

Supplementary material to:

Scanlon, J.D. Skull of the large non-macrostomatan snake *Yurlunggur* from the Australian Oligo-Miocene. *Nature* 2005-05-05789.

1. Revised diagnoses

Madtsoiidae Hoffstetter, 1961

Snakes of small to very large size; hypapophyses present only in anterior trunk; middle and posterior trunk vertebrae with moderately or well developed haemal keel (except a few near the cloacal region), often with short laterally paired projections on the posterior part of the keel. All trunk and caudal vertebrae with a parazygantral foramen (or sometimes several foramina) in a more or less distinct fossa lateral to each zygantral facet; prezygapophyseal processes absent; paracotylar foramina present; diapophyses relatively wide, exceeding width across prezygapophyses at least in posterior trunk vertebrae.¹⁹

***Yurlunggur* Scanlon, 1992**

Large snakes, adult mid-trunk vertebrae exceeding 35 mm in width, and total length estimated to exceed 6 m; neural spine low or moderate in height, overhanging zygantrum posteriorly, variable in height and shape within the column and between species; zygapophyses inclined at less than 30° (usually less than 22°) from horizontal, and approximately equal to diapophyses in width (usually slightly wider); 'paired hypapophyses' present in anterior to mid-trunk as lateral ridges on prominent median hypapophysis or haemal keel, but on posterior trunk forming a broad, nearly parallel-sided haemal keel with nearly flat or slightly concave ventral surface and lateral borders defined by distinct grooves, and sometimes with paired, short, conical free posterior processes^{8,23}. Anterior part of maxilla not flattened anteriorly but with narrow medial flange below narial chamber, and anterodorsal edge of dorsal process moderately steep; suborbital region with elongate dorsal facet in line with the maxilla, not forming an oblique trough. Pterygoid with teeth close to medial edge, facet for palatobasal articulation facing dorsally, and ectopterygoid process curving posteriorly (not simply triangular in palatal view).

Adult specimens of *Yurlunggur* are comparable in size to species of *Madtsoia*, *Gigantophis garstini*, and *Wonambi naracoortensis*, and considerably larger than species of *Alamitophis*, *Patagoniophis* and *Rionegrophis*, or *Wonambi barriei*. The neural spine is considerably lower and less steep than in *Madtsoia bai* and species

of *Wonambi*, and usually *Alamitophis* and *Rionegrophis*, but much higher (at similar positions in the column) than in *Patagoniophis parvus*, *Madtsoia laurasiae*, *Herensugea caristorum*, and probably also *Gigantophis garstini* (though the spine may be incomplete in all described material of this taxon). The neural canal is trifoliate in section, not triangular as in *Rionegrophis* or some specimens of *Patagoniophis*, and somewhat wider than deep. The condyle and cotyle are more oblique and depressed than in *Gigantophis garstini*, and the zygosphene relatively higher and narrower. The long axes of the postzygapophyseal facets are more oblique than in large species of *Madtsoia* and *Wonambi* (where they are nearly directly transverse) and the postzygapophyses are hence less distinct in dorso-ventral views from the interzygapophyseal ridge. The broad, flat or bifid haemal keel of posterior trunk vertebrae distinguishes *Yurlunggur* from taxa other than *Madtsoia* and *Herensugea* (this region has not been described in *Gigantophis*); *Madtsoia* differs in having paradiapophyses considerably more prominent laterally. Differs from *Wonambi naracoortensis* (the only other known non-pythonine Australian snake of comparable adult size) in having less steeply sloping zygapophyses, broader zygosphene, and lower neural arch and spine at equivalent regions of the column, lack of multiple additional 'pits' on areas of the vertebra including parazygantral face and roof of zygosphene, and in having the haemal keel of posterior trunk vertebrae defined laterally by distinct grooves rather than shallow depressions.

Features of the maxilla, palatine, pterygoid and/or dentary are comparable with but distinct from those in species of *Madtsoia*, *Wonambi*, *Nanowana*, *Patagoniophis* and *Alamitophis*. Characters of the anterior maxilla can be compared among *Wonambi naracoortensis*, both species of *Nanowana*, *Madtsoia camposi*, and *Yurlunggur* sp./spp. from Riversleigh; *Yurlunggur* is intermediate in proportions between *Wonambi* and *Nanowana+Madtsoia*. The pterygoid is comparable only among *Yurlunggur*, *Wonambi* spp. and *Nanowana godthelpi*; *Yurlunggur* and *Nanowana* resemble each other in the features mentioned, while *Wonambi* spp. have the teeth more distant from the medial edge, the facet narrow and facing medially more than dorsally, and a triangular ectopterygoid process. The dentary is most similar to *Wonambi*¹⁹, but the medioventral crest is much less prominent medially. Features of the braincase can be compared only with *Wonambi naracoortensis* among other madtsoiids, so their significance for generic diagnosis is currently unknown.

2. Additional cranial material, and condition of skull of QMF45391

In addition to material listed in the main text, referred cranial elements of *Yurlunggur* sp. or spp. from Riversleigh sites include other incomplete maxillae (e.g. **CS Site** QMF23046, QMF23049, QMF23050) and dentaries (e.g. **RV Site** QMF36441, **Upper Site** QMF51380, **Gag Site** QMF51381), well-preserved palatines (**CS Site** QMF24085, **WW Site** QMF51417, **Upper Site** QMF51416), pterygoids (**WH Site** QMF51378, **CS Site** QMF51379), and ectopterygoid (**WW Site** QMF19740)^{13,16-19}.

The cranial elements of QMF45391 (Fig. 1) were all more or less disarticulated within the rock but closely associated (often in immediate contact) with the articulated vertebral series and other vertebrae and ribs; apart from some elements shown in photographs (A. Gillespie and K. Black, UNSW; unpublished) and the two perfectly preserved frontals which remained in contact medially with each other and ventrally with one palatine (personal observations), precise information on their dispersion and orientations was generally not recorded between stages of acid processing. Reassembly as shown in Fig. 1 (by the author) followed unambiguous identification of each separate element, cleaning, and reattachment of broken pieces. The degree of staining of the bones varies through the deposit, so that pre-fossilisation breaks or disarticulations are often marked by colour or shade contrast in the figure. Positions of some elements of unusual morphology were established by precise interlocking contacts with other bones (e.g. ectopterygoid with pterygoid, postorbitofrontals with frontals and parietal, jugals with postorbitofrontals), possible because of the exceptionally fine preservation of bone surfaces in this specimen.

3. Morphological character list

The characters are numbered as in Lee & Scanlon (2002)¹⁵ [**LS**]; state definitions are modified in a few cases, and one multistate character is added ('60A'=264). *Yurlunggur* and *Wonambi* here replace composite 'Madtsoiidae' in **LS**, which was based mainly on *Wonambi* but included some data from *Yurlunggur*, *Nanowana* and other poorly known taxa. Changes to scoring of *Dinilysia* are based on Caldwell & Albino (2002)⁵ and interpretations in this work. Some notes are given on scoring of *Pachyrhachis* with reference to Polcyn et al. (2005), and *Eupodophis* with reference to Rage and Escuillié (2000) and Rieppel and Head (2004). References not cited in the *Letter* are detailed below.

1. Premaxilla. 0: anterior surface convex or straight. 1: anterior surface concave.
(*Yurlunggur* 0, *Wonambi* ?)
2. Ascending process of premaxilla. 0: long and contacting frontals, i.e. extends entire snout-frontal distance. 1: intermediate in length and not contacting frontals. 2: extremely reduced or absent. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* ?)
3. Ascending process of premaxilla. 0: process transversely expanded, partly roofing external nares. 1: process narrow or spine-like, separating but not roofing external nares. (*Yurlunggur* 1, *Wonambi* ?)
4. Ascending process of premaxilla. 0: without lateral flange. 1: with lateral flange forming dorsal margin of external naris. (*Yurlunggur* 0, *Wonambi* ?)
5. Nasal keel (process) of premaxilla. 0: absent. 1: moderately developed, short flange. 2: well developed, long process. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* ?)
6. Palatal (vomarine) process of premaxilla. 0: extensive overlapping contact with vomer. 1: non-overlapping, point contact with vomer. 2: not in contact with vomer. Ordered 0—1—2. (*Yurlunggur* ? - damaged, *Wonambi* ?).
7. Premaxilla-vomer contact. 0: flat overlap. 1: well-defined facet. (*Yurlunggur* ? - damaged, *Wonambi* ?)
8. Premaxillary palatal foramina. 0: paired. 1: single. 2: multiple. Ordered 1—0—2. (*Yurlunggur* 0, *Wonambi* ?)
9. Main body of premaxilla. 0: on anterior end of the snout. 1: on ventral surface of snout. (*Yurlunggur* 0, *Wonambi* 0 – facets on maxillae)
10. Snout shape. 0: tapering anteriorly in front of orbits. 1: spherical, expanded in front of orbits. (*Yurlunggur* 0, *Wonambi* 0)
11. Posterior margin of lateral process of premaxilla, in palatal view. 0: oriented anterolaterally. 1: oriented transversely, perpendicular to midline. 2: oriented posterolaterally. Ordered 0—1—2. (*Yurlunggur* 2, *Wonambi* ?)
12. Maxilla-premaxilla contact. 0: close, suture or strong abutting contact. 1: close but not abutting, connected by short ligament. 2: loose, widely separated. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0/1 - changed from 1/2; state assignments for other basal snakes may be questionable, but unchanged here). I am unaware of any extant snakes with a 'socketed' condition of the premaxilla comparable to that in *Yurlunggur*, it is certainly absent in most groups but might occur in some highly specialised fossorial snakes (e.g. uropeltids), and then as a likely 'reversal' associated with reinforcement of the snout.

