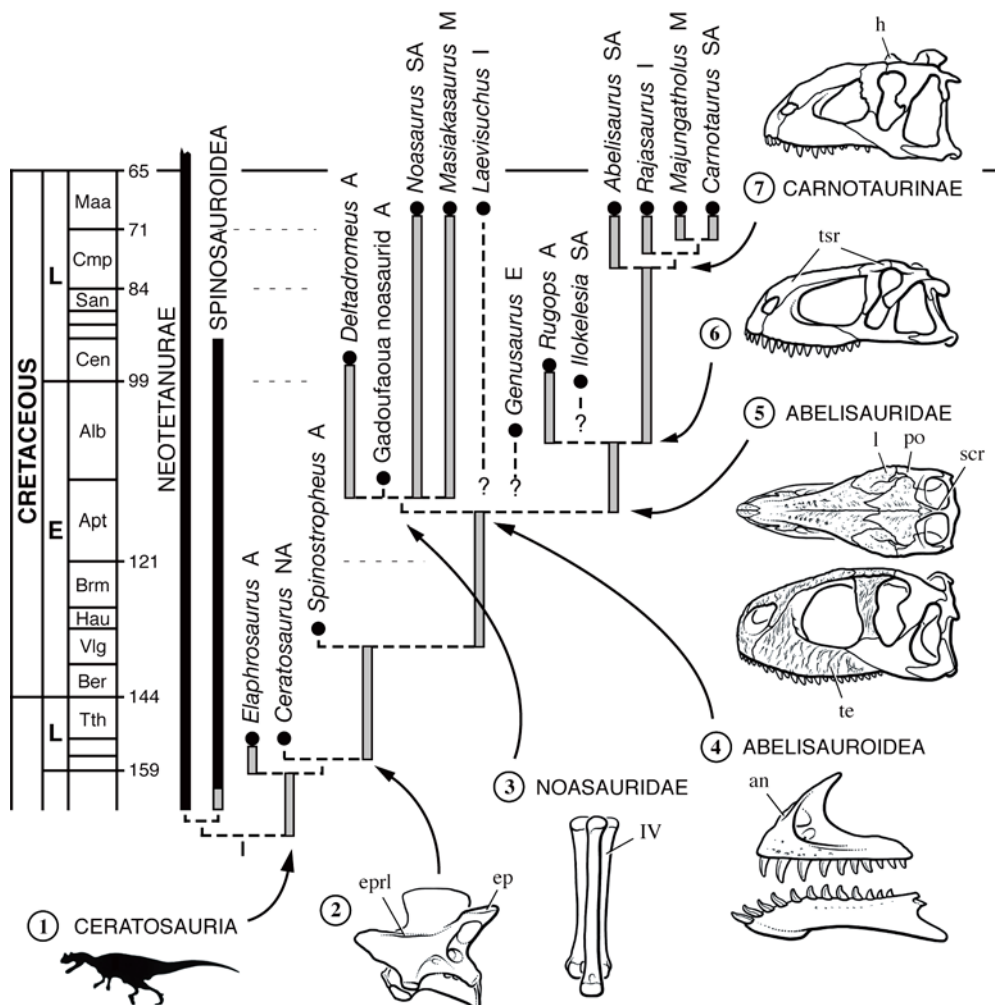


Basal Neotheropoda (Sereno et al., in review; Wilson et al., 2003)



Phylogenetic Analysis

The phylogenetic analysis summarized in the adjacent figure is based on 169 characters (66 cranial, 5 dental, 36 axial, 62 appendicular) scored for 21 ingroups, using *Herrerasaurus ischigualastensis* and *Eoraptor lunensis* as successive outgroups (Sereno et al., in review; Wilson et al., 2003). There are 6 multistate characters, 5 of which were ordered (47, 78, 83, 84, 91). The first cladistic use of each character appears in parentheses after the character. Characters with no citation are new to the analysis or are so modified from previous usage that attribution to a previous author may not constitute an accurate reference.

Maximum-parsimony analysis (Swofford, 1999) yielded two minimum-length tree of 205 steps, with the poorly known genera *Genusaurus* and *Ilokelesia* removed (CI = 0.86; RI = 0.93). The temporally-calibrated phylogeny uses a recent time scale (Gradstein et al., 1999).

