

## List of morphological characters.

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Morphological characters 1-399 are described below. The data matrix in nexus format forms Part 2 of this Electronic Supplement. This character list, and a similar matrix (with additional molecular data) are also available from TreeBASE (<http://www.treebase.org/treebase/>; accession number SN1715).

**Abbreviations and symbols:** char(s). = character(s); L = Lee (1998); LC = Lee and Caldwell (2000); RZ = Rieppel and Zaher (2000); Lxy, LCxy, RZxy = character xy as numbered in the respective reference; \* = soft-anatomical character newly analysed in the present study.

## Osteology

### Skull roof

1. **Premaxilla.** Paired (0); single (1).
2. **Premaxilla.** Does not contact frontals (0); contacts frontals (1).
3. **Premaxilla with median palatal ramus bearing foramina.** Absent (0); present (1).
4. **Premaxillary lateral foramina.** Present (0); absent (1). RZ (char. 2) state that "there are no such lateral premaxillary foramina in snakes, which therefore ... are coded as unknown" (page 30). This reasoning is puzzling, since the absence of foramina in [some] snakes clearly corresponds to state 1. The original polymorphic coding of snakes (0and1) is therefore retained, which coincidentally has the same effect as RZ's "unknown" coding.
5. **Premaxilla-maxilla contact.** Immobile and sutural (0); mobile and non-sutural (1).
6. **Maxillae.** Not in contact on palatal surface, behind premaxilla (0); in broad contact on palatal surface, behind premaxilla (1).
7. **Alveolar ridge of maxilla.** Straight in lateral view, not upturned at anterior end (0); upturned at anterior end near suture with premaxilla, resulting in a distinct notch (1).
8. **Dorsal process of maxilla.** On middle or anterior end of maxilla (0); on posterior half of maxilla (1). RZ (char. 5) note that *Pachyrhachis* should be coded with state 0, a correction to L, which has been made elsewhere (LC) as well.
9. **Dorsal process of maxilla.** Extends dorsomedially (0); extends dorsolaterally, overhanging mouth (1).
10. **Posterior process of maxilla.** Long, reaching or extending past middle of ventral margin of orbit (0); short, not reaching middle of ventral margin of orbit (1).
11. **Lacrimal.** Present, either permanently separate or fusing with prefrontal during ontogeny (0); absent, never present as a discrete element (1).

12. **Lacrimal foramen.** Single opening (0); double opening (1).
13. **Lacrimal foramen.** Not greatly enlarged (0); greatly enlarged (1).
14. **Snout shape.** Relatively short, rounded (0); long and very narrow, tapering to point (1).
15. **Jugal.** Present (0); absent (1). RZ (chars. 12, 240) argue that the putative jugal in *Pachyrhachis* "most probably" represents a displaced ectopterygoid. However, this interpretation is unlikely, for reasons discussed in LC. The elements interpreted as 'postorbitals' by Tchernov et al. (2000) are of the correct shape (sliver-shaped) and in the correct position (anteroventral region of orbit, nearly reaching the ventral 'foot' of the prefrontals) to be the jugals. Furthermore, there are other preserved elements (not identified by Tchernov et al.) which might correspond to the real posterior orbital elements, i.e. the postorbital and/or postfrontal (see chars. 31-33 below). Until the above interpretation and that of Tchernov et al. (2000) are carefully re-evaluated, jugal presence and other jugal characters are treated as unknown. All other snakes lack a jugal; the putative "jugal" identified by Estes et al. (1970) and discussed by RZ is the ventral end of the postorbital (pers. obs. of new specimens courtesy of M. Caldwell and A. Albino).
16. **Jugal.** Anterior process confined to medial surface of maxilla, jugal does not extend anteriorly beyond middle of orbit in lateral view (0); anterior process on dorsal surface of maxilla, jugal extends anteriorly beyond middle of orbit in lateral view (1).
17. **Jugal.** Does not extend anteriorly past orbit (0); extends anteriorly past orbit (1).
18. **Jugal.** Without large posterior process (0); with large posterior process (1).
19. **Jugal.** Lacking dermal sculpture (0); with dermal sculpture (1).
20. **Nasals.** Large (0); greatly reduced or absent (1).
21. **Nasals.** Paired elements (0); single median element (1). RZ (char. 14) code *Varanus* as polymorphic for this character rather than with state 1. However, a recent phylogeny of *Varanus* (Ast 2001) corroborates the interpretation (L; LC) that the fused condition is primitive for the genus.
22. **Nasal-prefrontal contact.** Present, nasal-prefrontal contact separating maxilla from frontal (0); absent, nasal and prefrontal separated by maxilla-frontal contact (1).
23. **External naris.** Not retracted, prefrontal and frontal both excluded from posterior narial margin by nasal and maxilla (0); slightly retracted, prefrontal (but not frontal) enters posterior narial margin (1); greatly retracted, prefrontal and frontal enter posterior narial margin (2). Ordered 0-1-2. RZ code *Pachyrhachis* as "unknown" but acknowledge the original coding (L) of a retracted naris as "most conceivable"; the latter coding thus is retained here.
24. **Prefrontal.** Smooth (0); with tubercle or rugosities near orbital margin (1).
25. **Antorbital ridge.** Absent (0); present, extending anteriorly from dorsal margin of orbit (1).
26. **Frontals.** Single median element (0); paired elements (1).
27. **Frontal.** Enters orbital margin (0); excluded from orbital margin (1). RZ (char. 21) question the coding of *Pachyrhachis* with state 1, due to the uncertain identity of a splint of bone on the orbital margin. However, under any of their three possible interpretations, the taxon still exhibits state 1 due to the prefrontal contacting the parietal and excluding the frontal from the orbital margin. The identity of the small sliver of bone lateral to this contact cannot change the inferred state.
28. **Frontals.** Lateral orbital margin straight or only very slightly concave (0); lateral orbital margin deeply concave (1). Not applicable in taxa where the frontal does not enter the orbit. RZ (char. 19) note that aigialosaurs have state 1, and this recoding is adopted here.
29. **Frontal shelf extending anteriorly to underlie nasal.** Absent (0); present (1).
30. **Frontoparietal suture.** In dorsal view, complex interdigitating contact (0); in dorsal view, simple straight or slightly curved contact (1). RZ subdivide state 1 into three states (simple contact transverse, anteriorly convex, or anteriorly concave). However, the second substate is uninformative (occurring only in some mosasaurs), the

third is informative only if snakes are subdivided. The suture in *Haasiophis*, as revealed by the photographs, is not quite the smooth U reconstructed in Tchernov et al.'s (2000) interpretive drawing. Rather, there is a small median flange of the parietal projecting between the frontals, making the suture slightly W-shaped, as in madtsoiids and *Pachyrhachis*.

31. **Postfrontal.** Present and large, extending beyond orbital margin (0); present and small, does not extend beyond orbital margin (1); absent, never present as a discrete element (2). Ordered 0-1-2. RZ (char. 23) code snakes as lacking a postfrontal. However, *Dinilyisia* has a large one (Estes et al. 1970; Lee and Caldwell, pers. obs. of new material). As a result, the original coding (0and2) is retained. *Pachyrhachis* is coded by RZ as unknown. However, the forked shape of the posterior orbital element in *Pachyrhachis* strongly suggests an incorporated, large postfrontal, which would still extend posteriorly beyond the orbit (state 0), regardless of the identity of a disputed sliver of bone. On the left side of *Haasiophis*, there is a rectangular element positioned directly over the maxilla-ectopterygoid junction, and extending anteromedially to underlap the frontal-parietal contact. This is shown in both the photograph and interpretive drawing, but not identified. On the right side, a similar distinct element is visible on the photograph, but interpreted in the drawing as the anterior part of an implausibly large right ectopterygoid (this means that the right element extends much further anteriorly, and is twice as large, as the well-preserved left element). The elements are in the correct position, and are of approximately the right shape, to be the postorbitofrontals. If this identification is correct, this means the elements interpreted as "postorbitals" by Tchernov et al. (2000) must be something else, and indeed they resemble jugals in shape and position (see chars. 15-19 above). Because of this uncertainty, characters of the postfrontal and postorbital are scored as unknown.
32. **Postfrontal.** Remains separate from postorbital throughout ontogeny (0); fusing with postorbital during ontogeny (1). RZ (char. 24) code *Pachyrhachis* as unknown, but state 1 appears more likely than state 0 (see previous character). Also, snakes were coded as unknown. However, *Dinilyisia* has a separate postfrontal (Estes et al. 1970), whereas (as noted by RZ) uropeltids have been observed to have a fused postfrontal (Baumeister 1908). Snakes thus are coded here with both possible states (which has the same effect, however, as RZ's "unknown" coding).
33. **Postfrontal** (or dorsomedial portion of single posterior orbital bone). Not forked medially, does not extend a long distance along frontal or parietal (0); forked medially, with an anterior process along the frontal and a posterior process along the parietal (1). RZ (char. 25) code snakes as unknown. However, basal snakes exhibit both states 0 (e.g. *Cylindrophis*) and 1 (*Dinilyisia*). Snakes thus are coded here with both possible states (which has the same effect, however, as RZ's "unknown" coding).
34. **Palpebral (superciliary) ossifications on dorsal margin of orbit.** Absent (0); present (1).
35. **Postorbital.** Present (0); absent (1).
36. **Postorbital ventral process.** Prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone (0); small, forming less than half of posterior orbital margin, postorbital primarily a temporal bone (1).
37. **Posterior margin of orbit.** Present and continuous (0); present but with small gap (1); very incomplete, less than 50% of posterior orbital margin bordered by bone (2). Ordered 0-1-2. RZ code *Pachyrhachis* with state 1, interpreting the ventral orbital element as an ectopterygoid. However, the original interpretation as a jugal (closing the orbital margin) appears more plausible, for reasons discussed in LC.
38. **Parietals.** Paired elements (0); single median element (1).
39. **Parietal tabs** (triangular flanges extending anteriorly into fossae on ventral surface of frontals). Present (0); absent (1). RZ (char. 31) have "difficulty in understanding" the definition of this character. However, they did not propose an improved definition and retained it unchanged. A full definition of this character can be found in Estes et al. (1988; char. 22).
40. **Pineal foramen.** Present (0); absent (1).
41. **Pineal foramen.** Entirely within parietal (0); on frontoparietal suture (1); entirely within frontal (2). Ordered 0-1-2.

