Appendix to Salisbury *et al*. (2006) The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia

Appendix

<u>Characters used in the phylogenetic analysis</u>

The data matrix included 176 discrete morphological characters and 43 ingroup taxa (see below). Characters and codings used in the phylogenetic analysis are based primarily on those listed in the works of Brochu (1997a, b, 1999, 2004a, b), with additional information from Benton & Clark (1988), Norell (1988, 1989), Norell & Clark (1990), Clark & Norell (1992), Buscalioni *et al*. (1992), Willis (1993), Clark (1994), Poe (1997), Buckley & Brochu (1999), Ortega *et al*. (2000), Buscalioni *et al*. (2001), Hua & Jouve (2004) and Brochu & Rincón (2004). For continuity and ease of comparison, numbers for characters 1-164 correspond with those used in Brochu (1999). Many of the characters were modified since, especially in the case of multistate characters, some states were no longer represented in the matrix or the polarity had changed due to the larger composition of the ingroup. Where characters have been rephrased or modified in line with the present study, this is noted accordingly.

A total of twelve new characters was added to the matrix. In cases where these were taken from other published sources the respective papers are cited. New characters that do not appear in previous analyses are marked with a dagger (†).

In most cases, character state 0 refers to the plesiomorphic condition; however, character polarity was determined by rooting the tree (Nixon & Carpenter 1993) and in some cases, state 1 represents the plesiomorphic condition. Character optimisation was based on comparison with outgroup taxa. The two outgroups selected for this analysis were *Theriosuchus* (based on *T. pusillus* and *T. guimarotae*) and *Goniopholis* (based on *G. simus*, *G. crassidens*, the Bernissart *G.* '*simus*' and the Isle of Wight *G.* '*crassidens*'). These taxa were considered sufficiently basal to the group of interest and most of their anatomy is known.

1. Ventral tubercle of proatlas at least one-half (0) or less than one half (1) the width of the dorsal crest. (Brochu 1999, character 1.)

2. Proatlas boomerang-shaped (0) strap-shaped (1) or massive and block-shaped (2). (Brochu 1999, character 2.)

3. Caudal half of axis neural spine wide (0) or narrow (1). (Adapted from Brochu 1999, character 3.)

4. Axis neural arch lacks (0) or possesses (1) a lateral process (''diapophysis''). (Adapted from Norell 1989, character 7.)

5. Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0) or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1). (Modified from Clark 1994, character 89.)

6. Axial hypapophysis located toward the center of the vertebral body (0) or toward the cranial end of vertebral body (1). (Adapted from Brochu 1999, character 6.)

7. Hypapophysis present on all cervical vertebrae, along with thoracic vertebrae I and II (0) or thoracic vertebrae I-III (1) or thoracic vertebrae I-IV (2). (Adapted from Brochu 1999, character 7.)

8. First postaxial cervical vertebra without a hypapophysis (0) or with a weakly developed hypopophysis (1) or with a prominant hypophysis (2). (Adapted from Clark & Norell 1992, character 11.)

9. Neural spines on the caudal cervical vertebrae as broad as those on the cranial cervical vertebrae (0) or neural spines on the caudal cervical vertebrae craniocaudally narrow compared with those on the cranial cervical vertebrae (1). (Adapted from Buckley & Brochu 1999, character 90.)

10. Proatlas with prominent cranial process (0) or lacks cranial process (1). (Adapted from Brochu 1999, character 10.)

11. Cranial half of axis neural spine oriented horizontally (0) or slopes cranially (1). (Adapted from Brochu 1999, character 11.)

12. Axis neural spine crested (0) or not crested (1). (Brochu 1999, character 12.)

13. Cranial sacral capitulum projects far cranially of tuberculum and is broadly visible in dorsal aspect (0) or cranial margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1). (Adapted from Brochu 1999, character 13.)

14. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1). (Brochu 1999, character 14.)

15. Atlantal ribs lack (0) or possess (1) large articular facets at cranial ends for each other. (Adapted from Brochu 1999, character 15)

16. Atlantal ribs without (0) or with (1) very thin medial laminae at cranial end. (Adapted from Brochu 1999, character 16)

17. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel (1). (Adapted from Brochu 1999, character 17.)

18. Thoracic and lumbar vertebrae amphicoelous (0) or weakly procoelous (1) or strongly procoelous (2). Ordered. (Adapted from several previous analyses, e.g. Benton

& Clark 1988; Norell & Clark 1990, character 10; Clark 1994, character 93; Brochu 1999, character 18.)

19. Axial hypapophysis grades into two low ridges caudally (0) or axial hypopophysis grades into a single ridge caudally (1). (Adapted from Brochu 1999, character 19.)

20. Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1). (Brochu 1999, character 20.)

21. Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0) or early in ontogeny (1). (Brochu 1999, character 21.)

22. Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1). (Adapted from Benton & Clark 1988.)

23. Cranial crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1). (Adapted from Brochu 1999, character 23.)

24. Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1). (Brochu 1999, character 24.)

25. Scapulocoracoid facet cranial to glenoid fossa uniformly narrow (0) or broad immediately cranial to glenoid fossa, and tapering cranially (1). (Adapted from Brochu 1999, character 25.)

26. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1). (Brochu 1999, character 26.)

27. Proximal extremity of ulna narrow and subangular in outline (0) or wide and rounded (1). (Brochu 1999, character 27.)

28. Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation ('wasp-waisted'; 2) or narrow, with dorsal indentation (3) or rounded with smooth border; caudal tip of blade very deep (4). (Adapted from Brochu 1999, character 28.)

29. M. teres major and m. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to the deltopectoral crest (0) or insert with common tendon; single insertion scar (1). (Adapted from Brochu 1999, character 29.)

30. Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2). (Brochu 1999, character 30.)

31. Cranial end of interclavicle flat (0) or rodlike (1). (Adapted from Brochu 1999, character 31)

32. Supraacetabular crest narrow (0) or broad (1). (Brochu 1999, character 32.)

33. Limb bones very long and slender; forelimb and hind limb approximately equal in length at maturity (0) or limb bones relatively robust; hind limb much longer than forelimb at maturity (1). (Polarity reversed from Brochu 1999, character 33.)

34. Cranial process of ilium prominent (0) or virtually absent (1). (Adapted from Benton & Clark 1988; Clark 1994, character 84; although the transformation recorded here is different.)

35. Dorsal osteoderms keeled (0) or not keeled (1). (Polarity reversed from Brochu 1999, character 35; adapted from Buscalioni *et al*. 1992, character 22.)

36. Biserial dorsal shield, dorsal osteoderms rectangular in outline with distinct medial and lateral parts either side of a sagittal keel (0); dorsal osteoderms segmented sagittally into rectangular paravertebral osteoderms and square to round accessory osteoderms (1); paravertebral osteoderms segmented (2). Ordered. (Adapted from Brochu 1999, character 36; Norell & Clark 1990, character 16; Clark 1994, character 95.)

37. Accessory osteoderms absent (0) or maximum of one longitudinal row of transversely contiguous accessory osteoderms (1) or maximum of two longitudinal rows of transversely contiguous accessory osteoderms (2) or maximum of three sagittal longitudinal rows of transversely contiguous accessory osteoderms (3). (Adapted from Brochu 1999, character 37; Norell & Clark 1990, character 12; Clark 1994, character 97.)

38. Nuchal shield grades continuously into dorsal shield (0) or nuchal shield differentiated from dorsal shield into four nuchal osteoderms in two parallel rows (1) or nuchal shield differentiated from dorsal shield into six nuchal osteoderms, with four central and two lateral (2) or nuchal shield differentiated from dorsal shield into more than four nuchal osteoderms in two parallel rows (3). (Adapted from Brochu 1999, character 38.)

39. Ventral osteoderms present, polygonal (0) or present, square (1) or present, paired ossifications that suture together (2) or absent (3). (Adapted from Clark 1994, character 100; Brochu 1999, character 39.)

40: Paravertebral osteoderms with a cranial articular surface (0) or smooth, without a cranial articular surface (1). (Adapted from Norell & Clark 1990, character 13; Clark 1994, character 96; Brochu 1999, character 40.)

41. Splenial with rostral perforation for mandibular ramus of cranial nerve V (0) or lacks rostral perforation for mandibular ramus of cranial nerve V (1). (Adapted from Brochu 1999, character 41.)

42. Mandibular ramus of cranial nerve V exits splenial rostrally only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V caudally (1) or splenial has double perforation for mandibular ramus of cranial nerve V caudally (2). (Adapted from Norell 1988, character 15; Norell 1989, character 8; Brochu 1999, character 42)

43. Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from the mandibular symphysis; rostral tip of splenial passes ventral to the Meckelian groove (1) or splenial excluded from the mandibular symphysis; rostral tip of splenial passes dorsal to the Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide 'V' within the mandibular symphysis (3) or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within the mandibular symphysis and forms narrow 'V' (4). (Adapted from Clark 1994, character 77.)

44. Articular-surangular suture simple (0) or with rostral process dorsal to the lingual foramen ('crocodyline process' of Aoki 1992; 1) or with rostral process ventral to lingual foramen (2). (Adapted from Brochu 1999, character 44)

45. Lingual foramen for articular artery and alveolar nerve on surangular entirely (0) or on surangular/angular suture (1) or on angular entirely (2). (Brochu 1999, character 45.)

46. Coronoid bounds caudal half of the medial intermandibular foramen (0) or completely surrounds the medial intermandibular foramen at maturity (1) or obliterates the medial intermandibular foramen at maturity (2). (Adapted from Norell 1988, character 12.)

47. Angular-surangular suture contacts external mandibular fenestra at caudal angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1). (Adapted from Norell 1988, character 40.)

48. Rostral processes of surangular unequal (0) or subequal to equal (1). (Adapted from Brochu 1999, character 48.)

49. Foramen aërum at extreme lingual margin of the retroarticular process (0) or set in from margin of the retroarticular process (1). (Adapted from Norell 1989, character 16.)

50. Retroarticular process projects caudally (0) or projects caudodorsally (1). (Adapted from Benton & Clark 1988; Clark 1994, character 71; Norell & Clark 1990, character 7.)

51. Surangular extends to the caudal end of the retroarticular process (0) or is pinched off rostral to the tip of the retroarticular process (1). (Adapted from Norell 1988, character 42.)

52. Alveoli for dentary teeth 3 and 4 nearly the same size and confluent (0) or fourth alveolus larger than third, and alveoli are separated (1). (Brochu 1999, character 52.)

53. Rostral-most dentary teeth directed rostrally (0) or directed rostrodorsally (1). (Adapted from Brochu 1999, character 53.)

54. Superior edge of coronoid slopes strongly cranially (0) or almost horizontal (1). (Adapted from Brochu 1999, character 54.)

55. Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1). (Brochu 1999, character 55)

56. Coronoid imperforate (0) or with a perforation caudal to the medial intermandibular foramen (1). (Adapted from Brochu 1999, character 56.)

57. Dorsal projection of hyoid cornu flat (0) or rodlike (1). (Brochu 1999, character 57.)

58. Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1). (Brochu 1999, character 58.)

59. Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1). (Brochu 1999, character 59.)

60. Sulcus between articular and surangular (0) or articular flush against surangular (1). (Brochu 1999, character 60.)

61. Surangular with spur bordering the dentary toothrow lingually for at least one alveolar length (0) or lacking such spur (1). (Brochu 1999, character 61.)

62. External mandibular fenestra absent (0) or present (1). (Clark 1994, character 75.)

63. Dorsal rostral projection of coronoid longer than ventral (0) or ventral projection longer than dorsal (1). (Adapted from Brochu 1999, character 63.)

64. External mandibular fenestra small; caudal intermandibular foramen not visible laterally (0) or external mandibular fenestra large; caudal intermandibular foramen visible laterally (1). (Adapted from Norell 1988, character 14.)

65. Surangular-dentary suture intersects external mandibular fenestra rostral to the rostrodorsal corner (0) or at the caudodorsal corner (1). (Adapted from Brochu 1999, character 65.)

66. Angular extends dorsally toward or beyond rostral end of the caudal intermandibular foramen; rostral tip acute (0) or does not extend dorsally beyond rostral end of the caudal intermandibular foramen; rostral tip very blunt (1). (Adapted from Brochu 1999, character 66.)

67. Surangular-angular suture lingually meets articular at ventral tip (0) or dorsal to ventral tip (1). (Brochu 1999, character 67.)

68. Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli. (Brochu 1999, character 68.)

69. Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1). (Adapted from Norell 1988, character 1.)

70. Postorbital bar massive (0) or slender (1). (Norell 1988, character 3.)

71. Rostral border of the secondary choanae is comprised of the palatines (0) or secondary choanae entirely surrounded by pterygoids (1). (Adapted from Benton & Clark 1988; Clark 1994, character 43; Norell & Clark 1990, character 1.)

72. Secondary choanae project caudoventrally (0) or rostroventrally (1) at maturity. (Adapted from Brochu 1999, character 72.)

73. Pterygoidal surface, lateral and rostral to the secondary choanae, flush with choanal margin (0) or pushed inward to form 'neck' (1). (Adapted from Brochu 1999, character 73.)

74. Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1). (Adapted from Norell 1988, character 5).

75. Quadratojugal forms the caudal angle of the infratemporal fenestra (0) or jugal forms the caudal angle of the infratemporal fenestra (1) or jugoquadratojugal suture lies at caudal angle of infratemporal fenestra (2). (Adapted from Norell 1989, character 10; Brochu 1999, character 75.)

76. Postorbital contacts neither quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3). (Adapted from Brochu 1999, character 76.)

77. Dentary tooth 4 occludes in notch between the premaxilla and the maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1). (Norell 1988, character 29.)

78. All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between 7th and 8th maxillary teeth; all other dentary teeth occlude lingually (1) or dentary teeth occlude in line with the maxillary toothrow (2). (Adapted from Norell 1988, character 5; Willis 1993, character 1.)

79. Naris projects rostrodorsally (0) or dorsally (1). (Adapted from Brochu 1999, character 79.)

80. Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in the infratemporal fenestra (1). (Adapted from Buscalioni *et al.* 1992, character 6.)

81. Frontoparietal suture deeply within supratemporal foramen; frontal prevents broad contact between the postorbital and the parietal (0) or suture makes modest entry into supratemporal foramen at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2). (Adapted from Brochu 1999, character 81.)

82. Supraoccipital exposure on dorsal skull table small (0), absent (1), large (2), or large such that parietal is excluded from caudal edge of the skull table (3). (Adapted from Norell 1988, character 11.)

83. Quadratojugal sends long rostral process along lower temporal bar (0) or sends modest process, or none at all, along lower temporal bar (1). (Adapted from Brochu 1999, character 83.)

84. Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares rostrally (1). (Adapted from Brochu 1999, character 84.)

85. Palatopterygoidal suture nearly at (0) or far from (1) caudal angle of the suborbital fenestra. (Adapted from Brochu 1999, character 85.)

86. Frontoparietal suture linear (0) or concavoconvex (1). (Polarity reversed from Brochu 1999, character 86.)

87. Supratemporal foramen with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of the supratemporal foramen near maturity (1) or supratemporal foramen closes during ontogeny (2). (Adapted from Norell 1988, character 9.)

88. Suborbital fenestra without (0) or with (1) caudal notch. (Adapted from Brochu 1999, character 88.)

89. Maxillary alveoli #4 and #5 same size and largest (0) or #5 largest (1) or #4 largest (2) or homodont (3). (Adapted from Norell 1988, character 1; Brochu 1999, character 89.)

90. Lateral edges of palatines parallel caudally (0) or flare caudally, producing a 'shelf' (1). (Adapted from Norell 1988, character 2.)

91. Ectopterygoid abuts maxillary toothrow (0) or maxilla broadly separates ectopterygoid from maxillary toothrow (1). (Norell 1988, character 19.)

92. Shallow fossa at rostromedial corner of supratemporal foramen (0) or no such fossa; rostromedial corner of supratemporal foramen smooth (1). (Adapted from Brochu 1999, character 92.)

93. Lacrymal makes broad contact with nasal; no caudal process of the maxilla (0) or maxilla sends caudal process within the lacrymal (1) or maxilla sends caudal process between the lacrymal and the prefrontal (2). (Adapted from Brochu 1999, character 93.)

94. Lateral edges of palatines smooth rostrally (0) or with lateral process projecting from palatines into suborbital fenestrae (1). (Adapted from Brochu 1999, character 94.)

95. Naris bisected by the nasals (0) or nasals contact the naris, but do not bisect it (1) or nasals excluded, at least externally, from the naris; nasals and premaxillae still in contact (2) or nasals and premaxillae not in contact (3). (Adapted from Norell 1988, character 3; Clark 1994, characters 13 and 14.)

96. Palpebral forms from single ossification (0) or from multiple ossifications (1). (Adapted from Norell 1988, character 8; Clark 1994, character 65.)

97. Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny. (Norell 1988, character 17.)

98. Caudomedial processes of pterygoid prominent and project ventrally (0) or small and project caudoventrally (1) or small and project caudally (2). (Adapted from Brochu 1999, character 98.)

99. Prefrontal pillar solid (0) or with large pneumatic sinus (prefrontal recess of Witmer 1997) (1).

100. Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1). (Norell 1988, character 27.)

101. Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1). (Brochu 1999, character 101.)

102. Caudal margin of otic aperture smooth and continuous with the paraoccipital process (0) or caudal margin of otic aperture inset (1). (Adapted from Brochu 1999, character 102)

103. Margin of orbit flush with skull surface (0) or dorsal edges of orbits upturned (1) or orbital margin forms a distinct collar (2). (Adapted from Brochu 1999, character 103)

104. Medial parietal wall of supratemporal foramen imperforate (0) or bearing smaller foramina (1). (Norell 1988, character 51.)

105. Lateral edge of suborbital fenestra straight (0) or bowed medially (1). (Brochu 1999, character 105.)

106. Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1). (Brochu 1999, character 106.)

107. Caudal rim of secondary choanae not deeply notched (0) or deeply notched (1). (Adapted from Brochu 1999, character 107.)

108. Rostral margin of palatine process rounded or pointed rostrally (0) or rostrally concave (1). (Adapted from Brochu 1999, character 108.)

109. Rostral ectopterygoid process tapers to a point (0) or forked (1). (Adapted from Brochu 1999, character 109.)

110. Palatine process extends (0) or does not extend (1) significantly beyond the rostral end of the suborbital fenestra. (Adapted from Willis 1993, character 2.)

111. Maxillary foramen for palatine ramus of CN-V small or not present (0) or very large (1). (Brochu 1999, character 111.)

112. Quadrate with small, ventrally-reflected medial hemicondyle (0) or with a small medial hemicondyle; dorsal notch for foramen aërum (1) or with a prominent dorsal projection between the hemicondyles (2) or with an expanded medial hemicondyle (3). (Brochu 1999, character 112.)

113. Basisphenoid expanded rostrocaudally ventral to the basioccipital (0) or forms a thin sheet (1). (Adapted from Brochu 1999, character 113.)

114. Quadratojugal spine low, near caudal angle of infratemporal fenestra (0) or high, between caudal and superior angles of infratemporal fenestra (1). (Adapted from Brochu 1999, character 114.)

115. Laterosphenoid bridge comprised entirely of laterosphenoid (0) or includes an ascending process of the palatine (1). (Adapted from Brochu 1999, character 115.)

116. Pterygoidoectopterygoidal flexure disappears during ontogeny (0) or remains throughout ontogeny (1). (Adapted from Brochu 1999, character 116.)

117. Lacrymal longer than prefrontal (0), or prefrontal longer than lacrymal (1), or lacrymal and prefrontal both elongate and nearly the same length (2). (Modified from Norell 1988, character 7.)

118. Palatine process generally broad rostrally (0) or in the form of thin wedge (1). (Adapted from Brochu 1999, character 118.)

119. Basisphenoid not broadly exposed ventral to the basioccipital at maturity in occipital aspect; pterygoid dorsoventrally short ventral to median eustachian opening (0) or basisphenoid broadly exposed ventral to the basioccipital in occipital aspect at maturity; pterygoid dorsoventrally tall ventral to median eustachian opening (1). (Adapted from Brochu 1999, character 119.)

120. Medial jugal foramen small (0) or very large (1). (Brochu 1999, character 120.)

121. Quadrate foramen aërum on mediodorsal angle (0) or on dorsal surface (1) of quadrate. (Brochu 1999, character 121.)

122. Sulcus on rostral braincase wall lateral to the basisphenoid rostrum (0) or braincase wall lateral to the basisphenoid rostrum smooth; no sulcus (1). (Adapted from Brochu 1999, character 122.)

123. Skull table surface slopes ventrally from median plane (0) or planar (1) at maturity. (Adapted from Brochu 1999, character 123.)

124. Incisive foramen absent or small, less than half the greatest width of premaxillae (0) or large, more than half the greatest width of premaxillae (1) or large, and intersects maxillopremaxillary suture (2). (Adapted from Brochu 1999, character 124.)

125. Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at the maxillopremaxillary suture (1). (Adapted from Norell 1988, character 22.)

126. Vomer entirely obscured by the maxillae and the palatines (0) or exposed on palate between the palatines (1). (Brochu 1999, character 126.)