Figure (Fig. 4 in Sereno et al., in review). Phylogenetic, temporal, and paleobiogeographic relationships among ceratosaurian theropods (169 characters, 205 steps; retention index = 0.93; see electronic Appendix on The Royal Society's Web site for discussion of phylogenetic nomenclature and phylogenetic analysis). Skeletal modifications include : **node 1**, a suite of cranial and postcranial characters that arose during the undocumented Early and Middle Jurassic history of the clade; **node 2**, prominent epipophyseal-prezygapophyseal lamina; **node 3**, metatarsal IV distal end reduced; **node 4**, anterolateral articulation for nasal process, intramandibular socket; **node 5**, groove-and-pit ornamentation, basic abelisaurid skull design; **node 6**, thickened skull roof; **node 7**, frontonasal horn. Area abbreviations: A, Africa; E, Europe; I, India; M, Madagascar; NA, North America; SA, South America. Anatomical abbreviations: an, articular surface for nasal; ep, epiphysis; epri, epipophyseal-prezygapophyseal lamina; h, horn; l, lacrimal; po, postorbital; scr, sagittal crest; te, textured external skull surface; tsr, thickened skull roof; IV, fourth metatarsal.

Character List and Matrix

The codings for the 169 characters (66 cranial, 5 dental, 36 axial, 62 appendicular) used in the analyses of Sereno et al. (in review) and Wilson & Sereno (2003) are listed below. There are 6 multistate characters, 5 of which were ordered (47, 78, 83, 84, 91). The first cladistic use of each character appears in parentheses after the character. Characters with no such citation are new to the analysis of Sereno et al. (in review) and Wilson et al. (2003). Two suprageneric ingroup taxa were scored on the basis of well known included genera (Spinosauroidea: *Suchomimus*, *Baryonyx*, *Torvosaurus*; Tetanurae: *Allosaurus*, *Sinraptor*).

1. Skull length: less (0), or more (1), than 3 times posterior skull height. (Sereno, 1999)
2. Skull, general external texture: smooth (0); sculptured (1). (Sampson et al., 1998)
3. Skull roof (frontal, nasal, lacrimal, postorbital), thickness: platelike (0); considerably thickened (1). (Novas, 1997)
4. Premaxilla, shape ventral to external naris: longer than deep (0); deeper than long (1). (Holtz, 1994)
5. Premaxilla, medial premaxillary foramen: absent (0); present (1).
6. Premaxilla posterolateral process, length: 2-3 times (0), or subequal to (1), transverse width at midlength. (modified from Carrano et al., 2002)
7. Premaxilla posterolateral process, form of articulation with maxilla: overlapping maxillary edge or anteromedial process (0); inserting into narrow slot between maxillary edge and anteromedial process (1). (modified from Carrano et al., 2002)
8. Premaxilla, palatal process: present (0); absent (1).
9. Premaxilla-maxilla arched diastema: absent (0); present (1). (Rowe, 1989)
10. Premaxilla-maxilla alveolar suture (portion of contact below premaxillary posterolateral process): present (0); absent (1). (Sereno, 1999)