13. Anterior (premaxillary) process of maxilla. 0: well developed, forming ventral margin of external naris. 1: poorly developed or absent, maxilla excluded from ventral margin of external naris. (*Yurlunggur* 0, *Wonambi* 0)
14. Dorsal (ascending or prefrontal) process of maxilla. 0: well developed. 1: poorly developed or absent. (*Yurlunggur* 0, *Wonambi* 0)
15. Anteromedial maxillary flange. 0: present, small horizontal shelf on medial surface of anterior end of maxilla. 1: absent, anterior end of maxilla without such shelf. (*Yurlunggur* 0, *Wonambi* 1, *Dinilysia* 0)
16. Lateral maxillary foramina. 0: present. 1: absent. (*Yurlunggur* 0, *Wonambi* 0)
17. Maxilla. 0: alveolar (tooth) row oriented longitudinally. 1: alveolar (tooth) row oriented transversely. (*Yurlunggur* 0, *Wonambi* 0)
18. Maxilla-palatine articulation. 0: located anteriorly, at or in front of anterior orbital margin. 1: located beneath anterior half of orbit. 2: located posteriorly, at same level as centre of orbit or further posterior. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0)
19. Palatine process of maxilla. 0: absent, medial margin of maxilla smooth or with (at most) indistinct swelling. 1: present, medial margin of maxilla with distinct process. (*Yurlunggur* 1, *Wonambi* 1)
20. Palatine process of maxilla. 0: does not approach pterygoid, palatine broadly enters suborbital fenestra. 1: contacts pterygoid, excluding palatine from suborbital fenestra. (*Yurlunggur* 0, *Wonambi* 0)
21. Palatine process of maxilla. 0: dorsomedial surface pierced by a large foramen. 1: not pierced. (*Yurlunggur* 0, *Wonambi* 0)
22. Ectopterygoid flange of maxilla. 0: maxilla without distinct posteromedial (ectopterygoid) expansion or flange. 1: maxilla with weak but distinct posteromedial (ectopterygoid) expansion or flange. 2: maxilla with large posteromedial (ectopterygoid) expansion or flange. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0; Pythoninae changed to 0&1, as *Morelia* and *Python* have state 1 and may be basal, see Scanlon 2001²⁴)
23. Posterior extent of maxilla. 0: does not reach middle of orbit. 1: reaches middle of orbit, or slightly further. 2: extends past posterior margin of orbit. Ordered 0—1—2. (*Yurlunggur* 2, *Wonambi* 2)
24. Nasal. 0: does not closely approach lateral process of premaxilla. 1: extends anteriorly to almost reach lateral process of premaxilla. (*Yurlunggur* 1, *Wonambi* ?)

25. Horizontal lamina of nasal. 0: narrow anteriorly, tapering to a point beside premaxilla. 1: horizontal lamina of nasal wide anteriorly, at most tapering only slightly to a blunt anterior end. (*Yurlunggur* 0, *Wonambi* ?; *Dinilysia* 0).
26. Horizontal lamina of nasal. 0: posterior margin wide. 1: posterior margin narrow, tapering to a posteromedial point. (*Yurlunggur* 0, *Wonambi* 0)
27. Nasal-frontal contact. 0: horizontal laminae of nasals and frontals in contact. 1: horizontal laminae of nasals and frontals not in contact. (*Yurlunggur* 0, *Wonambi* 0)
28. Nasal-frontal contact. 0: nasals overlap frontals dorsally. 1: frontals overlap nasals dorsally. 2: clasping junction, nasal fits into anterior groove in frontal and is thus overlapped and underlapped by frontal. Unordered. (*Yurlunggur* 0, *Wonambi* 2)
29. Nasal-frontal boundary: 0: concave posteriorly in dorsal view. 1: approximately straight and transverse. 2: convex posteriorly. 3: W-shaped, nasals project posteriorly into embayments in frontals. Unordered. (*Yurlunggur* 2, *Wonambi* 3)
30. Descending laminae of nasals. 0: not enlarged (shallow) anteriorly. 1: distinctly enlarged (very deep) anteriorly. (*Yurlunggur* ? - ventral margin damaged, *Wonambi* ?)
31. Anterior process of prefrontal. 0: moderately developed, triangular flange. 1: greatly reduced. 2: greatly elongated process. Ordered 1—0—2. (*Yurlunggur* 0, *Wonambi* 0)
32. Anterodorsal lappet of prefrontal. 0: absent or indistinct. 1: distinct process extending along lateral margin of nasal. (*Yurlunggur* 0 – possibly incipient, but not as in xenopeltids; *Wonambi* ?)
33. Prefrontal-nasal contact. 0: prefrontal separated from nasal by fissure continuous with external naris. 1: prefrontal contacts nasal. Character definition modified, combining states 0 and 2 of **LS**, and deleting state 3 which does not occur in the ingroup or proximal outgroups. (*Yurlunggur* 0, *Wonambi* ?).
34. Prefrontal-maxilla contact. 0: anterior process and ventrolateral margin of prefrontal contact maxilla. 1: anterior process of prefrontal does not contact maxilla and projects freely, only ventrolateral margin of prefrontal contacting maxilla. 2: anterior process and ventrolateral margin of prefrontal do not contact maxilla. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0)
35. Prefrontal-maxilla contact on facial region. 0: tight or interdigitating, relatively rigid. 1: flat or slightly convex surfaces, allowing rocking or sliding motion. (*Yurlunggur* 0, *Wonambi* 0). An additional distinction could be recognised within state 0; *Wonambi* has an interdigitating suture comparable to outgroups, *Yurlunggur* a looser

interlocking joint like anilioids. These states cannot yet be reliably distinguished in the other fossil taxa, so the original definition is retained.

36. Antorbital buttress of prefrontal. 0: lateral foot process does not contact palatine. 1: lateral foot process contacts palatine. (*Yurlunggur* 0, *Wonambi* ?)
37. Antorbital buttress of prefrontal. 0: medial foot process does not contact maxilla. 1: medial foot process contacts maxilla. (*Yurlunggur* 0, *Wonambi* ?)
38. Lateral process of palatine. 0: does not reach lateral edge of maxilla. 1: reaches lateral edge of maxilla. (*Yurlunggur* 0, *Wonambi* 0)
39. Outer orbital (lateral) margin of prefrontal, in lateral view. 0: slants anteroventrally. 1: vertical. (*Yurlunggur* 0, *Wonambi* 0 - inferred in **LS**).
40. Prefrontal lacrimal duct roof. 0: absent. 1: present, a horizontal flange extending anteriorly from lacrimal foramen. (*Yurlunggur* 0, *Wonambi* ?)
41. Prefrontal-frontal contact in dorsal view. 0: approximately straight. 1: curved, prefrontal fitting into deep embayment in frontal. (*Yurlunggur* 1, *Wonambi* 1)
42. Prefrontal-frontal contact in dorsal view. 0: oriented approximately parasagittally, prefrontals contact only lateral margins of frontals and are widely separated. 1: oriented anteromedially, prefrontals contact anterolateral margins of frontals and are moderately separated. 2: oriented anteromedially or transversely, prefrontals closely approaching or contacting one another. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0)
43. Prefrontal-frontal contact. 0: prefrontal sutured to or tightly buttressed against frontal. 1: prefrontal moveably articulated to frontal. (*Yurlunggur* 1, *Wonambi* 1 - **SL** coded *Madtsoiidae* with '?' since the prefrontal was unknown, but a mobile joint can be inferred in *Wonambi* because the maxilla-prefrontal contact was an interdigitating suture, hence relatively rigid, while the dorsal and lateral facets on the anterior frontal are smooth and consistent with mobility, and other structures indicate that palatomaxillary kinesis was present, if limited; Scanlon 2005¹³).
44. Antorbital (vertical) buttress of prefrontal. 0: broad, extends medially underneath lateral descending flanges of frontal. 1: narrow, does not extend medially to reach lateral descending flanges of frontal. (*Yurlunggur* 0, *Wonambi* 0)
45. Lacrimal foramen. 0: completely enclosed by prefrontal (and/or lacrimal, if distinct). 1: between prefrontal and palatine. 2: between prefrontal and maxilla. Unordered; description of state 0 modified. (*Yurlunggur* 2 – the second notch in the prefrontal, adjacent to the palatine, would be for the palatine nerve; *Wonambi* ?)