42. **Parietal table and jaw adductor muscles.** Parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (0); parietal table moderately wide, jaw adductors extend onto lateral margin only of dorsal surface of parietal (1); parietal table very wide, jaw adductors restricted entirely to ventral surface of parietal (2). Ordered 0-1-2.
43. **Parietal.** Main body of parietal does not extend far posteriorly, supraoccipital exposed in dorsal view (0); main body of parietal extends posteriorly, supraoccipital covered or nearly covered in dorsal view (1).
44. **Suspensorial ramus (posterolateral process) of parietal.** Well-developed (0); extremely short or absent (1).
45. **Upper temporal arch.** Complete, upper and lower temporal fenestrae separated (0); incomplete, upper and lower temporal fenestrae confluent (1).
46. **Temporal arch.** Without canthal crest (0); with canthal crest (1).
47. **Jugal-squamosal contact along upper temporal arch.** Absent (0); present (1).
48. **Dorsal process of squamosal.** Present (0); absent (1). RZ's (char. 41) coding of this character as unknown in *Pachyrhachis* is adopted here.
49. **Upper temporal fenestra.** Not restricted by postorbital (either widely open or restricted primarily by postfrontal) (0); restricted by postorbital (1). RZ (chars. 42, 43) code this and the next character as inapplicable in snakes, presumably because most of the latter lack a discrete postorbital (this character) and postfrontal (next character). However, *Dinilysia* (Estes et al. 1970) and possibly uropeltids (Baumeister 1908; RZ) have both elements and exhibit state 0 for both characters.
50. **Upper temporal fenestra.** Not restricted by postfrontal (either widely open or restricted primarily by postorbital), (0); restricted by postfrontal (1).
51. **Supratemporal.** Absent (0); present (1).
52. **Supratemporal.** In superficial position, on dorsolateral surface of parietal (0); in deep position, on ventrolateral surface of parietal (1).
53. **Supratemporal.** Confined to skull roof, does not extend along paroccipital process (0); extends along part of paroccipital process (1). RZ (char. 46) dispute this character and claim that neither mosasaurs nor snakes exhibit state 1. However, the supratemporal in mosasaurs has a long flange that extends along the lateral surface of the paroccipital process (e.g. Russell 1967, p. 34). Similarly, the supratemporal in *Dinilysia* extends along the long paroccipital process of the opisthotic-exoccipital (Estes et al. 1970, fig. 1). Madtsoiids also have this state (Scanlon 2005). Other snakes lack a long paroccipital process and cannot be coded. RZ's recoding of *Pachyrhachis* with 0 is not justified, since a well-developed paroccipital process is not exposed and may be absent; it is coded here as unknown. The codings adopted here for this character are discussed further in Scanlon (2005).
54. **Supratemporal.** Small, less than half the maximum width of the skull (0); large, at least half the maximum width of the skull (1). RZ code mosasaurs with state 0. However, this is a mistake since the supratemporal in mosasaurs is large but mostly hidden ventrally under the parietal (Russell 1967; Lee 1997). RZ appear to have been misled by the small exposure of the supratemporal in reconstructions of the skull in dorsal view. RZ also modify this character by changing it to supratemporal without or with free-ending posterior process, but this turns it into a very different character (one that furthermore is informative only if snakes are subdivided).
55. **Quadrate suspension.** Sutured to squamosal, pterygoid, and (sometimes) quadratojugal (0); mobile, articulates dorsally squamosal, supratemporal and opisthotic (1); mobile, articulates dorsally with supratemporal, little or no contribution from other elements (2); mobile, articulates dorsally with opisthotic, little or no contribution from other elements (3); mobile, articulates dorsally with squamosal, little or no contribution from other elements (4). Unordered. Mosasaurs were asserted by RZ (char. 49) to exhibit state 1 rather than 2. However, the articulation of the quadrate is almost entirely with the supratemporal (e.g. see Russell 1967, fig. 12), which largely excludes the opisthotic and the squamosal.
56. **Quadrate shaft orientation.** Slanting slightly anteroventrally, (0); slanting very anteroventrally, almost horizontal (1); approximately vertical (2); slanting posteroventrally (3). Ordered 1-0-2-3. This character has

been subdivided as suggested by RZ (char. 50), but the numbering of states is different here, to ensure that the primitive state is numbered 0. Also, RZ claim to have recoded *Pachyrhachis* with a posteriorly slanting quadrate, but this was the original coding (L, char. 50).

57. **Quadrate.** Tympanic crest (outer conch) is directed laterally and a well-developed wall (0); tympanic crest is directed laterally but a low ridge (1); distinct tympanic crest absent and external surface of quadrate only weakly concave (2). Ordered 0-1-2. RZ (char. 51) interpreted *Varanus* with state 1 rather than 0, due to a subjective difference in interpreting the boundary between states 0 and 1. As the crest in *Varanus* remains a wide wall and is wider than the other taxa coded with state 1, *Varanus* is coded here as having state 0.
58. **Quadrate.** With anteromedial (pterygoid) lappet (0); without anteromedial lappet (1).
59. **Quadrate shape.** Without large, posteroventrally curved, suprastapedial process (0); With large, posteroventrally curved, suprastapedial process (1).
60. **Mandibular articulation of quadrate.** Saddle-shaped, with lateral and medial condyles (0); flat, a single continuous condyle (1).
61. **Tympanic membrane.** Not ossified (0); ossified (1).

### Braincase and associated structures

62. **Orbitonasal fenestra.** Wide, not greatly restricted by either frontals or prefrontals (0); narrow, restricted largely by frontals and prefrontals (1).
63. **Ventral processes of frontals, forming lateral walls of olfactory tracts.** Not contacting anything below olfactory tracts (0); contacting one another below olfactory tracts (1); contacting parabasisphenoid below olfactory tracts (2). Unordered. As noted by RZ (char. 54), the original term for these processes ("ventromedial") was ambiguous, since it could apply also to the medial descending processes of alethinophidian snakes.
64. **Orbitosphenoid ossification.** Absent (0); present (1).
65. **Parietal downgrowths.** Absent or weakly developed ridges (0); prominent flanges (1). RZ (char. 56) code mosasaurs as lacking ridges and state that their condition is "closely comparable to *Varanus*". However, mosasaurs clearly have large descending flanges, as originally coded and previously noted (Lee 1997, fig. 3). Russell (1967, p. 29) noted that "though almost absent in *Varanus*, in all mosasaurs there are flattened descending alae from the parietal forming part of the medial wall of the supratemporal fenestra".
66. **Parietal downgrowths.** Pointed ventrally (0); sheet-like (1). RZ (char. 57) deleted this character as uninformative, claiming redundancy with character 44 here. This presumably was because at least slight parietal downgrowths are present whenever the jaw adductors insert on the lateral or dorsal margin of the skull table. This may be true, but the size of these downgrowths (previous character), and their shape, can still vary even in these taxa.
67. **Parietal downgrowths.** Not contacting parabasisphenoid or orbitosphenoid (0); contacting parabasisphenoid (1); contacting orbitosphenoid (2). Unordered.
68. **Optic foramina.** Not enclosed in bone (0); enclosed partly or entirely by frontals (1); enclosed by orbitosphenoid (2). Unordered. RZ (char. 60) further subdivided state 1, but this modification is only informative if snakes are subdivided into numerous terminals.
69. **Anterior brain cavity.** Floored only by cultriform process (0); floored by orbitosphenoid and cultriform process (1); floored by large descending frontal flanges and cultriform process (2). Unordered. The original definition of character states (L) was criticised by RZ (char. 61); LC have recognised this and refined the states.

70. **Trigeminal foramen or foramina.** Anterior margin not enclosed in bone (0); anterior margin enclosed by descending flange of parietal (1); anterior margin enclosed by orbitosphenoid and parabasisphenoid (2). Unordered. *Haasiophis* can be inferred to possess state 1, given its extensive descending parietal flange that meets the basisphenoid ventrally and the prootic posteriorly. (Both prootics are visible in ventral view, in the expected place on both sides of the basisphenoid, but are not labelled by Tchernov et al. 2000).
71. **Alar process of prootic.** Weakly developed (0); long process (1). RZ (char. 64) deleted this character from their analysis because they changed another character (RZ69) to be identical to the present one. RZ69 is deleted here, rather than being modified to be redundant with the present one; the latter is retained. Photographs of *Haasiophis* show a long alar process of the prootic between the supratemporal and the parietal; these are visible on both sides and are symmetrical, but are interpreted as part of the parietals by Tchernov et al. (2000). The elements interpreted as "prootics" by these authors are the lateral flanges of the pterygoid: they are clearly continuous with the pterygoid (as shown by both photographs and specimen drawings) and articulate with the ectopterygoid. As noted in Lee and Scanlon (2002), snakes which possess an alar process (e.g. *Dinilysia* and madtsoiids) have state 1.
72. **Alar process of prootic.** Directed dorsally (0); directed anterodorsally (1). RZ (char. 65) state that this character is inapplicable to *Pachyrhachis*, implying that the taxon lacks an alar process. However, the process might be present and, if so, is directed anterodorsally (see Lee and Caldwell 1998). Because of this uncertainty, it is here coded as unknown (which is effectively the same as RZ's coding of inapplicable). If the alar processes of the prootic in *Haasiophis* have been correctly identified here (see previous character), this taxon possesses state 1.
73. **Crista prootica** (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis). Well-developed lateral flange (0); reduced to weak ridge (1); absent (2). Ordered 0-1-2. State 2 is added, and coded for amphisbaenians, dibamids and snakes, as suggested by RZ (char. 66).
74. **Lateral head vein.** Not enclosed at all in bony canal (0); mostly or entirely enclosed in a bony canal on parabasisphenoid formed by an anteroventral continuation of the crista prootica (1).
75. **Foramen pro nervi facialis** (lateral exit on prootic for hyomandibular branch of the facial or VII nerve). Single (0); double (1). This character was deleted by RZ (char. 68) because of variability within terminals. However, it is retained here as such characters can be informative (e.g. Wiens 1998).
76. **Hypoglossal (XII) foramen.** Well-separated from jugular (X-XI) foramen (0); located very close to or confluent with jugular foramen (1).
77. **Occipital recess (recessus scalae tympani).** Open laterally (0); closed laterally (1). RZ (char. 70) code snakes as 1 rather than 0. However, many basal snakes have state 0 (Lee and Scanlon 2002), and snakes are thus coded with both states here.
78. **Stapes.** Light, with small footplate and slender shaft (0); robust, with large footplate and thick shaft (1). RZ's (char. 72) coding of snakes and skinks with both states is adopted here.
79. **Stapedial foramen.** Absent (0); present (1).
80. **Basisphenoid.** Without long posterolateral flanges (0); with long posterolateral flanges (1).
81. **Basipterygoid process.** Long, i.e. projecting far antero-laterally beyond the body of the basisphenoid (0); short or absent, i.e. not projecting very far beyond the body of the basisphenoid (1). RZ's (char. 74) criticism that this character should be coded as inapplicable in snakes (because the weak ridges in basal snakes might not be homologous to basipterygoid processes) is addressed by the rephrasing of state 1. In any case, the homology of the crests in basal snakes with the processes in lizards has yet to be refuted by character congruence (Lee and Scanlon 2002).
82. **Basal tubera.** Posteriorly located, very near to occipital condyle (0); anteriorly located, well away from occipital condyle (1). RZ (char. 76) claim that this character is inapplicable in snakes because the basal tubera are incorporated within the crista circumfenestralis. However, the position of the tubera can be determined nonetheless, and thus the character can be coded.