11. Premaxilla-maxilla suture, form of upper portion (immediately ventral to the premaxillary posterolateral process): butt joint (0); separated by pneumatic spaces (1).
12. Premaxilla-nasal suture, form: V-shaped (0); W-shaped (1).
13. Maxilla, promaxillary fenestra and antrum: absent (0); present (1).
14. Maxilla, position of principal row of labial neurovascular foramina: displaced dorsal to (0), or immediately above (1), the alveolar margin.
15. Maxilla, position of articular facet for distal end of anteroventral process of nasal: anterior or slightly anterolateral (0); lateral (1).
16. Maxilla, form of articular surface for nasal anteroventral process, and form of nasal anteroventral process: shallow facet, tapered anteroventral process (0); trough with terminal pit, blunt-tipped anteroventral process (1).
17. Maxilla, contact with ventral process of lacrimal: present (0); absent (1). (modified from Coria and Salgado, 2000)
18. Maxilla, form of articular surface for jugal posteroventral to antorbital fossa: partially (0), or entirely (1), laterally facing.
19. Maxilla, articular surface for jugal, width: 15% or less (0), or 25% or more (1), of the length of the suture. (modified from Sampson et al., 1998)
20. Lacrimal canal, position of anterior (internal) foramen: at midlength (0), or at proximal base (1), of ventral process.
21. Lacrimal canal, position of posterior (external) foramen: at midlength (0), or at proximal base (1), of ventral process.
22. Lacrimal antorbital pneumatic recess (into central body of lacrimal): absent (0); present (1). (Novas, 1992)
23. Lacrimal antorbital pneumatic recess, orientation: laterally partially exposed (0); laterally covered (by rim of fossa) (1).
24. Lacrimal-postorbital contact: absent (0); present (1). (Novas, 1992)
25. Lacrimal brow, form: horizontal shelf (0); ventrolaterally beveled surface (1).
26. Lacrimal-jugal articulation, form: jugal overlaps lacrimal (0); jugal overlaps lacrimal and inserts into a slot in lacrimal near orbital margin (1). (modified from Sereno et al., 1994)
27. Lacrimal ventral process, shape of distal end: flange-shaped, broadening distally (0); subtriangular, tapering distally (1). (modified from Sereno, 1999)
28. Nasal, form of narial margin (lateral view): asymmetrical U-shape (0); symmetrical C-shape (1).
29. Nasal-nasal suture, form: open (0); fused anteriorly (1). (Forster, 1999; Sereno, 1999)
30. Nasal posterolateral process: absent (0); present (1). (Sereno, 1999)
31. Nasal posterior process, position of distal end: offset lateral (0), or adjacent (1), to the midline.
32. Nasal posterior process, anteroposterior position of distal end: anterior (0), or dorsal (1), to the orbit.
33. Jugal, antorbital pneumatic recess (anterior ramus): present (0); absent (1).
34. Antorbital fossa, size (anteroposterior diameter): greater than anteroposterior diameter (0), or any diameter (1), of other skull openings. (modified from Rowe, 1989)

35. Antorbital fossa, position of anterior end: posterior (0), or ventral (1), to posterior end of external naris. (Sereno, 1999)
36. Antorbital fossa on ventral ramus of maxilla: present (0); absent (1). (modified from Lamanna et al., 2002)
37. Antorbital fossa, form of ventral margin on maxilla: rounded edge (0); raised, rounded rim (1). (modified from Rowe, 1989)
38. Antorbital fossa, external rim on anterior process of lacrimal: present (0); absent (1).
39. Antorbital fossa on ventral ramus of lacrimal: present (0); absent (1).
40. Postorbital orbital process, shape and dorsoventral position: rounded, posterodorsal orbital margin (0); triangular flange, posterior orbital margin (1).
41. Postorbital orbital process, continuity: continuous with (0), or inset from (1), remainder of ventral ramus. (modified from Sampson et al., 1998)
42. Postorbital posterior process, shape: elongate (0), or equilateral (1), triangle.
43. Squamosal anterior process, form of postorbital articulation: tongue-and-groove (0); squamous (1).
44. Squamosal anterior process, orientation (lateral view): anterior (0); anterodorsal (1). (Sereno, 1999)
45. Supratemporal fossa, postorbital participation: present (0); absent (1). (Sereno, 1999)
46. Frontal-parietal suture, form: open (0); fused (1). (Forster, 1999; Sereno, 1999)
47. Frontal-parietal skull table, shape (dorsal view): hourglass (0); subtriangular (1); frontal triangle with parietal sagittal crest (2) (ordered).
48. Frontal horn(s): absent (0); present (1). (modified from Novas, 1997)
49. Parietal posteromedian process (capping nuchal wedge): absent or rudimentary (0); present and thickened (1).
50. Parietal alae, orientation: posterolateral (0); lateral (1).
51. Quadrate lateral flange, maximum width: approximately 50 % of (0), or subequal to (1), transverse width of distal condyles. (modified from Forster, 1999)
52. Quadrate foramen, position: mid height (opening anteriorly) (0), or closer to quadrate head (opening posterodorsally) (1). (modified from Holtz, 2000)
53. Quadrate distal condyles, flattened or slightly concave anterior facet: absent (0); present (1).
54. Palatine anterior process, shape: tapered distally (0); expanded distally (1). (Sereno, 1999)
55. Supraoccipital nuchal wedge, position: anterior (0), or posterior (1), to occipital condyle.
56. Supraoccipital nuchal wedge, length from foramen magnum to summit: subequal to (0), or more than twice (1), vertical diameter of the occipital condyle. (modified from Forster, 1999)
57. Supraoccipital nuchal wedge and parietal alae, position of dorsal extremity: slightly (0), or considerably (1), above frontoparietal skull table. (modified from Sampson et al., 1998)
58. Exoccipital-opisthotic, participation in basal tubera: absent (0); present (1). (Sereno, 1999)

