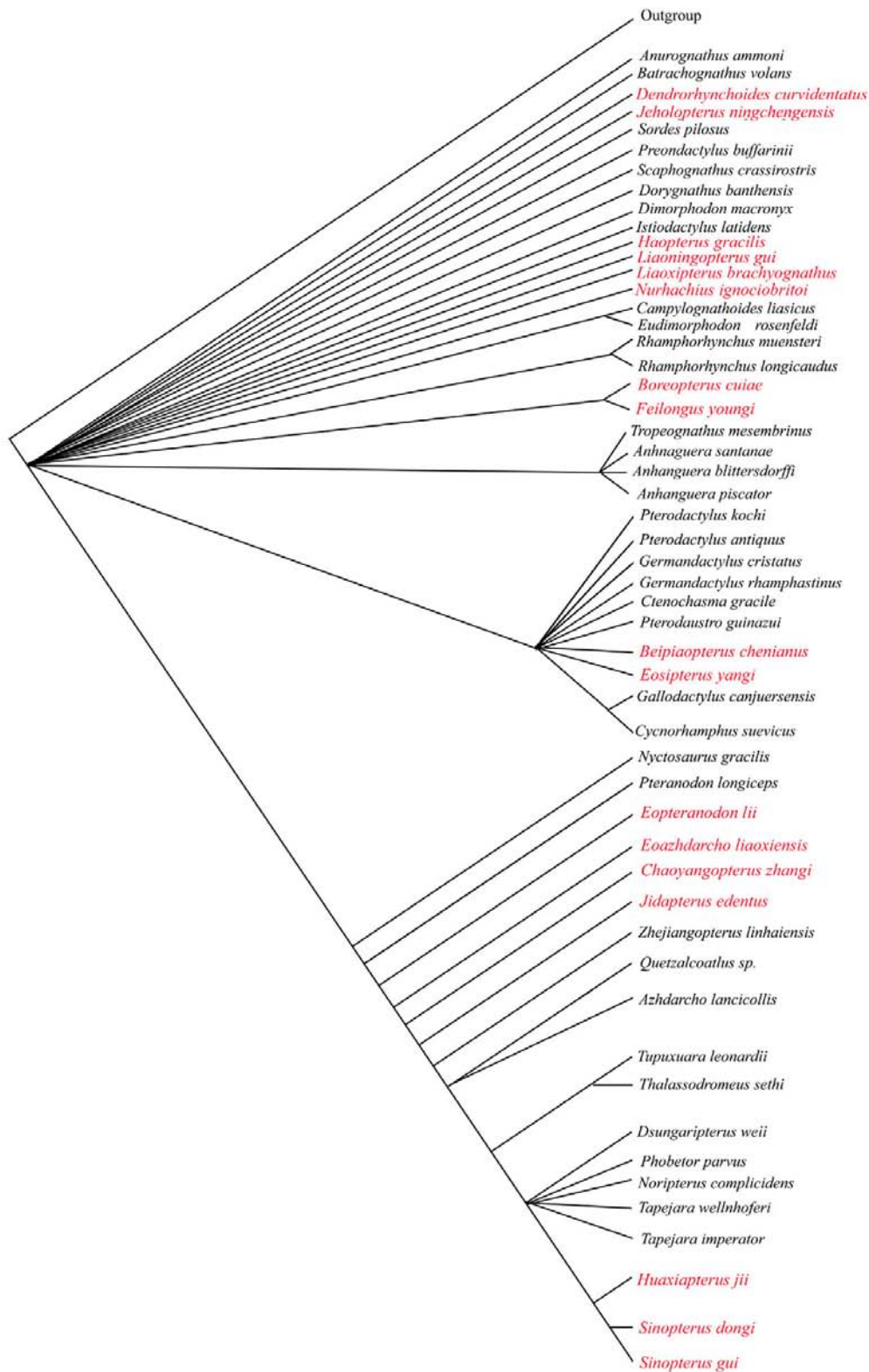


Fig. 4. Strict consensus tree of the Liaoning pterosaurs (in red).

and Begle, 1993), with branch-swapping options of the TBR (Tree Bisection and Regrafting) swapping algorithm method, and the limit of the MaxTree was set as 34000. Thirty-four thousand most parsimonious trees (MPTs) are found. The strict consensus tree shows (Fig. 4) that many Liaoning pterosaurs form unresolved polytomies. The results of the analysis show that: 1) *Beipiaopterus* and *Eosipterus* fall within the unresolved clade formed by *Pterodactylus*, *Germanodactylus*, *Ctenochasmas* and *Pterodaustro*; 2) *Eopteranodon*, *Eoazhdarcho*, *Chaoyangopterus*, *Jidapterus*, and *Zhejiangopterus* form successive outgroups to the more derived taxa, and 3) the Chinese tapejarid pterosaurs form a monophyletic group. The 50% majority-rule consensus tree produced better results (Fig. 5). The tree topology shows