127. Significant ventral quadrate process on lateral braincase wall (0) or quadratopterygoidal suture linear from basisphenoid exposure to the foramen ovale (1). (Brochu 1999, character 127.)

128. Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid lateral exposure at maturity. (Brochu 1999, character 128.)

129. Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall rostral to foramen ovale. (Adapted from Norell 1989, character 5.)

130. Capitate process of laterosphenoid oriented laterally (0) or rostrocaudally (1) toward the midline. (Adapted from Brochu 1999, character 130.)

131. Parietal and squamosal widely separated by the quadrate on the caudal wall of the supratemporal foramen (0) or the parietal and the squamosal approach each other on caudal wall of supratemporal foramen without actually making contact (1) or the parietal and the squamosal meet along caudal wall of the supratemporal foramen (2). (Adapted from Brochu 1999, character 131.)

132. Quadratosquamosal suture extends dorsally along caudal margin of the external auditory meatus (0) or extends only to the caudoventral corner of the external auditory meatus (1). (Adapted from Brochu 1999, character 132.)

133. Ectopterygoid extends along the medial face of postorbital bar (0) or stops abruptly ventral to the postorbital bar (1). (Brochu 1999, character 133.)

134. Rostral projection on postorbital bar prominent (0) or not prominent/absent (1). (Adapted from Norell 1989, character 2; Brochu 1999, character 134.)

135. Maxillary tooth row laterally convex or parallel (0) or laterally convex and flaring caudally (1) caudal to first six maxillary alveoli. (Adapted from Clark 1994, character 79; Brochu 1999, character 135.)

136. Medial process of prefrontal pillar expanded dorsoventrally (0) or rostrocaudally (1). (Adapted from Brochu 1999, character 136.)

137. Dorsal half of prefrontal pillar narrow (0) or expanded rostrocaudally in dorsal half (1). (Adapted from Norell 1988, character 41.)

138. Medial process of prefrontal pillar wide (0) or constricted (1) at base. (Brochu 1999, character 138.)

139. Ventral margin of orbit gently circular (0) or with prominent notch (1). (Brochu 1999, character 139.)

140. Mature skull table with broad lateral curvature; short caudolateral process of the squamosal (0); mature skull table with nearly horizontal sides; significant caudolateral process of the squamosal (1); mature skull table with nearly horizontal sides; caudolateral process of the squamosal greatly enlarged (2). (Adapted from Brochu & Rincón 2004, character 140.)

141. Exoccipital with prominent boss medial to the paroccipital process; process lateral to the caudal aperture of the cranioquadrate canal short (0) or exoccipital with small or no boss medial to the paroccipital process; process lateral to the caudal aperture of the cranioquadrate canal long (1). (Adapted from Brochu 1999, character 141.)

142. Premaxillary surface lateral to the naris smooth (0) or with deep notch (1). (Brochu 1999, character 142.)

143. Rostral canthi absent or very modest (0) or very prominent (1) at maturity. (Norell 1988, character 34; Brochu 1999, character 143.)

144. Preorbital ridges absent or very modest (0) or very prominent (1) at maturity. (Brochu 1999, character 144.)

145. Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1). (Brochu 1999, character 145.)

146. Dorsal process of the jugal flush with the lateral surface of the jugal (0) or considerably inset from the lateral surface of the jugal, and displaced ventral to the dorsal margin (1). (Adapted from Benton & Clark 1988; Norell & Clark 1990, character 3; Ortega *et al*. 2000, character 34; Brochu 1999, character 146.)

147. Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal. (Adapted from Norell 1988, character 46.)

148. Surface of the maxilla within the narial canal imperforate (0) or with multiple cecal recesses (1). (See Witmer 1995.)

149. Ectopterygoid extends (0) or does not extend (1) to caudal tip of the lateral pterygoid flange at maturity. (Adapted from Norell 1988, character 32.)

150. Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of exoccipital and quadrate. (Brochu 1999, character 150.)

151. Exoccipital terminates dorsal to basioccipital tuberosity (0) or sends a robust process ventrally and participates in the basioccipital tuberosity (1) or sends a slender process ventrally to the basioccipital tuberosity (2). (Adapted from Norell 1988, character 20; Clark 1994, characters 57 and 60; Brochu 1999, character 151.)

152. Secondary choanae not septate (0) or with a septum that remains recessed within the choanae (1) or with a septum that projects out of the choanae (2). (Adapted from Brochu 1999, character 152.)

153. Incisive foramen completely situated far from the premaxillary toothrow, at the level of the second or third alveolus (0) or abuts the premaxillary toothrow (1) or projects between first premaxillary teeth (2). (Brochu 1999, character 153.)

154. Parietal with sinus communicating with a pneumatic system (0) or solid, without a sinus (1). (Brochu 1999, character 154.)

155. Ventral scales have (0) or lack (1) follicle gland pores. (Poe 1996; Brochu 1999, character 155.)

156. Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two enlarged parallel rows (2). (Poe 1996; Brochu 1999, character 156.)

157. Median pelvic keel scales form two parallel rows along most of tail length (0) or form single row along tail (1) or merge with lateral keel scales to form Y-shaped keel (2). (Poe 1996; Brochu 1999, character 157.)

158. Lingual osmoregulatory pores small (0) or large (1). (See Taplin & Grigg 1989.)

159. Tongue with (0) or without (1) keratinised surface. (See Taplin & Grigg 1989.)

160. M. caudofemoralis with a single head (0) or with double head (m. caudofemoralis longus and m. caudofemoralis brevis; 1). (See Frey *et al.* 1989.)

161. Naris circular or keyhole-shaped (0) or wider than long (1). (Brochu 1999, character 161.)

162. Suranguloarticular suture oriented rostrocaudally (0) or bowed strongly laterally (1) within glenoid fossa. (Adapted from Brochu 1999, character 162.)

163. Postorbitosquamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table. (Adapted from Brochu 1999, character 163.)

164. Rostral foramen for palatine ramus of cranial nerve VII ventrolateral (0) or ventral (1) to basisphenoid rostrum. (Adapted from Brochu 1999, character 164.)

165. Caudal maxillary alveoli round (0) or mediolaterally compressed (1). (From Brochu 2004b, character 165.)

166. Dentary symphysis extends to sixth through eighth dentary alveolus (0) or to fourth or fifth alveolus (1) or beyond eighth dentary alveolus (2). (Adapted from Brochu 2004b, character 166.)

167. Largest dentary alveolus immediately caudal to fourth is: 13 or 14 (0); 13 or 14 and a series behind it (1); 10, 11, or 12 (2); or, all alveoli are of a uniform size (3). (Adapted from Brochu 2004b, character 167.)

168. Prefrontal pillars transversely expanded at their dorsal half and columnar ventrally (0); narrow or longitudinally expanded at their dorsal part and columnar ventrally (1). (From Buscalioni *et al*. 2001, character 165; modified from Ortega *et al*. 2000, character 30.)

†169. Height of peduncle of neural arch on caudal cervical vertebrae approximately equivalent to that of peduncle on neural arch of each of the thoracic, sacral and cranial-most caudal vertebrae (0) or considerably greater (1).

170. Cervical vertebrae all amphicoelous (0) or some amphicoelous and some procoelous (1) or all procoelous (2). Ordered. (Adapted from Norell & Clark 1990, character 8.)

171. Caudal vertebrae all amphicoelous (0) or first caudal vertebra opisthoceolous or procoelous, remainder of caudal vertebrae amphicoelous (1) or first caudal vertebra opisthoceolous or procoelous, remainder of caudal vertebrae procoelous, with the degree of procoely decreasing terminally (2) or first caudal vertebra biconvex, remainder of caudal vertebrae procoelous, with the degree of procoely decreasing terminally (3). Ordered. (Adapted from Norell & Clark 1990, character 9.)

172. Secondary choanae situated near the rostral margin of the pterygoids (0) or towards the caudal margin of the pterygoids (1). (Adapted from Clark 1994, character 44.)

†173. Distal extremity of the ulna expanded transversely with respect to the long axis of the bone; maximum width equivalent to that of the proximal extremity (0) or proximal extremity of the ulna considerably wider than the distal extermity (1).

174. Occipital surface ventral to basioccipital condyle slopes rostroventrally (0) or is roughly parallel to the transverse plane ('verticalised' basicranium, sensu Tarsitano 1985) (1). (Adapted from Hua & Jouve 2004, character 167.)

175. Postorbital bar continuous with the lateral edge of the dorsal part of the postorbital (0) or postorbital bar inset from the lateral edge of the dorsal part of the postorbital (1). (Norell & Clark 1990, character 3.)

176. Antorbital fenestra present (0) or absent (1). (Benton & Clark 1988; Norell & Clark 1990, character 2.)

Taxon-character matrix

Key advanced neosuchian and basal eusuchian taxa considered in this analysis were *Bernissartia fagessii* (Norell & Clark 1990), *Susisuchus anatoceps* (Salisbury *et al*. 2003a) and *Hylaeochampsa vectiana* (Clark & Norell 1992). Species of *Borealosuchus* (Brochu 1997b, 1999), and well-known basal gavialoids, alligatoroids and crocodyloids were also included. The number of extant taxa was selectively reduced in order to eliminate ambiguous portions of the tree that are remote from the problem at hand, and to reduce computation time. Advanced neosuchian and basal eusuchian taxa not considered in the analysis include taxa that are either poorly known or could not be examined firsthand: *Shamosuchus* spp., (Efimov 1988, Turner *et al*. 2005); *Stomatosuchus inermis* (Stromer 1925); *Aegyptosuchus peyeri* (Stromer 1933); *Aigialosuchus villadensis* (Persson 1960); *Tadzhikosuchus* spp. (Efimov 1988); *Dolichochampsa minima* (Gasparini & Buffetaut 1980); and *Rugosuchus nonganesis* (Wu *et al*. 2001). We are not convinced of the taxonomic validity of *Allodaposuchus precedens* as defined by Buscalioni *et al*. (2001), so refrained from using it in the main analysis. (An analysis that included *Allodaposuchus* was nevertheless carried out; see Appendix.) The 'Glen Rose form' (Langston 1974), often considered a basal eusuchian (e.g., Benton & Clark 1988; Brochu 1999), was also not included. Much of the material previously considered representative of the Glen Rose form is now thought to belong to the atoposaurid *Pachycheilosuchus* (see Rogers 2003). Until such time as the Glen Rose form is formally described, we are of the opinion that it is best left out of discussions on origins of Eusuchia and Crocodylia. An undescribed neosuchian from the Barremian Calizas de la Huéguina Formation of Las Hoyas, Spain (Ortega & Buscalioni 1995) was also not considered.

