

Phylogenetic Data

Electronic Supplementary Material 4 for:

**“First complete sauropod dinosaur skull from the Cretaceous
of the Americas and the evolution of sauropod dentition”**

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In order to resolve the phylogenetic position of *Abydosaurus* amongst sauropods, we conducted a cladistic analysis based on the data matrix of Wilson (2002) with modified taxonomic and character scope.

Ingroup terminal taxa were restricted to neosauropods, because ample character evidence supports placement of *Abydosaurus* within that group, and non-neosauropods are not known to survive into post-'Neocomian' age rocks. We further tailored ingroup composition by bundling several genera into higher-level terminal taxa because *Abydosaurus* shares none of the diagnostic features of their constituent genera or subgroups. Flagellicaudata, Rebbachisauridae and Saltasauridae were all assumed to be monophyletic (e.g., Upchurch et al. 2004; Curry Rogers 2005; Wilson 2005; Harris 2006; Sereno et al. 2007), and scorings were created by collapsing scorings for constituent genera. Ingroup genera included *Haplocanthosaurus*, *Jobaria*, *Camarasaurus*, *Brachiosaurus*, *Euhelopus* and *Malawisaurus*, all of which are diagnosed by autapomorphies (Wilson 2002:appendix C). Several other genera are known from the Early Cretaceous of North America (e.g., *Astrodon*, *Cedarosaurus*, *Venenosaurus*, *Sauroposeidon*, *Paluxysaurus*), but cranial remains are quite rare and overlap with *Abydosaurus* is limited. Where anatomical overlap is present, these genera can be clearly distinguished *Abydosaurus*. Inclusion of the many fragmentary taxa is beyond the scope of the present analysis. The taxonomic scope we have chosen precludes testing whether *Abydosaurus* is a non-neosauropod or a member of one of the higher-level taxa. However, a result in which *Abydosaurus* is positioned as outgroup to all other ingroup taxa or to one of the higher-level terminal taxa would suggest that the aforementioned results should be considered.

The reduced taxonomic scope the analysis necessitated removal of characters whose scorings do not vary within Neosauropoda, either because they distinguish amongst basal clades or because they vary between genera subsumed within higher-level terminal taxa. We augmented the data matrix by including autapomorphies of neosauropod genera listed by Wilson (2002:appendix C) that are shared with *Abydosaurus*. We implemented the scoring changes detailed by Wilson (2005) and Wilson and Upchurch (2009), as well as many of those listed Harris (2006) and Rose (2007). The resultant matrix included 151 characters scored in 10 ingroup taxa and two outgroup taxa (*Omeisaurus*, *Shunosaurus*) that were chosen based on their completeness and unanimous acceptance of their phylogenetic position outside Neosauropoda.

Taylor (2009) recently suggested that the North American species *Brachiosaurus altithorax* is generically distinct from the African species *B. brancai*, which is known from abundant material including a complete skull and many craniodental elements. Based on numerous differences between overlapping parts of both holotypes, Taylor (2009) proposed that the African species should be known as *Giraffatitan brancai*. While we are open to this possibility, we do not believe that it is sufficiently justified at present because the identified differences have not been defended as separating genera, rather than species, populations, or individuals. The sister-taxon relationship between the two species recovered in the phylogenetic analysis performed by Taylor (2009) neither supports nor refutes their generic-level separation. At this point, we consider the decision to recognize the African species as a genus apart to be arbitrary. We choose to retain the original nomenclature in this contribution. In our

phylogenetic analysis, the scoring for *Brachiosaurus* includes data from both species, following the Wilson (2002) analysis from which ours is derived.

Character List

The following list includes 151 character statements derived from Wilson (2002) with the following modifications. Four characters (4, 52, 87, 92) have been incorporated from the autapomorphy list from Wilson (2002:appendix C), two new characters (3, 44) have been added, and coding of two characters (51, 68) has been modified. Apart from these changes, character information is identical to Wilson (2002); please see that text for character attributions. Character data is fairly evenly distributed throughout the skeleton: there are 60 cranial characters (40%), 47 axial characters (31%), and 44 appendicular characters (29%).