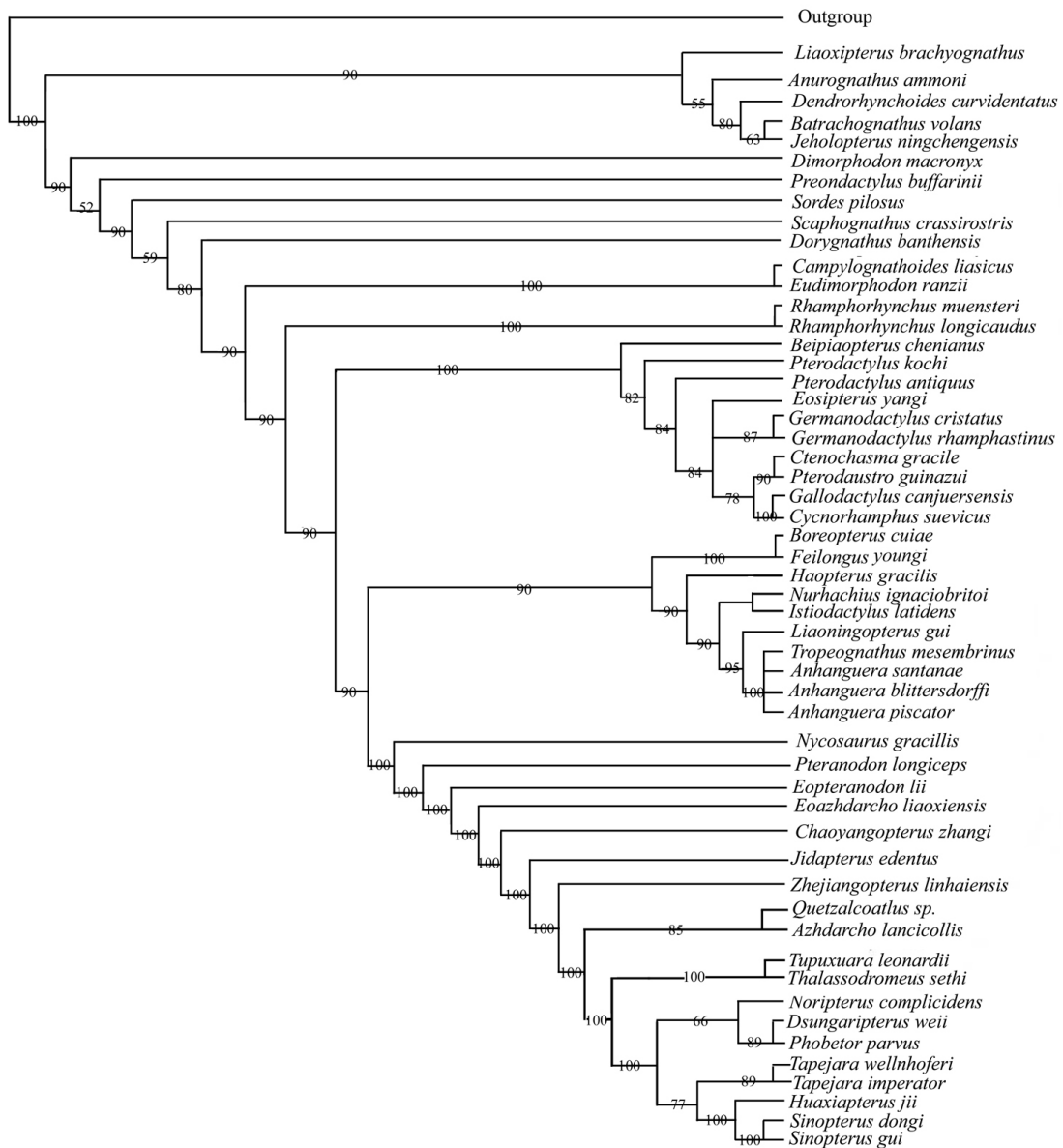


Fig. 5. 50% majority-rule tree including all Liaoning pterosaurs.

that: 1) *Liaopterus* is basal to (*Anurognathus* (*Dendrorhynchoides* (*Batrachognathus* + *Jeholopterus*))); 2) *Jeholopterus* is more derived than *Dendrorhynchoides*; 3) *Beipiaopterus* is a basal form of Ctenochasmatoidea; 4) *Eosipterus*, Germanodactylidae, Ctenochasmatidae, and Gallodactylidae form an unresolved polytomy, placing *Eosipterus* within Ctenochasmatoidea, as previously suggested by Unwin *et al.* (2000); 5) *Feilongus* and *Boreopterus* are sister taxa, which are basal to the clade formed by *Haopterus* and the derived forms Istiodactylidae and Anhangueridae; 6) *Liaoningopterus* is a basal Anhangueridae; 7) *Eopteranodon*, *Eoazhdarcho*, *Chaoyangopterus*, *Jidapterus*, *Zhejiangopterus*, and the Chinese tapejarids occupy, respectively, the same position as in the strict consensus tree, and 8) *Liaopterus* is a basal Anurognathidae. We infer the current position of *Liaopterus* to be wrong due to numerous missing characters for this taxon, and because *Liaopterus* differs from Anurognathid pterosaurs in both tooth morphology and lower jaw structure.

Because numerous characters are missing for *Liaopterus* (represented by an incomplete lower jaw), a second analysis was run without this taxon. This analysis provided a better-resolved tree. The strict consensus of 34000 MPTs (Fig. 6) shows that: 1) anurognathid pterosaurs form a monophyletic group, and *Anurognathus* is a basal form of Anurognathidae; 2) *Batrachognathus*, *Dendrorhynchoides*, and *Jeholopterus* form an unresolved tritomy; 3) *Beipiaopterus*, *Eosipterus*, and other ctenochasmatoid pterosaurs form an unresolved polytomy; 4) *Boreopterus* and *Feilongus* form a clade, which is basal to the clade of (*Haopterus* + (Istiodactylidae + Anhangueridae)); 5) *Liaoningopterus* is a basal form of Anhangueridae, and 6) the relative systematic positions of *Eopteranodon*, *Eoazhdarcho*, *Chaoyangopterus*, *Jidapterus*, and *Zhejiangopterus* does not differ from previous analyses. The 50% majority-rule consensus of the second cladistic analysis is better resolved and delivers results identical to the 50% majority-rule consensus of the first cladistic analysis (Fig. 7).