83. **Posterior opening of vidian canal.** Situated within basisphenoid (0); at basisphenoid-prootic suture (1); at suture between prootic and epiphysial ossification in the region of the basal tubera (2). Unordered.
84. **Opisthotic.** Flange extending between basal tubera and paroccipital process weak or absent, most of the stapes exposed in ventral view (0); wide horizontal flange extending posterolaterally from basal tubera to paroccipital process, obscuring much of the stapes in ventral view (1).
85. **Supraoccipital.** Does not contact parietal, unossified gap persists between the two elements (0); abuts parietal, the two elements meet but contact is non-sutural, and a tiny gap might remain between the two elements along part of the dorsal edge of the supraoccipital (1); sutural contact with parietal, entire anterodorsal edge of supraoccipital contacts parietal (2). Ordered 0-1-2.
86. **Supraoccipital.** Situated ventral or posteroventral to parietal, does not form part of posterior skull roof (0); situated posterior to parietal, forms part of posterior skull roof (1). RZ (char. 81) code skinks and pygopodids as polymorphic for this character; skinks are accepted as polymorphic here, but pygopodids remain coded with state 0, since only highly derived forms (e.g. *Lialis*) have state 1.
87. **Exoccipital.** Discrete element, not fusing with opisthotic until well into postembryonic ontogeny (0); not present as discrete element, fusing with opisthotic within embryo (1).
88. **Occipital condyle.** Single continuous convex projection, posterior surface of condyle straight in ventral view (0); two discrete convex projections arranged horizontally, posterior surface of condyle concave in ventral view (1).
89. **Posttemporal fenestra.** Present as an opening (0); completely closed via sutural contact of the skull roof and otic region of braincase (1). RZ (char. 80) deleted this character, alleging redundancy with their char. 91. However, the two characters vary largely independently (as can be seen from the codings). For example, the supraoccipital can contact the parietal firmly, but there can be large posttemporal fenestra, as in mosasaurs (see Scanlon 2005 for further discussion).

## Palate and associated structures

90. **Septomaxilla-maxilla contact.** Septomaxilla extensively sutured to the dorsal surface of the palatal flange of the maxilla (0); septomaxilla not sutured to maxilla (1). RZ (char. 85) acknowledge that both mosasaurs and snakes lack a septomaxilla-maxilla contact, but prefer to code snakes as "not applicable" rather than with state 1, since the other contacts of the septomaxilla differ between snakes and mosasaurs. Such prejudgements of homology appear unwarranted, and the lack of contact in mosasaurs and snakes is coded as potentially homologous here (to be tested by character congruence). However, RZ's coding of iguanids as polymorphic (based on a pers. comm. from R. Etheridge) is provisionally adopted.
91. **Septomaxillae.** Separated in midline by distinct cartilaginous gap, without raised crest (0); closely approaching each other in the midline in a raised crest (1). RZ (char. 86) criticise this character (discussed by Estes et al. 1988, char. 86) because the two septomaxilla are "always separated by each other by the internasal septum" (RZ, p.37). However, it is not the separation per se that is the critical variable, but the degree of separation and the presence of a midline crest (Estes et al. 1988).
92. **Median flange of septomaxilla.** Short, not reaching level of prefrontal (0); long, extends posteriorly to reach level of prefrontal (1).
93. **Dorsal surface of septomaxilla** (roof of Jacobson's organ). Flat or concave, Jacobson's organ small (0); expanded dorsally and convex, Jacobson's organ large (1).
94. **Opening of Jacobson's organ.** Enclosed partly by maxilla and vomer, confluent posteriorly with choana (0); enclosed fully by maxilla and vomer, sometimes with a tiny contribution from the septomaxilla, not confluent with choana (1); enclosed fully by vomer and septomaxilla only, not confluent with choana (2). Unordered.
95. **Vomers.** Paired (0); fused (1).

96. **Vomer.** With little or no sutural contact with maxilla behind opening of Jacobson's organ, most of lateral margin free (0); with extensive sutural contact with maxilla behind opening of Jacobson's organ, entire lateral margin meets maxilla (1). RZ (char. 98) argue that this character should be coded as unknown in *Pachyrhachis*, as the vomer is not preserved. However, the relevant area of the maxilla is known and suggests state 0 (Lee and Caldwell 1998).
97. **Vomer.** Small, less than half the length of maxilla (0); long, at least half the length of the maxilla (1). *Haasiophis* has been coded with state 1 here, as the vomer is as long as in other taxa with state 1. It is, however, slightly less than half the length of the maxilla, due to the enlarged maxilla in this taxon.
98. **Vomer.** Main posterior portion broad, plate-like (0); main posterior portion narrow, rod-like (1). RZ code basal snakes with a posteriorly broad vomer, but as some (e.g. typhlopids) have a narrow vomer, snakes are coded with both states here.
99. **Vomer.** Anterior or anteromedial to palatine (0); entirely medial to palatine (1). RZ (char. 98) argue that this character should be coded as unknown in *Pachyrhachis*, as the vomer is unknown. However, as the palatine reaches the snout region, there is no room for the palatine anterior to it, and it must have been completely medial (Lee and Caldwell 1998).
100. **Secondary palate.** Absent (0); present, formed by medial extension of ventrolateral edge of the "scroll-like" palatine (1).
101. **Palatine-vomer contact.** Short, length of contact less than half the length of vomer (0); extensive, length of contact forming at least half the length of vomer (1).
102. **Palatine-vomer contact.** Immobile, sutural contact (0); mobile, non-sutural contact (1).
103. **Palatine.** Long: as long as vomer (0); short: half as long as vomer (1). RZ (char. 98) suggest *Pachyrhachis* should be coded as unknown because the vomer is "not known". However, even if the putative vomer (Lee and Caldwell 1998) is not accepted, the length of the palatine (almost half that of the skull) in *Pachyrhachis* implies state 0.
104. **Palatines.** Well separated from one another by anterior extension of interpterygoid vacuity (0); contacting or almost contacting one another along most of their midline, obliterating interpterygoid vacuity (1).
105. **Palatine.** Without distinct medially-directed process (0); with distinct rectangular process projecting medially from the middle portion of the palatine to the skull midline (1).
106. **Choanal groove of palatine.** Short or absent (0); long groove leading posteriorly from choana along ventral surface of palatine (1).
107. **Ectopterygoid.** Does not enter cheek (0); enters cheek as a sliver sandwiched between maxilla and jugal (1).
108. **Ectopterygoid-palatine contact.** Absent, maxilla enters suborbital fenestra (0); present, maxilla excluded from suborbital fenestra (1). Mosasaurs were coded as unknown by RZ (char. 102). However, as both states are known to occur (Williston, 1898; Russell 1967) they should be coded as polymorphic instead.
109. **Suborbital fenestra.** Present and large (0); present but small (1); absent, i.e. completely closed (2). Ordered 0-1-2.
110. **Interpterygoid vacuity.** Open and narrow (0); open and wide (1); narrow and closed by a broadened parasphenoid (2). Ordered 1-0-2.
111. **Pterygoid-vomer contact.** Present, palatal ramus of pterygoid meets vomer anteriorly (0); absent, palatal ramus does not reach vomer (1).
112. **Pterygoid.** With triangular depression on ventral surface, extending from suborbital foramen towards basicranial articulation (0); without such depression (1).
113. **Pterygoid.** Anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process (0); anterior process distinctly set off from lateral process, the two portions meeting at a distinct 'corner' (1).

114. **Anterolateral process of pterygoid.** Absent, pterygoid with only anterior and lateral processes (0); present, extending along lateral margin of palatine (1).

115. **Epipterygoid.** Present (0); absent (1).

## Lower jaw

116. **Mandibular symphysis.** Rigid: anterior tips of dentary with a distinct, flat symphyseal area (0); mobile: anterior tips of dentary smoothly rounded and without distinct symphyseal area (1).

117. **Mental foramina on lateral surface of dentary.** Three or more foramina (0); two or fewer foramina (1). RZ (char. 111) argue that *Pachyrhachis* possesses one foramen rather than two foramina, but either interpretation implies state 1.

118. **Dentary.** With large posterodorsal extension covering much of the lateral surface of coronoid process (0); with small posterodorsal extension onto anterolateral part of coronoid process (1); does not cover lateral surface of coronoid process (2). Ordered 0-1-2.

119. **Meckel's canal.** Open groove on ventromedial or medial surface of dentary (0); enclosed tube within dentary, upper and lower borders of groove meeting in a sutural contact (1); enclosed tube within dentary, upper and lower borders completely fused together (2). Ordered 0-1-2.

120. **Anterior (symphyseal) end of Meckel's canal.** Extends along ventral margin of lower jaw (0); confined to medial surface of lower jaw (1). RZ (char. 115) recode *Pachyrhachis* with the ventral condition. However, the canal is clearly medial in this taxon (Haas 1980, fig. 3) and in the very similar *Haasiophis* (Tchernov et al. 2000, fig. 1).

121. **Intramandibular septum of Meckel's canal.** Poorly developed, does not approach level of the posteriormost tooth (0); well-developed, extends posteriorly to nearly the level of the posteriormost tooth (1). Contrary to RZ (char. 116), all snakes, including scolecophidians, exhibit state 1 (Lee and Scanlon 2001).

122. **Subdentary shelf.** Large (0); weakly developed (1); absent (2). Ordered 0-1-2. RZ (char. 117) correctly note that this character should apply only to taxa with pleurodonty, but code mosasaurs and snakes (which have true thecodonty: Caldwell et al. 2003) with state 2 rather than as inapplicable.

123. **Posterior margin of lateral surface of dentary.** No notch present (0); shallow notch present (1); deep notch present (2). Ordered 0-1-2. RZ (char. 118) retain this character unchanged but argue it should not be ordered; this possibility is tested in the 'unordered' analysis of the present study.

124. **Dentary-postdentary articulation.** Dentary overlapped extensively by coronoid, surangular, and prearticular (0); dentary overlapped mainly by prearticular (1); dentary overlapped mainly by surangular (2). Unordered. The states and codings are modified here according to RZ's (char. 119) suggestions.

125. **Splénial.** Large, extending anteriorly past middle of tooth row (0); small, only reaching middle of tooth row (1); absent (2). Ordered 0-1-2. As noted by RZ (char. 120), some basal snakes have a large splénial. In addition, others lack a splénial (Lee and Scanlon 2002). Snakes have been coded with all three states.

126. **Splénial.** Extends posteriorly onto postdentary bones, past apex of coronoid process (0); extends posteriorly onto postdentary bones but does not reach level of apex of coronoid process (1); does not substantially overlap postdentary elements, splénial with loose vertical contact with angular (2). Ordered 0-1-2. RZ (char. 121) suggest recoding state 2 (a loose vertical splénial-angular contact) into two states, one for mosasaurs and one for alethinophidians. However, this subdivision would render this character autapomorphic for both taxa (and thus uninformative), and is not justified, since the morphology of the splénial-angular contact in mosasaurs and basal snakes is very similar (Lee et al. 1999). RZ further code scolecophidians with an extensive contact. However, this applies to typhlopids only, with leptotyphlopids and anomalepedids possessing a vertical contact (as do other basal snakes). For this reason, snakes are coded with state 2 here.

