

Phylogenetic relationships among basal birds

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Abstract

A cladistic numerical analysis using a large number of characters and Mesozoic avian taxa is presented and the phylogenetic relationships of the Alvarezsauridae, the Confuciusornithidae and the Enantiornithes are discussed in light of this new study. It is concluded that (1) the Alvarezsauridae are the sister group of Aves, (2) the Confuciusornithidae share a sister group relationship with the Ornithothoraces (Enantiornithomorpha and Ornithuromorpha), and (3) the Enantiornithes are not closely related to *Archaeopteryx*, and thus "Sauriurae" is a paraphyletic group.

Keywords

Birds, Mesozoic, systematics, evolution.

Appendix 1: Character list

Appendix 2: Character matrix

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Appendix 1: Character list

Character list and character states used for the present cladistic analysis.

Skull and mandible

1. Rostral portion of the premaxillae unfused (0) or fused (1) in adults.
2. Maxillary process of the premaxilla restricted to its rostral portion (0), or subequal or longer than the facial contribution of the maxilla (1).
3. Frontal process of the premaxilla short (0), relatively long, approaching the rostral border of the antorbital fenestra (1), or very long, extending caudally near the level of lacrimals (2).
4. Premaxillary teeth: present (0), absent (1).
5. Toothed (0) or toothless (1) maxilla and dentary.
6. Caudal margin of naris far rostral than (0), or nearly reaching or overlapping (1), the rostral border of the antorbital fossa.
7. Dorsal ramus of the maxillary nasal process: present (0), absent (1).
8. Cup-shaped caudal maxillary sinus: absent (0), present (1).
9. Rostral margin of the jugal away (0) or very close to the caudal margin of the osseous external naris (1).
10. Jugal process of palatine: present (0), absent (1).
11. Ectopterygoid: present (0), absent (1).
12. Squamosal incorporated to the braincase forming a zygomatic process: absent (0), present (1).
13. Postorbital: present (0), absent (1).
14. Postorbital–jugal contact: present (0), absent (1).
15. Quadratojugal sutured to the quadrate (0), or joined through a ligamentary articulation (1).
16. Quadratojugal–squamosal contact: present (0), absent (1).
17. Lateral, round cotyle on the mandibular process of the quadrate (quadratojugal articulation): absent (0), present (1).
18. Quadrate orbital process (pterygoid ramus) broad (0), or sharp and point-shaped (1).
19. Quadrate pneumaticity: absent (0), present (1).
20. Quadrate articulating only with the squamosal (0), or with both prootic and squamosal (1).
21. Quadrate distal end with two, transversely aligned condyles (0), or with a triangular, condylar pattern, usually composed of three distinct condyles (1).
22. Caudal tympanic recess opens on the rostral margin of the paraoccipital process (0), or into the columellar recess (1).
23. Basicranial fontanelle on the ventral surface of the basisphenoid (basisphenoid recess): present (0), absent (1).
24. Deeply notched rostral end of the mandibular symphysis: absent (0), present (1).
25. Coronoid bone: present (0), absent (1).
26. Articular pneumaticity: absent (0), present (1).
27. Dentary tooth implantation: teeth in individual sockets (0), or teeth in a communal groove (1).
28. Teeth with serrated crowns (0), or unserrated crowns (1).

Vertebral column and ribs

29. Atlantal hemiarches unfused (0), or fused forming a single arch (1).
30. One or more pneumatic foramina piercing the centra of midcranial cervicals, caudal to the level of the parapophysis–diapophysis: present (0), absent (1).
31. Cranial cervical vertebrae heterocoelous: absent (0), present (1).
32. Prominent carotid processes in the intermediate cervicals: absent (0), present (1).
33. Postaxial cervical epiphyses prominent, projecting further back from the postzygapophysis (0), or weak, not projecting further back from the postzygapophysis, or absent (1).
34. Prominent (50% or more the height of the centrum's cranial articular surface) ventral processes of the cervicothoracic vertebrae: absent (0), present (1).
35. Cervicothoracic vertebrae with parapophyses located at the same level as the prezygapophyses: absent (0), present (1).
36. Thoracic vertebrae count 13 or 14 (0), less than 13 (1), or less than 11 (2).
37. Wide vertebral foramen in the midcaudal thoracic vertebrae, vertebral foramen/articular cranial surface ratio (vertical diameter) larger than 0.40: absent (0), present (1).
38. Hyposphene–hypantrum accessory intervertebral articulations in the thoracic vertebrae: present (0), absent (1).
39. Lateral side of the thoracic centra: weakly or not excavated (0), deeply excavated by a groove (1), or by a broad fossa (2).
40. Parapophyses located in the cranial (0), or central (1) part of the centra of the thoracic vertebrae.
41. Sinsacrum formed by less than 8 (0), or 8 or more vertebrae (1).
42. Sinsacrum procoelous: absent (0), present (1).
43. Caudal portion of the sinsacrum forming a prominent ventral keel: absent (0), present (1).
44. Convex caudal articular surface of the sinsacrum:

Appendix 1, continued.

- absent (0), present (1).
45. Caudal vertebra prezygapophyses: present (0), absent (1).
 46. Distal caudal vertebra prezygapophyses: elongate, exceeding the length of the centrum by more than 25% (0), or shorter (1).
 47. Procoelic caudals: absent (0), present (1).
 48. First caudal with a ventrally sharp centrum: absent (0), present (1).
 49. Proximal haemal arches elongate, at least 3 times longer than wider (0), shorter (1), or absent (2).
 50. Pygostyle: absent or rudimentary (fewer than three elements) (0), present (1).
 51. Pygostyle longer than or equal to (0), or shorter than (1), the combined length of the free caudals.
 52. Caudal vertebrae count larger than 35 (0), less than 25 or 26 (1), less than 15 (2).
 53. Ossified uncinat processes: absent (0), present (1).
- Thoracic girdle and sternum*
54. Coracoid and scapula articulate through a wide, sutured articulation (0), or through more localized facets (1).
 55. Scapula articulated at the shoulder (proximal) end of the coracoid (0), or well below to it (1).
 56. Humeral articular facets of the coracoid and the scapula placed in the same plane (0), or forming a sharp angle (1).
 57. Procoracoid process on coracoid: absent (0), present (1).
 58. Coracoid shape: short (0), elongated with trapezoidal profile (1), or strut-like (2).
 59. Distinctly convex lateral margin of coracoid: absent (0), present (1).
 60. Bicipital tubercle (= acrocoracoidal process): present (0), or absent (1).
 61. Supracoracoid nerve foramen of coracoid centrally located (0), or displaced (often as an incision or even without passing through) toward the medial margin of the coracoid (1).
 62. Supracoracoid nerve foramen opening into an elongate furrow medially and separated from the medial margin of the coracoid by a thick bony bar: absent (0), present (1).
 63. Broad, deep fossa on the dorsal surface of the coracoid: absent (0), present (1).
 64. Sternocoracoidal process on the sternal half of the coracoid: absent (0), present (1).
 65. Scapular caudal end blunt and usually expanded (0), or tapered to a sharp point (1).
 66. Scapular shaft straight (0), or sagittally curved (1).
 67. Prominent acromion in the scapula: absent (0), present (1).
 68. Dorsal and ventral margins of the furcula: subequal in width (0), ventral margin distinctly wider than the dorsal margin (1).
 69. Boomerang-shaped furcula, with interclavicular angle of approximately 90° (0), or U-shaped furcula, with an interclavicular angle of less than 70° (1).
 70. Hypocleidium: absent or poorly developed (0), or well developed (1).
 71. Sternum subquadrangular to transversally rectangular (0), or longitudinally rectangular (1).
 72. Distinctly carinate sternum, more prominent than a faint ridge: absent (0), present (1).
 73. Sternal carina near to or projecting rostrally from the cranial border of the sternum (0), or not reaching the cranial border of the sternum (1).
 74. Lateral process of the sternum: absent (0), present (1).
 75. Prominent distal expansion in the lateral process of the sternum: absent (0), present (1).
 76. Medial process of the sternum: absent (0), present (1).
 77. Rostral margin of the sternum broad and parabolic: absent (0), present (1).
 78. Wide V-shaped caudal end of the sternum: absent (0), present (1).
 79. Costal facets of the sternum: absent (0), present (1).
- Thoracic limb*
80. Proximal and distal humeral ends twisted (0), or expanded nearly in the same plane (1).
 81. Humeral head concave cranially and convex caudally (0), or globe shaped, craniocaudally convex (1).
 82. Superior margin of the humeral head concave in its central portion, rising ventrally and dorsally: absent (0), present (1).
 83. Ventral tubercle of the humerus projected ventrally (0), proximally (1), or caudally, separated from the humeral head by a deep capital incision (2).
 84. Humerus with distinct transverse ligamental groove: absent (0), present (1).
 85. Pneumatic fossa in the caudoventral corner of the proximal end of the humerus: absent or rudimentary (0), well developed (1).
 86. Prominent, subquadrangular-shaped (i.e., subequal length and width) deltopectoral crest of the hu-