The data matrix is based primarily on that of Brochu (1997a, b, 1999, 2004a, b). Where characters have been modified, taxa have been re-scored accordingly, based either on our own examination of the original material or on descriptions and illustrations provided in the literature. Following Brochu (1999), *Australosuchus clarkae* was selected as a representative of Mekosuchinae sensu Salisbury & Willis (1996). Crocodylines were reduced to five taxa (*Crocodylus cataphractus*, *Crocodylus porosus*, *Osteolaemus tetrapsis*, '*Crocodylus*' *robustus* and '*Crocodylus*' *megarhinus*), tominstomines to four (*Tomistoma schlegelii*, *Tomistoma lusitanica*, *Gavialosuchus americanus* and '*Crocodylus*' *spenceri*), alligatoroids to twelve (*Leidyosuchus canadensis*, *Diplocynodon darwinii*, *Baryphracta depoponiae*, *Brachychampsa* *montana*, *Stangerochampsa mccabei*, *Navajosuchus mooki*, *Hassiaciosuchus haupti*, *Alligator mississippiensis*, *Paleosuchus trigonatus*, *Caiman yacare*, *Caiman latirostris* and *Melanosuchus niger*) and gavialoids to seven (*Eothoracosaurus mississippiensis*, *Thoracosaurus macrorhychus*, *Thecochampsoides minor*, *Eogavialis africanus*, *Gryposuchus columbianus*, *Siquisiquesuchus venezuelensis* and *Gavialis gangeticus*).

Codings for *Eothoracosaurus mississippiensis*, *Thoracosaurus macrorhychus*, *Thecochampsoides minor*, *Eogavialis africanus* and *Gryposuchus columbianus* were based primarily on those provided in Brochu (2004a), *Siquisiquesuchus venezuelensis* on those provided in Brochu & Rincón (2004), and *Navajosuchus mooki* and *Hassiaciosuchus haupti* on those provided in Brochu (2004b).

Codings for *Allodaposuchus precedens* (*sensu* Buscalioni *et al*. 2001) were based on those provided in Buscalioni *et al*. (2001) and Hua & Jouve (2004). However, where it appeared to us that the scores provided in these papers conflicted with the descriptions and illustrations provided in Buscalioni *et al*. (2001), they were changed accordingly or left as 'unknown'.

Character codings for newly added taxa are based on the following sources.

Goniopholis simus: BMNH 41098 and 41098a (holotype), BMNH R5814 and IPB R359.

Goniopholis crassidens: BMNH 3798 (holotype).

Isle of Wight *Goniopholis* '*crassidens*': BMNH R3876.

Bernissart *Goniopholis* '*simus*': IRScNB R1537 and IRScNB R1539.

Theriosuchus pusillus: BMNH 48216 (lectotype) and BMNH 48330 (paratype).

Theriosuchus guimarotae: IPFUB Gui Croc 7308 (holotype), 7352, 7441, 7545, 7564, 8037, 7349, 7550, 7555, 7381, 7394, 73133, 73134, 73135, 7475, 7614, 8138, 8148, 7351, 7360, 7426, 7429, 7560, 75108, 7526, 7743, 7809, 7910, 8033, 8111, 8132, 7472, 8028, 7423, 7584, 7363, 7388, 7395, 73137, 73138, 73139, 7422, 7478, 7552, 7575, 75109, 75110, 7633, 7654, 7658, 7682, 7725, 7744, 7811, 7906, 7913, 8024, 8047, 8052, 8114, 8133, 8136, 8218, 8248, 7369, 7629, 7727, 7810, 8123, 7480, 7570, 8017, 8217, 7548, 7549, 8116, 7420, 7542, 7661, 7674, 7675, 7908, 8142, 8230, 7391, 7457, 7641, 7668, 7580, 7678, 7680, 8130, 7350, 7366, 7389, 7396, 73140, 73141, 73142, 7428, 7839, 7482, 7543, 7544, 7553, 7564, 7568, 7577, 7585, 7599, 75112, 75113, 75127, 7617, 7618, 7621, 7624, 7625, 7643, 7722, 7723, 7728, 7909, 8010, 8016, 8135, 8139, 8210, 8212, 7348, 7397, 7562, 8025, 8039, 8053, 8221, 8231, 73125, 7659, 8141, 8232, 75104, 7579, 8245, 7301, 7352, 7355, 7357, 7359, 7374, 7375, 7376, 7377, 7379, 7380, 7383, 7385, 7392, 73101, 73128, 73129, 73130, 73131, 73132, 7415-3, 7416, 7417, 7419, 7421, 7424, 7425, 7430, 7431, 7432, 7434, 7437, 7438, 7441-1-6, 7442, 7458, 7459, 7461, 7462, 7463, 7464, 7465, 7466, 7467, 7468, 7469, 7470, 7471, 7472, 7473, 7474, 7496, 74108, 7563, 7565, 7566, 7572, 7583, 75105, 75106, 75107, 75118, 75134, 75135, 7623, 7627, 7650, 7685, 7729, 7730, 7912, 8012, 8014, 8015, 8019, 8026, 8031, 8037, 8041, 8057, 8058, 8113, 8118, 8125, 8137, 8146, 8147, 8159, 8160, 8216, 8226, 8227, 8228, 8236, 8246, 8247.

Susisuchus anatoceps: SMNK 3804 PAL (holotype).

Institutional abbreviations for reference specimens: **BMNH**, Natural History Museum, London (formerly the British Museum of Natural History); **IPB**, Institut für Paläontologie der Universität Bonn, Germany; **IPFUB**, Institut für Paläontologie der Freien Universität Berlin, Germany; **IRScNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Germany.

A Nexus or MacClade version of the matrix is available from the corresponding author upon request.

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Matrix
                                             1 11111 11112 22222 22223 33333 33334
                                   12345 67890 12345 67890 12345 67890 12345 67890

Theriosuchus spp.                  ?000? 1?11? 000?? ??000 ?0000 00000 00000 00010
Goniopholis spp.                   ?000? 0?00? 000?? ?00?? ?0000 000?0 00000 00000
Bernissartia fagesii               ??11? 1211? 010?? ??00? ?0?0? 0000? ?0000 11010
Susisuchus anatoceps               ????? ???1? ??01? ??0?0 ?000? 00??? ??0?0 21310
Hylaeochampsa vectiana             ????? ????? ????? ????? ????? ????? ????? ?????
Isisfordia duncani                 ?00?0 1?101 100?? ?11?? ?000? ?01?? ?0000 21110
Allodaposuchus precedens           ????? ????? ????? ????? ????? ????? ????? ?????
Borealosuchus formidabilis         00000 10110 1100? ?02?0 00000 00010 00001 20?20
Borealosuchus wilsoni              ????? ??11? ??0?? ????? ?0000 0001? ??001 20?20
Borealosuchus acutidentatus        ????? ????? ????? ????? ????? ?0??? ????? ?????
Borealosuchus sternbergii          00000 1?110 11000 01210 00000 00010 00001 2???0
Leidyosuchus canadensis            ????0 1???? ??0?? ????? ?0000 1?01? ??110 2??11
Eothoracosaurus mississippiensis   ????? ????? ????? ????? ??000 ????? ?01?1 2???0
Thecoachampsoides minor            ???1? 1???? 0???? ??21? ?00?0 ?100? ?0101 20??0
Siquisiquesuchus venezuelensis     ????? ????? ????? ????? ??1?? ????? ??1?? ?????
Thoracosaurus macrorhynchus        ??11? 1?1?? 0???? ??21? ????? 0??0? ???01 2???0
Eogavialis africanum               ????? 1???? ??0?? ???11 ????? ????? ???0? ????0
Gryposuchus colombianus            ??1?0 ????? 00??? ????? ??000 ????? ????? ????0
Gavialis gangeticus                02110 10100 00000 00210 00000 01001 00100 ?0030
Pristichampsus spp                 ??000 101?? 01??? ??20? ?0000 0111? ?0100 2???0
Diplocynodon darwinii              10000 0?210 01010 00201 ?000? 1141? ?0110 21120
Baryphracta deponiae               10??0 0???0 ????? ?02?? ?0??? 1?4?? ??110 2??20
Stangerochampsa mccabei            ??00? 1?21? 0101? ??21? ?0000 11010 00111 2??10
Brachychampsa montana              10001 ??211 11?10 002?1 0?000 11010 001?0 23110
Alligator mississippiensis         10001 10211 01010 01201 11101 11110 00110 22130
Navajosuchus mooki                 ????? ????? ??0?? ??201 ?0??? 11?1? ??110 21110
Hassiacosuchus haupti              00??1 ????1 ????? ?1201 1000? 11?1? ??1?? 21?10
Caiman yacare                      10001 10211 10010 11201 11011 11110 00110 21220
Caiman latirostris                 10001 10211 10000 11201 110?1 11110 00110 21220
Melanosuchus niger                 10001 10211 1?010 11201 11011 11110 00110 22220
Paleosuchus trigonatus             10001 11210 01011 11201 10011 11312 10110 21320
Crocodylus cataphractus            10000 1021? 00110 0?201 01001 11212 00110 21130
Crocodylus porosus                 11100 11211 00100 01201 01000 11212 00110 21231
Osteolaemus tetraspis              ??100 11211 00100 ?1201 01001 11112 01110 21110
'Crocodylus' robustus              ????? ????? ??1?? ??20? ????? ?111? ?111? ????0
'Crocodylus' megarhinus            ????? ???0? ????? ??2?? ????? ????? ????? ?????
Tomistoma schlegelii               02100 10211 00100 01201 00001 11111 00110 21330
Tomistoma lusitanica               ????? ????? ????? ??2?? ????? ????? ????0 2???0
Gavialosuchus americanus           02100 1?210 00100 0020? ?0101 1?11? ??11? 2???0
'Crocodylus' spenceri              ????? ????? ????? ??2?? ????? ????? ????? ?????
Brachyuranochampsa eversolei       ????? ????? ????? ????? ????? ????? ????? ?????
'Crocodylus' acer                  ????? ????? ????? ????? ????? ????? ????? ?????
'Crocodylus' affinis               00000 10211 10110 01201 00000 11110 00110 2???0
Asiatosuchus germanicus            00100 1?211 00??? ?1201 ?000? 11?1? ??11? ????0
Prodiplocynodon langi              ????? ????? ????? ????? ????? ????? ????? ?????
Australosuchus clarkae             ????? 1?2?? ????? ??2?? ????? 1??1? ??1?0 2???0
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Matrix continued