59. Laterosphenoid head, location of articular socket: split between the frontal and postorbital (0); postorbital only (1). (Sereno, 1999)
60. Basisphenoid fontanelle: absent (0); present (1). (Forster, 1999; Sereno, 1999)
61. External mandibular fenestra, position of anterior end: posterior (0), or ventral (1), to last dentary tooth. (Sereno, 1999)
62. Dentary anterior end, shape: rounded (0); expanded dorsoventrally (1). (Forster, 1999; Sereno, 1999)
63. Dentary-surangular articulation, form: narrow V-shaped notch (0); broad U-shaped socket (1). (modified from Carrano et al., 2002)
64. Dentary, medial articular prong for surangular (separate from dorsal prong that is exposed laterally): absent (0); present (1).
65. Dentary posteroventral process, length: long (0); short (1), extending only as far posteriorly as the dentary posterodorsal process. (Sereno, 1999)
66. Prearticular-angular foramen: absent (0); present (1). (Sereno, 1999)
67. Premaxillary tooth row, position of posterior end: ventral (0), or anterior (1), to the external naris. (Sereno, 1999)
68. Maxillary tooth row, position of posterior end: ventral (0), or anterior (1), to the ventral ramus of the lacrimal. (modified from Gauthier, 1986)
69. Crown height (largest maxillary crowns): 20-30% (0), or 10-15% (1), of height of snout at midlength. (modified from Martinez et al., 1993)
70. Tooth rows, transverse curvature: minor (0); marked (1). (Sereno, 1999)
71. Dentary tooth 3, size: subequal (0), or enlarged (1), relative to dentary tooth 2. (Sereno, 1999)
72. Axial intercentrum length: 25-35% (0), or 40-70% (1), axial centrum length. (Sereno, 1999)
73. Axial anterior pleurocoel: absent (0); present (1). (Rowe, 1989)
74. Axial neural canal, vertical diameter: more (0), or less (1), than 30% vertical diameter of centrum. (Sereno, 1999)
75. Axial spinopostzygapophyseal lamina, form: straight or gently concave (0); deeply notched (1). (modified from Gauthier, 1986)
76. Axial prezygapophyses, form: raised facet (0); anteriorly-projecting shelf (1). (modified from Sereno, 1999)
77. Axial transverse process, size: rounded prominence (0); cylindrical process (1). (modified from Sereno, 1999)
78. Mid cervical (C3-C6) centrum length: less than 3 (0), 3 (1), or more than 4 (2), times centrum height (ordered). (Sereno, 1999)
79. Postatlantal cervical centra, form of articular surfaces: amphicoelous (0); marked opisthocoely (1). (Sereno, 1999)
80. Postaxial cervical centra, pleurocoel (anterior): absent (0); present (1). (Rowe, 1989)
81. Postaxial presacral vertebrae, posterior pleurocoel: absent (0); present (1). (Sereno et al., 1994)
82. Postaxial presacral vertebrae, posterior pleurocoel, form: open fossa (0); partially sharp-rimmed and invaginated (1).