Cranial

1. Posterolateral processes of premaxilla and lateral processes of maxilla, shape: without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1).
2. Premaxillary anterior margin, shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1).
3. Prenarial-antorbital snout length: less than 1/3 skull length (0); greater than 1/3 skull length (1).
4. Premaxilla and maxilla, sutural contact: flat (0); overlapping and sinuous (1).
[*Nemegtosaurus* autapomorphy #2; modified from Wilson 2002]
5. Preantorbital fenestra: absent (0); present (1).

6. Subnarial foramen and anterior maxillary foramen, position: well distanced from one another (0); separated by narrow bony isthmus (1).
7. Antorbital fenestra, maximum diameter: much shorter than (0) or subequal to (1) orbital maximum diameter.
8. External nares, position: terminal (0); retracted to level of orbit (1); retracted to a position between orbits (2).
9. External nares, maximum diameter: shorter (0) or longer (1) than orbital maximum diameter.
10. Orbital ventral margin, anteroposterior width: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1).
11. Lacrimal, anterior process: present (0); absent (1).
12. Jugal-ectopterygoid contact: present (0); absent (1).
13. Jugal, contribution to antorbital fenestra: very reduced or absent (0); large, bordering approximately one-third its perimeter (1).
14. Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1).
15. Postorbital, posterior process: present (0); absent (1).
16. Frontal contribution to supratemporal fossa: present (0); absent (1).
17. Frontal, anteroposterior length: approximately twice (0) or less than (1) minimum transverse breadth.
18. Parietal occipital process, dorsoventral height: short, less than the diameter of the foramen magnum (0); deep, nearly twice the diameter of the foramen magnum (1).
19. Parietal, contribution to posttemporal fenestra: present (0); absent (1).
20. Parietal, distance separating supratemporal fenestrae: less than (0) or twice (1) the long axis of supratemporal fenestra.
21. Supratemporal fenestra: present (0); absent (1).
22. Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1).
23. Supratemporal fenestra, maximum diameter: much longer than (0) or subequal to (1) that of foramen magnum.
24. Supratemporal region, anteroposterior width: temporal bar longer (0) or shorter (1) anteroposteriorly than transversely.

25. Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1).
26. Squamosal-quadratojugal contact: present (0); absent (1).
27. Quadratojugal, anterior process length: short, anterior process shorter than dorsal process (0); long, anterior process more than twice as long as dorsal process (1).
28. Quadrate fossa, depth: shallow (0); deeply invaginated (1).
29. Quadrate fossa, orientation: posterior (0); posterolateral (1).
30. Palatobasal contact, shape: pterygoid with small facet (0), dorsomedially oriented hook (1), or rocker-like surface (2) for basipterygoid articulation.
31. Pterygoid, transverse flange (i.e., ectopterygoid process) position: posterior of orbit (0); between orbit and antorbital fenestra (1); anterior to antorbital fenestra (2).
32. Pterygoid, quadrate flange size: large, palatobasal and quadrate articulations well separated (0); small, palatobasal and quadrate articulations approach (1).
33. Pterygoid, palatine ramus shape: straight, at level of dorsal margin of quadrate ramus (0); stepped, raised above level of quadrate ramus (1).
34. Vomer, anterior articulation: maxilla (0); premaxilla (1).
35. Paroccipital process, ventral non-articular process: absent (0); present (1).
36. Basipterygoid processes, length: short, approximately twice (0) or elongate, at least four times (1) basal diameter.
37. Basisoccipital depression between foramen magnum and basal tubera: absent (0); present (1).
38. Basisphenoid/basipterygoid recess: present (0); absent (1).
39. Basisphenoid-quadrates contact: absent (0); present (1).
40. Basipterygoid processes, orientation: perpendicular to (0) or angled approximately 45 degrees to (1) skull roof.
41. Dentary, depth of anterior end of ramus: slightly less than that of dentary at midlength (0); 150 percent minimum depth (1).
42. Dentary, anteroventral margin shape: gently rounded (0); sharply projecting triangular process or "chin" (1).
43. Dentary symphysis, orientation: angled 15 degrees or more anteriorly to (0) or perpendicular to (1) axis of jaw ramus.
44. Dentary posteroventral process, shape: single (0); forked (1).