46. Jugal. 0: present. 1: absent. (*Yurlunggur* 0, *Wonambi* ?) **LS** coded Madtsoiidae with '?', but presence of a jugal has been predicted [Refs 10,11,13,16] and is now confirmed in QMF45391. The similarly situated element in *Dinilysia*, which differs in extending further dorsally to contact the parietal slightly more extensively, is consequently also identified as a jugal (contra Caldwell & Albino 2002⁵), but codings for alethinophidians are not changed, provisionally accepting the usual identification of the postorbital. Identity of the putative jugals in *Pachyrhachis* remains controversial (Polcyn et al. 2005) but the alternatives are no better supported by evidence intrinsic to the specimen. The argument of Polcyn et al. that they represent the symmetrically broken ventral portions of very long postorbitals is only parsimonious in the context of the assertion that 'Jugals are unknown in all other snakes' (ibid. p. 13). If *Pachyrhachis* is recoded with state 1 in the present analysis, this would optimise as a loss independent of that in Serpentes; i.e., in the current context it is more parsimonious to retain the interpretation of *Pachyrhachis* in **LS** (after Scanlon 1996¹⁶), which was based partly on the finished rather than broken appearance of the lateral tips of both postorbitals as figured by Haas (1979). *Pachyrhachis* is here recoded as '?' - uncertain. Presence of jugals in *Haasiophis* is also considered likely, but also uncertain (**LS**). In *Eupodophis* (new material described by Rieppel and Head 2004) the posterior ends of the 'ectopterygoids' of MSNM V 3661 are symmetrically splayed laterally to nearly contact the distal ends of the postorbitals on both sides (inexplicable as due to dorso-ventral compression of a horizontal element), and widely separated from any preserved part of the pterygoids (better preserved in MSNM V 4014, including the large, posteriorly located ectopterygoid processes, identified by Rieppel and Head as parts of the 'prootics'). These 'ectopterygoids' are thus more likely jugals; an actual ectopterygoid may be the right-side element labelled 'c' ('coronoid) in Rieppel and Head (2004, fig. 6), which is similar in shape to the ectopterygoid of *Yurlunggur* and ventrally overlaps another element (unlabelled in the same fig.) which may be the ectopterygoid process of the pterygoid. Here coded as '?' – uncertain, due to the crushed and incomplete preservation of all known cranial material in *Eupodophis*.
47. Postorbitofrontal ossification(s) in adults. 0: one discrete ossification, conventionally termed the postorbital or postorbitofrontal. 1: no postorbital or postfrontal. Modified from **LS** by deletion of original state 1, to distinguish jugal (previous character) from the other elements. (*Yurlunggur* 0, *Wonambi* ?, *Dinilysia* 0)

48. Postorbitofrontal ossification(s). 0: strongly forked medial margin, anterior and posterior rami tightly clasping frontoparietal suture. 1: weakly forked or straight medial margin overlapping frontoparietal suture. 2: medial margin not forked and without distinct anterior and posterior rami, abutting skull roof laterally. Ordered 0—1—2. Character definition modified, intermediate state added (*Yurlunggur* 1, *Wonambi* ?; *Dinilysia* 1).
49. Prefrontal and postorbitofrontal ossification(s). 0: widely separated, frontal broadly enters orbit. 1: narrowly separated, frontal narrowly enters orbit. 2: in contact, frontal excluded from orbit.. Ordered 0—1—2. (*Yurlunggur* 2, *Wonambi* 0 – *Wonambi* has a large, prominent supraorbital process of the frontal, while the equivalent structure in *Yurlunggur* is small and overlapped laterally by the postorbitofrontal).
50. Lateral process of parietal (at suture with frontal). 0: lateral process distinct. 1: lateral process absent. This is referred to as the ‘postorbital process’ and is distinct from the ‘lateral wing’ of some taxa. (*Yurlunggur* 0, *Wonambi* 0).
51. Posterior orbital margin. 0: complete, closed by postorbital contacting jugal. 1: complete, closed by postorbital contacting ectopterygoid-maxilla unit. 2: incomplete. Unordered. (*Yurlunggur* 0, *Wonambi* ?, *Dinilysia* 0 – changed from 0/1) (*Pachyrhachis* recoded from 0 to 0/1, see character 46)
52. Frontal shape. 0: frontals gradually tapering anteriorly. 1: frontals rectangular, at most slightly constricted in middle. 2: frontals gradually tapering posteriorly. 3: frontals greatly constricted in middle. Unordered. (*Yurlunggur* 2, *Wonambi* 1)
53. Anterior tab of frontal. 0: distinct and well-defined. 1: poorly defined or absent. (*Yurlunggur* 0, *Wonambi* 0)
54. Frontal-parietal contact (dorsal aspect). 0: mostly straight and transverse, slight median notch in frontals at most. 1: Anteriorly concave, i.e. frontals extending posteriorly into broad median embayment in parietals. 2: complex W or M shape. Unordered. (*Yurlunggur* 1, *Wonambi* 2 – comparable with the conditions in *Dinilysia* and *Pachyrhachis* and coded with the same state [as in **LS**], though relatively straighter and smoother than in these taxa).
55. Subolfactory (lateral descending) processes of frontal. 0: not contacting one another ventromedially. 1: meeting ventromedially, below medial descending processes of frontal if present. (*Yurlunggur* 1, *Wonambi* 1)
56. Medial descending processes of frontal. 0: absent. 1: present. (*Yurlunggur* 1, *Wonambi* 1) (*Pachyrhachis* rescored ? – unknown)

57. Medial descending processes of frontal. 0: not meeting subolfactory (lateral descending) frontal processes, interolfactory pillar incomplete ventrally. 1: meeting ascending projections of the subolfactory processes at the mesial frontal suture. 2: fused to subolfactory frontal processes, mesial frontal suture obliterated. Ordered 0—1—2. Character definition modified by addition of state 0 and relabelling of other states. (*Yurlunggur* 0, *Wonambi* ? – both processes incompletely known).
58. Mesial frontal suture. 0: on ventral portion of interolfactory pillar. 1: on middle of interolfactory pillar. (*Yurlunggur* not applicable, *Wonambi* ?).
59. Length of main body of parietal (i.e. excluding supraorbital or posterior processes). 0: short, at most 40% skull (snout-occiput) length. 1: intermediate, between 40 and 55% of skull length. 2: long, at least 55% of skull length. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 1)
60. Suture between frontal and parietal descending flanges. 0: in lateral view, suture between frontal and parietal extends approximately vertically, or slightly anterodorsally. 1: suture greatly inclined anterodorsally, i.e. closer to the horizontal than the vertical. 2: suture curved, extending vertically in its ventral portion and becoming horizontal more dorsally. Unordered. (*Yurlunggur* 1, *Wonambi* 0)
- 60A.** Optic (=ophthalmic) fenestra. 0: not defined, incomplete ventrally. 1: bordered by frontal, parietal and sphenoid. 2: sphenoid separated from border of foramen by frontal and/or parietal. Unordered, because state 2 could have been attained before ossification of parasphenoid rostrum in orbital region (component of platytrabic condition characterising Ophidia). Used by Scanlon (1996¹⁶) as part of the same unordered multistate character as the following, but not in recent published analyses; discussed by Underwood (1967), McDowell (1967), and Estes et al. (1970¹). Added as last column of matrix, to retain consistent labelling of other characters. (*Yurlunggur* 1, *Wonambi* 1)
61. Optic foramen. 0: posteriorly located, posterior border forming a deep notch in parietal. 1: intermediate position, posterior border formed by straight margin of parietal. 2: anteriorly located, posterior border within frontal. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 1 – changed from 0/1 in **LS**).
62. Optic foramen. 0: opening faces anterolaterally. 1: opening faces laterally. (*Yurlunggur* 1, *Wonambi* 1)
63. Anterior (supraorbital) process of parietal. 0: absent or poorly developed. 1: enlarged, extending along at least 40% of lateral margin of frontal. Definition

modified (cutoff at 40% rather than 50%) to capture the striking difference between *Wonambi* and *Yurlunggur*. (*Yurlunggur* 1, *Wonambi* 0)