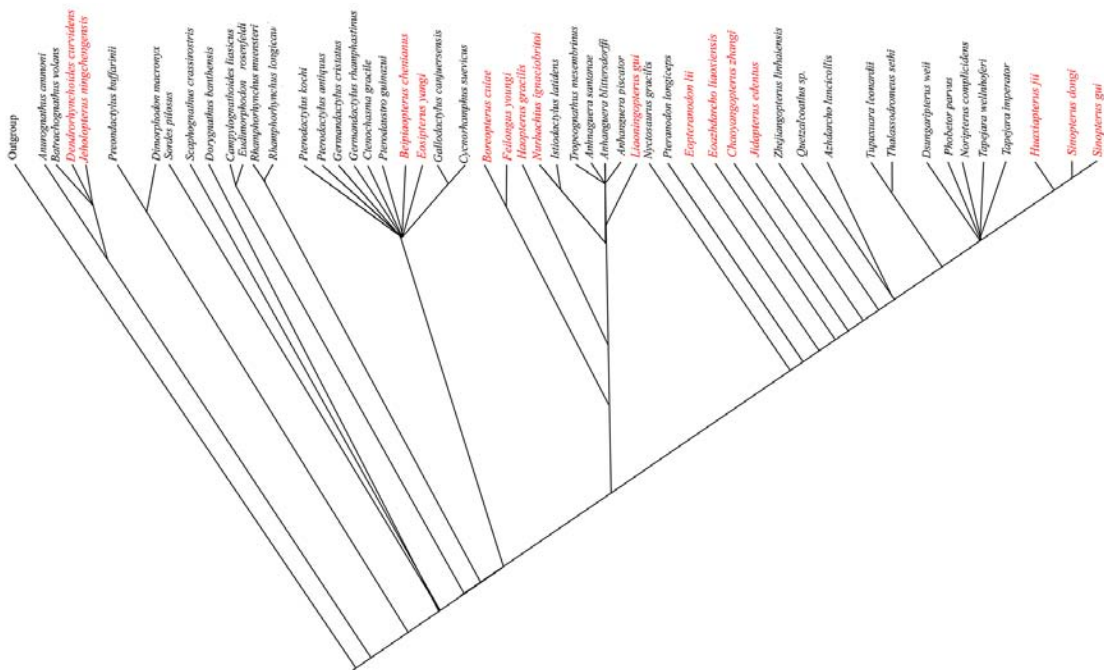


Fig. 6. Strict consensus tree (excluding *Liaopterus*) of the Liaoning pterosaurs (in red).

DISCUSSION AND CONCLUSION

The preliminary phylogenetic analysis (based on 50% majority-rule consensus) of Liaoning pterosaurs indicates that some pterosaurs can be safely assigned to specific family, such as *Dendrorhynchoides* and *Jeholopterus* to Anurognathidae, *Nurhachius* to Istiodactylidae, *Liaoningopterus* to Anhangueridae, and *Sinopterus dongi*, *Sinopterus gui* and *Huaxiapterus jii* to Tapejaridae. *Beipiaopterus* is possibly a basal form of ctenochasmatoid pterosaur, whereas *Eoispterus* is more derived than *Beipiaopterus* and forms a clade with *Pterodactylus antiquus*. *Eoispterus*, Germanodactylidae, Ctenochasmatidae, and Gallodactylidae form an unresolved polytomy. *Boreopter* and *Feilongus* form a clade basal to *Haopterus* and to other ornithocheiroids. The fewer number of teeth in *Haopterus* may indicate that the reduction of the tooth