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- merus: absent (0), present (1).
87. Prominent bicipital crest of the humerus, cranioventrally projecting: absent (0), present (1).
 88. Ventral face of the humeral bicipital crest with a small fossa for muscular attachment: absent (0), present (1).
 89. Humeral distal condyles mainly located on distal (0), or cranial (1) aspect.
 90. Humerus with two (0), or a single, distal condyle (1).
 91. Well-developed brachial depression on the cranial face of the distal end of the humerus: absent (0), present (1).
 92. Well-developed olecranal fossa on the caudal face of the distal end of the humerus: absent (0), present (1).
 93. Distal end of the humerus very compressed cranio-caudally: absent (0), present (1).
 94. Ulna shorter (0), or longer or nearly equivalent (1), than the humerus.
 95. Ulnar shaft considerably thicker than the radial shaft, radial shaft/ulnar shaft ratio larger (0), or smaller (1), than 0.70.
 96. Olecranon process of ulna: relatively small (0), hypertrophied, nearly one-third (1) or one-half (2) the length of the ulna.
 97. Proximal end of the ulna with a well-defined area for the insertion of the m. brachialis anticus: absent (0), present (1).
 98. Semilunate ridge on the dorsal condyle of the ulna: absent (0), present (1).
 99. Shaft of radius with a long longitudinal groove on its ventrocaudal surface: absent (0), present (1).
 100. U-shaped to heart-shaped ulnare (scapholunar): absent (0), present (1).
 101. Semilunate carpal and proximal ends of metacarpals unfused (0), semilunate fused to the alular (I) metacarpal (1), semilunate fused to the major (II) and minor (III) metacarpals (2), or fusion of semilunate and all metacarpals (3).
 102. Distal end of metacarpals: unfused (0), or partially or completely fused (1).
 103. Intermetacarpal space: absent or very narrow (0), at least, as wide as the maximum width of minor metacarpal (III) shaft (1).
 104. Extensor process on alular metacarpal (I): absent or rudimentary (0), or well developed (1).
 105. Minor metacarpal (III) projecting distally more than the major metacarpal (II): absent (0), present (1).
 106. Round-shaped alular metacarpal (I): absent (0), present (1).
 107. Alular metacarpal (I) large, massive, depressed, and quadrangular-shaped: absent (0), present (1).
 108. Alular digit (I) long, exceeding the distal end of the major metacarpal (0), or short, not surpassing this metacarpal (1).
 109. Alular digit (I) large, robust, and dorsoventrally compressed: absent (0), present (1).
 110. Prominent ventral projection of the lateroproximal margin of the proximal phalanx of the alular digit (I): absent (0), present (1).
 111. Ungual phalanx of major digit (II): present (0), absent (1).
 112. Ungual phalanx of major digit (II) much smaller than the unguals of the alular (I) and minor (III) digits: absent (0), present (1).
 113. Proximal phalanx of the minor digit (III) much shorter than the remaining nonungual phalanges of this digit: absent (0), present (1).
 114. Ungual phalanx of minor digit (III): present (0), absent (1).
 115. Proximal phalanx of major digit (II) of normal shape (0), or flat and cranio-caudally expanded (1).
 116. Intermediate phalanx of major digit (II) longer (0), or shorter to equivalent (1), than proximal phalanx.
 117. Alular unguinal phalanx with two, ventroproximal foramina: absent (0), present (1).
- Pelvic girdle*
118. Pelvic elements unfused (0), or fused or partially fused (1).
 119. Preacetabular process of ilium twice as long as postacetabular process: absent (0), present (1).
 120. Small acetabulum, acetabulum/ilium length ratio equal or smaller than 0.11: absent (0), present (1).
 121. Postacetabular process shallow and pointed, less than 50% of the depth of the preacetabular wing at the acetabulum: absent (0), present (1).
 122. Orientation of proximal portion of pubis: cranially to subvertically oriented (0), retroverted, separated from the main synsacral axis by an angle ranging between 65° than 45° (1), or more or less parallel to the ilium and ischium (2).
 123. Prominent antitrochanter: caudally directed (0), or dorsocaudally directed (1).
 124. Iliac brevis fossa: present (0), absent (1).
 125. Pubic pedicel cranioventrally (0), or ventrally or caudoventrally (1) projected.
 126. Supracetabular crest on ilium: well-developed (0), absent or rudimentary (1).
 127. Supracetabular crest extending throughout the ac-