45. External mandibular fenestra: present (0); absent (1).
46. Surangular depth: less than twice (0) or more than two and one-half times (1) maximum depth of the angular.
47. Surangular ridge separating adductor and articular fossae: absent (0); present (1).
48. Splenial posterior process, position: overlapping angular (0); separating anterior portions of prearticular and angular (1).
49. Coronoid, size: extending to dorsal margin of jaw (0); reduced, not extending dorsal to splenial (1); absent (2).
50. Tooth rows, shape of anterior portions: narrowly arched, anterior portion of tooth rows V-shaped (0); broadly arched, anterior portion of tooth rows U-shaped (1); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (2).
51. Tooth rows, length: extending to orbit (0); restricted anterior to orbit (1); restricted anterior to external naris (1); restricted anterior to subnarial foramen (2).
52. Crowns in upper and lower tooth rows, relative diameters: subequal (0); lower crowns smaller than upper crowns. [*Nemegtosaurus* autapomorphy #17; modified from Wilson 2002]
53. Occlusal pattern: interlocking, V-shaped facets (0); high-angled planar facets (1); low-angled planar facets (2).
54. Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlap (1).
55. Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2).
56. Marginal tooth denticles: present (0); absent on posterior edge (1); absent on both anterior and posterior edges (2).
57. Dentary teeth, number: greater than 20 (0); 17 or fewer (1).
58. Replacement teeth per alveolus, number: two or fewer (0); more than four (1).
59. Teeth, orientation: perpendicular (0) or oriented anteriorly relative (1) to jaw margin.
60. Teeth, longitudinal grooves on lingual aspect: absent (0); present (1).

Axial

61. Presacral bone texture: solid (0); spongy, with large, open internal cells, “camellate” (Britt, 1993, 1997) (1).

62. Atlantal intercentrum, occipital facet shape: rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter than that of ventral aspect (1).
63. Cervical vertebrae, number: 9 or fewer (0); 10 (1); 12 (2); 13 (3); 15 or greater (4).
64. Cervical neural arch lamination: well developed, with well defined laminae and coels (0); rudimentary; diapophyseal laminae only feebly developed if present (1).
65. Cervical pneumatopores (pleurocoels), shape: simple, undivided (0); complex, divided by bony septa (1).
66. Anterior cervical centra, height:width ratio: less than 1 (0); approximately 1.25 (1).
67. Anterior cervical neural spines, shape: single (0); bifid (1).
68. Mid-cervical centra, aEI (anteroposterior length/average of width and height of posterior face): 2.5-3.0 (0); >4 (1).
69. Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (1).
70. Posterior cervical and anterior dorsal bifid neural spines, median tubercle: absent (0); present (1).
71. Dorsal vertebrae, number: 15 (0); 14 (1); 13 (2); 12 (3); 11 (4); 10 or fewer (5).
72. Dorsal neural spines, length: approximately twice (0) or approximately four times (1) centrum length.
73. Middle and posterior dorsal neural arches, centropostzygapophyseal lamina (cpol), shape: single (0); divided (1).
74. Middle and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present (1).
75. Middle and posterior dorsal neural arches spinopostzygapophyseal lamina (spol) shape: single (0); divided (1).
76. Middle and posterior dorsal neural spines, shape: tapering or not flaring distally (0); flared distally, with pendant, triangular lateral processes (1).
77. Middle and posterior dorsal neural spines, orientation: vertical (0); posterior, neural spine summit approaches level of diapophyses (1).
78. Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).
79. Posterior dorsal neural arches, hyosphene-hypantrum articulations: present (0); absent (1).