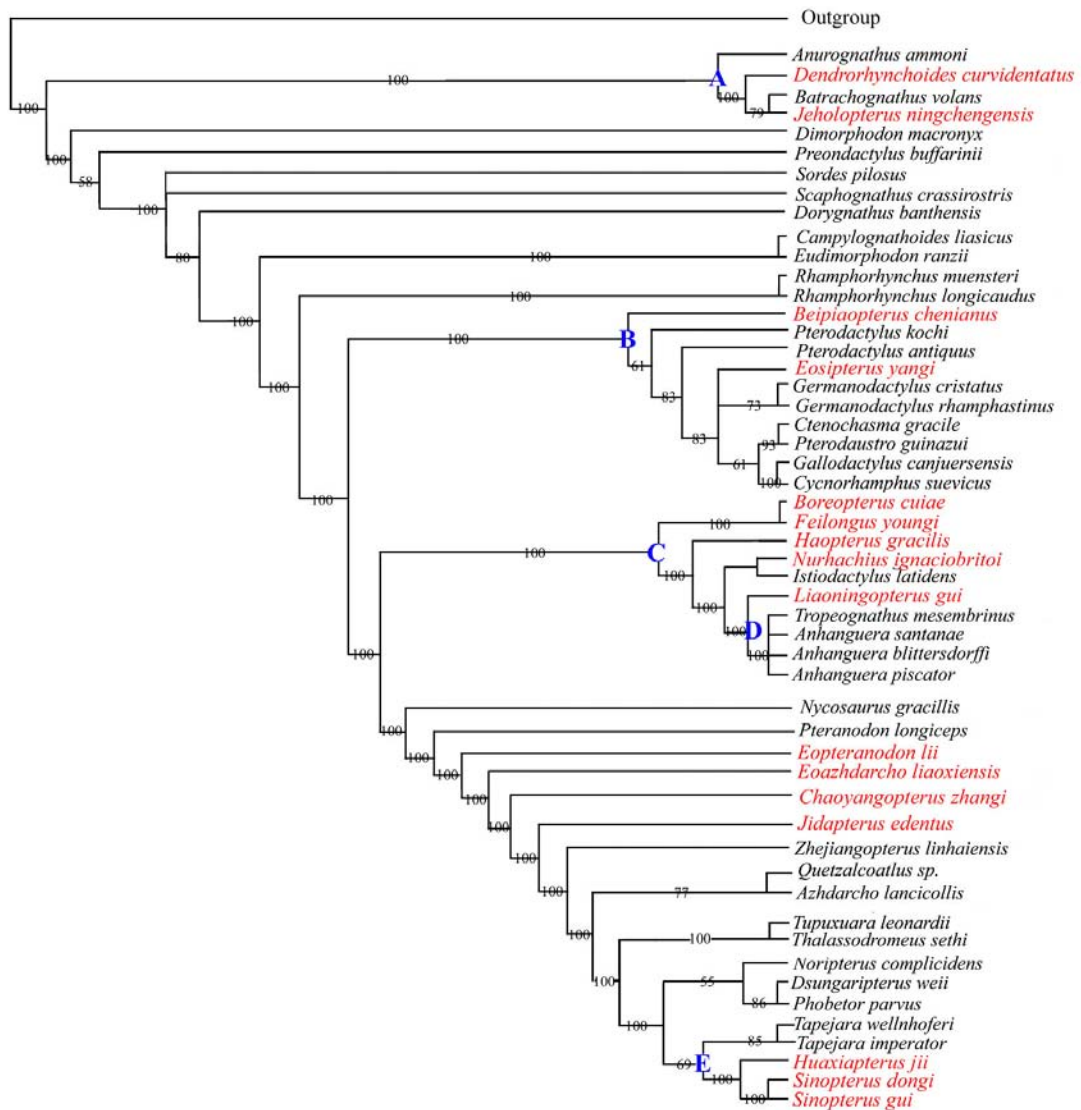


Fig. 7. 50% majority-rule tree (excluding *Liaoxipterus*), of the Liaoning pterosaurs (in red). A: Anurognathidae; B: Ctenochasmatoidea; C: Ornithocheiroidea; D: Anhangueridae; E: Tapejaridae

number is a derived character of this taxon. *Eopteranodon*, *Eoazhdarcho*, *Chaoyangopterus*, and *Jidapterus* are successive outgroups to *Zhejiangopterus* and other azhdarchids. *Eopteranodon* and *Eoazhdarcho* are potentially primitive forms of Azhdarchoidea. Finally, the Chinese tapejarids, *Sinopterus* and *Huaxipterus*, share several unique cranial characters with *Tapejara* and together appear to be more closely related to each other than to other azhdarchoids. *Sinopterus* and *Huaxipterus* have elongate skulls and weakly developed cranial crests and seem to be less derived than *Tapejara*, which possesses a short and deep skull and a large cranial crest. Tupuxuarids (*Tupuxuara* and *Thalassodromeus*) have often been linked with the family Tapejaridae, but the present phylogenetic analyses show that tupuxuarids are basal to the clade formed by Dsungaripteridae and Tapejaridae. Thus the term Tapejaridae is restricted to *Tapejara*, *Sinopterus*, and *Huaxipterus* as mentioned by Lü *et al.* (in press).

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서부 요녕성과 그 주변 지역에서 산출된 익룡의 계통발생학적 분석

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요약: 최근 많은 익룡 화석들이 서부 요녕성과 그 주변 지역에서 발견되었다. 총 17 속 18 종이 명명되었고 이중 4속만이 분명한 과(科)로 분류된다. 익룡의 산출 상태가 불완전하기 때문에 (어떤 것들은 몸뼈만 산출되고 어떤 것들은 머리뼈만 산출된다) 이들 익룡들 간에 자세한 관계는 분명하지 않다. Kellner의 수정된 데이터에 기초해 요녕성과 그 주변에서 산출된 익룡들의 관계를 PAUP을 이용해 분석하였다. 이 분석을 위해 outgroup을 포함해 총 56 종에 대해 80개의 특징을 이용하였다. 나타난 결과는 *Dendrorhynchoides* 와 *Jeholopterus* 는 Anurognathidae에 속한다. *Boreopterus* 와 *Feilongus* 는 함께 만드는 그룹은 다른 ornithocheirid 익룡들 중 가장 원시적이며 *Liaoningopterus* 는 Anhangueridae에 속하는 원시적인 익룡이다. *Beipiaopterus* 은 아마도 ctenochasmatoid 익룡의 원시적인 종일 가능성이 있다. *Eosipterus* 는 Germanodactylidae 의 원시적인 종이다. *Eoazhdarcho* 과 *Eopteranodon* 는 Azhdarchoidea 의 원시적인 종이다. *Chaoyangopterus* 와 *Jidapterus* 역시 이 그룹에 속할 수도 있으나 *Eopteranodon* 와 *Eoazhdarcho* 보다는 더 진화된 형태다. 3종의 중국산 tapejarid 익룡은 하나의 monophyletic 그룹을 형성한다.

주요어: 계통발생학적 분석, 익룡, 요녕성, 중국

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Appendix 1. Characters for phylogenetic analysis of the inter-relationships among pterosaurs (modified from Kellner (2004), with additional taxa and recoded and additional characters as noted following the characters) and data matrix (0= plesiomorphic character state; 1~7=derived characters; ?=missing data; - = character not applicable).

Skull

1. Dorsal margin of the skull:
 - 0- Straight or curved downwards
 - 1- concave
 - 2- wave-like (modified)
2. Lower jaw:
 - 0- lateral compressed
 - 1- comparatively broad (modified)
3. Rostral part of the skull anterior to the external nares:
 - 0- reduced
 - 1- elongated (less than half of skull length)
 - 2- extremely elongated (more than half of skull length)
4. Rostral end of premaxillae/maxillae downturned:
 - 0- absent
 - 1- present
5. Posterior margin of nasoantorbital fenestra:
 - 0- straight
 - 1- concave (from Unwin, 2003)
6. Position of the external naris:
 - 0- above the premaxillary tooth row
 - 1- displaced posterior to the premaxillary tooth row
7. Orbit:
 - 0- smaller than the antorbital opening
 - 1- larger than the antorbital opening (from Unwin, 2003)
8. Naris and antorbital fenestra:
 - 0- separated
 - 1- confluent, short than 45% of the skull length
 - 2- confluent, longer than 45% of the skull length
9. Orbit comparatively small and positioned very high in the skull
 - 0- absent
 - 1- present
10. Orbit pear-shaped:
 - 0- absent
 - 1- present
11. Position of the orbit relatively to the nasoantorbital fenestra (naris+antorbital fenestra):
 - 0- same level or higher
 - 1- orbit lower than the dorsal rim of the nasoantorbital fenestra
12. The tip of the lower jaw:
 - 0- pointed
 - 1-expanded (new)
13. Premaxillary sagittal crest:
 - 0-absent