64. Posterior border of parietal. 0: with distinct median notch. 1: without distinct median notch. (*Yurlunggur* 1, *Wonambi* 1)
65. Posterior border of parietal. 0: without median projection over supraoccipital. 1: with median projection over supraoccipital. (*Yurlunggur* 0, *Wonambi* 0; this and preceding character scored for *Yurlunggur* based on the intact supraoccipital, as the posterior margin of the parietal is slightly worn).
66. Posterolateral (supratemporal or suspensorial) process of parietal. 0: well developed, posterolateral margin of parietal with a distinct flange. 1: reduced, posterolateral margin of parietal with a triangular corner. 2: absent, posterolateral margin of parietal rounded. Ordered 0—1—2. (*Yurlunggur* 0 based on outline of parietal contact surfaces in QMF45111, as parietal margins are damaged in QMF45391; *Wonambi* ?).
67. Descending flange of parietal. 0: without horizontal crest. 1: with very large horizontal crest, extending from orbital region towards prootic. (*Yurlunggur* 1, *Wonambi* 1)
68. Descending flange of parietal. 0: does not contact anterior margin of base of basiptyergoid process. 1: broadly contacts anterior margin of base of basiptyergoid process. (*Yurlunggur* 0 based on reconstruction using QMF45391, F45111, and F23041; *Wonambi* 0)
69. Supratemporal. 0: large, quadrate contacts supratemporal but not otic capsule. 1: vestigial, quadrate contacts supratemporal and otic capsule. 2: absent, quadrate contacts otic capsule only. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0).
70. Supratemporal. 0: posterior end projecting greatly beyond otic capsule. 1: posterior end projecting slightly beyond otic capsule. 2: posterior end not projecting beyond otic capsule. Ordered 0—1—2. (*Yurlunggur* 0/1, *Wonambi* 0/1; the large paroccipital process in each rules out state 2; state 0 could be assigned by assuming the quadrate and compound [each known in only one of the taxa] are similar in both). Probably, the supratemporal in *Yurlunggur* had a free posterolateral extension equal to or greater (relatively) than any extant booid, because the parietal is relatively short, paroccipital processes not especially prominent posteriorly, and proportional similarity of other jaw elements to those of *Nanowana* spp. makes it likely the compound was about equal in length to the dentary, as in *N. godthelpi*.

71. Supratemporal. 0: does not substantially cover dorsolateral surface of prootic. 1: covers almost the entire dorsolateral surface of prootic. (*Yurlunggur* 0, *Wonambi* 0).
72. Supratemporal. 0: anterior tip well behind anterior margin of prootic. 1: anterior tip slightly behind anterior margin of prootic. 2: anterior tip in line with or in front of anterior margin of prootic. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 0, based on supratemporal facet on parietal in each taxon).
73. Quadrate. 0: without small ossification (extracolumella or stylohyal) on medial surface, contacting stapes. 1: with such ossification. (*Yurlunggur* 0, *Wonambi* ?; *Dinilyisia* 0 based on Ref. 5 [the element is present but not fused to the quadrate]). The identification of a stylohyal near the ventral end of the quadrate in *Pachyrhachis* (Polcyn et al. 2005) is unconvincing, as it is merely a convexity of the medial margin (also present in *Yurlunggur*, QMF45391) rather than the disc-like structure typical of macrostomatans, and has no apparent connection to the stapes which is preserved in association with a groove near the dorsal edge of the quadrate; this taxon is here recoded as ?, uncertain.
74. Dorsoposterior (=suprastapedial) process of quadrate. 0: distinct, large. 1: indistinct, small or absent. (*Yurlunggur* 0, *Wonambi* ?)
75. Dorsoposterior (suprastapedial) process of quadrate. 0: projects posteroventrally, forming acute angle with quadrate shaft. 1: projects posteriorly, forming approximately a right or slightly obtuse angle with quadrate shaft. 2: projects posterodorsally, forms very obtuse angle with quadrate shaft in lateral view. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* ?)
76. Length of quadrate shaft (i.e. excluding suprastapedial process). 0: short, maximum length along shaft no more than 25% of snout-occiput length. 1: long, more than 25% of snout-occiput length. (*Yurlunggur* 0, *Wonambi* ?)
77. Cephalic condyle of quadrate. 0: situated dorsally, approximately level with dorsal margin of prootic. 1: situated ventrally, well below level of dorsal margin of prootic. (*Yurlunggur* 0, *Wonambi* 0; inferred from braincase in each).
78. Quadrate shaft. 0: inclined slightly anteroventrally. 1: inclined greatly anteroventrally. 2: vertical. 3: inclined posteroventrally. Ordered 1—0—2—3. (*Yurlunggur* 2/3, *Wonambi* ?; *Dinilyisia* 2/3). Polcyn et al.(2005) describe the condition in *Pachyrhachis* as ‘posteroventrally inclined’ but their fig. 10 shows it as nearly vertical; the original scoring is retained.

79. Septomaxilla. 0: projects anterolaterally, overlapping lateral process of premaxilla and/or anterior tip of the maxilla. 1: does not project anterolaterally, not overlapping lateral process of premaxilla or anterior tip of maxilla. (*Yurlunggur* 1, *Wonambi* ?)
80. Dorsolateral flange of septomaxilla. 0: blunt, without spine, expansion or calcified ligament. 1: with spine projecting posterolaterally. 2: with posterior expansion projecting posteromedially towards frontal. 3: with calcified ligament. Unordered. (*Yurlunggur* 1, *Wonambi* ?)
81. Septomaxilla. 0: maxilla, but not septomaxilla, contributes to posterior border of the external naris. 1: septomaxilla with lateral flange contributing to the posterior border of the external naris. (*Yurlunggur* 0, *Wonambi* 0)
82. Septomaxilla-frontal contact. 0: posteromedial flange of septomaxilla short, not contacting frontal. 1: posteromedial flange of septomaxilla long, contacting frontal adjacent to midline on lower part of interolfactory pillar. (*Yurlunggur* 0 – based on lack of space for contact on the frontal although septomaxillae are incomplete posteriorly; *Wonambi* ?). (*Pachyrhachis* rescored ? – unknown)
83. Fenestra for duct of Jacobson's organ. 0: faces ventrally. 1: faces posteroventrally. (*Yurlunggur* 0, *Wonambi* ?) (*Pachyrhachis* rescored ? – unknown)
84. Vomer. 0: does not enter lateral margin of fenestra for Jacobson's organ. 1: forms posterior part of lateral margin of fenestra for Jacobson's organ. (*Yurlunggur* 0, *Wonambi* ?)
85. Vomeronasal nerve. 0: does not pierce the ridge on the vomer forming the posterior wall of the vomeronasal organ. 1: pierces ridge *via* a single large foramen (sometimes with one or two additional small foramina). 2: pierces ridge through a cluster of numerous small foramina. Unordered. (*Yurlunggur* 1 – large foramen present; *Wonambi* ?)
86. Medial fenestra in vomeronasal cupola. 0: posterior ends of sagittal flanges of vomer and septomaxilla with small or no contact, and large intervening fenestra or embayment. 1: posterior ends of sagittal flanges of vomer and septomaxilla in extensive contact, with small or no intervening fenestra. (*Yurlunggur* ? – septomaxilla incomplete posteriorly; *Wonambi* ?)
87. Palatine length (excluding posteromedial process). 0: short anteroposteriorly (much shorter than vomer). 1: intermediate in length anteroposteriorly (as long as vomer). 2: long anteroposteriorly (much longer than vomer). Ordered 0—1—2. (*Yurlunggur* 2 – palatine 39.5, vomer 32 mm in QMF45391; *Wonambi* 1 – reconstruction, Scanlon & Lee 2000¹¹).