	44444	44445	55555	55556	6	6	666	66667	77777	77778
	12345	67890	12345	67890	1	2	345	67890	12345	67890
Theriosuchus spp.	0000?	?00?0	111??	???01	1	{01}	?00	00011	00000	21000
Goniopholis spp.	00000	?0000	001??	????1	1	1	?00	00000	000?0	00010
Bernissartia fagesii	0000?	???00	100??	?00?1	1	0	???	0?000	0???0	10000
Susisuchus anatoceps	?????	????1	1????	????1	?	?	???	??10	????0	11010
Hylaeochampsa vectiana	?????	?????	?????	?????	?	?	???	????0	100??	1?0?0
Isisfordia duncani	?????	?????	?????	?????	?	1	???	??01?	100?0	??0??
Allodaposuchus precedens	?????	?????	?????	?????	?	?	???	????0	10?00	10210
Borealosuchus formidabilis	00000	00?01	0010?	00100	1	1	000	00001	100?0	?0200
Borealosuchus wilsoni	??102	00001	0010?	0???0	1	1	?00	00001	10000	10200
Borealosuchus acutidentatus	?????	?????	?????	?????	?	?	?00	00001	????0	?020?
Borealosuchus sternbergii	00000	00001	00100	000?0	0	1	000	00001	10000	10100
Leidyosuchus canadensis	00000	00111	1010?	0???1	?	1	000	00001	10000	10000
Eothoracosaurus mississippiensis	??30?	??001	1?1??	????0	?	?	???	??2?0	100?0	1021?
Thecoachampsoides minor	?0300	00001	1110?	0??00	?	1	?00	?02?0	100?0	10210
Siquisiquesuchus venezuelensis	??30?	0??01	?110?	0????	?	?	???	??2?0	1???0	?021?
Thoracosaurus macrorhynchus	??300	??001	11???	????0	?	1	000	00200	100?0	10210
Eogavialis africanum	?030?	?10?1	111??	????1	?	1	?00	00200	10000	10210
Gryposuchus colombianus	?0300	00001	11110	0???0	0	1	000	00200	10010	10210
Gavialis gangeticus	00300	00001	11100	00100	0	1	000	00200	10000	10210
Pristichampsus spp	00001	?0??1	?11??	?????	?	1	?00	000?1	100?0	10000
Diplocynodon darwinii	00101	00111	101??	000?1	?	1	?00	00011	1?0?0	11000
Baryphracta deponiae	??0??	?0111	1?1??	?????	?	1	?00	??011	100?0	11010
Stangerochampsa mccabei	01000	001?1	111??	?????	1	1	?01	10011	11010	21010
Brachychampsa montana	10100	?0111	111??	?00?1	1	1	?00	?0011	11010	21010
Alligator mississippiensis	11201	00111	11110	00011	1	1	010	00011	11010	21010
Navajosuchus mooki	0100?	?01?1	111??	?????	?	1	001	??1?1	110?0	2100?
Hassiacosuchus haupti	0?0??	?0111	111??	????1	?	1	?00	??111	????0	21000
Caiman yacare	11220	11111	01101	00111	0	1	000	11011	11010	21111
Caiman latirostris	11220	11111	01101	0??1?	?	1	000	11011	11010	21011
Melanosuchus niger	11220	11111	01101	0??11	1	1	000	11011	11010	21011
Paleosuchus trigonatus	12200	21111	01111	10111	1	1	000	11011	11010	21011
Crocodylus cataphractus	10111	01001	01110	0100?	0	1	000	00001	10011	00211
Crocodylus porosus	10111	01001	01110	01001	1	1	000	00001	10011	00211
Osteolaemus tetraspis	10111	01001	01110	01001	1	1	000	00001	10111	00210
'Crocodylus' robustus	10111	00011	01110	0??01	1	1	000	00001	10111	00211
'Crocodylus' megarhinus	101??	?0001	011??	????1	1	1	?00	00001	10002	?0211
Tomistoma schlegelii	10400	01001	01100	00000	0	1	000	00201	10000	10210
Tomistoma lusitanica	??4??	?0001	01???	?????	?	1	?00	00201	10000	10211
Gavialosuchus americanus	??412	????1	01110	00???	?	1	000	002?1	10000	1021?
'Crocodylus' spenceri	??411	?0?01	??1??	????1	?	1	?00	00??1	100??	?0210
Brachyuranochampsa eversolei	?????	?????	?????	?????	?	?	???	????1	100?0	?0210
'Crocodylus' acer	?????	?????	?????	?????	?	?	???	??01	100?0	?0211
'Crocodylus' affinis	10100	00001	01110	00001	1	1	000	00001	100?0	1011?
Asiatosuchus germanicus	000??	?0001	011??	?00??	1	1	?00	000?1	100?0	10000
Prodiplocynodon langi	?????	?????	?????	?????	?	?	???	????1	10??0	?001?
Australosuchus clarkae	10111	?0001	011??	????1	1	1	?00	00001	????2	00211

Matrix continued

				1	11111	11111	11111	11111
	88888	88889	99999	99990	00000	00001	11111	11112
	12345	67890	12345	67890	12345	67890	12345	67890
Theriosuchus spp.	03100	00000	00100	00000	00100	00000	000?0	01000
Goniopholis spp.	01000	00000	00012	00000	00000	00000	0000?	00000
Bernissartia fagesii	00?01	00000	1?101	?00?0	00001	00?00	?010?	000?0
Susisuchus anatoceps	02?0?	00?3?	?12?2	?0??0	0?000	0????	00???	?0??0
Hylaeochampsa vectiana	00?01	000?0	0110?	??0?0	00200	?0000	?01??	0101?
Isisfordia duncani	00?0?	?0??0	01?1?	??00?	?0?00	?0000	?000?	??00?
Allodaposuchus precedens	0000?	11???	00???	??0?0	0?000	?0?0?	001?0	???11
Borealosuchus formidabilis	00001	00000	01002	00000	00000	00000	0010?	02110
Borealosuchus wilsoni	100?1	00000	01002	?0000	00000	00?00	?0100	0211?
Borealosuchus acutidentatus	1000?	00?0?	01002	?00?0	00000	???0?	?0???	?2???
Borealosuchus sternbergii	00001	10100	01012	?0000	00000	00000	0010?	00011
Leidyosuchus canadensis	00001	10100	11011	?0000	01001	00000	01110	00010
Eothoracosaurus mississippiensis	00?11	10030	01?02	?00?0	00000	00000	001??	?0100
Thecoachampsoides minor	10011	10030	01002	?0000	0?100	00000	030??	?0100
Siquisiquesuchus venezuelensis	?0?1?	?0?30	01?0?	?02??	00200	??000	?00??	??10?
Thoracosaurus macrorhynchus	00011	00030	01002	??000	00100	00000	0010?	1010?
Eogavialis africanum	11011	10030	01002	?0000	00200	00000	00000	00100
Gryposuchus colombianus	10011	00030	01102	?0200	00200	00000	?0000	00100
Gavialis gangeticus	10001	00030	01103	00200	00200	00000	00000	00100
Pristichampsus spp.	20001	10000	01001	?0000	00100	00000	021?0	00010
Diplocynodon darwinii	00001	00101	?1002	?0000	01000	00000	?111?	00010
Baryphracta deponiae	00001	01?01	??00?	?0??0	0?00?	000?0	?1?1?	000??
Stangerochampsa mccabei	10000	10121	11201	?00?0	01000	00000	0111?	00010
Brachychampsa montana	12000	10111	11201	?0000	01000	00100	01110	00010
Alligator mississippiensis	21000	00121	11100	00010	01100	10000	01111	01010
Navajosuchus mooki	20000	?0?21	11101	?0000	0100?	00?00	?1???	00??0
Hassiacosuchus haupti	2100?	10???	?1101	???00	0100?	0????	?1???	?0???
Caiman yacare	23000	11121	11101	00001	01111	01000	01110	10010
Caiman latirostris	23000	01121	11101	00000	01111	01000	01110	10010
Melanosuchus niger	23000	01121	11101	00000	01111	01000	01110	10010
Paleosuchus trigonatus	22000	01121	11011	11000	011?0	01100	01110	10010
Crocodylus cataphractus	20101	10110	01002	00100	01100	10010	03100	00101
Crocodylus porosus	20101	10110	01001	00100	01100	10010	03100	00001
Osteolaemus tetraspis	20101	01110	01010	11100	01101	00001	03100	00011
‘Crocodylus’ robustus	21101	11110	01011	?0100	01100	10001	03100	00001
‘Crocodylus’ megarhinus	2?101	?0100	01201	?0100	01100	00000	?3100	00001
Tomistoma schlegelii	20101	00010	01102	00100	01100	00001	03100	00001
Tomistoma lusitanica	20?11	00010	01002	?0100	01100	00000	03100	00101
Gavialosuchus americanus	21?11	10?10	0?102	?0100	01100	00000	031?0	001?1
‘Crocodylus’ spenceri	20?01	10010	01101	?0?00	0?100	??000	?31??	001??
Brachyuranochampsa eversolei	20001	00110	01001	??000	01000	?0?0?	031??	00?0?
‘Crocodylus’ acer	2000?	10110	01001	?00?0	0?000	?0001	03100	0000?
‘Crocodylus’ affinis	20001	10110	01001	?0000	01000	00001	131?0	00000
Asiatosuchus germanicus	1000?	00?10	010?1	?0000	01000	00001	131??	000??
Prodiplocynodon langi	10001	?010?	01?01	?00??	01000	?0001	131?0	0?01?
Australosuchus clarkae	2010?	10?1?	01001	?0?00	01100	0?000	0110?	00001