- 1- confined to the anterior portion of the skull
 - 2- high, displaced backwards, near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit, and extending backwards
 - 3- low, displaced backwards near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit but not extending backwards
 - 4- starting at the anterior portion of the skull and extended posteriorly above the occipital region
 - 5- starting at the posterior half of the nasoantorbital fenestra
 - 6- low, positioned in the middle portion of the rostrum not reaching the nasoantorbital fenestra.
 - 7- low, positioned in the middle portion of the rostrum extending until the middle part of the nasoantorbital fenestra.
14. Tip of the premaxilla expanded:
 - 0- absent
 - 1- present, with premaxillary end high
 - 2- present, with premaxillary end dorsoventrally flattened.
 15. Posterior ventral expansion of the maxilla:
 - 0-absent
 - 1-present
 16. Rostrum:
 - 0- high, with convex outline
 - 1- low with straight or concave dorsal outline
 - 2- anterior region of rostrum low, but antorbital region expanded dorsally
 - 3- anterior region of rostrum high, but antorbital region flat (modified from Unwin, 2003)
 17. Foramen on nasal process:
 - 0- absent
 - 1- present
 18. Caudal end of mandible with distinct dorsal 'coronoid' eminence
 - 0- present
 - 1- absent (from Unwin, 2003)
 19. Bony frontal crest:
 - 0- absent
 - 1- low and blunt
 - 2- low and elongated
 - 3- high and expanded posteriorly
 20. Bony parietal crest:
 - 0- absent
 - 1- present, blunt
 - 2- present, laterally compressed and posteriorly expanded, with a rounded posterior margin
 - 3- present, consisting the base of the posterior portion of the cranial crest
 21. Posterior region of the skull rounded with the squamosal displaced ventrally:
 - 0- absent
 - 1- present
 22. Posterior of the quadrate relative to the ventral margin of the skull:
 - 0- vertical or subvertical
 - 1- inclined about 120° backwards
 - 2- inclined about 150° backwards
 23. Position of the articulation between the skull and mandible:
 - 0- under the posterior half of the orbit or further backwards

- 1- under the middle part of the orbit
- 2- under the anterior half of the orbit
- 24. Helical jaw joint:
 - 0- absent
 - 1- present
- 25. Supraoccipital:
 - 0- does not extend backwards
 - 1- extends backwards
- 26. Foramen pneumaticum piercing the supraoccipital:
 - 0- absent
 - 1- present
- 27. Expanded distal ends of the paroccipital processes:
 - 0- absent
 - 1- present
- 28. Nasal process of maxilla:
 - 0- vertical-subvertical
 - 1- inclined backwards (from Unwin, 2003)
- 29. Palatal ridge:
 - 0- absent
 - 1- present (modified)
- 30. Maxilla-nasal contact:
 - 0- narrow
 - 1- broad
 - 2- absent (modified from Unwin, 2003)
- 31. Mandibular rami:
 - 0- at the same level
 - 1- elevated well above symphysis (from Unwin, 2003)
- 32. Mandibular symphysis:
 - 0- absent or very short
 - 1- present, at least 30% of mandibular length
- 33. Anterior tip of the dentary downturned:
 - 0- absent
 - 1- present
- 34. Ventral margin of skull:
 - 0- straight or slightly convex
 - 1- curved downwards (modified from Unwin, 2003)
- 35. Dentary bony sagittal crest:
 - 0- absent
 - 1- blade-like and shallow
 - 2- massive and deep (modified)
- 36. Position and present of teeth:
 - 0- teeth present, evenly distributed along the jaws
 - 1- teeth absent from the anterior portion of the jaws
 - 2- teeth confined to the anterior part of the jaws
 - 3- jaw toothless
- 37. Location of largest teeth:
 - 0- rostral half of dentition

- 1- caudal half (from Unwin, 2003)
38. Variation in the size of the anterior teeth in the upper and lower:
0- absent
1- present (modified)
39. Teeth with a broad and oval base (dsungaripterid-like tooth):
0- absent
1- present (modified)
40. Multicusped teeth:
0- absent
1- present
41. Peg-like teeth:
0- absent
1- present, 15 or less on each side of the jaws
2- present, more than 15 on each side of the jaws
42. Long slender teeth (*Ctenochasma*-like tooth)
0- absent
1- present (modified)
43. Laterally compressed and triangular teeth:
0- absent
1- present

Axial skeleton

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

Pectoral girdle

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

Forelimb

59. Proportional length of the humerus relative to the metacarpal IV (hu/mcIV):
 0- $\text{hu/mcIV} > 2.50$
 1- $1.5 < \text{hu/mcIV} < 2.5$
 2- $0.4 < \text{hu/mcIV} < 1.5$
 3- $\text{hu/mcIV} < 0.40$
60. Proportional length of the humerus relative to the femur (hu/fe):
 0- $\text{hu/fe} \leq 0.8$
 1- $1.4 > \text{hu/fe} > 0.8$
 2- $\text{hu/fe} > 1.40$ (modified)
61. Proportional length of the humerus + ulna relative to the femur + tibia (hu+ul/fe+ti):
 0- humerus plus ulna about 80% or less of femur plus tibia length ($\text{hu+ul/fe+ti} < 0.8$)
 1- humerus plus ulna larger than 80% of femur plus tibia length ($\text{hu+ul/fe+ti} > 0.8$)
62. Pneumatic foramen on the proximal part of the humerus:
 0- absent
 1- present on ventral side (modified)
63. Pneumatic foramen on the proximal part of the first wing phalange:
 0- absent
 1-present (new)