83. Cervical epipophyseal-prezygapophyseal ridge/lamina, form and distribution: absent (0); rounded ridge in mid cervicals C4-C6 (1); prominent crest or lamina in all postaxial cervicals (2) (ordered). (modified from Coria and Salgado, 2000)
84. Cervical epiphyses, form: ridgelike or subconical if extended (0); mid cervical epiphyses anteroposteriorly extended with anterior corner (1); all anteroposteriorly extended (2) (ordered). (modified from Bonaparte et al., 1990)
85. Cervical epiphyses, height (dorsoventral distance from edge of postzygapophyseal facet): less (0), or more (1), than 50% of height of the posterior centrum face. (modified from Novas, 1997)
86. Postatlantal cervical vertebrae, pneumatic fossa on neural arch ventral to postzygapophysis: absent (0); present (1).
87. Mid cervical (C4-6) neural spines, orientation: vertical (0); posterodorsally inclined (1).
88. Dorsal centrum length: subequal to (0), or more than 2.5 times (1), centrum height. (Sereno, 1999)
89. Mid dorsal parapophyses, form: short process (0); process with cylindrical shaft (1).
90. Posterior dorsal parapophyses, position: anteroventral to diapophysis and ventral to prezygodiapophyseal lamina (0); anterior to diapophysis and joined with prezygodiapophyseal lamina (1).
91. Sacral number: 3 (primordial sacral pair, 1 dorsosacral) (0); 5 (primordial sacral pair, 1 dorsosacral, 2 caudosacrals) (1); 6 (primordial sacral pair, 2 dorsosacrals, 2 caudosacrals) (2) (ordered). (modified from Bonaparte, 1991)
92. Sacrum shape, dorsal view: subrectangular (0); subtriangular (1). (Sereno, 1999)
93. Mid sacral centra, ventral margin: horizontal (0); dorsally arched (1). (Sereno, 1999)
94. Mid sacral centra, transverse dimensions: similar to adjacent sacrals (0); strongly constricted (1). (Sereno, 1999)
95. Sacral transverse processes, relations: separate (0); fused (1). (Rowe, 1989)
96. Sacral neural spines, relations: separate (0); fused (1). (Rowe, 1989)
97. Sacral neural arches, development of paramedian fossae: poorly developed (0); divided by vertical septa (1).
98. Anterior caudal transverse processes, form: subrectangular or distally tapering (0); distally expanding (1). (Coria and Salgado, 2000)
99. Anterior caudal neural spines, anterior flange for interspinous articulation: absent (0); present (1). (Sereno, 1999)
100. Distal caudal centrum length: 3 to 4 (0), or approximately 7 (1), times centrum height. (Sereno, 1999)
101. Distal caudal prezygapophyses, maximum length: at least 30% or less (0), or at least 40% (1), overlap of preceding centrum. (Sereno, 1999)
102. Cervical ribs, pneumatic recesses near rib articular processes: absent (0); present (1). (Sampson et al., 1998)
103. Mid cervical (C4-8) ribs, lateral process for articulation with successive rib spine: absent (0); present (1).

104. Mid cervical (C4-8) ribs, form of lateral process for articulation with successive rib spine: ridge (0); flange (1).
105. Caudosacral ribs, attachment position: ventral margin (0), or angled toward posterodorsal corner (1), of postacetabular process. (Sereno, 1999)
106. Chevron base, paired anterior and posterior processes: absent (0); present (1). (Sereno et al., 1994)
107. Anterior chevrons, midshaft shape: transversely flattened (0); rod-shaped (1).
108. Scapular glenoid, shape: approximately twice as long as (0), or subequal to (1), its transverse width.
109. Coracoid posterior process, shape: hook-shaped (0); rounded corner (1). (Sereno et al., 1996)
110. Humeral head, shape and size: subcylindrical, approximately 50% of maximum width of proximal end (0); subspherical, approximately 70% or more of maximum width of the proximal end (1). (modified from Coria et al., 2000)
111. Humeral lateral tuberosity, position: proximal (0), or distal (1), to medial tuberosity.
112. Humeral deltopectoral crest, size (measured from the anterior margin of midshaft): subequal to (0), or less than (1), anteroposterior shaft diameter at midshaft. (modified from Carrano et al., 2002)
113. Humeral shaft axis, form: sigmoid (0); straight (1). (Holtz, 1994)
114. Humeral distal condyles, form: convex, rounded anteriorly (0); nearly flat (1). (Carrano et al., 2002)
115. Distal carpal 1, distal articulation: metacarpal I (0); metacarpals I and II (1). (Gauthier, 1986)
116. Manual digits and metacarpals, longest: digit III, metacarpal III (0); digit II, metacarpal II (1). (Sereno, 1999)
117. Metacarpal I length: longer (0), or shorter (1), than phalanx 1 or ungual of digit I. (Sereno, 1999)
118. Metacarpal III, mid shaft transverse diameter, and III-ungual length: subequal to digit II (0); diameter 55% or less metacarpal II, ungual length less than 70% II-ungual (1). (modified from Sereno et al., 1994)
119. Manual digit V: present (0); absent (1). (Gauthier, 1986)
120. Pelvic girdle sutures, form: open (0); fused (1). (Rowe, 1989)
121. Iliac length: shorter (0), or longer (1), than femoral length. (modified from Novas, 1991)
122. Iliac supracetabular crest, form: shelf-like with straight edge in lateral view (0); pendant with convex margin in lateral view (1). (Gauthier, 1986)
123. Iliac preacetabular process, position of anteroventral corner: anteroventral extremity of process (0); proximal to the anterior margin of the process (1).
124. Iliac postacetabular process, form of posterior margin: convex (0); concave (1). (Sereno, 1999)
125. Iliac postacetabular process, form of lateral attachment scar: subtle (0); pronounced scar (1). (Sereno, 1999)
126. Iliac pubic peduncle, orientation of distal articular end: approximately 45° (0), or 60° (1), from the horizontal. (modified from Sereno, 1999)
127. Iliac pubic peduncle, anterodorsal margin: present (0); rudimentary or absent (1).