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- etabulum (0), or extending only over the cranial half of the acetabulum (1).
128. Ischium with a dorsal process approaching, or abutting to, the ventral margin of the ilium: absent (0), present (1).
129. Ischiadic terminal processes forming a symphysis: present (0), absent (1).
130. Ischium two-thirds or less (0), or more than two-thirds (1), the length of the pubis.
131. Obturator process of ischium: prominent (0), or reduced or absent (1).
132. Pubic apron one-third or more the length of the pubis (0), shorter (1), or absent (absence of symphysis) (2).
133. Pubis shaft laterally compressed throughout its length: absent (0), present (1).
134. Pubic foot: present (0), absent (1).
135. Laterally compressed and kidney-shaped proximal end of pubis: absent (0), present (1).
- Pelvic limb*
136. Femur with distinct fossa for the capital ligament: absent (0), present (1).
137. Femoral neck: present (0), absent (1).
138. Femoral anterior trochanter separated from the greater trochanter (0), or fused to it forming the trochanteric crest (1).
139. Femoral posterior trochanter: absent to moderately developed (0), or hypertrophied (1).
140. Conical and strongly distally projected lateral condyle of femur: absent (0), present (1).
141. Femur with prominent patellar groove: absent (0), present (1).
142. Femoral popliteal fossa distally bounded by a complete transverse ridge: absent (0), present (1).
143. Tibiofibular crest in the lateral condyle of femur: absent (0), poorly developed (1), prominent (2).
144. Fossa for the femoral origin of the *M. tibialis cranialis*: absent (0), present (1).
145. Caudal projection of the lateral border of the distal end of the femur: absent (0), present (1).
146. Tibia, calcaneum and astragalus unfused or poorly co-ossified (sutures still visible) (0), or complete calcaneo-astragalar-tibial fusion (1).
147. Cranial cnemial crest on tibiotarsus: absent (0), present (1).
148. Round proximal articular surface of tibiotarsus: absent (0), present (1).
149. Medial border of medial articular facet strongly projects proximally: absent (0), present (1).
150. Extensor canal on tibiotarsus: absent (0), present (1).
151. Wide and bulbous medial condyle of the tibiotarsus: absent (0), present (1).
152. Narrow, deep intercondylar sulcus on tibiotarsus that proximally undercuts the condyles: absent (0), present (1).
153. Proximal end of the fibula prominently excavated by a medial fossa (0), or nearly flat (1).
154. Fibula with the tubercle for the *M. iliofibularis* cranio-laterally (0), laterally (1), or caudolaterally or caudally (2) directed.
155. Fibula reaching the proximal tarsals (0), or greatly reduced distally, without reaching these elements (1).
156. Metatarsals II, III and IV completely (or nearly completely) fused one to each other: absent (0), present (1).
157. Distal tarsals free (0), or completely fused to the metatarsals (1).
158. Metatarsal V: present (0), absent (1).
159. Proximal end of metatarsal III in the same plane as metatarsals II and IV (0), reduced, not reaching the tarsals (arctometatarsalian condition) (1), or plantarily displaced with respect to metatarsals II and IV (2).
160. Well-developed tarsometatarsal intercondylar eminence: absent (0), present (1).
161. Tarsometatarsal vascular distal foramen completely enclosed by metatarsals III and IV: absent (0), present (1).
162. Trochlea metatarsal II broader than the trochlea of metatarsals III: absent (0), present (1).
163. Completely reverted hallux (arch of unguis phalanx of digit I opposing the arch of the unguis of digits II, III and IV): absent (0), present (1).
164. Metatarsal IV significantly thinner than metatarsals II and III: absent (0), present (1).
165. Plantar surface of tarsometatarsus excavated: absent (0), present (1).
166. Tubercle on the dorsal face of the metatarsal II: absent (0), present (1).
167. Hypotarsus: absent (0), present (1).
- Integument*
168. Feathers: absent (0), present (1).
169. Alula: absent (0), present (1).