Matrix continued

	11111	11111	11111	11111	11111	11111	11111	11111
	22222	22223	33333	33334	44444	44445	55555	66666
	12345	67890	12345	67890	12345	67890	12345	67890
Theriosuchus spp.	10100	00000	00000	?0?00	?0000	10??0	01???	?????
Goniopholis spp.	0?100	00??0	??000	00000	00000	0?0?0	?1???	?????
Bernissartia fagesii	0??0?	?????	0??00	??00	00000	10?00	001??	?????
Susisuchus anatoceps	0?1??	?????	2??00	???00	10000	0???0	?????	?????
Hylaeochampsa vectiana	??0??	000?1	0000?	0?000	0?000	000?0	00???	?????
Isisfordia duncani	0?1??	?????	000??	????0	1????	10?10	01???	?????
Allodaposuchus precedens	100??	?0011	00000	???00	0000?	0??10	10???	?????
Borealosuchus formidabilis	0?100	000??	000?1	01001	10000	10?10	001??	?????
Borealosuchus wilsoni	?01??	??0??	00001	?1?01	1????	1??10	001??	?????
Borealosuchus acutidentatus	??10?	??0??	????1	???01	1????	1???0	001??	?????
Borealosuchus sternbergii	00100	00001	00011	?1?01	10000	10010	0010?	?????
Leidyosucihus *canadensis*	10100	00001	00010	01001	10000	10010	0010?	?????
Eothoracosaurus mississippiensis	0?0?0	?????	?0?00	???01	10001	00???	00???	?????
Thecoachampsoides minor	00000	0?0?1	0000?	0?001	10001	00?1?	100??	?????
Siquisiquesuchus venezuelensis	0?0??	??0??	???0?	???12	10001	00???	1????	?????
Thoracosaurus macrorhynchus	00000	0?0?0	?0000	?0?01	10001	00?10	000??	?????
Eogavialis africanum	000?0	0?0?0	0000?	00011	10001	00?10	1000?	?????
Gryposuchus colombianus	00000	00000	0000?	???12	10001	00?10	100??	?????
Gavialis gangeticus	00000	00000	0000?	00011	10001	00010	10000	00000
Pristichampsus spp.	0?100	0?1?1	01010	???01	10000	10?10	001??	?????
Diplocynodon darwinii	1?100	0?0??	11?10	???01	10000	10?10	001??	?????
Baryphracta deponiae	1?1??	0????	???10	???01	10000	1??1?	?0???	?????
Stangerochampsa mccabei	1?120	0?0?1	2?110	???01	10001	10?10	011??	?????
Brachychampsa montana	10120	00001	11110	?1?01	10001	10?10	011??	?????
Alligator mississippiensis	10100	00001	21110	11001	11000	10010	02101	10011
Navajosuchus mooki	1?11?	??0?1	21110	???01	10001	10?10	0?1??	?????
Hassiacosuchus haupti	1?1??	??0??	21?10	?1?01	10001	10?10	0????	?????
Caiman yacare	10100	00001	21110	11001	10000	10010	21201	11011
Caiman latirostris	10100	00001	21110	11001	10100	10010	21201	21011
Melanosuchus niger	10101	00001	21110	11001	10100	10010	21201	21011
Paleosuchus trigonatus	10100	00001	21110	11001	10000	10010	21101	12011
Crocodylus cataphractus	01100	01111	00010	11101	10000	10110	00110	10101
Crocodylus porosus	01100	01111	00010	11101	10010	11110	00110	10101
Osteolaemus tetraspis	01100	01111	00010	11101	10010	10011	00110	10101
'Crocodylus' robustus	0?100	01111	00010	11101	10010	10011	001??	?????
'Crocodylus' megarhinus	01100	0?11?	00010	???01	10000	10?10	001??	?????
Tomistoma schlegelii	01100	11111	00010	11101	10001	10010	00110	10101
Tomistoma lusitanica	01100	1?1??	0001?	11?01	10001	10?10	001??	?????
Gavialosuchus americanus	??100	0?1??	0001?	???01	10001	10?10	0011?	?????
'Crocodylus' spenceri	??100	011??	???10	???01	10001	10?10	001??	?????
Brachyuranochampsa eversolei	0?1?0	0?1??	???10	???01	10001	10?10	001??	?????
'Crocodylus' acer	01100	011??	00010	?1?01	10001	10?10	001??	?????
'Crocodylus' affinis	01100	0?1??	00010	???01	10000	10?10	0011?	?????
Asiatosuchus germanicus	0?100	??1??	00?10	???01	10000	10?10	001??	?????
Prodiplocynodon langi	01100	001?1	???10	?1001	1000?	10?10	001??	?????
Australosuchus clarkae	01100	0?111	01010	?1?01	10001	10010	0?11?	?????

Matrix continued

	11111	11111	11111	1
	66666	66667	77777	7
	12345	67890	12345	6
Theriosuchus spp.	00??0	02001	10000	0
Goniopholis spp.	00??0	00?00	00100	1
Bernissartia fagesii	00??0	02000	30?01	1
Susisuchus anatoceps	0???0	???10	0?001	1
Hylaeochampsa vectiana	??0?0	??0??	?1?11	1
Isisfordia duncani	??0?0	?3?02	20001	1
Allodaposuchus precedens	??0?0	??0??	?1?11	1
Borealosuchus formidabilis	000?0	03112	31011	1
Borealosuchus wilsoni	000?0	12?12	31111	1
Borealosuchus acutidentatus	000?0	1????	??111	1
Borealosuchus sternbergii	000?0	02?12	31111	1
Leidyosuchus canadensis	00010	00???	31?11	1
Eothoracosaurus mississippiensis	00??0	23??2	31?1?	1
Thecoachampsoides minor	000?0	23??2	?1??1	1
Siquisiquesuchus venezuelensis	00??0	23???	????1	1
Thoracosaurus macrorhynchus	000?0	23???	31??1	1
Eogavialis africanum	000?0	23???	?1??1	1
Gryposuchus colombianus	000?0	23???	31?01	1
Gavialis gangeticus	00000	23102	31101	1
Pristichampsus spp.	010?1	02?02	31111	1
Diplocynodon darwinii	000?0	00112	31111	1
Baryphracta deponiae	0?0?0	?0???	?1??1	1
Stangerochampsa mccabei	000?0	01?12	?1111	1
Brachychampsa montana	000?0	01?12	?1111	1
Alligator mississippiensis	00110	10112	31111	1
Navajosuchus mooki	001?0	01???	?1111	1
Hassiacosuchus haupti	0?1?0	01???	??1?1	1
Caiman yacare	00110	12112	31111	1
Caiman latirostris	00110	12112	31111	1
Melanosuchus niger	00110	12112	31111	1
Paleosuchus trigonatus	00110	12112	31111	1
Crocodylus cataphractus	01010	03112	31111	1
Crocodylus porosus	01010	02112	31111	1
Osteolaemus tetraspis	01110	02112	31111	1
‘Crocodylus’ robustus	01110	021??	31111	1
‘Crocodylus’ megarhinus	010?0	02???	31?11	1
Tomistoma schlegelii	01010	03112	31111	1
Tomistoma lusitanica	0?0?0	03???	31?11	1
Gavialosuchus americanus	010?0	03112	31??1	1
‘Crocodylus’ spenceri	0?0?0	03???	31?11	1
Brachyuranochampsa eversolei	0?0?0	?????	?1?11	1
‘Crocodylus’ acer	0?0?0	?????	?1?11	1
‘Crocodylus’ affinis	010?0	02?12	31111	1
Asiatosuchus germanicus	000?0	00112	31111	1
Prodiplocynodon langi	0?0?0	??1??	?1?11	1
Australosuchus clarkae	010?0	02??2	???11	1

Phylogenetic analysis

The data matrix was analysed with PAUP 4.0b10 (Swafford 2003). Ten heuristic searches were completed, using Random Stepwise Addition in each one. Selected European species of *Goniopholis* and *Theriosuchus* were used as sequential outgroups for rooting purposes. Analyses were run with most multistate characters unordered; however characters 18, 36, 170 and 171 were ordered, since higher states unambiguously include lower ones in these characters, and the transformations are supported by recent biomechanical analyses (Salisbury 2001; Salisbury & Frey 2001).

The analyses resulted in the recovery of six optimal trees (length, 482 steps; consistency index, 0.4710; homoplasy index, 0.5311; retention index, 0.7686; rescaled consistency index, 0.3620). The strict consensus tree of this analysis was the same as the one shown in figure 4a of the paper. Bootstrap support for each node was assessed using ten randomised heuristic iterations of 1 x 10^6 bootstrap replicates, with the branch-swapping option disabled.

A run that included *Allodaposuchus precedens* (*sensu* Buscalioni *et al*. 2001) resulted in 3 optimal trees (length, 489 steps; consistency index, 0.462; homoplasy index, 0.538; retention index, 0.765; rescaled consistency index, 0.354). A strict consensus of this analysis resulted in a tree that was identical to that shown in figure 4a, but with *Allodaposuchus* as the sister taxon to *Hylaeochampsa*.

Apomorphy list and bootstrap support indices

The tree used to derive these apomorphies is identical to the one shown in Fig. 4a, except for the position of *Asiatosuchus germanicus*, which is here considered the most basal crocodyloid.

* = ACCTRANS optimisation only
** = DELTRANS optimisation only

Numbers in square brackets indicate bootstrap support greater than 50%.

Bernissartia fagesii + *Susisuchus anatoceps* + Eusuchia [62]
*12(1), 36(1), *37(1), 76(1), **82(0), 85(1), *92(1), *113(1), *130(1), *137(1), *152(0), *171(2), 175(1)

Bernissartia fagesii
3(1), 4(1), 7(2), **12(1), **52(0), 53(0), 62(0), **69(0), 91(1), 95(1), 105(1), **113(1), **152(0), 171(3)

Susisuchus anatoceps + Eusuchia
*28(1), *29(1), 36(2), *38(1), 50(1), *52(1), *69(1), *71(1), **92(1), 141(1), *149(1)

Susisuchus anatoceps
38(3), 77(1), 79(1), 82(2), 89(3), 93(2), 131(2), 146(0), 169(1), 171(0)

Eusuchia
18(1), **71(1), **149(1), 170(2), **171(2)

Hylaeochampsa vectiana + Crocodylia [57]
*18(2), *27(1), *33(1), *39(3), *69(0), **113(1), 119(1), **130(1), **152(0), *171(3), 172(1), *173(1), 174(1)

Hylaeochampsa vectiana
103(2), 117(1), 123(0), 141(0), 146(0)

Crocodylia
**18(2), **69(0), *70(1), 86(1), 93(0), 140(1), 168(1), **171(3), **173(1)

Gavaloidea + *Borealosuchus*
10(1), 14(0), 19(1), *28(0), 35(1), 37(0), *38(0), *58(1), 60(0), *61(0), 78(2), *118(1)

Borealosuchus [59]
11(1), **12(1), *27(0), **29(1), *33(0), *39(2), 51(0), 52(0), **170(1), 135(1), 137(1), 169(1)

Borealosuchus formidabilis + *Borealosuchus wilsoni* + *Borealosuchus acutidentatus* [74]
**39(2), **61(1), 86(0), 117(2), **118(1)

Borealosuchus formidabilis
**58(1), 167(3), 173(0)

Borealosuchus wilsoni + *Borealosuchus acutidentatus* [83]
*43(1), *45(2), 81(1), 166(1)

Borealosuchus wilsoni
**43(1), **45(2)

Borealosuchus sternbergii
17(1), *58(0), **61(0), 78(1), 88(1), 94(1), *118(0), 120(1), 134(1)

Gavialoidea [95]
*2(2), *3(1), *4(1), *9(0), *12(0), *29(0), *30(1), **33(1), 43(3), 68(2), *70(0), 79(1), 84(1), 89(3), **118(1), 119(0), 123(0), *130(0), *137(0), 145(1), 146(0), *153(0), 166(2), 167(3)

Thoracosaurus macrorhynchus + *Thecoachampsoides minor* + *Eogavialis africanum* + *Gavialis gangeticus* + *Siquisiquesuchus venezuelensis* + *Gryposuchus colombianus*
**3(1), **4(1), 103(1), **153(0), *174(0)