127. **Splénial-dentary contact.** Extensive bony contact (0); reduced bony contact, much intervening connective tissue (1). RZ (char. 123) delete this character because they find it "difficult to understand" (p. 40). However, it was fully described in Estes et al. (1988: 158) and thus is retained here. On the other hand, mosasaurs and *Pachyrhachis* are coded as unknown because of the uncertainty regarding soft-tissue inferences in fossil material.
128. **Splénial-angular contact.** Not, or very slightly, exposed in lateral view (0); greatly exposed in lateral view (1).
129. **Anteromedial process of coronoid.** Long, extensive overlap on medial surface of dentary in front of coronoid process (0); short, coronoid does not greatly overlap medial surface of dentary in front of coronoid process (1). As noted by RZ (char. 125), the coronoid lies medial to the posterior dentary in most basal snakes (except uropeltids). Snakes are coded with state 0. RZ recommend coding this character as not applicable in snakes; presumably because the coronoid is a simple plate anteriorly without clear anteromedial and anterolateral processes. However, snakes can still be coded based on the contacts of the coronoid.
130. **Anterolateral process of coronoid.** Absent, coronoid does not overlap lateral surface of dentary (0); present, overlapping lateral surface of dentary (1). Snakes lack this process and are coded with state 0; RZ (char. 126) coded them as "inapplicable", for reasons which are not clear.
131. **Coronoid.** Anteromedial margin robustly contacts splénial (0); anteromedial margin with tiny point contact, or does not contact splénial (1). Snakes are coded with state 1 since this is found in *Dinilysia*, some scolecophidians and all basal alethinophidians. Although RZ state that all scolecophidians have state 0, this condition is found only in typhlopids.
132. **Coronoid.** Ventral margin of medial surface straight or convex (0); ventral margin of medial surface concave (1). RZ (char. 128) recommend coding dibamids and amphisbaenians as polymorphic; this has been done by LC and is also adopted here.
133. **Subcoronoid fenestra on medial surface of the mandible.** Fenestra absent, prearticular expands dorsally and contacts the entire ventral edge of the coronoid, surangular covered by these elements in medial view (0); fenestra present as distinct gap between coronoid and prearticular, surangular exposed in medial view (1). RZ (char. 129) recommend coding taxa lacking a discrete surangular as inapplicable (or discarding the character). However, even in taxa where the surangular is fused to adjacent elements, the presence of a medial fenestra exposing the lateral wall of the 'surangular' portion of the fused bone can be determined.
134. **Disarticulated surangular.** Extends far into the dentary and terminates in a point (0); extends some distance into the dentary and terminates in a blunt end (1); extends a short distance (at most) into the dentary and terminates in a blunt end (2); extends over lateral surface of dentary (3). Unordered. RZ (char. 130) claim that mosasaurs do not have state 2, because the surangular does not extend into the dentary. However, this condition represents an exaggerated form of state 2, and in RZ's matrix mosasaurs are actually coded with state 2.
135. **Surangular.** Does not extend dorsally to overlap posterior part of coronoid process (0); with flange extending dorsally to overlap posterior part of coronoid process (1).
136. **Surangular.** Does not form large portion of articular cotyle (0); forms half of articular cotyle (1).
137. **Angular.** Present (0); absent (1).
138. **Angular.** With wide exposure on medial surface of the mandible (0); not exposed, or exposed as only a very narrow splint, on the medial surface of the mandible (1).
139. **'Finger-like' angular process.** Absent (0); present (1).
140. **Prearticular** (or prearticular portion of compound element). In medial view with dentary and splénial removed, extends only a short distance in front of coronoid process, not past posterior teeth (0); extends well anterior to coronoid process, past posterior teeth (1). RZ claim that the condition in *Pachyrhachis* is unknown, but erosion of the left angular (right in ventral view) clearly reveals that the prearticular portion of the

compound bone extends far anterior to the coronoid (e.g. Lee and Caldwell 1998, fig. 4). However, RZ's recoding of snakes with 0 is accepted here.

141. **Prearticular crest.** Absent (0); moderately well-developed (1); prominent, with embedded angular process (2). Ordered 0-1-2.
142. **Adductor fossa.** Faces dorsomedially, medial margin low and rounded (0); faces dorsally, medial margin developed into vertical flange (1). The redefinition and recoding of this character by RZ (char. 137) is adopted here.
143. **Adductor fossa.** Narrow transversely, does not bulge medially (0); inflated transversely, bulges medially (1).
144. **Articular.** Fused with prearticular and surangular (0); fused with prearticular but not surangular (1); separate from both prearticular and surangular (2). Ordered 0-1-2. The descriptions of states 0 and 2 were inadvertently switched in L (see RZ, char. 139); this was corrected in LC.
145. **Retroarticular process size.** Intermediate, between 1 and 2 times articular cotyle (0); short, < articular cotyle (1); long, > 2 times articular cotyle (2). Ordered 1-0-2.
146. **Retroarticular process position.** In line with rest of mandible (0); offset medially, resulting in a lateral 'step' where it joins the rest of the mandible (1).
147. **Retroarticular process orientation.** Extends straight posteriorly (0); extends slightly medially (1); extends greatly medially (2). Ordered 0-1-2. State 2 is added following RZ (char. 141), who noted that the medial inflection might be slight or very great. However, their addition of another character state (process reduced) is not valid, since the resultant character conflates orientation and size. Their additional state is considered part of character 145 (retroarticular process size).
148. **Retroarticular process.** Dorsal surface with distinct sulcus or pit (0); dorsal surface smooth, lacking pit (1). RZ (char. 142) recommended coding taxa with a reduced process (*Pachyrhachis* and some snakes) as not applicable, which was the approach adopted by LC. However, snakes which have a long retroarticular process, such as scolecophidians, have state 1, so this terminal as a whole can be coded.
149. **Retroarticular process.** Dorsomedial margin smooth and featureless (0); dorsomedial margin with discrete tubercle or flange (1).
150. **Retroarticular process.** Tapering, narrow distally (0); not tapering, broad distally (1).
151. **Retroarticular process.** Not twisted posteriorly, posterior dorsal surface directed dorsally (0); twisted posteriorly, posterior dorsal surface directed dorsomedially (1). RZ (char. 145) comment that this is inapplicable to taxa with a reduced process, such as *Pachyrhachis*; this approach was also previously adopted (L, LC), thus the need for this qualification is unclear.

## Dentition

152. **Marginal teeth.** Pleurodont, teeth set in a continuous groove (0); acrodont, teeth ankylosed to jaw margin (1); thecodont, teeth ankylosed in discrete alveoli and separated by well-developed interdental plates (2). Unordered. RZ (char. 146) claim that scolecophidians and mosasaurs lack alveoli. However, true interdental plates separating adjacent teeth are present in both these groups (Scanlon and Lee 2000; Caldwell et al. 2003).
153. **Marginal teeth.** Without sharp carinae (0); with sharp carinae on anterior and posterior edges (1); with sharp carinae on lateral and medial edges (2). Unordered. RZ (char. 147) discard the original formulation of this character (carinae absent / present) as "misleading", because the carinae in varanoids and in snakes are positioned differently. The state 'carinae present' therefore is subdivided into two unordered derived states here, with no a priori assumption of homology between them.
154. **Bases of marginal teeth.** Smooth, external dentine not infolded (0); dentine infolded at least externally, resulting in longitudinal grooves (1). The original character referred to plicidentine, which strictly speaking is

an infolding of the enamel on the external and internal surfaces and thus difficult to confirm in many forms (see RZ, char. 148). As redefined here, however, *Pachyrhachis*, mosasaurs, and some basal fossil snakes can be coded with state 1.

155. **Marginal teeth.** Crowns closely spaced (0); crowns separated by large gaps (1). RZ (char. 149) comment that the crown separation in mosasaurs and terrestrial varanoids is due to wide flaring bases, but do not state why this makes the character carry "little phylogenetic information". However, they retain it unmodified, which is also done here.
156. **Marginal teeth.** Without high pedestals (0); with high pedestals (1).
157. **Position of replacement teeth.** Lingual to functional tooth (0); posterolingual to functional tooth (1); no true replacement teeth (2). Unordered.
158. **Resorption pits associated with replacement teeth.** Extending into tooth crown (0); Restricted to bone of attachment at base of teeth (1). This redefinition of character states follows RZ (char. 151). However, their subdivision of state 1 into two states (pits in bone of attachment small or large) has not been followed, since this subdivision is not cladistically informative, with one of the substates being an autapomorphy of mosasaurs. Otherwise, codings follow RZ (char. 151).
159. **Orientation of replacement teeth.** Erupt upright, growing straight upwards into functional position (0); erupt horizontally, and then rotating through ninety degrees about the base into functional position (1). RZ's (char. 152) argument that recumbent replacement teeth in numerous mosasaur specimens are taphonomic artefacts is unlikely (LC).
160. **Premaxillary teeth.** Five or more (0); four or fewer (1). *Haasiophis* has a very small and narrow premaxilla and can be inferred to possess state 1.
161. **Median premaxillary tooth.** Absent (0); present (1). Although Tchernov et al. (2000) state that *Haasiophis* lacks premaxillary teeth, this cannot be confirmed, because the ventral surface of the element is largely covered by the maxillae.
162. **Median premaxillary tooth.** Not enlarged (0); much larger than other premaxillary teeth (1).
163. **Premaxillary teeth** (apart from median tooth). Similar size or larger than anterior maxillary teeth (0); distinctly smaller than anterior maxillary teeth (1).
164. **Maxillary teeth.** Thirteen or more tooth positions (0); between twelve and nine tooth positions (1); eight or fewer tooth positions (2). Ordered 0-1-2.
165. **Dentary teeth.** Thirteen or more tooth positions (0); twelve to nine tooth positions (1); eight or fewer tooth positions (2). Ordered 0-1-2.
166. **Palatine teeth.** Present (0); absent (1).
167. **Palatine teeth.** Small conical denticles (0); similar in size to marginal teeth (1).
168. **Pterygoid teeth.** Present (0); absent (1).
169. **Pterygoid teeth.** Small conical denticles (0); large and recurved teeth (1). RZ (char. 162) claimed that the original formulation of this character was uninformative (pterygoid teeth much smaller or similar in size to marginal teeth), arguing that they are always smaller than the marginal teeth. However, there remains a clear difference between the shagreen of small pterygoid teeth in typical 'lizards' and the long, recurved pterygoid teeth in mosasaurs and snakes with dentigerous pterygoids, and the redefined character relates to this.
170. **Egg teeth.** Single (0); paired (1).