Appendix 2: Character matrix

Character matrix used in the present cladistic analysis. Character state 0 is plesiomorphic; character states 1 and 2 are apomorphic. Entries with n are not comparable character states; ? entries are either not preserved or unknown.

	10	20	30	40	50	60	70
Allosauroidae	000000000	000000000	000000000	000000000	000000000	n00000000	000000000
Troodontidae	00000000?	0000??010	0110??10?	000100000	0?0000000	n?10000100	00?0??0??
Velociraptorina	000000000	00000000?	000000000	000000000	000000010	n010000100	0000001000
Archaeopteryx	0010010001	000111000?	01??1?0100	0?1000??00	00?0010?10	n100000100	0000001000
Rahonavis	?????????	?????????	?????????	????0?1020	010?010010	n??1?????	????001???
Mononykus	?????????	?????????	?1?????1?	0111?1100	?11??11??	n?0000001	0000000???
Shuvuuia	000?000?01	?001110001	010?1?1100	0111?1100	0111011100	n?0000001	0000000???
Alvarezsaurus	?????????	?????????	?????????	?1?0??00	000?01110?	n?00000??	0????00???
Patagonykus	?????????	?????????	?????????	0?????1000	?111??11??	n?00?0001	000???????
Confuciusornis	102111000?	0000111??1	0??1?0nn??	0?11?01120	0100010?21	0110000200	1000000000
Changchengornis	1??1110???	?????????	0??1?0nn??	?????????2?	0?0001???	01?00?0200	1000?00000
Noguerornis	?????????	?????????	?????????	?????????	?0???????	?????????	?????????1
Iberomesornis	?????????	?????????	?????????	??101??00	0000010011	010????200	1??010??11
Patagopteryx	?????????	?1??111011	1?1??0??11	1111011100	11011n10??	?01110200	1000111???
Vorona	?????????	?????????	?????????	?????????	?????????	?????????	?????????
Concornis	?????????	?????????	?????????	?????????11	?0?0??001?	?011102010	1110?0?111
Sinornis	1010010???	????????0??	??????01??	?????????11	1??0??0?21	?101??0210	1110101?21
Gobipteryx	1021111101	0??????0??	0??010nn??	?????????	?1??010?21	??1?1?02?0	??10??11?1
Eoalulavis	?????????	?????????	?????????0?	??110??2?	???????????	?011102010	1110111111
Neuquenornis	?????????	?????????	?????????	?????????11	???????????	??11?0210	1110?01110
Ambiortus	?????????	?????????	?????????0?	11??0??2??	???????????	??1111200	10????11010
Hesperornis	1121011111	1111111101	11001011?1	1101021120	000?1n0020	021100120n	0000010000
Ichthyornis	1?210??2??	?111111111	?????10111	1111021120	1?00010?21	1??1111200	10011100??
Anas	1121111111	1111111111	011011nn10	1111021100	10001n0021	1211111200	1001111010
	80	90	100	110	120	130	140
Allosauroidae	00n?????00	000000000	000000000	n00000000	000000000	00n0000001	000000000
Troodontidae	?????????	?0?0?0???	??000????	000000000	000000000	000011n000	00????0000
Velociraptorina	00n0n00000	000000000	000000000	000000000	000000000	010011n000	0000000000
Archaeopteryx	?0n???????	?000000000	00?0000000	0000000000	0000000010	10n?11n?20	00000?1000
Rahonavis	?????????	?????????	????10100?	?????????	?????????010	100111n110	0000?01100
Mononykus	1100n00001	0010000011	000002000?	1100001011	??????11??	?10?001???	????1001?1
Shuvuuia	1100n00001	0010000011	000002000?	1000001011	??????1?00	0100001011	12111?0???
Alvarezsaurus	?????????	?????????	?????????	?????????	??????0?00	0?00000???	?????0?0?
Patagonykus	?????????	00100?0011	001?01?0??	1??0?01011	????????0??	?00?000???	?1100??001
Confuciusornis	10n1000110	0001010?10	0000101?01	2000000000	01100001?0	?11111n110	1101?101?0
Changchengornis	10n?????1?0	?0??1?1???	??0?010???	?000000000	0110010???	???????????	?10???????
Noguerornis	?????????	00????0???	??10??0?0?	3?10110?0?	???????????	?????????10?	???????????
Iberomesornis	?????????	00?0?00?20	0??110???	???????????	?????????1??	?????????1?1	1?0???????
Patagopteryx	??????1??1	00??000010	0000100?0?	?11??0?0?0	0??00?100	010011n011	12010?0?0?
Vorona	?????????	?????????	?????????	?????????	?????????	?????????	?????101?0
Concornis	11111110?0	0121?01110	0?1110????	?0?0?010?	0??011???	????????111	010??00???
Sinornis	11111110?0	012?101110	01?110?111	3000110100	0?01010?00	11??1n1?1	1??0?0110
Gobipteryx	?????????	?????????	0??11?111?	?00?1?????	????0?????	????1?????	?1?1?????
Eoalulavis	10n0nn0000	1121001110	0111101?1?	?01?1?010?	0?0?010???	???????????	?????????11?
Neuquenornis	11011?????	??2?1?????	11111??1?	3000110???	???????????	???????????	?????????1?
Ambiortus	?11???????	10?10000??	????1?????	3??0?10???	0??11n???	???????????	???????????
Hesperornis	10n0n0101n	10n0000nn	000nnnnnnn	nnnnnnnnnn	nnnnnnnn101	021111?011	1211010100
Ichthyornis	110??1?1?1	1021000110	110110110?	3111000100	1nn?11?1?	?21?11n111	1211?10100
Anas	1101001011	1021100010	1100101101	3111000100	1nn111n101	021111n111	1211010100