80. Posterior dorsal neural spines, shape: rectangular through most of length (0); “petal” shaped, expanding transversely through 75 percent of its length and then tapering (1).
81. Sacral vertebrae, number: 3 or fewer (0); 4 (1); 5 (2); 6 (3).
82. Sacral vertebrae contributing to acetabulum: numbers 1-3 (0); numbers 2-4 (1).
83. Sacral neural spines, length: approximately twice (0) or four times (1) length of centrum.
84. Caudal bone texture: solid (0); spongy, with large internal cells (1).
85. Caudal vertebrae, number: more than forty-five (0); thirty-five or fewer (1).
86. Caudal transverse processes: persist through caudal 20 or more posteriorly (0); disappear by caudal 15 (1); disappear by caudal 10 (2).
87. Caudal 1 transverse process, shape: blade-shaped (0); with prominent ventral bulge (1).
[*Brachiosaurus* autapomorphy #12; modified from Wilson 2002]
88. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or platycoelous (0); procoelous (1); opisthocoelous (2).
89. Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl): absent (0); present and extending onto lateral aspect of neural spine (1).
90. Anterior caudal neural arches, prespinal lamina (prsl): absent (0); present (1).
91. Anterior caudal neural arches, postspinal lamina (posl): absent (0); present (1).
92. Anterior caudal vertebrae, prdl: absent (0); present (1). [*Brachiosaurus* autapomorphy #13; modified from Wilson 2002]
93. Anterior caudal neural arches, postspinal fossa: absent (0); present (1).
94. Anterior caudal neural spines, transverse breadth: approximately 50 percent of (0) or greater than (1) anteroposterior length.
95. Anterior caudal transverse processes, shape: triangular, tapering distally (0); “wing-like”, not tapering distally (1).
96. Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1).
97. Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1).
98. Distalmost biconvex caudal centra, length-to-height ratio: less than 4 (0); greater than 5 (1).
99. Distalmost biconvex caudal centra, number: 10 or fewer (0); more than 30 (1).
100. Cervical ribs, length: much longer than centrum, overlapping as many as three subsequent vertebrae (0); shorter than centrum, little or no overlap (1).
101. Dorsal ribs, proximal pneumatocoels: absent (0); present (1).

102. Anterior dorsal ribs, cross-sectional shape: subcircular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1).
103. "Forked" chevrons with anterior and posterior projections: absent (0); present (1).
104. "Forked" chevrons, distribution: distal tail only (0); throughout middle and posterior caudal vertebrae (1).
105. Chevrons, "crus" bridging dorsal margin of haemal canal: present (0); absent (1).
106. Chevron haemal canal, depth: short, approximately 25 percent (0) or long, approximately 50 percent (1) chevron length.
107. Chevrons: persisting throughout at least 80 percent of tail (0); disappearing by caudal 30 (1).

Appendicular

108. Scapular acromion process, size: narrow (0); broad, width more than 150 percent minimum width of blade (1).
109. Scapular blade, shape: acromial edge not expanded (0); rounded expansion on acromial side (1); racquet-shaped (2).
110. Scapular glenoid, orientation: relatively flat or laterally facing (0); strongly beveled medially (1).
111. Scapular blade, cross-sectional shape at base: flat or rectangular (0); D-shaped (1).
112. Coracoid, proximodistal length: less than (0) or approximately twice (1) length of scapular articulation.
113. Sternal plate, shape: oval (0); crescentic (1).
114. Humeral proximolateral corner, shape: rounded (0); square (1).
115. Humeral midshaft cross-section, shape: circular (0); elliptical, with long axis oriented transversely (1).
116. Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0); exposed on anterior portion of humeral shaft (1).
117. Ulnar proximal condylar processes, relative lengths: subequal (0); unequal, anterior arm longer (1).
118. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1).
119. Radius, distal breadth: slightly larger than (0) or approximately twice (1) midshaft breadth.