## Axial skeleton

171. **Centra.** Not constricted anterior to condyle, i.e. condyle not wider than posterior end of centrum (0); slightly constricted anterior to condyle, i.e. condyle slightly wider than posterior end of centrum (1); greatly constricted anterior to condyle, i.e. condyle much wider than posterior end centrum (2). Ordered 0-1-2.
172. **Vertebral articular surfaces.** Vertical, condyles (if present) facing posteriorly, much of the articular surface is visible in ventral view (0); slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articular surface is visible in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articular surface is visible in ventral view (2). Ordered 0-1-2.
173. **Shape of articular surfaces in mid-dorsal vertebrae.** Oval, horizontal (mediolateral) dimension wider than vertical (dorsoventral) dimension (0); circular (1). RZ (char. 166) note that some snakes (scolecophidians) have oval cotyles; this was recognised in LC, where snakes were coded with both states.
174. **Centra.** Notochordal, i.e. perforated by persistent notochord in adults (0); not notochordal, i.e. not perforated by persistent notochord in adults (1).
175. **Centra.** Amphicoelous (0); procoelous (1).
176. **Neural spines.** Tall processes (0); low ridges (1).
177. **Zygosphenes and zygantra.** Present (0); absent (1). RZ (chars. 169, 170) recommend combining both these characters into one character, which they treat as unordered. However, treating the characters as two separate characters captures the putative homology of accessory vertebral articulations across all taxa (this character), while at the same time considering the variability of the structures as potentially informative (next character). This treatment therefore is not redundant, as argued by RZ.
178. **Zygosphenes and zygantra.** Type A, articular surface of zygosphene faces dorsally (0); type B, articular surface of zygosphene faces ventrolaterally (1). Inapplicable in taxa without these structures.
179. **Intercentra on mid-presacral vertebrae.** Present (0); absent (1). Some pygopodids retain intercentra (Kluge 1987).
180. **Number of presacral vertebrae.** 23 to 25 (0); 22 or fewer (1); 26 (2); 27 to 50 (3); 50 to 119 (4); 120 to 150 (5), 150 or more (6). Ordered 1-0-2-3-4-5-6.
181. **Number of cervical vertebrae.** Seven or fewer (1); eight (0); nine or ten (2); more than ten (3). Ordered 1-0-2-3.
182. **Transverse processes of anterior presacrals.** On anterior end of centrum (0); on middle of centrum (1).
183. **Hypapophyses on anterior presacrals.** Only extending to the posterior end of the sixth presacral at most (0); extending to the seventh presacral or beyond (1). RZ (char. 174) delete this character and claim that snakes cannot be coded because they lack a cervical region. This argument might apply to char. 181 above (number of cervicals), but cannot apply to the present character. Snakes have presacral vertebrae, and the number of these vertebrae bearing hypapophyses can be determined readily.
184. **Dorsoposterior flange on atlas neural arch.** Present, directly overlying axis neural arch (0); absent (1).
185. **Anterior presacral intercentra** (excluding atlas and axis intercentra). Not sutured or fused to preceding centrum (0); sutured to preceding centrum (1); fused to preceding centrum (2). Ordered 0-1-2.
186. **Anterior presacral intercentra.** Not sutured or fused to following centrum (0); sutured to following centrum (1); fused to following centrum (2). Ordered 0-1-2.
187. **Pachyostosis of mid-presacral vertebrae and ribs.** Absent (0); present (1).
188. **Caudal transverse processes.** Single processes throughout caudal region (0); double processes in some caudals (1).
189. **Caudal transverse processes.** Two prongs converging distally (0); two prongs diverging distally (1).

190. **Caudal transverse processes.** Project laterally or posterolaterally (0); project anterolaterally (1).
191. **Caudal autotomy septa.** Present in some caudals (0); absent in all (1).
192. **Caudal autotomy septa.** Anterior to, or within, transverse processes (0); posterior to transverse processes (1). This character was taken from Estes et al. (1988), who recognised two very similar states. RZ (char. 182) noted that state one could have been subdivided into two states, but nevertheless retained the same two states.
193. **Pedestals on caudal vertebrae for chevrons / haemapophyses.** Weakly developed, barely raised above the surface of the centrum (0); prominent raised tubercles (1). RZ (char. 185) recode this and the following two characters as inapplicable in snakes, thus implicitly assuming that the haemapophyses of snakes are non-homologous with the chevrons of other squamates. However, the two structures are very similar in position (posteroventral margin of caudal centrum) and structure (distal separation of the rami of a chevron would produce a pair of rod-like haemapophyses). Furthermore, at least some basal snakes (*Podophis*, *Wonambi*) have typical squamate chevrons (Rage and Escuillie 2000; Scanlon and Lee 2000). For this reason, the original assumption of homology is retained.
194. **Chevrons / haemapophyses.** Articulate with caudal centra (0); sutured or fused to caudal centra (1).
195. **Caudal chevron / haemapophysis position.** At posteroventral margin of centrum (0); situated more anteriorly, some distance from posteroventral margin of centrum (1).
196. **Body shape.** Round, ribs smoothly curved (0); laterally compressed, middle and distal regions of ribs totally straight (1).
197. **Ribs.** Begin from third (or more anterior) presacral vertebra (0); begin from fourth (or more posterior) presacral vertebrae (1). RZ (char. 186) noted that as originally defined, using the term cervical vertebra, this character might be considered inapplicable in snakes (which lack a clearly defined cervical region). The modified character is applicable to snakes.
198. **Ribs.** Proximal end without anteroventral pseudotuberculum (0); proximal end with anteroventral pseudotuberculum (1).
199. **Ribs.** Proximal end without posterodorsal pseudotuberculum (0); proximal end with posterodorsal pseudotuberculum (1).
200. **Distally forked cloacal ribs** ('lymphapophyses'). Absent (0); present (1). RZ (char. 189) argue that *Pachyrhachis* might have more than a single lymphapophysis. This, however, would not change its coding.
201. **Tail.** Cylindrical or only slightly laterally compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1).
202. **Neural spines of posterior caudal vertebrae.** Projecting dorsally or posterodorsally (0); projecting almost horizontally, highly inclined posteriorly (1).

### Shoulder girdle and forelimbs

203. **Scapulocoracoid.** Present and large (0); present but reduced (1); absent (2). Ordered 0-1-2.
204. **Emargination on anterodorsal edge of scapula.** Absent (0); present (1).
205. **Anterior (primary) coracoid emargination.** Absent (0); present (1).
206. **Posterior (secondary) coracoid emargination.** Absent (0); present (1).
207. **Clavicle.** Present (0); absent (1).
208. **Clavicle.** Follows contour of anterior margins of scapulocoracoid (0); curves anteriorly away from scapulocoracoid (1).

209. **Clavicles.** Rod-like, at most only slightly expanded proximally, and with no notch or fenestra (0); greatly expanded proximally, usually with notch or fenestra (1).
210. **Interclavicle.** Present (0); absent (1).
211. **Interclavicle.** Cross-shaped, with lateral processes (0); simple rod, without lateral processes (1).
212. **Interclavicle.** Anterior process small or absent (0); anterior process large (1).
213. **Ossified sternum.** Present (0); absent (1).
214. **Sternal fontanelle.** Absent (0); present (1).
215. **Sternal fontanelle.** Single (0); paired (1).
216. **Number of rib attachment points to sternum.** Five pairs (0); four pairs (1); three pairs (2); two pairs or fewer (3). Ordered 0-1-2-3.
217. **Postxiphisternal inscriptional ribs.** None united along the ventral midline (0); one or more pairs united along the ventral midline to form continuous chevron-shaped structures (1).
218. **Forelimbs.** Large (0); small (1); absent (2). Ordered 0-1-2.
219. **Ectepicondylar foramen of humerus.** Present (0); absent (1).
220. **Epipodials.** Parallel (0); distally diverging (1).
221. **Forelimb.** 'Foot': olecranon large, carpals well-ossified, digits independently movable and with well-developed joints (0); 'flipper': olecranon small, carpals poorly ossified, digits joined by webbing or sheath, and with poorly developed joints (1).

## Pelvic girdle and hindlimbs

222. **Pelvis.** Present and large (0); present and small (1); absent (2). Ordered 0-1-2.
223. **Pelvic elements** (ilium, ischium, pubis). Elements distinct, but strongly sutured together (0); co-ossified into a single pelvic bone (1); elements distinct, weakly united in non-sutural contacts (2). Ordered 1-0-2. RZ (char. 207) argue that aigialosaurs have a firmly sutured pelvis, rather than a weakly sutured one as originally coded. However, the pelvis is only well-known in one aigialosaur, where the sutures appear to be weaker than in typical varanoids, with both pubes and ischia taphonomically separated from each other (Carroll and DeBraga 1992, fig. 12; Lee, pers. obs.). Aigialosaurs thus are coded with either state 0 or 2. RZ also claim that the weakly sutured pelvises of snakes that possess all three elements (e.g. pythons, some scolecophidians) are not closely comparable, but retain their coding with state 2, which is also done here. In *Haasiophis* the pelvis is represented by at least two isolated elements, implying state 2.
224. **Sacral blade of ilium.** With anterior bulge or process (0); without anterior process (1).
225. **Pubis.** Short in length, symphyseal process directed ventrally (0); intermediate in length, symphyseal process anteroventrally (1); greatly elongated, symphyseal process directed anteriorly (2). Ordered 0-1-2. RZ (char. 209) delete this character because it is "difficult to understand" (p. 46). However, it was first used in Estes et al. (1988, char. 124) where the three states were clearly defined. The symphyseal process is directed ventrally and medially in all squamates. However, in some squamates, it is elongated so that it points slightly (state 1) or greatly (state 2) anteriorly as well.
226. **Pubic plate.** Oriented parasagittally, wide in lateral view (0); oriented transversely, narrow in lateral view (1).
227. **Pubis.** Expanded distally, at symphyseal margin (0); not expanded distally (1).
228. **Hindlimbs.** Well-developed (0); reduced (1); absent (2). Ordered 0-1-2.
229. **Femur.** Gracile (0); stout (1).

230. **Femur.** Curved in dorsoventral plane (0); not curved (1). RZ (char. 213) delete this character from analysis, because the condition in *Pachyrhachis* is uncertain because of crushing, and because (at least in *Pachyrhachis*) the character is at least partly correlated with the previous one, since a small stout femur is unlikely to be curved. The character is retained here, but made independent of limb reduction by coding it as inapplicable in taxa with greatly reduced femora (including *Pachyrhachis*).
231. **Distal end of tibia.** Gently convex for astragalocalcaneal articulation (0); with notch fitting into a ridge on astragalocalcaneum (1). As noted by RZ (char. 214), this character might be considered inapplicable in mosasaurs and snakes, which unlike other squamates lack a distal epiphysis. However, rather than being deleted (as in RZ) it is retained here, but coded as inapplicable in mosasaurs and snakes.
232. **Astragalus and calcaneum.** Co-ossified (0); separate (1). RZ (char. 215) provisionally retain this character but argue that it is subject to ontogenetic variation and due to paedomorphosis. This, however, would apply to many other characters which nevertheless are useful phylogenetic markers.
233. **Hindlimb.** 'Foot': fifth metatarsal fully hooked, tarsals well-ossified, digits independently movable and with well-developed joints (0); 'flipper': fifth metatarsal partially hooked or not hooked, tarsals poorly ossified, digits joined by webbing or sheath and with poorly developed joints (1).