Appendix 2, continued.

	150	160	170
<i>Allosauroidae</i>	0000000000	0000000000	0000000??
<i>Troodontidae</i>	0?00000000	00?0100010	0000000??
<i>Velociraptorina</i>	0000000000	0000000000	0000010??
<i>Archaeopteryx</i>	0?0?000?00	00??000000	001000010
<i>Rahonavis</i>	0010000000	00?2100?00	00100101?
<i>Mononykus</i>	0000000010	001?10??10	00?0000??
<i>Shuvuuia</i>	00??00??10	0011100010	00?00001?
<i>Alvarezsaurus</i>	?????0???0	00??00??0?	00?0?00??
<i>Patagonykus</i>	0000000000	00??00??00	??????0??
<i>Confuciusornis</i>	??1??1??00	10?1101000	001011010
<i>Changchengornis</i>	?????1????	????10100?	??100?01?
<i>Noguerornis</i>	??????????	??????????	????????1?
<i>Iberomesornis</i>	0????0010?	?????00?00	0?10?????
<i>Patagopteryx</i>	012?010000	1111111100	1000101??
<i>Vorona</i>	011?100000	1111111000	10?0100??
<i>Concornis</i>	0???11010?	1????01?00	0111??1?
<i>Stornis</i>	011?01??00	111?10??00	????1?0??
<i>Gobipteryx</i>	??????0100	1?1?101100	?1?1010??
<i>Eoalulavis</i>	??????????	??????????	????????11
<i>Neuquenornis</i>	0???1?????	?????0??0?	0111?????
<i>Ambiortus</i>	??????????	??????????	????????1?
<i>Hesperornis</i>	1121011001	0012111121	1000000??
<i>Ichthyornis</i>	112?011001	00?2111121	10?0001??
<i>Anas</i>	1121011001	0012111121	101000111