Thecoachampsoides minor + *Eogavialis africanum* + *Gavialis gangeticus* + *Siquisiquesuchus venezuelensis* + *Gryposuchus colombianus* [67]
**27(1), 81(1), 113(0), 151(1), *112(3), *130(1)

Thecoachampsoides minor
112(3), *130(1)

Eogavialis africanum + *Gavialis gangeticus* + *Siquisiquesuchus venezuelensis* + *Gryposuchus colombianus* [68]
*35(0), 103(2), **130(0), 139(1)

Gavialis gangeticus + *Siquisiquesuchus venezuelensis* + *Gryposuchus colombianus* [79]
**61(0), 86(0), 93(1), 98(2), **174(0)

Siquisiquesuchus venezuelensis + *Gryposuchus colombianus* [67]
*74(1), 140(2)

Siquisiquesuchus venezuelensis
23(1)

Gryposuchus colombianus
54(1), **74(1)

Gavialis gangeticus
**2(2), **9(0), **30(1), **35(0), **39(3), **58(1), 84(0), 95(3)

Eogavialis africanum
20(1), 47(1), 60(1), 82(1)

Thoracosaurus macrorhynchus
**1(0), *86(0), 116(1), **130(0)

Pristichampsus spp. + Brevirostres [63]
**8(2), 20(1), **26(1), **34(1), **38(1), *54(1), **88(1), *95(1), **102(1), *112(1), *128(1), *134(1), *136(1), **137(1), 156(1), 160(1), 164(1), **169(1)

Brevirostres [52]
*8(2), *26(1), *34(1), **48(1), **49(1), *88(1), **91(1), *102(1), **112(1), **114(1), **121(1), 167(0), *169(1)

Alligatoroidea [76]
*1(1), *28(0), *39(1), 48(1), 49(1), *52(0), *59(1), 91(1), **112(1), 114(1), 121(1), *128(0), *155(1), *159(1), **167(0)

Leidyosuchus canadensis
40(1), **52(0), *54(0), 94(1), 105(1), *136(0)

Diplocynodontidae + Globidonta [76]
**1(1), **12(1), 69(1), *74(1), 77(1), *79(1), 90(1), 131(1), 132(1), *133(1)

Diplocynodon darwinii + *Baryphracta deponiae* [88]
6(0), 10(0), 28(4), 39(2), *45(1), 86(0), *95(2)
Diplocynodon darwinii
43(1), **45(1), **52(0), *79(0), **95(2)

Baryphracta deponiae
**79(1), 87(1)

Globidonta [94]
5(1), *52(1), *66(1), 72(1), **74(1), 76(2), **79(1), 81(1), 85(0), *89(1), 93(2), *124(2), **133(1), 145(1), 152(1), 167(1)

Stangerochampsa mccabei + *Navajosuchus mooki* + *Hassiacosuchus haupti* + Alligatoridae
*17(1), *21(1), 42(1), 89(2), 131(2)

Stangerochampsa mccabei
19(1), 35(1), 65(1), **66(1), **124(2)

Navajosuchus mooki + *Hassiacosuchus haupti* + Alligatoridae
**17(1), **21(1), *25(1), *28(1), 81(2), *82(1), 93(1), *124(0), 163(1)

Alligatoridae [95]
*22(1), **25(1), **28(1), *39(2), 41(1), 43(2), **59(1), 86(0), 103(1), **136(1), 145(0), **155(1), **159(1), 166(1), *167(0)

Alligator mississippiensis
**22(1), 23(1), 37(2), 39(3), 45(1), **54(1), 64(1), *66(0), **82(1), 95(0), 99(1), 106(1), 115(1), 117(1), 142(1), 152(2), **167(0)

Camininae [100]
16(1), 24(1), *38(2), **39(2), *46(1), 47(1), 51(0), 55(1), 58(1), **66(1), 67(1), 80(1), *82(2), 87(1), *104(1), 107(1), 116(1), 151(2), *157(1), 167(2)

Caiman yacare + *Caiman latirostris* + *Melanosuchus niger* [99]
11(1), 12(0), **22(1), **38(2), 44(2), **46(1), *54(0), 82(3), **104(1), 105(1), 153(2), **157(1),

Caiman yacare
61(0), 78(1), 86(1), 100(1)

Caiman latirostris + *Melanosuchus niger* [86]
143(1), 156(2)

Caiman latirostris
14(0)

Melanosuchus niger
37(2), 125(1)

Paleosuchus trigonatus
7(1), 10(0), 15(1), *22(0), 28(3), 30(2), 31(1), 38(3), 42(2), 46(2), **54(1), 56(1), **82(2), 93(0), 94(1), 96(1), 97(1), 108(1), 157(2)

Navajosuchus mooki + *Hassiacosuchus haupti* [66]
*1(0), 68(1), 79(0), *124(1)

Navajosuchus mooki
65(1), *82(0), **124(1)

Hassiacosuchus haupti
**1(0), **82(1)

Brachychampsa montana
11(1), 37(3), 41(1), 43(1), 82(2), **89(1), 108(1), **124(2)

Crocodyloidea [55]
*3(1), *12(0), *13(1), 17(1), 51(0), 81(1), *89(1), 110(1), 111(1), 112(3), *122(1), **128(1), *129(1), *154(1), *158(1)

Prodiplocynodon langi + ‘*Crocodylus*’ *affinis* + *Brachyuranochampsa eversolei* + ‘*Crocodylus*’ *acer* + Crocodylidae
*41(1), *43(1), 79(1), **122(1), *162(1), *167(2)

‘*Crocodylus*’ *affinis* + *Brachyuranochampsa eversolei* + ‘*Crocodylus*’ *acer* + Crocodylidae [52]
**13(1), **28(1), **41(1), **43(1), **54(1), *78(1), 81(2), **89(1), 119(0), *127(1), *138(1), **154(1), **162(1)

Brachyuranochampsa eversolei + ‘*Crocodylus*’ *acer* + Crocodylidae
*14(0), *25(1), *30(1), *44(1), *45(1), 78(2), 111(0), *120(1), **127(1), 145(1)

Crocodylidae [64]
**3(1), **14(0), **25(1), **44(1), 83(1), 98(1), 103(1), 110(0), **120(1), **129(1), **136(1), **138(1), **158(1)

Australosuchus clarkae + ‘*Crocodylus*’ *megarhinus* + Crocodylinae
*1(1), *7(1), *22(1), *30(2), **45(1), *57(1), 75(2), 76(0), 80(1)

‘*Crocodylus*’ *megarhinus* + Crocodylinae
145(0)

Crocodylinae [68]
**22(1), **30(2), *47(1), **57(1), 74(1), 75(1), *106(1), *144(1)

Crocodylus
**1(1), 28(2), **39(3), **47(1), **106(1), 109(1), 148(1)

Crocodylus cataphractus
3(0), *7(0), 14(1), 61(0), 95(2), 118(1), *144(0), 167(3)

Crocodylus porosus
2(1), **7(1), 25(0), 38(2), 40(1), **144(1), 147(1)

Osteolaemus tetraspis + '*Crocodylus*' *robustus* [95]
32(1), *39(1), 73(1), 87(1), 94(1), *96(1), 110(1), **144(1), 150(1), 163(1)

Osteolaemus tetraspis
**7(1), **47(1), 80(0), 86(0), 95(0), **96(1), 97(1), 105(1), *106(0), 119(1)

'*Crocodylus*' *robustus*
*47(0), 49(1), 82(1), **106(1)

'*Crocodylus*' *megarhinus*
9(0), 89(0), 93(2)

Australosuchus clarkae
112(1), 132(1)

'*Crocodylus*' *spenceri* + *Gavialosuchus americanus* + *Tomistoma* [65]
*2(2), *38(3), 43(4), *61(0), *68(2), 88(0), 93(1), 118(1), 167(3)

Gavialosuchus americanus + *Tomistoma*
**2(2), *45(0), *60(0), **68(2), *84(1), 95(2)

Tomistoma
*44(0), *54(0), 86(0), 126(1)

Tomistoma schlegelii
**30(1), **38(3), **39(3), **44(0), 47(1), **54(0), **60(0), **61(0), *84(0), 110(1), 118(0)

Tomistoma lusitanica
80(1), **84(1), 93(0)

Gavialosuchus americanus
10(0), 17(0), 23(1), 45(2), 82(1), **84(1)

'*Crocodylus*' *spenceri*
**45(1)

Brachyuranochampsa eversolei
86(0)

'*Crocodylus*' *acer*
80(1)
'*Crocodylus*' *affinis*
*3(0), 11(1), **78(1)

Prodiplocynodon langi
*89(0)

Asiatosuchus germanicus
**3(1), 86(0), **89(1), **167(0)

Pristichampsus spp.
**12(1), **28(1), 45(1), 81(2), 103(1), 112(2), **128(1), 132(1), 162(1), 165(1)

Isisfordia duncani
9(0), 11(1), *12(0), 17(1), **28(1), **38(1), 94(1), *113(0), *152(1), 167(3)

Discussion

A revised differential diagnosis for Eusuchia

Following Huxley (1875), Eusuchia is considered an apomorphy-based taxon, referral to which is dependant on the possession of the following unique combination of traits: procoelous cervical, thoracic and lumbar vertebrae (shared with *Brillanceausuchus*, *Pachycheilosuchus* and *Junggarsuchus*; *Theriosuchus pusillus* may also have some procoelous cervical vertebrae); caudal vertebra I with a condyle on the terminal end of the vertebral body, remainder of caudal vertebrae procoelous, with the degree of procoely decreasing terminally (shared with *Bernissartia* and *Pachycheilosuchus*); secondary choanae entirely surrounded by pterygoids (possibly also found in *Brillanceausuchus*); sagittally segmented paravertebral osteoderms (shared with *Susisuchus*; a similar condition also occurs in distantly related forms such as *Simosuchus, Gobiosuchus* and *Notosuchus* – see below).