### Miscellaneous osteological characters

234. **Body proportions.** Head moderately large with respect to trunk region (0); head extremely small with respect to trunk region (1).
235. **Dorsal body osteoderms.** Absent (0); present (1).
236. **Ventral body osteoderms.** Absent (0); present (1).
237. **Separable cranial osteoderms.** Absent (0); present only in periphery of skull table (1); present over entire skull table (2). Ordered 0-1-2.
238. **Separable cranial osteoderms.** Few and large (0); many and small (1).
239. **Separable cranial osteoderms.** Tightly connected to skull roof, though separable (0); very loosely connected to skull roof (1).
240. **Rugosities on skull roof bones formed by overlying cephalic scales.** Rugosities absent (0); rugosities present, no vermiculate sculpture (1); rugosities present, along with vermiculate sculpture (2). Ordered 0-1-2.
241. **Scleral ossicles.** Present (0); absent (1).
242. **Scleral ossicles.** Fifteen or more (0); fourteen (1); thirteen or fewer (2). Ordered 0-1-2.
243. **Scleral ossicles.** Complex and irregular in shape (0); square in shape (1).
244. **Hyoid apparatus.** Second epibranchials present (0); second epibranchials absent (1).
245. **Hyoid apparatus.** Second ceratobranchials present (0); second ceratobranchials absent (1).
246. **Epiphyses.** Present on both appendicular and axial skeleton (0); present on appendicular skeleton, absent on axial skeleton (1); absent on both appendicular and axial skeleton (2). Ordered 0-1-2. This represents a combination of the two epiphysial characters, as suggested by RZ (chars. 227, 228). Aigialosaurs possess state 1, mosasaurs possess state 2.
247. **Fusion of long bone epiphyses.** Fuse to diaphyses at the same time, or after, fusion of braincase elements (0); fuse to diaphyses before fusion of braincase elements (1).
248. **Postcloacal bones.** Absent (0); present (1).

## Soft anatomy

### External morphology

249. **Complex dewlap apparatus (gular fan).** Absent (0); present (1).
250. **Cephalic scales.** Numerous and small (0); few and enlarged (1).
251. **Scales in mid-dorsal row.** Larger than other dorsal scales (0); same size as other dorsal scales (1).
252. **Dorsal body scales.** Mostly small and granular, only a few isolated large scales at most (0); all large and flat (1).
253. **Enlarged dorsal body scales.** Polygonal (0); cycloid (1).
- \*254. **Tympanic membrane.** Absent, auditory area covered by scaly skin (0); present, auditory area with smooth tympanum (1). Data from Wever (1978) and author's observations. Note that under this definition (after Wever 1978), taxa sometimes described as having "scaly" tympanic membranes (e.g. xenosaurids: McDowell and Bogert 1954; Estes et al. 1988) are coded as lacking a tympanum.
- \*255. **Tympanic membrane.** Superficial, flush or almost flush with skin and meatal cavity absent (0); recessed, large meatal cavity present (1). Data from Wever (1978) and author's observations. Not applicable in taxa lacking a tympanic membrane.
256. **Femoral or preanal pores.** Absent (0); present (1). Eublepharids and diplodactylines primitively possess pores, whereas the primitive condition in gekkonids is uncertain (Kluge 1967).
- \*257. **Generation glands.** Absent (0); escutcheon type present (1); beta type present (2). The homologies of the two types of gland are debated (e.g. Kluge 1983), and this character is thus treated as unordered. Gekkonines s. l. primitively have beta glands, the escutcheon type is restricted to sphaerodactylines.
- \*258. **Specialised toe pads with fine lamellae.** Absent (0); present (1). Not applicable in limb-reduced taxa.
259. **Tail length.** Long, i.e. more than 38% of snout-vent length (0); short, i.e. less than 38% of snout vent length (1).

### Cartilaginous structures

260. **Inferior alary process of anterior nasal copula.** Small (0); large (1).
261. **Apical foramen of anterior nasal copula.** Present, copula perforated by medial branch of ethmoid nerve (0); absent, medial branch of ethmoid nerve passes ventral to copula (1).
262. **Superior nasal fenestra of parietectal cartilage.** Present (0); absent (1). Contrary to Hallermann (1998), a fenestra is present in cordylids but absent in xanthusiids (Malan 1946).
263. **Course of medial branch of ethmoid nerve.** Through groove on premaxilla (0); through groove on septomaxilla (1).
264. **Paraseptal cartilage.** Well-developed and anteroposteriorly complete (0); reduced and anteroposteriorly incomplete, or absent (1).
265. **Planum antorbitale of nasal capsule.** Complete posteriorly, separating cavum antorbitale from choanal duct (0); incomplete posteriorly, cavum antorbitale continuous with choanal duct (1).
266. **Foramen olfactorius leading into ethmoidal region.** Small (0); large (1). Contrary to Hallermann (1998), a large foramen is present in gekkonids (Malan 1946).

267. **Nasopharyngeal cavity.** Nasal passage not separated from oral cavity (0); nasal passage partially separated from oral cavity (1); nasal passage fully separated from oral cavity (2). Ordered 0-1-2. Contrary to Hallermann (1998), some basal snakes exhibit state 0 (McDowell 1972). The presence of a bony palate in xantusiids also appears to be variable (Savage 1963).
268. **Interorbital septum.** Present (0); absent (1).
269. **Commissura sphenethmoidalis connecting nasal capsule and interorbital septum.** Present, complete (0); present, incomplete (1); absent (2). Ordered 0-1-2.
270. **Processus supraoccipitalis (tectum synoticum).** Present (0); absent (1).
271. **Epicoracoid cartilage.** Extensive, contacting mesoscapula and usually suprascapula (0); reduced, does not contact mesoscapula nor suprascapula (1).

## Musculature

272. **Insertion of adductor mandibulae posterior on lower jaw.** Not extending into Meckel's canal (0); extending slightly into Meckel's canal, but lacking median tendon (1); extending greatly into Meckel's canal, with median tendon (2). Ordered 0-1-2.
273. **Origin of adductor mandibulae internus (pars pseudotemporalis superficialis) on skull roof.** Restricted to anterior margin of temporal fenestra (0); extending posteriorly along entire medial margin of temporal fenestra but not onto supratemporal (1); extending posteriorly along entire medial margin of temporal fenestra and onto supratemporal (2). Ordered 0-1-2, and inapplicable in taxa where this muscle is lost (Schwenk 2000).
274. **Separate insertion (= "anterior head") of adductor mandibulae internus (pars pseudotemporalis profundus).** Absent (0); present (1).
275. **Depressor palpebris inferior of eyelid.** Present (0); absent (1).
276. **Musculus extracolumellaris of middle ear.** Absent (0); present (1).
277. **Meatal closure muscle of tympanum.** Absent or vestigial (0); partially encircles tympanum, i.e. L- or C-shaped (1); fully encircles tympanum, i.e. O-shaped (2). Ordered 0-1-2. Data from Wever (1978) and Kluge (1987).
278. **Musculus mandibulohyoideus of throat.** Absent (0); present (1). Schwenk (2000) suggests that this is a more appropriate name for the muscle than is *geniohyoideus*.
279. **Musculus hyoglossus of tongue.** Divided into two bundles only (0); subdivided into multiple bundles (1).
280. **Intrinsic circular muscle system of tongue.** Incomplete ring (0); complete ring but weakly developed (1); complete ring and well-developed (2). Ordered 0-1-2.
281. **Musculus rectus abdominis lateralis of abdomen.** Absent (0); present (1).
282. **Musculus intercostalis ventralis of abdomen.** Present (0); absent (1).
283. **Musculus transversus penis of hemipenis.** Well-developed (0); greatly reduced or absent (1).
284. **Musculus transversus penis of hemipenis.** Fibres extend transversely (0); fibres extend obliquely or longitudinally (1).
285. **Musculi retractores laterales of hemipenis.** Anterior and posterior muscles present (0); single muscle present of uncertain homology, which might represent the anterior, posterior, or combined muscle (1); anterior muscle present only (2). Unordered.
286. **Musculi retractores laterales of hemipenis.** Widely separated (0); close together or partially fused (1).

287. **Musculus retractor lateralis anterior of hemipenis.** Originates lateral to hemipenis (0); originates dorsal to hemipenis (1).
288. **Musculus retractor lateralis posterior of hemipenis.** Originates lateral to hemipenis (0); originates dorsal to hemipenis (1).
289. **Musculus retractor lateralis posterior of hemipenis.** Not situated within hemipenial sheath (0); situated substantially within hemipenial sheath (1).

### Brain and nervous system

290. **Nucleus sphericus of accessory olfactory bulb.** Weakly to moderately developed, diffuse (0); strongly developed, discrete (1); extremely well developed, discrete (2). Ordered 0-1-2.
291. **Brain organisation.** Lacertomorph pattern (0); dracomorph pattern (1).
292. **Pituitary gland.** Distal lobe a regular mass, lying ventral to intermediate lobe (0); distal lobe greatly enlarged anteriorly and thin posteriorly, distal lobe therefore lies mostly anteroventral to intermediate lobe (1).
293. **Ulnar nerve in forelimb.** Superficial (0); deep (1).
294. **Innervation of muscles of lower leg.** Peroneal nerve (0); interosseous nerve (1).

### Middle and inner ear

295. **Internal (quadrate) process of extracolumella.** Present (0); absent (1).
296. **Spindle body in cochlear duct.** Absent (0); present (1).
297. **Limbic mound (vestibular lip) of cochlear duct.** Absent or very weak (0); distinct, simple ridge (1); large recurved flange (2). Ordered 0-1-2.
298. **Shape of limbus.** Circular to slightly oval (0); greatly elongated anteroposteriorly (1).
299. **Anteroventral region of limbus.** Not intruded by periotic sac (0); accommodates long posterodorsal projection – the accessory scala tympani – from periotic sac (1); accommodates short anterior projection from periotic sac (2). Unordered.
300. **Basal papilla.** Does not extend all the way across limbus, large margin of limbic tissue present at either end (0); extends almost all the way across limbus, only a narrow strip of limbic tissue present at one end (1).
301. **Basal papilla.** Simple continuous strip, not or only slightly constricted (0); with deep constriction that almost or completely separates the strip into two portions (1).
302. **Basal papilla and membrane.** Posterodorsal extremity not tapered (0); posterodorsal extremity tapered (1).
303. **Restraint system for cilia of hair cells.** Cells attached to tectorial membrane (0); cells attached to tectorial membrane and inertial bodies (sallets) (1); cells attached to inertial bodies (sallets and culmen) only (2). Ordered 0-1-2.
304. **Tectorial membrane.** Present (0); absent (1).
305. **Arrangement of inertial bodies and tectorial membrane.** Inertial bodies situated at both ends of tectorial membrane (0); inertial bodies situated alongside entire length of tectorial membrane (1).
306. **Otic sac.** Small to moderate in size (0); greatly enlarged (1).