88. Horizontal (palatal) lamina of vomer. 0: posterior end narrow, tapering to a point; choana wide. 1: posterior end expanded; choana narrow. (*Yurlunggur* 1, *Wonambi* ?)
89. Vertical (posterior dorsal) lamina of vomer. 0: small or absent. 1: well developed. (*Yurlunggur* 0, *Wonambi* ?)
90. Palatine-vomer contact. 0: medial (choanal) process of palatine with extensive contact with vomer. 1: tiny point contact. 2: no contact. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0).
91. Palatine-vomer articulation. 0: medial (choanal or vomerine) processes of palatines do not project ventromedially to separate vomers. 1: medial processes of palatines project ventromedially to separate the posterior portions of the vomers. (*Yurlunggur* 1, *Wonambi* ?).
92. Medial (choanal or vomerine) process of palatine. 0: anteroposteriorly broad plate of bone. 1: narrow finger-like process. (*Yurlunggur* 0, *Wonambi* 0) In *Eupodophis*, the slender process reconstructed by Rieppel and Head (2004, fig. 10) may not represent the complete process; this and the preceding two characters are hence scored as '?', uncertain.
93. Medial (choanal or vomerine) process of palatine. 0: without distinct, large anterior flange. 1: with distinct, large plate-like anterior flange, abutting vomer posterolaterally. (*Yurlunggur* 1, *Wonambi* 1)
94. Anterior process of palatine. 0: no anterior process, only medial (choanal or vomerine), lateral (maxillary) and posteromedial (pterygoid) processes present. 1: narrow ("dentigerous") process present, in addition to medial, lateral and posteromedial processes. 2: wide horizontal plate present. Unordered. (*Yurlunggur* 1, *Wonambi* 1)
95. Anterior process of palatine. 0: contacting vomer-septomaxilla complex. 1: not contacting vomer-septomaxilla complex. (*Yurlunggur* 0 – palatine and septomaxilla with facet-like structures; *Wonambi* ?).
96. Palatine-maxilla contact . 0: palatine sutured to maxilla. 1: palatine meets maxilla in a mobile joint. 2: palatine does not contact maxilla. Ordered 0—1—2. Wording modified, 'mobile' substituted for 'loose'. (*Yurlunggur* 1, *Wonambi* 1). Excluded as 'uninformative' for this analysis, which is an artifact of combining outgroup taxa (all with state 0) as a single terminal; state 2 occurs uniformly in only one ingroup taxon.

97. Lateral (maxillary) process of palatine. 0: situated in middle or anterior end of main body of palatine. 1: at posterior end of main body of palatine. (*Yurlunggur* 0, *Wonambi* 0)
98. Lateral process of palatine. 0: pierced by foramen or constricted notch for palatine nerve (= sphenopalatine branch of facial nerve). 1: lacking foramen. Description of state 0 modified. (*Yurlunggur* 1, *Wonambi* 1 – process damaged in *W. naracoortensis* but foramen absent in palatines referred to *W. barriei*^{11,16})
99. Articulation of palatine with pterygoid. 0: short. 1: long. (*Yurlunggur* 0, *Wonambi* 0)
100. Pterygoid tooth row curvature. 0: concave medially. 1: straight to slightly convex medially. (*Yurlunggur* 0, *Wonambi* 0)
101. Ectopterygoid process of pterygoid. 0: well developed, a large rectangular or triangular lateral process. 1: poorly developed, a small rounded lateral flange. 2: absent. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0 – observed in *W. barriei*^{11,13,16}). This character was not considered by Polcyn et al. (2005), but their surface reconstructions of the *Pachyrhachis* holotype skull (ibid. fig. 5) and serial sections (ibid. fig. 7) show the lateral process of the pterygoid on left and right sides. As noted previously^{15,16}, these structures are nearly obscured in dorsal view by the coronoids, and have been mistaken for them in other works. They are more clearly visible in *Haasiophis* and *Eupodophis*, but similarly identified as ‘coronoids’ or ‘prootics’ in previous work (Tchernov et al. 2000, Rieppel et al. 2003, Rieppel and Head 2004).
102. Ectopterygoid attachment to pterygoid. 0: anterior to basipterygoid process. 1: lateral to basipterygoid process. 2: posterior to basipterygoid process. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 1)
103. Pterygoid quadrate ramus. 0: robust, plate-like. 1: gracile, rod-like. (*Yurlunggur* 0, *Wonambi* 0 – based on *W. barriei*, Scanlon 1996¹⁶).
104. Pterygoid medial margin. 0: with distinct medial spur in region of basicranial articulation. 1: with smooth medial bulge. 2: with straight margin. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 1)
105. Pterygoid quadrate ramus. 0: with a shallow groove along ventromedial surface, or no groove. 1: with a very deep groove along ventromedial surface, becoming dorsomedial posteriorly. (*Yurlunggur* 0, *Wonambi* 0)
106. Pterygoid quadrate ramus. 0: vertical or oblique sheet. 1: approximately horizontal sheet. (*Yurlunggur* 0, *Wonambi* 0)

107. Pterygoid quadrate ramus. 0: terminates near jaw joint. 1: projects posteriorly well past jaw joint. (*Yurlunggur* ?, *Wonambi* ?; unknown in madtsooids but state 0 can be expected).
108. Ectopterygoid. 0: large. 1: small. 2: absent. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0). For alternative identification of the ectopterygoid in *Eupodophis*, see remarks to character 46 above.
109. Ectopterygoid-pterygoid contact. 0: clasps pterygoid on both dorsal and ventral surfaces. 1: simple overlap on only ventral surface of pterygoid. 2: simple overlap on only dorsal surface of pterygoid. 3: simple contact on only lateral edge only of pterygoid. Unordered. (*Yurlunggur* 0, *Wonambi* 0/1).
110. Ectopterygoid-maxilla contact. 0: posterior tip of the maxilla abuts ectopterygoid. 1: posterior tip of the maxilla is lifted off ectopterygoid and projects freely. (*Yurlunggur* 0, *Wonambi* 0)
111. Ectopterygoid-maxilla contact. 0: anterior end of ectopterygoid restricted to posteromedial edge of maxilla. 1: ectopterygoid invades significantly the dorsal surface of the maxilla. (*Yurlunggur* 1, *Wonambi* 1)
112. Ectopterygoid shape. 0: distal end of ectopterygoid with single anterior process projecting dorsally along maxilla. 1: distal end of ectopterygoid with two anterior processes projecting dorsally along maxilla. (*Yurlunggur* 0, *Wonambi* 0; anterolateral edge sigmoid in both, but no distinct lateral process).
113. Lateral edge of the ectopterygoid. 0: straight or slightly curved, lacking distinct angulation. 1: distinctly angulated, a distinct 'corner' present between the anterior (parasagittally oriented) and posterior (posteromedially oriented) portions of the lateral margin. (*Yurlunggur* 1, *Wonambi* 1 – margin strongly curved through more than 90 degrees, if not distinctly angled at any one point). (*Pachyrhachis* rescored ? – unknown)
114. Cultriform process. 0: anterior one-third broad posteriorly and tapering anteriorly. 1: anterior one-third narrow throughout. (*Yurlunggur* 0, *Wonambi* 0)
115. Interchoanal keel of cultriform process. 0: absent. 1: present, a sagittal flange extending ventrally between the medial processes of the palatines. (*Yurlunggur* 1, *Wonambi* 1 – inferred from ridge on most anterior preserved portion in SAMP30178A, and medial contact surface on palatine).
116. Parabasisphenoid transverse width behind frontal descending flanges. 0: narrow, without concave ventral surface. 1: broad and ventrally concave. (*Yurlunggur* 1, *Wonambi* 1)

117. Basipterygoid process. 0: prominent, i.e. a pedicel or flange projecting far laterally with distinct distal facet. 1: weak, consisting of a crest or mound without a distinct distal facet. 2: absent. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0)
118. Distal surfaces (facets or crests) of basipterygoid processes. 0: long axes oriented obliquely, or transversely in ventral view. 1: long axes oriented parasagittally in ventral view. (*Yurlunggur* 1, *Wonambi* 1)
119. Parabasisphenoid (= sphenoid). 0: sphenoid wing absent, no triangular dorsolateral prominence lateral to alar process of dorsum sellae. 1: sphenoid wing present as triangular prominence distinct from alar process, extending up anterior margin of prootic below the trigeminal notch. (*Yurlunggur* 0, *Wonambi* 0^{13,18})
120. Ventral surface of parabasisphenoid. 0: smooth posteriorly, lacking keel. 1: with median keel in posterior region, at level of posterior openings of vidian canals. 2: with pair of parasagittal keels. Unordered. (*Yurlunggur* 1, *Wonambi* 1)
121. Basioccipital-parabasisphenoid suture. 0: positioned midway between fenestra ovalis and trigeminal foramen. 1: posteriorly positioned, closer to fenestra ovalis than to trigeminal foramen. 2: anteriorly positioned, closer to trigeminal foramen than to fenestra ovalis. Ordered 1—0—2. (*Yurlunggur* 0, *Wonambi* 0)
122. Basioccipital. 0: with short posterolateral flanges. 1: with long posterolateral processes. (*Yurlunggur* 0, *Wonambi* 0)
123. Posterior opening of vidian canal. 0: within basisphenoid, not bordered by prootic. 1: partly bordered by prootic (i.e. on basisphenoid-prootic suture) or entirely within prootic. (*Yurlunggur* 1, *Wonambi* 1)
124. Vidian canal. 0: does not open intracranially. 1: opens intracranially, emerging on internal surface of sphenoid (primary opening) then emerging externally on sphenoid-parietal suture (secondary opening). (*Yurlunggur* 0, *Wonambi* 0)
125. Vidian canals. 0: symmetrical. 1: asymmetrical, left larger than right or *vice versa*. (*Yurlunggur* 0, *Wonambi* 0).
126. Hypophysial pit (sella turcica). 0: without distinct anterior bony boundary. 1: bounded anteriorly by distinct ridge. (*Yurlunggur* 1, *Wonambi* 1) (this and some several following characters scored for the outgroup taxon *Lanthanotus* based on CT sections in Maisano 2001)
127. Cerebral carotid artery. 0: opens into posterior region of hypophysial pit, near posterior transverse wall. 1: opens into middle region of hypophysial pit, well away from posterior transverse wall. (*Yurlunggur* 1, *Wonambi* 1)