Remarks on the possible sagittal segmentation of the dorsal osteoderms in Gobiosuchus*,* Simosuchus *and* Notosuchus

Sagittal segmentation of the dorsal osteoderms may have evolved independent to the condition seen in eusuchians in the basal mesoeucrocodylian *Gobiosuchus kielanae* (Osmólska *et al*. 1997) and the notosuchids *Simosuchus clarki* (Buckley *et al*. 2000) and *Notosuchus terrestris* (Pol 2005). However, in none of these taxa has the configuration of the dorsal osteoderms been described in detail, nor the relationship between the exact position of the osteoderms and the underlying axial skeleton. As the material referred to these taxa has not been examined firsthand, we are unclear exactly how the segmentation of the dorsal shield has progressed from the plesiomorphic biserial condition seen in other crocodyliforms, or if it has progressed at all (see Salisbury & Frey 2001). Sagittal segmentation of the dorsal shield in transition from Neosuchia to Eusuchia can be traced as a series of discrete steps, with forms such as *Bernissartia* and the Calizas de la Huéguina neosuchian displaying a condition that is intermediate between more basal taxa, in which the dorsal shield is biserial (e.g. *Goniopholis* and *Theriosuchus*), and *Susisuchus*, *Isisfordia* and crocodylians, in which the dorsal shield comprises a tetraserial paravertebral shield and multiple sagittal rows of accessory osteoderms (Ortega & Buscalioni 1995; Salisbury & Frey 2001). Some dyrosaurids may also display a condition comparable to that in *Bernissartia* (Salisbury 2001; Salisbury & Frey 2001). To what extent the sagittal segmentation of the dorsal shield occurred (if at all) in the lineages leading to *Gobiosuchus*, *Simosuchus* and *Notosuchus* is currently unclear, and will require more detailed investigations before any informative comparisons with the neosuchian-eusuchian transition can be carried out.

Regardless of how the dorsal shield of *Gobiosuchus*, *Simosuchus* and *Notosuchus* evolved, as with *Susisuchus* and eusuchians (Salisbury 2001), the configuration seen in these animals would have resulted in an increased capacity for lateral flexion of the trunk. However, with amphicoelous vertebrae, the capacity to sustain high-walking would have been impeded in animals with a mass greater than approximately 50 kg (Salisbury 2001). Given that all three taxa each possess other anatomical characteristics indicative of a predominantly terrestrial lifestyle, this biomechanical constraint on size may explain why they were small animals.

References

Aoki, R. 1992 Fossil crocodilians from the late Tertiary strata in the Sinda Basin, eastern Zaire. *Afr. Study Monogr.* **17**, 67-87.

Benton, M. J. & Clark, J. M. 1988 Archosaur phylogeny and the relationships of the Crocodilia. In *The phylogeny and classification of tetrapods. Systematics Association Special Volume No. 35A.*, vol. 1: Amphibians, Reptiles, Birds. (ed. M. J. Benton), pp. 295-338. Oxford: Clarendon Press.

Brochu, C. A. 1997a A review of "*Leidyosuchus*" (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *J. Vert. Paleont.* **17**, 679-697.

Brochu, C. A. 1997b Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Syst. Biol.* **46**, 479-522.

Brochu, C. A. 1999 Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *J. Vertebr. Paleontol. Memoir 6* **19**, 9-100.

Brochu, C. A. 2004a A new Late Cretaceous gavialoid crocodylian from eastern North America and the phylogenetic relationships of thoracosaurs. *J. Vertebr. Paleontol.* **24**, 610-633.

Brochu, C. A. 2004b Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *J. Vertebr. Paleontol.* **24**, 857-873.

Brochu, C. A. & Rincón, A. D. 2004 A gavialoid crocodylian from the Lower Miocene of Venezuela. *Spec. Pap. Palaeontol.* **71**, 61-79.

Buckley, G. A. & Brochu, C. A. 1999 An enigmatic new crocodile from the Upper Cretaceous of Madagascar. *Spec. Pap. Palaeontol.* **60**, 149-175.

Buscalioni, A. D., Ortega, F., Weisampel, D. B. & Jianu, C. M. 2001 A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Hateg Basin, Romania. Its relevance in the Phylogeny of Eusuchia. *J. Vertebr. Paleontol.* **21**, 74-86.

Buscalioni, A. D., Sanz, J. L. & Casanovas, M. L. 1992 A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *N. Jb. Geol. Paläont., Mh. Abh.* **187**, 1-29.

Clark, J. M. 1994 Patterns of evolution in Mesozoic crocodyliformes. In *In the shadow of the dinosaurs* (ed. N. C. Fraser & H.-D. Sues), pp. 84-97. New York: Cambridge.

Clark, J. M. & Norell, M. A. 1992 The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. *Am. Mus. Novit.* **3032**, 1/19.

Densmore, L. D. 1983 Biochemical and immunological systematics of the order Crocodylia. *Evol. Biol.* **15**, 397-465.

Densmore, L. D. & Owen, R. D. 1989 Molecular systematics of the order Crocodilia. *Am. Zool.* **29**, 831- 841.

Efimov, M. B. 1988 On the fossil crocodiles of Mongolia and the USSR. *Trans. Joint Soviet-Mongolian Paleontol. Exped.* **34**, 81-90.

Frey, E., Riess, J. & Tarsitano, S. F. 1989 The axial tail musculature of recent crocodiles and its phyletic implications. *Am. Zool.* **29**, 857 - 862.

Gasparini, Z. & Buffetaut, E. 1980 *Dolichochampsa minima*, n. g. n. sp., a representative of a new family of eusuchian crocodiles from the Late Cretaceous of northern Argentina. *N. Jb. Geol. Paläont., Mh.* **1980**, 257-271.

Gatesy, J., G. Amato, M. Norell, R. Desalle, and C. Hayashi. 2003. Combined support for wholesale taxic atavism in gavialine crocodylians. *Syst. Biol*. 52: 403-422.

Harshman, J., Huddleston, C. J., Bollback, J. P., Parsons, T. J. & Braun, M. J. 2003 True and False gharials: a nuclear gene phylogeny of Crocodylia. *Syst. Biol*. **52**, 386-402.

Hua, S. & Jouve, S. 2004 A primitive marine gavialoid from the Paleocene of Morocco. *J. Vert. Paleontol.* **24**, 341-350.

Huxley, T. H. 1875 On *Stagonolepis robertsoni*, and on the evolution of the Crocodilia. *Q. J. Geol. Soc.* **31**, 423-438.

Langston, W. J. 1974 Nonmammalian Comanchean tetrapods. *Geoscience and Man* **8**, 77-102.

Nixon, C. K. & Carpenter, J. M. 1993 On outgroups. *Cladistics* **9**, 413-426.

Norell, M. A. 1988 Cladistic approaches to evolution and paleobiology as applied to the phylogeny of alligatorids. Unpublished PhD Thesis: Yale University.

Norell, M. A. 1989 The higher level relationships of the extant crocodilia. *J. Herpetol.* **23**, 325-335.

Norell, M. A. & Clark, J. M. 1990 A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bull. Inst. r. Sci. Nat. Belg.* **60**, 115-128.

Ortega, F. & Buscalioni, A. D. 1995 Las Hoyas crocodiles, an evidence of the transition model of the eusuchian dorsal armour configuration. In *II International Symposium on Lithographic Limestones*, pp. 53-56. Lleida-Cuenca, Spain: Ediciones de la Universidad Autónoma de Madrid.

Ortega, F., Gasparina, Z., Buscalioni, A. & Calvo, J. O. 2000 A new species of *Araripesuchus* (Crocodylomorpha, mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). *J. Vert. Paleontol.* **20**, 57-76.

Osmólska, H., Hua, S. & Buffetaut, E. 1997 *Gobiosuchus kielanae* (Protosuchia) from the Late Cretaceous of Mongolia: anatomy and relationships. *Acta Palaeontol. Polonica* **42**, 257-289.

Persson, P. O. 1960 Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). *Ark. Min. Geol.* **2**, 431-478.

Poe, S. 1996 Data set incongruence and the phylogeny of crocodilians. *Syst. Biol.* **45**, 393-414.

Pol, D. 2005 Postcranial remains of *Notosuchus terrestris* Woodward (Archosauria: Crocodyliformes) from the Upper Cretaceous of Patagonia, Argentina. *Ameghiniana* **42**, 21-38.

Rogers, J. V. I. 2003 *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. *J. Vert. Paleontol.* **23**, 128-145.

Taplin, L. E. & Grigg, G. C. 1989 Historical zoogeography of the eusuchian crocodilians: a physiological perspective. *Am. Zool.* **29**, 885 - 901.

Turner, A. H., Norell, M. & Pol, D. 2005 Anatomy and relationships of *Shamosuchus djadochetaensis* (Crocodyliformes, Neosuchia) from the Late Cretaceous of Mongolia. *J. Vert. Paleont.* **25**, 125A.

Salisbury, S. W. 2001 A biomechanical transformation model for the evolution of the eusuchian-type bracing system. Unpublished PhD Thesis: The University of New South Wales.

Salisbury, S. W. & Frey, E. 2001 A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians. In *Crocodilian biology and evolution* (ed. G. C. Grigg, F. Seebacher & C. E. Franklin), pp. 85-134. Chipping Norton: Surrey Beatty & Sons.

Salisbury, S. W., Frey, E., Martill, D. M. & Buchy, M.-C. 2003a A new mesosuchian crocodilian from the Lower Cretaceous Crato Formation of north-eastern Brazil. *Paläontograph., Abt.* **270**, 3-47.

Salisbury, S. W. & Willis, P. M. A. 1996 A new crocodylian from the early Eocene of southeastern Queensland and a preliminary investigation of the phylogenetic relationships of crocodyloids. *Alcheringa* **20**, 179-223.

Stromer, E. 1925 Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 7. *Stomatosuchus inermis* Stromer, ein schwach bezahnter Krokodilier und 8. Ein skelettrest des Pristiden *Onchopristis numidus* Haug sp. *Abh. Bayer. Akad. Wiss., Math.-nat. Abt.* **30** (6), 1-9.

Stromer, E. 1933 Wirbeltierreste der Baharije-Stufe. 12. Die procoelen Crocodilia. *Akad. Wiss., Math.-nat. Abt., N.F.* **15**, 1-5.

Swofford, D. L. 2003. PAUP*. Sinauer Associates, Sunderland, Massachusetts.

White, P. S. & Densmore, L. D. I. 2001 DNA sequence alignments and data analysis methods: their effect on the recovery of crocodylian relationships. In *Crocodilian biology and evolution* (ed. G. C. Grigg, F. Seebacher & C. E. Franklin), pp. 29-37. Chipping Norton, NSW: Surrey Beatty & Sons.

Willis, P. M. A. 1993 *Trilophosuchus rackhami*, gen. et sp. nov., a new crocodilian from the early Miocene Limestones of Riversleigh, northwestern Queensland. *J. Vert. Paleontol.* **13**, 90-98.
Witmer, L. M. 1995 Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. *J. Morph.* **225**, 269-327.
Witmer, L. M. 1997 The evolution of the antorbital cavity in archosaurs: a study in soft-tissue reconstruction in the fossil record with analysis of the function of pneumacity. *J. Vert. Paleontol. Memoir 3* **17**, 1-73.
Wu, X.-C., Cheng, Z.-W. & Russell, D. A. 2001 Cranial anatomy of a new crocodyliform (Archosauria: Crocodylomorpha) from the Lower Cretaceous of Song-Liao Plain, northeastern China. *Can. J. Earth Sci.* **38**, 1653-1663.