307. **Periotic (perilymphatic) cistern.** Not divided into saccular and cochlear parts (0); fully divided into saccular and cochlear parts (1).

### Olfactory and vomerolfactory organs

308. **Jacobson's organ.** Weakly developed (0); moderately developed (1); extremely well developed (2). Ordered 0-1-2.
309. **Jacobson's organ opening and choanal groove.** Choanal groove long, reaches opening of Jacobson's organ (0); choanal groove short, does not reach opening of Jacobson's organ (1); choanal groove absent (2). Ordered 0-1-2.
310. **Jacobson's organ epithelium.** Poorly developed, less than 2.5 receptor cells for each supporting cell (0); intermediate, between 2.5 and 8 receptor cells for each supporting cell (1); well-developed, more than 8 receptor cells for each supporting cell (2). Ordered 0-1-2.
311. **Olfactory epithelium.** Poorly developed, less than 2 receptor cells for each supporting cell (0); intermediate, between 2 and 4 receptor cells for each supporting cell (1); well-developed, more than 4 receptor cells for each supporting cell (2). Ordered 0-1-2.
312. **Vestibulum of nasal cavity.** Short (0); greatly elongated (1).
- \*313. **Concha.** Well-developed (0); greatly reduced or absent (1). Data from Parsons (1970), Frost and Etheridge (1989), and references therein.
314. **Conchal shape.** Central (conchal) space small or absent, entire external nasal gland lies lateral to nasal capsule (0); central space large, accommodating part of external nasal gland (1).
315. **Size of external nasal gland.** Small (0); large (1).

### Oral glands

316. **Dental glands** (serous glands opening at the base of the teeth). Absent on both jaws (0); present on both jaws (1).
317. **Labial glands** (mucous or muco-serous glands opening into the lips). Present on both jaws (0); absent on upper jaws only (1); absent on both upper and lower jaws (2). Ordered 0-1-2.
318. **Gland of Gabe on lower jaw.** Absent (0); present (1).

### Tongue and hyoid apparatus

319. **Tongue shape.** Short and wide (0); long and narrow (1).
320. **Tongue cross-section.** Thick (vertically) in cross-section and not greatly broadened (0); very flat and broad (1).
321. **Notching of free part of tongue.** Not notched (0); notched less than 10% of total length of tongue (excluding posterior limbs) (1); notched between 10 and 20% (2); notched between 20 and 40% (3); notched more than 40% (4). Ordered 0-1-2-3-4. Dibamids are coded with state 0 (after Greer 1985), but one genus might have a slight notch (Schwenk 2000).
322. **Tines of tongue tip.** Not drawn out into long, tapering points (0); drawn out into long, tapering points (1).

323. **Relationship of tongue to sublingual plicae.** Entire tongue rests above sublingual plicae (0); anterior portion lies between rather than above sublingual plicae (1).
324. **Foretongue.** Not much wider than width of the internal hyoglossus muscle bundles (0); much wider than width of the internal hyoglossus muscle bundles (1).
325. **Bipartite tongue.** Absent, hydrostatic length change distributed along entire tongue (0); present, hydrostatic length change localised within foretongue (1). This character was previously described as “foretongue retractibility” (e.g. McDowell 1972), but Schwenk (2000) notes that the above description is more accurate.
326. **Hindtongue.** Fleshy and solid (0); modified into sheath (1).
327. **Glandular epithelium of tongue.** Present on foretongue and hindtongue (0); absent on hindtongue only (1); absent on hindtongue and foretongue (2). Ordered 0-1-2.
328. **Taste buds on tongue.** Present (0); absent (1).
329. **Lingual mucocytes.** Present over entire tongue (0); absent on foretongue but present on hindtongue (1); absent on both foretongue and hindtongue (2). Ordered 0-1-2.
330. **Lingual mucocytes.** Few serous glands, i.e. mostly muco-serous (0); many serous glands (1).
331. **Lingual scales.** Absent (0); present (1).
332. **Lingual scale arrangement.** Irregular (0); in diagonal rows across tongue (1).
333. **Lingual scale morphology.** With smooth posterior edges (0); with crenulated or irregular posterior edges (1).
334. **Dorsal lingual plicae** (transverse, imbricate folds across dorsal tongue surface). Absent (0); present on hindtongue only (1); present on hindtongue and foretongue (2). Ordered 0-1-2.
335. **Ventral lingual plicae** (transverse, imbricate folds across ventral surface of tongue). Absent (0); present on foretongue (1).
336. **Covering of main body of tongue.** High-profile papillae (0); low-profile papillae (1); papillae absent, replaced by smooth keratinised epithelium (2). Ordered 0-1-2.
337. **Reticulation of tongue papillae.** Papillae not reticular (0); reticular on foretongue only (1); reticular on foretongue and hindtongue (2). Ordered 0-1-2.
338. **Shape of tongue papillae.** Tops convex, not flat (0); tops flat (1). In both gekkotans and xantusiids, these papillae form a smooth pad on the region of the tongue, used to wipe the eye (Schwenk 2000).
339. **Pointed epithelial apices on papillae of hindtongue.** Absent (0); present (1).
340. **Tongue keratinization.** Absent (0); ventral pallets present on ventral surface of foretongue (1); keratinous covering present over tines of tongue tip (2). Unordered.
341. **Ventral pallet shape.** Does not project laterally, covered by main body of tongue in dorsal view (0); projects laterally beyond margins of main body of tongue, and visible in dorsal view (1).
342. **Sublingual glands on floor of mouth under free part of tongue.** Diffuse and irregular in transverse section (0); dense and round in transverse section (1).
343. **Sublingual glands on floor of mouth under free part of tongue.** Paired (0); scattered (1).
344. **Entoglossal process of hyoid.** Single continuous cartilage (0); distal end detached and connected to proximal portion by ligaments (1).
345. **Laryngo-hyoid ligament.** Without dorsolateral branches (0); with dorsolateral branches extending ventral to laryngeal cartilage (1).
346. **Hypohyal.** Short or absent (0); long (1).
- \*347. **Wing-like hyoid cornu.** Absent (0); present (1). From Kluge (1987).

## Eye and orbital structures

348. **Eye.** Well-developed with sharply formed lens and fully differentiated retinal visual cells, animal very responsive to light when constructing burrows (0); poorly developed with vaguely formed lens and incompletely differentiated retinal visual cells, animal poorly responsive to light when constructing burrows (1).
349. **Visual cells of retina.** Rods present (0); rods absent (1).
350. **Pupil shape.** Vertical (0); round (1).
351. **Eye covering.** Eye exposed, upper and lower eyelids present (0); eye covered by single transparent spectacle (1); eye covered by opaque scales (2). Ordered 0-1-2.
352. **Lacrimal duct.** Single (0); double (1).
353. **Anterior opening of lacrimal duct.** Enters oral cavity directly, near opening of duct of Jacobson's organ (0); enters duct of Jacobson's organ (1); enters main lumen of Jacobson's organ (2). Ordered 0-1-2.

## Visceral organs and histology

354. **Lungs.** Subequal in size (0); left lung reduced (1); right lung reduced (2). Unordered.
355. **Lungs.** Single-chambered (0); partially divided into numerous chambers by septae (1); multichambered, divided fully into numerous chambers (2). Ordered 0-1-2.
356. **Lungs.** Without intrapulmonary bronchi or 'pseudobronchus' (0); with intrapulmonary bronchi, one in each lung (1); with single 'pseudobronchus' between lungs (2). Unordered.
357. **Ventricle of heart.** Apex attached to pericardium by ligamentous gubernaculum cordis (0); apex free from pericardium, gubernaculum cordis absent (1).
358. **Fundic glands of stomach.** Body of gland consisting of both mucous (cyanophilic) and serous (erythrophilic) cells (0); mucous cells lost, body of gland consisting of serous (erythrophilic) cells only (1).
359. **Fundic glands of stomach.** Distinct neck cells absent (0); distinct neck cells present (1).
360. **Pancreas.** Elongated or multilobed (0); compact (1).
361. **Main bile salt.** Cholic or allocholic acid (0); varanic acid (1); pythocholic acid (2). Unordered.

## Circulatory system

362. **Carotid duct connecting carotid and systemic arches.** Present (0); absent (1).
363. **Stapedial artery.** Passes anterior to stapes (0); passes through stapes via stapedial foramen (1); passes posterior to stapes (2). Ordered 0-1-2.

## Cloaca and genitalia

364. **Cartilaginous apical horns within hemipenis.** Absent (0); present (1).
365. **Hemipenial sheath.** Absent (0); present (1).
366. **Hypoischium.** Well-developed (0); vestigial or absent (1).
367. **Urinary bladder.** Present (0); absent (1).
368. **Post-cloacal sacs.** Absent (0); present (1).
369. **Cloacal gland.** Discrete ventral gland present in both sexes (0); discrete gland absent in males but present in females (1); discrete gland absent in both sexes (2). Ordered 0-1-2.
370. **Cloacal glands.** Ventral glands a single mass (0); ventral glands divided into two or more discrete masses (1).
371. **Cloacal glands.** Discrete dorsolateral glands absent in both sexes (0); dorsolateral glands present in males only (1); dorsolateral glands present in both sexes (2). Ordered 0-1-2.

## Spermatozoon

372. **Acrosome of spermatozoon.** Circular in cross-section (0); flattened in cross-section (1).
373. **Perforatorium.** Rod-like, constant diameter throughout (0); gradually tapering anteriorly (1).
374. **Perforatorial base plate.** Absent or indistinct (0); well-developed and distinct (1).
- \*375. **Perforatorial base plate.** Knob-like, i.e. ovoid (0); stopper-like, i.e. truncated cone (1).
376. **Epinuclear translucent space.** Absent (0); indistinct and small (1); distinct and large (2). Ordered 0-1-2.
377. **Midpiece.** Short (0); moderate in length (1); long (2). Ordered 0-1-2.
378. **Mitochondria of midpiece.** Round (0); intermediate (1); long (2). Ordered 0-1-2.
379. **Shape of elongate mitochondria.** Straight and columnar (0); curved and sinuous (1).
380. **Dense bodies.** Intramitochondrial (0); regular rings (1); scattered (2); linear series (3); stellate spiral (4); two groups (5). Unordered.
381. **Multilaminar membranes.** Absent (0); present (1).

## Behaviour and ecology

- \*382. **Eye-licking.** Absent (0); present (1).
- \*383. **Complex vocalisations produced by vocal cords.** Absent, only single distress calls at most (0); present, multiple chirps (1). Although eublepharids are capable of simple distress calls (Underwood 1954; Bauer, pers. comm.), the vocalisations are not as intricate as in other gekkotans (Kluge 1987). *Sphenodon* and some agamids (Moody 1980), lacertids (Böhme et al. 1985; Arnold 1984) and scincids (Greer 1989) can utter squeaks, but again these involve the passage of air through the glottis rather than true vocal cords, and are not complex multiple calls.
- \*384. **Prey prehension.** Small prey captured on dorsal surface of tongue (0); small prey captured using jaws exclusively (1). From Schwenk (1988, 1993, 2000).