128. Dorsum sellae (crista sellaris). 0: well developed. 1: greatly reduced. (*Yurlunggur* 0, *Wonambi* 0)
129. Dorsum sellae (crista sellaris). 0: oriented anterodorsally, overhanging the posterior portion of hypophysial pit. 1: oriented dorsally, not overhanging hypophysial pit. (*Yurlunggur* 1, *Wonambi* 1)
130. Laterosphenoid bridge. 0: absent, V2 and V3 exits of trigeminal foramen confluent. 1: present, fuses to prootic forming vertical bar between exits of V2 and V3. (*Yurlunggur* 0, *Wonambi* 0). The structures in *Haasiophis* and *Eupodophis* previously interpreted as lateral flanges of the prootics and to imply the presence of 'laterosphenoids' (Tchernov et al. 2000, Rieppel et al. 2003, Rieppel and Head 2004) are here considered ectopterygoid processes of the pterygoids; on either view, there is no evidence for division of the foramen in either taxon.
131. Alar process of prootic. 0: long distinct process projecting anteriorly well past trigeminal (V) foramen. 1: short process not projecting past trigeminal (V) foramen. (*Yurlunggur* 0, *Wonambi* 0). Extent of semicircular canal unknown in fossils other than *Yurlunggur*, so state definitions from **LS** retained.
132. Trigeminal foramen, anterior margin. 0: closed by parietal at least medially; upper and lower anterior processes of prootic may touch superficially lateral to the parietal. 1: closed by prootic, deep contact or fusion of prootic processes excludes parietal from opening. (*Yurlunggur* 0, *Wonambi* 0)
133. Exit foramen for the facial (VII) nerve (hyomandibular branch, if distinct). 0: located outside the opening for the mandibular branch of the trigeminal nerve (V3, or V2+V3). 1: located within the opening. (*Yurlunggur* 0, *Wonambi* 0)
134. Sulcus connecting exit foramen of palatine branch of facial (VII) nerve with posterior opening of vidian canal. 0: weakly recessed, with shallow and smooth margins. 1: deeply recessed, with sharply defined anterior and often also posterior margins. 2: embedded, closed laterally forming a tunnel in prootic. Ordered 0-1-2. (*Yurlunggur* 1, *Wonambi* 1). The outgroup could be assigned state 1 if the anterior margin is identified with part of the crista prootica of lizards (see Scanlon 2005¹³).
135. Crista circumfenestralis. 0: juxtastapedial recess bordered by crests which may extend directly laterally but do not converge. 1: juxtastapedial recess surrounded by crests which converge to partly enclose stapedial footplate, much of footplate remains exposed laterally. 2: juxtastapedial recess surrounded by crests which converge to largely enclose stapedial footplate. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0; these taxa differs mainly in the orientation of the crests, not the degree

to which they enclose the recess, so they are assigned the same state).

(*Pachyrhachis* rescored 0 – unknown)

136. Supratemporal-supraoccipital contact. 0: supratemporal and supraoccipital separated by dorsal exposures of parietal and exoccipital. 1: supratemporal and supraoccipital separated by dorsal exposures of prootic, parietal and exoccipital. 2: supratemporal and supraoccipital in contact. Unordered. (*Yurlunggur* 0/2, *Wonambi* 0/2 – no supratemporals yet identified; supraoccipital forms dorsal margin of facet on paroccipital process occupied by supratemporal but possibly also part of the parietal, which may have intervened).
137. Paroccipital process. 0: long process. 1: distinct flange. 2: indistinct bump or absent. Ordered 0—1—2. (*Yurlunggur* 0, *Wonambi* 0 – smaller than *Dinilysia*, larger than any extant snake)
138. Supraoccipital. 0: external (dorsoposterior) surface with no, or very weak transverse ridge. 1: external surface with moderate transverse ridge. 2: external surface with very high transverse ridge. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* ?)
139. Supraoccipital dorsal exposure. 0: long, sagittal dimension more than 50% transverse dimension. 1: short, sagittal dimension less than 50% transverse dimension. (*Yurlunggur* 0, *Wonambi* 0 – changed from 1, see Scanlon 2005¹³).
140. Supraoccipital-prootic contact. 0: narrow, less than half supraoccipital-parietal contact. 1: broad, subequal to or as long as supraoccipital-parietal contact. (*Yurlunggur* 0, *Wonambi* 0).
141. Exoccipital separation dorsal to foramen magnum. 0: exoccipitals widely separated above foramen magnum. 1: exoccipitals with tiny point contact above foramen magnum. 2: exoccipitals in extensive median contact above foramen magnum. Ordered 0—1—2. (*Yurlunggur* 2, *Wonambi* 1; ventral surface of supraoccipital in QMF45391 indicates a longer overlap on the exoccipitals than revealed by exoccipital in *Wonambi*). (*Pachyrhachis* rescored 0 – unknown, following Polcyn et al. 2005)
142. Exoccipital separation ventral to foramen magnum. 0: exoccipitals separated below foramen magnum, not in contact along dorsal midline of occipital condyle. 1: exoccipitals in contact below foramen magnum, along dorsal midline of occipital condyle. (*Yurlunggur* 1, *Wonambi* 1) (*Pachyrhachis* rescored 0 – unknown)

143. Occipital condyle. 0: dorsal surface deeply concave, i.e. with deep "fovea dentis".
1: dorsal surface slightly concave at most, i.e. with shallow or no "fovea dentis". (*Yurlunggur* 0, *Wonambi* 0)
144. Stapedial shaft. 0, straight. 1, angulated. (*Yurlunggur* ?, *Wonambi* ?) The long stapedial shaft is now known in *Pachyrhachis* (Polcyn et al. 2005) but neither state can be assigned to this taxon as the curve in the shaft is probably an artifact of crushing and the footplate is unknown.
145. Stapedial shaft. 0, slender and longer than diameter of stapedial footplate. 1, thick and not longer than diameter of footplate. (*Yurlunggur* ?, *Wonambi* ?)
(*Pachyrhachis* 0) Based on the probably rather long supratemporals in *Yurlunggur*, a similarly long stapedial shaft can be predicted, but this might not be the case if the compound was extremely short (cf. *Archaeophis turkmenicus*, Tatarinov 1988).
146. Distal end of stapes. 0, associated with dorsal tip of suprastapedial process of quadrate. 1, associated with ventral end of suprastapedial process and dorsal end of quadrate shaft, i.e. cephalic condyle. 2, associated with middle or ventral half of quadrate shaft. Ordered 0 – 1 – 2. (*Yurlunggur* ? – apparently 1 if stapedial facet correctly identified; *Wonambi* ?; *Pachyrhachis* ? – uncertain, due to two putative locations of the stapes-quadrate articulation, the dorsal groove in which the stapes lies, and the ventromedial bump identified as a stylohyal by Polcyn et al. 2005)
147. Dentary length. 0: dentary long, more than 40% of main mandible length, i.e., length excluding retroarticular process. 1: dentary short, less than 40% of main mandible length. (*Yurlunggur* 0 – compound unknown but dentary more than 72 mm, so state 1 would require unknown supratemporal to exceed 90 mm, considered implausible; *Wonambi* 0).
148. Mental foramina on lateral surface of dentary. 0: two or more. 1: one.
(*Yurlunggur* 0, *Wonambi* 1 – partial dentary referred to *W. barriei* has state 0, but here based on *W. naracoortensis*. All other known madtsoiid dentaries have 2 or 3 foramina^{13,19}).
149. Posterolateral margin of dentary. 0: notch absent, posterolateral margin of dentary straight or slightly concave, dorsoposterior and ventroposterior processes indistinct. 1: with shallow notch, processes short. 2: with deep notch, processes long. Ordered 0—1—2. (*Yurlunggur* 2, *Wonambi* 2)
150. Dentary posterior margin. 0: dorsal posterior process does not extend much further than ventral posterior processes. 1: dorsal process extends much further