64. Deltopectoral crest of humerus with elongate rectangular profile
 0- absent
 1- present (from Unwin, 2003)
65. Metacarpals I-III:
 0- disparate lengths
 1- the same length (from Unwin, 2003)
66. Distal end of the humerus
 0- oval or D-shaped
 1- subtriangular
67. Proportional length of the ulna relative to the metacarpal IV (ul/mcIV):
 0- ulna 3.6 times longer than metacarpal IV (ul/mcIV>3.6)
 1- length of ulna between four and two times the length of metacarpal IV (3.6>ul/mcIV>2)
 2- ulna less than two times the length of metacarpal IV (ul/mcIV<2)
68. Diameter of radius and ulna:
 0- subequal
 1- diameter of the radius about half that of the ulna
 2- diameter of the radius less than half that of the ulna
69. Distal syncarpals:
 0- unfused
 1- fused in a rectangular unit
 2- fused in a triangular unit
70. Pteroid:
 0- absent
 1- present, shorter than half the length of the ulna
 2- present, longer than half the length of the ulna
71. Metacarpals I-III:
 0- articulating with carpus
 1- metacarpal III articulates with carpus, metacarpals I and II reduced
 2- not articulating with carpus
72. Proportional length of the first phalanx of manual digit IV relative to the metacarpal IV (ph1d4/mcIV)
 0- both small and reduced
 1- both enlarged with ph1d4 over twice the length of mcIV
 2- both enlarged with ph1d4 less than twice the length of mcIV
73. Proportional length of the first phalanx of manual digit IV relative to the tibiotarsus (ph1d4/ti):
 0- ph1d4 reduced
 1- ph1d4 elongated and less than twice the length of ti (ph1d4/ti smaller than 2.00)
 2- ph1d4 elongated about or longer than twice the length of ti (ph1d4/ti subequal /larger than 2.00)
74. Proportional length of the second phalanx of manual digit IV relative to the first phalanx of manual digit IV (ph2d4/ph1d4):
 0-both short or absent
 1-elongated with the second phalanx about the same size or longer than first (ph2d4/ph1d4 larger than 1.0)
 2-elongated with the second phalanx up to 30% shorter than first (ph2d4/ph1d4 between 0.7 and 1.0)
 3-elongated with the second phalanx more than 30% shorter than first (ph2d4/ph1d4 smaller than 0.7)
75. Deltopectoral crest of humerus tonge-shaped, with necked base:
 0-absent

1-present (from Unwin, 2003)

76. Unguals of manus and pes:

0- similar in size

1- 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):

0- femur about twice or longer than metacarpal IV ($fe/mcIV > 2.0$)

1- femur longer but less than twice the length of metacarpal IV ($1.0 < fe/mcIV < 2.0$)

2- femur about the same length or shorter than metacarpal IV ($fe/mcIV < 1.0$)

78. Length of metatarsal III:

0- more than 30% of the tibia length

1- less than 30% of the tibia length

79. Fifth pedal digit:

0- with four phalanges

1- with two phalanges

2- with 1 or no phalanx (extremely reduced)

80. Last phalanx of pedal digit V:

0- reduced or absent

1- elongated, straight

2- elongated, curved

3- elongated, very curved (boomerang-shaped)

Appendix

	1	10	20	30	35
<i>Ornithosuchus longidens</i>	0	0	0	0	0
<i>Herrerasaurus ischigualastensis</i>	0	0	0	0	0
<i>Scleromochlus taylori</i>	0	0	0	?	?
<i>Anurognathus ammoni</i>	0	1	0	0	0
<i>Batrachognathus volans</i>	?	1	0	0	?
<i>Dendrorhynchoides curvidentatus</i>	0	1	0	0	?
<i>Jeholopterus ningchengensis</i>	0	1	0	0	?
<i>Sordes pilosus</i>	0	0	1	0	0
<i>Preondactylus buffarinii</i>	0	0	1	0	0
<i>Scaphognathus crassirostris</i>	0	0	1	0	0
<i>Dorygnathus banthensis</i>	0	0	1	0	0
<i>Dimorphodon macronyx</i>	0	0	1	0	0
<i>Campylognathoides liasicus</i>	0	0	1	0	0
<i>Eudimorphodon ranzii</i>	0	0	1	0	0
<i>Rhamphorhynchus muensteri</i>	0	0	1	0	0
<i>Rhamphorhynchus longicaudus</i>	0	0	1	0	0
<i>Pterodactylus kochi</i>	0	0	1	0	0
<i>Pterodactylus antiquus</i>	0	0	1	0	0
<i>Germanodactylus cristatus</i>	0	0	1	0	0
<i>Germanodactylus rhamphastinus</i>	0	0	1	0	0
<i>Ctenochasma gracile</i>	1	0	2	0	0
<i>Pterodaustro guinazui</i>	1	0	2	0	0
<i>Gallodactylus canjuersensis</i>	1	0	1	0	0
<i>Cycnorhamphus suevicus</i>	1	0	1	0	0
<i>Nyctosaurus gracilis</i>	0	0	1	0	0
<i>Pteranodon longiceps</i>	1	0	2	0	1
<i>Istiodactylus latidens</i>	0	0	1	0	0
<i>Tropeognathus mesembrinus</i>	2	1	1	0	1
<i>Anhanguera santanae</i>	2	0	1	0	1
<i>Anhanguera blittersdorffi</i>	2	0	1	0	1
<i>Anhanguera piscator</i>	2	0	1	0	1
<i>Dsungaripterus weii</i>	2	0	1	0	0
<i>Phobetor parvus</i>	2	0	1	0	0
<i>Noripterus complicidens</i>	?	?	?	?	?
<i>Tupuxuara leonardii</i>	0	0	1	0	0
<i>Thalassodromeus sethi</i>	0	0	1	0	0
<i>Tapejara wellnhoferi</i>	2	0	1	0	1
<i>Tapejara imperator</i>	0	0	1	0	1
<i>Quetzalcoalus sp.</i>	0	0	1	0	0
<i>Azhdarcho lancicollis</i>	?	?	?	?	?
<i>Beipiaopterus chenianus</i>	?	?	?	?	?
<i>Boreopterus cuiaei</i>	1	0	2	0	1
<i>Zhejiangopterus linhaiensis</i>	0	0	1	0	0
<i>Sinopterus dongi</i>	2	0	1	0	1
<i>Sinopterus gui</i>	?	0	1	0	1
<i>Jidapterus edentus</i>	0	0	2	0	1
<i>Haopterus gracilis</i>	0	0	1	0	0
<i>Chaoyangopterus zhangii</i>	0	0	?	?	?
<i>Liaoningopterus</i>	0	0	1	0	?
<i>Liaoxipterus brachyognathus</i>	?	?	?	?	?
<i>Huaxiapterus jii</i>	2	0	0	1	0
<i>Eopteranodon lii</i>	?	0	2	0	1
<i>Eoazhdarcho liaoxiensis</i>	?	0	?	?	?
<i>Feilongus youngi</i>	1	0	2	0	1
<i>Nurhachius ignaciobritoi</i>	0	0	1	0	0
<i>Eosipterus yangi</i>	?	?	?	?	?