120. Carpal bones, number: 3 or more (0); 2 or fewer (1).
121. Carpal bones, shape: round (0); block-shaped, with flattened proximal and distal surfaces (1).
122. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1).
123. Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90 degree arc (0); U-shaped, subtending a 270 degree arc (1).
124. Longest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1).
125. Metacarpal I, length: shorter than (0) or longer than (1) metacarpal IV.
126. Metacarpal I, distal condyle shape: divided (0); undivided (1).
127. Metacarpal I distal condyle, transverse axis orientation: beveled approximately 20 degrees proximodistally (0) or perpendicular (1) with respect to axis of shaft.
128. Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or less (1); absent or unossified (2).
129. Manual phalanx I.1, shape: rectangular (0); wedge-shaped (1).
130. Manual nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).
131. Pelvis, anterior breadth: narrow, ilia longer anteroposteriorly than distance separating preacetabular processes (0); broad, distance between preacetabular processes exceeds anteroposterior length of ilia (1).
132. Pubis, ambiens process development: small, confluent with (0) or prominent, projecting anteriorly from (1) anterior margin of pubis.
133. Puboischial contact, length: approximately one-third (0) or one-half (1) total length of pubis.
134. Ischial blade, length: much shorter than (0) or equal to or longer than (1) pubic blade.
135. Ischial blade, shape: emarginate distal to pubic peduncle (0); no emargination distal to pubic peduncle (1).
136. Ischial distal shaft, shape: triangular, depth of ischial shaft increases medially (0); bladelike, medial and lateral depths subequal (1).
137. Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50 degrees with each other (0); flat, nearly coplanar (1).

138. Femoral midshaft, transverse diameter: subequal to (0), 125-150 percent, or (1) at least 185 percent (2) anteroposterior diameter.
139. Femoral shaft, lateral margin shape: straight (0); proximal one-third deflected medially (1).
140. Tibia, distal breadth: approximately 125 percent (0) or more than twice (1) midshaft breadth.
141. Fibular distal condyle, size: subequal to shaft (0); expanded transversely, more than twice midshaft breadth (1).
142. Astragalus, shape: rectangular (0); wedge-shaped, with reduced anteromedial corner (1).
143. Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1).
144. Astragalus, posterior fossa shape: undivided (0); divided by vertical crest (1).
145. Astragalus, transverse length: 50 percent more than (0) or subequal to (1) proximodistal height.
146. Calcaneum: present (0); absent or unossified (1).
147. Metatarsal I proximal condyle, transverse axis orientation: perpendicular to (0) or angled ventromedially approximately 15 degrees to (1) axis of shaft.
148. Metatarsal I distal condyle, transverse axis orientation: perpendicular to (0) or angled dorsomedially to (1) axis of shaft.
149. Metatarsal I distal condyle, posterolateral projection: absent (0); present (1).
150. Pedal digit I ungual, length: shorter (0) or longer (1) than metatarsal I.
151. Osteoderms: absent (0); present (1).

Character–Taxon Matrix

The following are scores for 151 characters in 10 terminal taxa and 2 outgroups.

Characters include state “0” (= primitive), states “1-4” (derived), “?” for missing information, and “9” for inapplicable data. All characters are binary except 21

(characters 6, 16, 20, 30, 43, 51, 53, 56, 63, 65, 70, 71, 81, 82, 97, 98, 99, 104, 109,

120, 129). All multistate characters were treated as unordered except one that codes positional change and is presumed to transform in an ordered fashion in development

(51). The text block below is formatted so that it can be copied and placed in PAUP.

#NEXUS

Begin data;
Dimensions ntax=12 nchar=151;
Format symbols="0~9";

Matrix

Omeisaurus

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0100000210?01000000000????00?11000100?
0001001001000000111100101010000010011110

Shunosaurus

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00003191000920000000?0190001000000000?999?
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Flagellicaudata

001011120111101111101?111100?201001010111001010?231202211?001?01010?15?1?
10000?21100100111?011011110011001100100010?1011110000111010100010001110011110

Rebbachisauridae

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000?0

Haplocanthosaurus

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000101110????????????0

Jobaria

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3010000930011100002100010001100000???0001?
001110100010110011100001110001011100011100110?0

Camarasaurus

110010011111010111010101100101101100010010001111111001121000002010101030001101
00210001000110010009900?101011101000101101111100111001101110001110011010

Brachiosaurus

111010011101010111000101111100101100110010011111212100121000103010010930011101
002100?11001110000???011??10?1101000101101111111101101101111011100110?0

Euhelopus

01?010?1??1??10?????0??????1??01??????100?1?????11?01121?101?
4011011120010101?03?0?????????????????011?????10100?110?????????????0??
011110011?00110?0