- posteriorly than ventral process. (*Yurlunggur* ? – ventral process incomplete; *Wonambi* 1)
151. Posteromedial shelf of dentary. 0: not exposed medially. 1: exposed medially. (*Yurlunggur* 0 – covered by splenial as far as known in QMF45391, and posteromedial margin of complete shelf in dentary QMF45073 with dorsal contact surface for coronoid; *Wonambi* ?)
152. Meckel's canal (groove). 0: lacks floor anteriorly, open ventrally anterior to level of anterior inferior alveolar foramen. 1: floored by a horizontal ventral lamina for its full length. 2: enclosed anteriorly, with ventral and medial lamina. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 1).
153. Splenial. 0: splenial present as discrete element. 1: splenial not present as discrete element. (*Yurlunggur* 0, *Wonambi* 0 – inferred from more or less distinct facets on dentary).
154. Splenial size. 0: small, extends no more than 50% of distance from intramandibular joint to symphysis. 1: large, extends more than 50% of distance from intramandibular joint to symphysis. (*Yurlunggur* 1, *Wonambi* ?)
155. Splenial-angular joint. 0: vertical in medial view. 1: highly oblique in medial view. Only scorable in taxa with a straight, simple joint. (*Yurlunggur* 0, *Wonambi* ?; 'straight and simple' are relative terms: the splenial joint surface in QMF45391 is generally similar to *Cylindrophis*, *Morelia*, and other taxa previously coded with state 0)
156. Foramen within splenial (= anterior mylohyoid foramen). 0: present. 1: absent. The name of the foramen was stated incorrectly in **LS** as 'inferior alveolar foramen', which normally passes anterodorsal to the splenial and not through it; see Rieppel and Zaher (2000) and following character. (*Yurlunggur* 0, *Wonambi* ?)
157. Dorsal margin of splenial. 0: deeply notched, posterior region of notch bordered dorsally by anterodorsal spine. 1: moderately notched, posterior region of notch not bordered dorsally by anterodorsal spine. 2: smooth, not notched. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* ?; *Dinilysia* 0 based on Estes et al. 1970¹)
158. Splenial-coronoid contact. 0: posterior end of splenial in broad contact with coronoid. 1: posterior end of splenial only just reaches coronoid. 2: posterior end of splenial does not contact coronoid. Not applicable in taxa lacking either element. Ordered 0—1—2. (*Yurlunggur* 0 – both splenials with coronoid facets well preserved; *Wonambi* ?).

159. Splenial lateral exposure. 0: Anterior portion of splenial not exposed laterally. 1: Anterior portion of splenial greatly exposed laterally. (*Yurlunggur* 0, *Wonambi* ?)
160. Coronoid. 0: coronoid large and distinct. 1: coronoid greatly reduced and sometimes fused to compound. 2: coronoid never present as distinct element. Ordered 0—1—2. (*Yurlunggur* 0 – distinct coronoid facets on dentary and splenial; *Wonambi* 0 – large facet on compound)
161. Coronoid. 0: with posteroventral process or expansion. 1: without posteroventral process or expansion. (*Yurlunggur* ?; *Wonambi* ? – facet on compound preserves shape of posterior but not anterior margin of coronoid, so overall shape unclear)
162. Coronoid lateral exposure. 0: coronoid overlaps lateral surface of surangular and is exposed in lateral view. 1: coronoid does not overlap lateral surface of surangular, but projects dorsally beyond it and is thus well exposed in lateral view. 2: coronoid entirely medial to surangular and is largely covered in lateral view. Ordered 0—1—2. (*Yurlunggur* ?, *Wonambi* ? – possible narrow lateral overlap; *Dinilysia* 0 – apparently considerable overlap)
163. Coronoid-angular contact. 0: coronoid and angular separated by prearticular, or prearticular portion of compound bone. 1: coronoid contacts angular. (*Yurlunggur* ?, *Wonambi* ? – close approach at least, but compound incomplete anteromedially)
164. Coronoid process. 0: well developed, distinct projection lateral to adductor fossa. 1: poorly developed or absent, smooth rounded crest at most. (*Yurlunggur* ?, *Wonambi* ?)
165. Surangular eminence. 0: compound postdentary element without dorsal eminence. 1: surangular portion of compound with dorsal crest or process lateral to adductor fossa. 2: prearticular portion of compound with ascending process medial to adductor fossa. Unordered. (*Yurlunggur* ?, *Wonambi* 1, *Dinilysia* changed to 1 based on Caldwell & Albino 2002⁵, contra Estes et al. 1970¹ due to distortion in mandible of holotype)
166. Adductor fossa. 0: posterior region exposed medially, prearticular dorsal margin lower than surangular dorsal margin. 1: posterior region exposed dorsally only; prearticular about equal in height to surangular. 2: posterior region exposed laterally only, prearticular higher than surangular. Ordered 0—1—2. (*Yurlunggur* ?, *Wonambi* 1, *Dinilysia* changed to 1 – see previous character)
167. Anterior surangular foramen. 0: situated posteriorly, below apex of coronoid process or more posterior. 1: situated anteriorly, between apex and anterior limit of coronoid process. 2: situated far anteriorly, in front of anterior limit of coronoid

- process. Ordered 0—1—2. (*Yurlunggur*?, *Wonambi* 2 – not 1, as foramen would be overlapped by dentary and thus anterior to coronoid process)
168. Lateral crest of compound element, extending anteriorly from articular cotyle along ventrolateral surface of mandible. 0: absent or weak. 1: strongly developed. State descriptions modified from ‘absent’ and ‘present’. (*Yurlunggur*?, *Wonambi* 0)
169. Articular-surangular fusion. 0: articular and surangular not fully fused in region of articular facet. 1: articular and surangular fully fused in region of articular facet. (*Yurlunggur*? – articular region known but incomplete; *Wonambi* 0)
170. Retroarticular process length. 0: long, longer than articular facet. 1: short, not longer than articular facet. (*Yurlunggur* 1, *Wonambi* 1)
171. Dorsal flange of retroarticular process. 0: absent. 1: present. (*Yurlunggur*?, *Wonambi* 0)
172. External grooves and ridges on tooth bases. 0: present, surface of bases of mature tooth crowns with vertical ridges and grooves. 1: absent, surface of bases of mature tooth crowns smooth. (*Yurlunggur* 0, *Wonambi* 0). Radial infolding of the tooth base is present in both taxa¹⁷, and unless demonstrated otherwise it is parsimonious to regard this as homologous to the more extensively folded dentine and enamel (‘plicidentine’) in varanoids.
173. Premaxillary teeth. 0: present. 1: absent. (*Yurlunggur* 1, *Wonambi*?).
174. Premaxillary tooth number. 0: three or more alveoli on each side of the midline. 1: one or two alveoli on each side. Not applicable when teeth are absent; parsimony-uninformative for this analysis, excluded.
175. Maxillary teeth. 0: nearly uniform in size, at most only slightly larger in middle of tooth row, with uniform gradation. 1: distinctly larger near middle of tooth row, smaller anteriorly and posteriorly. 2: distinctly larger near anterior end of tooth row, smaller in middle and posteriorly. Unordered. (*Yurlunggur* 0, *Wonambi* 0).
176. Maxillary teeth. 0: nine or more alveoli. 1: eight or fewer alveoli. (*Yurlunggur* 0, *Wonambi* 0)
177. Dentary teeth. 0: eight or more alveoli. 1: seven or fewer alveoli. (*Yurlunggur* 0, *Wonambi* 0)
178. Alveoli (in middle of maxilla and dentary). 0: not expanded transversely. 1: wider transversely than anteroposteriorly. (*Yurlunggur* 1, *Wonambi* 1)
179. Palatine teeth. 0: absent. 1: present. (*Yurlunggur* 1, *Wonambi* 1)
180. Palatine teeth. 0: nine or more alveoli. 1: eight or fewer alveoli. (*Yurlunggur* 0, *Wonambi* 0)