Appendix

	36	40	50	60	70
<i>Ornithosuchus longidens</i>	0	0	0	0	0
<i>Herrerasaurus ischigualastensis</i>	0	0	0	0	0
<i>Scleromochlus taylori</i>	?	0	0	0	0
<i>Anurognathus ammoni</i>	0	0	0	0	0
<i>Batrachognathus volans</i>	0	0	0	0	0
<i>Dendrorhynchoides curvidentatus</i>	0	0	0	0	0
<i>Jeholopterus ningchengensis</i>	0	0	0	0	0
<i>Sordes pilosus</i>	0	0	0	0	0
<i>Preondactylus buffarinii</i>	0	0	0	0	0
<i>Scaphognathus crassirostris</i>	0	0	0	0	0
<i>Dorygnathus banthensis</i>	0	0	0	0	0
<i>Dimorphodon macronyx</i>	0	0	0	0	0
<i>Campylognathoides liasicus</i>	0	0	0	0	0
<i>Eudimorphodon ranzii</i>	0	0	0	0	0
<i>Rhamphorhynchus musensteri</i>	0	0	0	0	0
<i>Rhamphorhynchus longicaudus</i>	0	0	0	0	0
<i>Pterodactylus kochi</i>	0	0	0	0	0
<i>Pterodactylus antiquus</i>	0	0	0	0	0
<i>Germanodactylus cristatus</i>	0	0	0	0	0
<i>Germanodactylus rhamphastinus</i>	0	0	0	0	0
<i>Ctenochasma gracile</i>	0	0	0	0	0
<i>Pterodaustro guinazui</i>	0	0	0	0	0
<i>Gallodactylus anjuersensis</i>	2	0	0	0	0
<i>Cynorhamphus suevicus</i>	2	0	0	0	0
<i>Nyctosaurus gracilis</i>	3	-	-	0	0
<i>Pteranodon longiceps</i>	3	-	-	0	0
<i>Istiodactylus latidens</i>	0	0	0	0	0
<i>Tropeognathus mesembrinus</i>	0	0	1	0	0
<i>Anhanguera santanae</i>	0	0	1	0	0
<i>Anhanguera blittersdorffi</i>	0	0	1	0	0
<i>Anhanguera piscator</i>	0	0	1	0	0
<i>Dsungaripterus weii</i>	1	1	0	1	0
<i>Phobetor parvus</i>	1	1	0	1	0
<i>Noriopterus complidens</i>	?	?	?	?	?
<i>Tupuxuara leonardii</i>	3	-	-	-	-
<i>Thalassodromeus sethi</i>	3	-	-	-	-
<i>Tapejara wellnhoferi</i>	3	-	-	-	-
<i>Tapejara imperator</i>	3	-	-	-	-
<i>Quetzalcoatlus sp.</i>	3	-	-	-	-
<i>Azhdarcho lancicollis</i>	3	-	-	-	-
<i>Beipiaopterus cheniamus</i>	?	?	?	?	?
<i>Boreopteris cuiiae</i>	0	0	1	0	0
<i>Zhejiangopterus linhaiensis</i>	3	-	-	-	-
<i>Sinopterus dongi</i>	3	-	-	-	-
<i>Sinopterus gui</i>	3	-	-	-	-
<i>Jidapterus edentus</i>	3	-	-	-	-
<i>Haopterus gracilis</i>	0	0	1	0	0
<i>Chaoyangopterus zhangii</i>	3	-	-	-	-
<i>Liaoningopterus</i>	2	0	1	0	0
<i>Liaoxipterus brachyognathus</i>	2	0	0	0	1
<i>Huaxipterus jii</i>	-	-	-	-	-
<i>Eopteranodon lii</i>	-	-	-	-	-
<i>Eoazhdarcho liaoxiensis</i>	-	-	-	-	-
<i>Feilongus youngi</i>	2	0	1	0	0
<i>Nurhachius ignaciobritoii</i>	2	-	0	0	0
<i>Eosipterus yangi</i>	?	?	?	?	?