Malawisaurus

11?0???1??1?????????????????????????????????100?????11???1210?01??1000109?000?
111103?????10101111001??01?0911?????01110000??1??111?????????1111110?????????1

Lithostrotia

0?1?19?1?101010110?10101001112111?10??10?01011?0?121102210001??
100009400001111032011201011?0101100?
110911101011111019911111299101011121101101111001

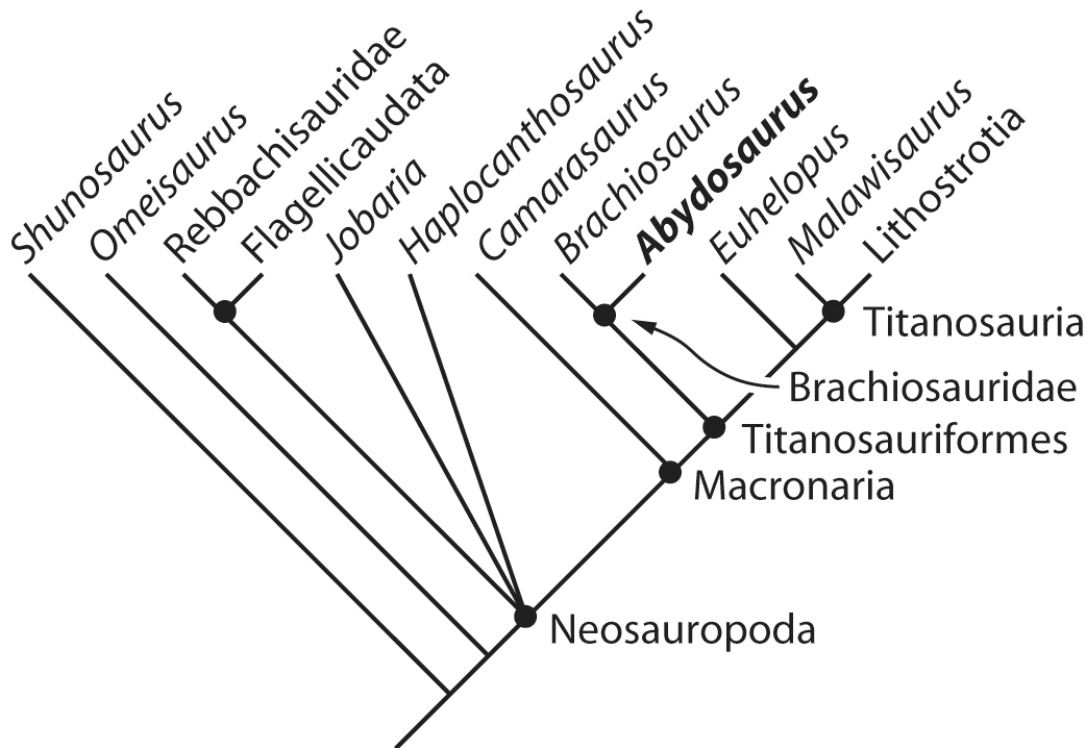
Abydosaurus

111110010101010?100001011011001?0?001000000110??21212012101010??10?
0?????????????????????10??1?????????????????110??010?????11?
111?????????????????????0

;
END;

Trees

The low number of terminal taxa allowed for use of “branch-and-bound” treebuilding methods, which guarantee discovery of the shortest tree (Swofford 2001). Five most parsimonious trees were discovered that differed in the positions of *Jobaria* and *Haplocanthosaurus* within Macronaria (TL=235; CI=0.63; RI=0.60; RC=0.45). Apart from this uncertainty, tree topology is consistent that of Wilson (2002). *Abydosaurus* could be scored for almost 50% of the characters, which resolved it within Macronaria as the sister taxon to *Brachiosaurus* (decay index = 3).



ESM3 Figure 1. Phylogenetic position of *Abydosaurus*. Strict consensus of 5 most parsimonious trees generated by analysis of 151 characters in 10 neosauropod ingroup taxa. The position of *Jobaria* and *Haplocanthosaurus* relative to other neosauropods is unstable, but *Abydosaurus* is nest within Titanosauriformes as the sister-taxon to *Brachiosaurus* (decay index = 3).

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