128. Iliopubic contact, form: butt joint (0); peg-in-socket (1). (Sampson et al., 2001)
129. Ilioischial contact, form: butt joint (0); peg-in-socket (1).
130. Ilioischial articulation, width of distal end: subequal to (0), or smaller than (1), iliac-pubic articulation (1). (Serenio et al., 1994)
131. Pubic fenestra: absent (0); present (1). (Rowe, 1989)
132. Pubic shaft axis, form: straight (0); bowed anteriorly (1). (Rowe, 1989)
133. Pubic shaft, distal half, transverse width of blade-shaped medial portion: subequal to (0), or twice the width of (1), rod-shaped lateral portion. (Serenio, 1999)
134. Pubic foot: present (0); absent (1). (Holtz, 1994)
135. Pubic foot, symphyseal area: absent or restricted to distal margin (0); broad median contact (1). (Serenio, 1999)
136. Pubic foot, anteroposterior length: longer (0), or shorter (1), than ischial foot. (Serenio, 1999)
137. Ischial antitrochanter, form of nonarticular acetabular margin: concave (0); concave so as to undercut the antitrochanter (1).
138. Ischial antitrochanter, size: less (0), or subequal to or greater (1), than adjacent articular surface for ilium. (Serenio, 1999)
139. Ischial obturator notch (or foramen): absent (0); present (1). (Serenio et al., 1994)
140. Ischial shaft, cross-sectional shape (paired): broad contact, rod-like (0); separated dorsally, V-shaped. (Serenio, 1999)
141. Ischial foot: absent (0); present (1). (Bonaparte et al., 1990)
142. Femoral anterior trochanter, form: sigmoid (0); blade-shaped (1). (Serenio et al., 1994)
143. Femoral anterior trochanter, dimorphism: absent (0); present (1). (Rowe, 1989)
144. Tibial cnemial crest, width (lateral view): tapers distally, or less than 50% of proximal end (0); expands distally, or more than 50% of proximal end (1), distally. (cnemial crest measured from anterior margin of shaft)
145. Tibial cnemial crest, lateral fossa: absent (0); present (1).
146. Tibial proximal end, tibiofibular crest: absent (0); present (1). (Forster, 1999; Serenio, 1999)
147. Tibial midshaft proportions, transverse versus anteroposterior: subequal (0); transverse width 135-150% of anteroposterior width (1). (Serenio, 1999)
148. Tibiofibular shaft contact distal to tibiofibular crest: absent (0); present (1).
149. Tibial crest (distal to tibiofibular crest) with flattened articular edge for fibular shaft: absent (0); present (1). (Martinez et al., 1986)
150. Tibial distal end, lateral extension of posterolateral flange (= calcaneum, posterior articular facet for tibial posterolateral flange): partially (0), or nearly completely (1), backs the distal end of fibula and calcaneum. (modified from Serenio et al., 1994)
151. Fibular fossa: absent (0); present (1). (Rowe, 1989)
152. Fibular fossa, form: oval, opens medially (0); crescentic, invaginated anteriorly, opens posteromedially (1).
153. Fibular shaft ventral to tibiofibular crest, position relative to tibial shaft: lateral (0); anterior (1).

Dilophosaurus

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Carnotaurus

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SPINOSAUROIDEA

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NEOTETANURAE

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