Appendix

	71	80
<i>Ornithosuchus longidens</i>	0 0 0 0 0 0 0 0 0 0	0
<i>Herrerasaurus ischigualastensis</i>	0 0 0 0 0 0 0 0 0 2	0
<i>Scleromochlus taylori</i>	? ? ? ? ? 0 ? ? ? ?	
<i>Anurognathus ammoni</i>	0 1 1 ? 0 1 0 0 1 ?	
<i>Batrachognathus volans</i>	? ? ? ? 0 1 ? ? ? ?	
<i>Dendrorhynchoides curvidentatus</i>	0 1 1 2 0 1 0 0 ? ?	
<i>Jeholopterus ningchengensis</i>	0 1 1 2 0 1 1 0 1 1	
<i>Sordes pilosus</i>	0 1 1 1 0 1 0 0 1 3	
<i>Preondactylus buffarinii</i>	0 1 1 1 0 0 0 0 ? ?	
<i>Scaphognathus crassirostris</i>	0 1 1 1 1 1 0 0 1 3	
<i>Dorygnathus banthensis</i>	0 1 1 1 0 1 1 0 1 3	
<i>Dimorphodon macronyx</i>	0 1 1 1 0 1 1 0 1 1	
<i>Campylognathoides liasicus</i>	0 1 2 1 0 1 1 0 1 0	
<i>Eudimorphodon ranzii</i>	0 ? ? ? 0 1 1 ? ? ?	
<i>Rhamphorhynchus muensteri</i>	0 1 2 2 1 1 1 0 1 2	
<i>Rhamphorhynchus longicaudus</i>	0 1 2 2 1 1 1 0 1 2	
<i>Pterodactylus kochi</i>	0 2 1 2 0 1 2 0 2 0	
<i>Pterodactylus antiquus</i>	0 2 1 2 0 1 2 0 2 0	
<i>Germanodactylus cristatus</i>	? 2 1 2 0 0 2 1 ? ?	
<i>Germanodactylus rhamphastinus</i>	? 2 1 ? 0 0 2 ? ? ?	
<i>Ctenochasma gracile</i>	? 2 1 2 ? 0 2 0 2 0	
<i>Pterodaustro guinazui</i>	? 2 1 2 0 0 2 0 2 0	
<i>Galloedactylus canjuersensis</i>	? ? 1 2 0 1 ? 1 ? ?	
<i>Cycnorhamphus suevicus</i>	0 2 1 2 0 0 2 1 ? ?	
<i>Nyctosaurus gracilis</i>	2 2 2 2 0 ? 2 0 ? ?	
<i>Pteranodon longiceps</i>	2 2 2 2 0 0 2 0 2 0	
<i>Istiodactylus latidens</i>	? ? ? 1 0 ? ? ? ? ?	
<i>Tropeognathus mesembrinus</i>	? ? ? ? ? ? ? ? ? ?	
<i>Anhanguera santanae</i>	1 ? ? ? ? ? ? ? ? ?	
<i>Anhanguera blittersdorffi</i>	? ? ? ? ? ? ? ? ? ?	
<i>Anhanguera piscator</i>	1 1 2 0 0 1 2 1 2 0	
<i>Dsungaripterus weii</i>	0 2 1 2 0 0 2 1 2 0	
<i>Phobetor parvus</i>	? ? ? ? 0 0 ? ? ? ?	
<i>Noripterus complicidens</i>	? 2 1 2 ? 0 2 1 2 0	
<i>Tupuxuara leonardii</i>	? 2 1 3 ? ? 2 ? ? ?	
<i>Thalassodromeus sethi</i>	? ? ? ? ? ? ? ? ? ?	
<i>Tapejara wellnhoferi</i>	? 2 1 ? ? ? 2 1 2 0	
<i>Tapejara imperator</i>	? ? ? ? ? ? ? ? ? ?	
<i>Quetzalcoatlus sp.</i>	? 2 1 3 0 ? 2 ? 2 0	
<i>Azhdarcho lancicollis</i>	? ? ? ? ? ? ? ? ? ?	
<i>Beipiaopterus chenianus</i>	? 1 1 3 0 1 2 0 2 0	
<i>Boreopterus cuiaie</i>	? 2 1 2 ? 1 2 1 2 0	
<i>Zhejiangopterus linhaiensis</i>	? 2 1 3 0 0 2 ? ? ?	
<i>Sinopterus dongi</i>	? 2 1 2 0 0 2 1 2 0	
<i>Sinopterus gui</i>	? 2 1 ? 0 ? 2 ? ? ?	
<i>Jidapterus edentus</i>	1 2 1 3 0 0 2 1 2 0	
<i>Haopterus gracilis</i>	0 2 ? 2 0 1 ? ? 2 0	
<i>Chaoyangopterus zhangii</i>	2 2 1 3 0 ? 2 1 2 0	
<i>Liaoningopterus</i>	? ? ? ? ? ? ? ? ? ?	
<i>Liaoxipterus brachyognathus</i>	? ? ? ? ? ? ? ? ? ?	
<i>Huaxiapterus jii</i>	1 2 1 2 0 0 2 1 ? ?	
<i>Eopteranodon lii</i>	? 2 1 2 0 ? 2 1 ? ?	
<i>Eoazhdarcho liaoxiensis</i>	2 2 1 2 0 0 2 ? ? ?	
<i>Feilongus youngi</i>	? ? ? ? ? ? ? ? ? ?	
<i>Nurhachius ignaciobritoii</i>	1 2 ? 2 0 ? 2 ? ? ?	
<i>Eosipterus yangi</i>	0 2 1 2 0 0 2 0 2 0	



Plate 1. A: *Eosipterus yangi* (GMV 2117); B-1: Skeleton of *Dendrorhynchoides curvidentatus* (GMV 2128), B-2: Close-up the teeth of *Dendrorhynchoides curvidentatus*. Scale in mm; C: *Sinopterus gui* (BPV-077); D: *Jidapterus edentus* (CDA 01); E: *Boreopterus cuiiae* (JZMP-04-07-3); F-1: *Huaxiapterus jii* (GMN-03-11-001, now the specimen is transferred to Changzhou China Dinosaur Park: CDM V30001); F-2: Close-up the skull of *Huaxiapterus jii*.



Plate 2. G-1: new specimen of *Jeholopterus ningchengensis* (stored in the Institute of Geology, Chinese Academy of Geological Sciences); G-2: Close-up the skull of *Jeholopterus ningchengensis*, showing the fossilized soft tissues surrounded. Scale in mm; H: *Eoazhdarcho liaoxiensis* (GMN-03-11-002); I-1: *Liaopterus brachyognathus* (CAR-0018), I-2: Close-up of the mandibular symphysis of *Liaopterus brachyognathus* (CAR-0018). Scale in mm; J: *Eopteranodon lii* (BPV-078); K-1: skeleton of an istiodactylid pterosaur (LPM 00023), K-2: Close-up the tooth of an istiodactylid pterosaur (LPM 00023). Scale in mm.