- \*385. **Tongue protrusion.** Part of tongue remains behind mandibular symphysis even during maximum protrusion (0); entire tongue, including posterolateral limbs, can protrude past mandibular symphysis (1). From Schwenk (1988).
- \*386. **Tongue flicks.** Flicks without substrate contact rare (0); flicks without substrate contact common (1). From Schwenk (1993).
- \*387. **Vertical oscillations during tongue flicks.** Absent (0); present (1). From Schwenk (1993).
- \*388. **Vertical oscillations during tongue flicks.** Always one vertical oscillation per tongue flick (0); single and multiple vertical oscillations occur (1). From Schwenk (1993), except that this character is not applicable in taxa without vertical oscillations (see previous character).
- \*389. **Chemosensory discrimination of prey from nonprey odors.** Absent (0); present (1). From Schwenk (1993). Since that study, primitive iguanids and gekkonids have been shown to be unable to identify prey chemicals (Cooper 1995; contra Schwenk 1993), although some taxa in each group have evolved this ability. Chameleons and cordylids were coded as unknown by Schwenk (1993); they have state 0, and both states, respectively (Cooper 1994, 1995). Amphisbaenians appear to be unable to discriminate between prey and artificial odors (Lopez and Salvador 1992), and have been tentatively coded with state 0.
- \*390. **Strike-induced chemosensory searching.** Absent (0); brief (1); prolonged (2). Character and distribution taken from Cooper (1994, 1995) and references therein. Ordered 0-1-2.
- \*391. **Foraging mode.** Unable to locate food or prey trails without visual cues (0); able to locate food or prey trails without visual cues (1). From Schwenk (1993).
- \*392. **Foraging mode.** Ambush foraging (0); active foraging (1). Data from Cooper (1994), with additional taxon codings taken from Cooper and Steele (1999), Cooper and Whiting (1999), Perry (1999), and Schwenk (2000). *Sphenodon* has been interpreted as an ambush forager (Cooper 1994; Schwenk 2000). Gekkonids were coded with both states by Cooper (1994). However, additional studies of more taxa have suggested that ambush foraging is primitive (Cooper 1995; Perry 1999; Schwenk 2000). Amphisbaenians, not considered in Cooper (1994), have been described as both lying in wait for prey, and actively searching for prey trails (Gans and Klemmer 1968; Mattison 1986; Schwenk 2000). Although snakes have very diverse foraging strategies, basal forms such as scolecophidians and anilioids appear to be active foragers (e.g. Rajendran 1985; Schwenk 2000).
- \*393. **Reproductive mode.** Oviparous (0); viviparous (1). Viviparity is here defined to mean live young, i.e. the entire continuum between 'ovoviviparity' and placental viviparity. All basal iguanids, agamids, chameleons, gekkonids and lacertids are oviparous, although some derived taxa in each group have evolved viviparity (Lee and Shine 1998).
- \*394. **Clutch size.** Variable (0); fixed at one (1); fixed at two (2). This character does not form a clear morphocline, and is unordered. Xantusiids (McDowell and Bogert 1954), pygopodids (Kluge 1987), and basal gekkonids (Kluge 1987) ovulate and lay two eggs or young at a time; dibamids appear to always to have one egg, although few specimens have been examined (Greer 1985). All other squamate groups have variable clutch sizes.
- \*395. **Habitat.** Terrestrial, partly or entirely surface-living (0); totally fossorial (1); marine (2). This character does not form a morphocline, and is unordered. Modern snakes have been coded with both states, since some basal forms are totally fossorial (e.g. most but not all scolecophidians; Webb and Shine 1992), whereas others are partly surface-living (e.g. aniliids).
- \*396. **Territorial behaviour.** Males defend no or small parts of home range, e.g. a burrow or crevice (0); males defend large parts of home range (1). Data from Stamps (1977) as reviewed by Martins (1994). Martins (1994) subdivided state 1 into two states, defence of immediate surroundings and defence of specific geographic areas, but admitted that this distinction was dubious because of insufficient information in most cases. The two states have been combined here. Also, contrary to Martins (1994), chameleons were described with both states (Stamps 1977). Basal snakes have not been reported to defend home ranges (e.g. Rajendran 1985; J. Scanlon, pers. comm.). Of the taxa not considered by Stamp, detailed studies have not mentioned defence of home

ranges in pygopodids, xenosaurids, helodermatids or amphisbaenians (Gans and Klemmer 1968; Greer 1989; Brown and Carmony 1991; Ballinger et al. 1995), and these taxa have been tentatively coded with state 0.

\*397. **Territorial behaviour.** Head-bobbing, head-butting and push-up displays between agonistic males absent (0); present (1). Data from Stamps (1977) and Carpenter and Ferguson (1977). Chameleons have been tentatively coded with state 1; they exhibit head-bobbing as well as head-butting, and have a rocking display (Stamps 1977; Carpenter and Ferguson 1977) that appears to be equivalent to the push-up display modified for an arboreal context. Limbless forms have been coded as not applicable; it is difficult to see how such head-bobbing, head-butting and push-ups could be performed if the head is against the ground, oscillates during locomotion, and if the forelimbs are poorly developed or absent. A description of aggression in *Xenosaurus* only mentioned fighting and biting (Ballinger et al. 1995), and xenosaurids thus have been tentatively assumed to have state 0.

\*398. **Egg shell.** Parchment (0); calcareous (1).

\*399. **Ability to undergo major short-term colour changes.** Absent (0); present (1). Data from Stamps (1977), Frost and Etheridge (1989), Greer (1989), Brown and Carmony (1991).

## Characters from recent analyses, excluded here

**Supratemporal-prootic contact.** Absent (0); present (1). L48, LC58. As suggested by RZ48, this character equates rather different states in mosasaurs and snakes, and has been deleted.

**Cultriform process.** Curved in lateral view (0); straight (1). L62. This character is difficult to quantify, subject to distortion during drying, and impossible to score on taxa where the relevant region is unossified. This character was thus deleted by LC. RZ62 also recommended deletion of this character.

**Lacrimial.** Separate throughout ontogeny (0); fusing with prefrontal during ontogeny (1). LC12. Not cladistically informative; derived state uniformly present in only one taxon.

**Lacrimial foramen.** Bordered at least partly by facial elements, i.e. lacrimial or maxilla (0); entirely within antorbital flange of prefrontal (1). L11. This was interpreted as a mosasauroid-snake synapomorphy by L. However, the lacrimial foramen appears to be absent in mosasaurs, which thus cannot be coded. This character was thus deleted by LC; RZ11 also recommended deletion.

**Parietal.** Approximately half as long as skull, or shorter (0); more than half as long as skull (1). LC41. Not cladistically informative; derived state uniformly present in only one taxon.

**Parietal downgrowths.** Not sutured to prootic (0); sutured to prootic (1). L58, LC71. This character is deleted here. It is correlated with character 68: well-developed downgrowths will always strongly contact the prootic. RZ58 attempted to redefine the character as 'prootic alar process present/absent', but this amounts to a totally new character (since the presence of the process, and its contact with the parietal, are largely independent).

**Squamosal.** Present (0); absent (1). LC50. Not cladistically informative; derived state uniformly present in only one taxon.

**Otic region.** Region of braincase containing fenestra ovalis not expanded laterally (0); region of braincase containing fenestra ovalis expanded laterally (1). L71. This character was interpreted as diagnosing a *Sineoamphisbaena* + dibamid + amphisbaenian clade (Wu et al. 1996; L). However, it was deleted by LC, because the lateral expansion in *Sineoamphisbaena* is correlated with the general broadness of the skull, whereas in dibamids and amphisbaenians (and indeed all miniaturised squamates) the otic region is proportionately large due to allometry.

**Footplate of stapes.** Not tightly surrounded by ridges projecting from the lateral surface of the braincase elements (0); tightly surrounded by flanges from prootic and opisthotic (1). L73. This was interpreted as a mosasauroid-snake synapomorphy. However, the flanges in mosasaurs tightly encircle only a tiny area around the stapes,

whereas those in snakes encircle a much greater area and might be argued to fail the test of similarity. This character was thus deleted by LC; RZ73 also recommended deletion.

**Basipterygoid process.** Articular facet at distal end is a small, subcircular area (0); articular facet at distal end is a large, anteroposteriorly elongated area (1). L75. This character is very variable within terminal taxa and very difficult to quantify, and was deleted by LC. RZ75 also recommended deletion.

**Posterior opening of vidian canal.** Situated anteriorly, well in front of the posterior end of the basisphenoid (0); situated posteriorly, near the posterior end of the basisphenoid (1). L78, LC89. As noted by RZ78, this character is rather vague and also partly related to the present character 83, and thus is deleted.

**Dentary.** Straight in lateral view, with straight dorsal edge (0); curved in lateral view, with concave dorsal (alveolar) edge (1). L112, LC124. RZ112 question the state in *Pachyrhachis* and also code mosasaurs as polymorphic. As this character is extremely variable, even between young and old adults, and difficult to quantify, it is deleted here.

**Anterior tip of splenial.** LC134. On ventral edge of dentary (0); on medial surface of dentary (1). This character is closely correlated with character 120 (position of anterior portion of Meckel's canal), and thus is deleted.

**Splenial-angular contact.** In medial view overlapping, irregular, and with limited mobility (0); in medial view abutting, straight (vertical), and highly mobile (1). L124, LC136. As noted by RZ124, this character overlaps strongly with characters 126 and 127, thus it is deleted from the present analysis.

**Pubic tubercle.** On posterodorsal end of pubis (0); more anteroventrally placed, occupying shaft of pubis (1). This character was interpreted as a scleroglossan synapomorphy (Estes et al. 1988; L). However, there are no clear differences between scleroglossans and other squamates (i.e. iguanians), and this character was deleted by LC.

**Epiphyses on appendicular skeleton.** L228, LC256. Present (0); absent (1). This character has been combined with a related character (246 above), as suggested by RZ228.

**Pelvis.** External to rib cage, sacral contacts present (0); internal to rib cage, sacral contacts absent (1). RZ234. This character was noted by Caldwell and Lee (1997) to be an autapomorphy of snakes above *Pachyrhachis*, and thus not informative at this level of analysis. On the other hand, RZ234 claimed that dibamids exhibit the derived state. However, most of the pelvis lies external to the sacral ribs in this taxon, and only a small anterior part of it encroaches into the posterior ribcage.

**Cartilaginous processus ascendens of supraoccipital.** Present (0); absent (1). RZ232. This is a soft-anatomy character and included here as part of that character set. It was used previously by Hallermann (1998, char. 144).

**Femur and tibia/fibula development.** RZ235-6. As acknowledged by RZ, these are correlated with the other limb-reduction characters included here, and should not be included as well (they were included by RZ for heuristic reasons).

**Medial frontal flanges, posterior process of dentary, long palatine, anterior process of palatine, suprapedial process.** RZ231, 233, 237-239. These were new characters added by RZ to resolve relationships within snakes, but are informative only if snakes are subdivided into multiple terminals, which does not apply at the current level of analysis.

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