181. Pterygoid teeth. 0: present. 1: absent. (*Yurlunggur* 0, *Wonambi* 0)
182. Pterygoid teeth. 0: twelve or more alveoli. 1: eleven to nine alveoli. 2: eight or fewer alveoli. Ordered 0—1—2. (*Yurlunggur* 1&2, *Wonambi* 1).
183. Median (basihyal) element. 0: present, uniting hyoid cornua. 1: absent. (*Yurlunggur* ?, *Wonambi* ?).
184. First branchial arch elements. 0: present. 1: absent, replaced by caudal extensions of the lateral edge of the basihyal. (*Yurlunggur* ?, *Wonambi* ?)
185. Hyoid cornua. 0: diverging sharply posteriorly. 1: diverging only slightly posteriorly. 2: parallel. (*Yurlunggur* ?, *Wonambi* ?)
186. Number of presacral vertebrae. 0: less than 120. 1: 120-160. 2: 160-200. 3: over 200. Ordered 0—1—2—3. (*Yurlunggur* 1/2/3, *Wonambi* 1/2/3, *Dinilysia* 1/2/3 – each known from associated skeletons just complete enough to exclude state 0)
187. Number of caudal vertebrae. 0: more than 20. 1: fewer than 20. (*Yurlunggur* ?, *Wonambi* ?)
188. Dorsoposterior process on atlas neural arch, overlying axis neural arch. 0: present, well developed. 1: absent or very weak. (*Yurlunggur* 0 [*Y. camfieldensis*, inferred from axis NTMP908-4, Scanlon 2004²³] & 1 [QMF45391], *Wonambi* ?).
189. Second (axis) intercentrum. 0: not fused to anterior region of axis centrum, suturally connected at most. 1: fused to anterior region of axis centrum. (*Yurlunggur* 0 [*Y. camfieldensis*, Scanlon 2004²³] & 1 [QMF45391], *Wonambi* ?).
190. Neural spine height. 0: well-developed process. 1: low ridge, or absent. (*Yurlunggur* 0, *Wonambi* 0)
191. Posterior margin of neural arch. 0: shallowly concave in dorsal view. 1: with deep, V-shaped embayment in dorsal view exposing much of centrum in front of condyle. (*Yurlunggur* 1, *Wonambi* 1)
192. Zygosphene roof. 0: with deeply concave anterior edge, i.e. deeply notched between zygosphenal facets. 1: with shallowly concave anterior edge, i.e. slightly notched between facets. 2: with straight or slightly sinuous anterior edge, i.e. not uniformly concave. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 1)
193. Condyles of mid-trunk vertebrae. 0: oval, sagittal dimension much less than transverse diameter. 1: round, sagittal dimension similar to transverse dimension. (*Yurlunggur* 1, *Wonambi* 1)
194. Condyles of mid-trunk vertebrae. 0: facing very dorsally, ventral edge (at most) of condyle surface exposed in ventral view. 1: facing posteriorly, or posterodorsally, much of condyle surface exposed in ventral view. (*Yurlunggur* 1, *Wonambi* 1)

195. Precondylar constriction of centrum. 0: absent or very weak. 1: moderate. 2: strong. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 1)
196. Orientation of zygapophyses of mid-trunk vertebrae. 0: steeply inclined medially, 30° or more from the horizontal. 1: moderately inclined medially, between 15° and 30° from the horizontal. 2: not inclined medially, less than 15° from horizontal. Ordered 0—1—2. (*Yurlunggur* 1, *Wonambi* 0&1)
197. Paracotylar foramina (foramen on anterior surface between cotyle and transverse process). 0: present on most or all vertebrae. 1: present on no, or few, vertebrae. (*Yurlunggur* 0, *Wonambi* 0)
198. Parazygantral foramina (foramen on posterior surface of neural arch, between zygantrum and postzygapophyseal facets). 0: absent on all vertebrae. 1: numerous small pits (but no large foramina) in parazygantral area. 2: one (or several) large foramen present on each side. Unordered. State descriptions modified for clarity (see Scanlon 2005¹³). (*Yurlunggur* 2, *Wonambi* 2).
199. Subcentral foramina. 0: uniform throughout column, small and paired in most vertebrae. 1: irregular, being either small and paired, absent, or single and large, in different vertebrae. (*Yurlunggur* 0, *Wonambi* 0)
200. Prezygapophyseal process. 0: absent. 1: present as a small process extending slightly laterally from prezygapophyseal facet. 2: present as a prominent process extending laterally or anterolaterally from prezygapophyseal facet. Ordered 0—1—2. State descriptions slightly modified. (*Yurlunggur* 0, *Wonambi* 0)
201. Hypapophyses. 0: present on anterior eight cervicals or fewer. 1: present up to at least cervical ten, but absent in mid- and posterior trunk. 2: present throughout trunk, but poorly developed in posterior trunk. 3: present throughout trunk, well developed throughout. Ordered 0—1—2—3. (*Yurlunggur* 1, *Wonambi* 1)
202. Ventral surface of centra. 0: mid-trunk vertebrae with smooth, transversely convex ventral surface. 1: mid-trunk vertebrae bearing single median haemal keels. (*Yurlunggur* 1, *Wonambi* 1)
203. Lymphapophyses. 0: No forked free ribs or lymphapophyses. 1: three or more free-ending cloacal vertebrae with lymphapophyses. (*Yurlunggur* ?, *Wonambi* 1)
204. Caudal vertebrae. 0: with posteroventral projections. 1: without posteroventral projections. (*Yurlunggur* 0, *Wonambi* 0; *Anilius* changed to 1 following Szyndlar and Rage 2003, see Scanlon 2005¹³)
205. Posteroventral elements of caudals. 0: articulate with centrum. 1: fuse with centrum. (*Yurlunggur* 0, *Wonambi* 0)

206. Posteroventral elements of caudals. 0: distally fused (chevrons). 1: distally separated (haemapophyses). 2: single median element (caudal hypapophyses). Unordered. (*Yurlunggur*?, *Wonambi* 0)
207. Ribs. 0: tuber costae (= tuberculum, tuberculiform process, dorsal process) of rib absent or weakly developed. 1: tuber costae well developed. (*Yurlunggur* 1, *Wonambi* 1)
208. Ribs. 0: slender throughout body. 1: thickened and heavily ossified (pachyostotic) in middle region of body. (*Yurlunggur* 0, *Wonambi* 0)
209. Cervical region. 0: present, at least 20 anterior vertebrae bearing ribs distinctly shorter and thinner than ribs of other trunk vertebrae. 1: absent, only the first few anterior vertebrae bear short, thin ribs. (Not scorable, by this definition, on disarticulated material)
46. Pelvic girdle. 0: three elements present. 1: two elements present. 2: single element present. 3: no elements present. Ordered 0—1—2—3. (*Yurlunggur*?, *Wonambi*?)
47. Pelvis. 0: external to sacral or cloacal ribs. 1: internal to sacral or cloacal ribs. (*Yurlunggur*?, *Wonambi*?)
48. Hindlimb. 0: present, with distinct femur, tibia and fibula. 1: vestigial, with one bone (femur) only, and sometimes a single distal spur. 2: absent. Ordered 0—1—2. (*Yurlunggur*?, *Wonambi*?)
- 213-263 (soft anatomy and behaviour, see **SL**) unknown in *Yurlunggur* and *Wonambi* '264': see 60A, above.

4. Data matrix

#NEXUS

BEGIN DATA;

DIMENSIONS NTAX=30 NCHAR=264;

FORMAT SYMBOLS= " 0 1 2 3" MISSING=? GAP=- ;

MATRIX

```

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Lanthanotus       010000000000000010--0000000-00000-
0000010000002000-000--1---000000000000000000000000?0100-000-000000000000000-
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000000000000-
00100000000000000000?????????0????????????????????????????????001000??0000-??00
Varanus           0(01)1000000000000000--00000003-00000-
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0--0000000000000000-0000000-00000-00100001-0000000000000000000100-0-1-
0000000000-

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Anomalepididae -2-1?(12)-211(02)210-11-0--01110012000121--00-0-11-
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Xenopeltis 0110(12)0000011010000--12110(01)0-
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Pythoninae (01)2-02(12)-
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-
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Ungaliophiinae
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00211000011101(01)11010110(01)01001(01)100(23)01(01)11002-
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BEGIN ASSUMPTIONS;
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[2] 1.0 2.0 .  1.0
[3] 2.0 3.0 1.0 .
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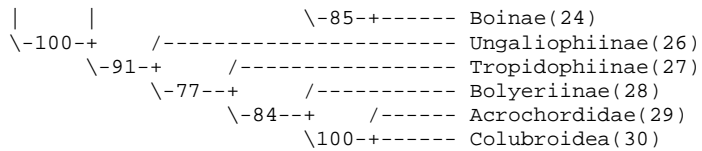
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OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ;
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TYPESET * UNTITLED = unord: 1 3-4 7 9-10 13-17 19-21 24-30 32-33 35-41
43-47 50-56 58 60 62-65 67-68 71 73-74 76-77 79-86 88-89 91-95 97-100 103
105-107 109-116 118-120 122-133 136 139-140 142-145 147-148 150-151 153-156
159 161 163-165 168-181 183-184 187-191 193-194 197-199 202-209 211 214-231
234-237 239 244 247-248 250-251 254 256-257 259 261-264, ord: 2 5-6 11-12 18
22-23 34 42 48-49 57 59 61 66 69-70 72 75 87 90 96 101-102 104 108 117 134-
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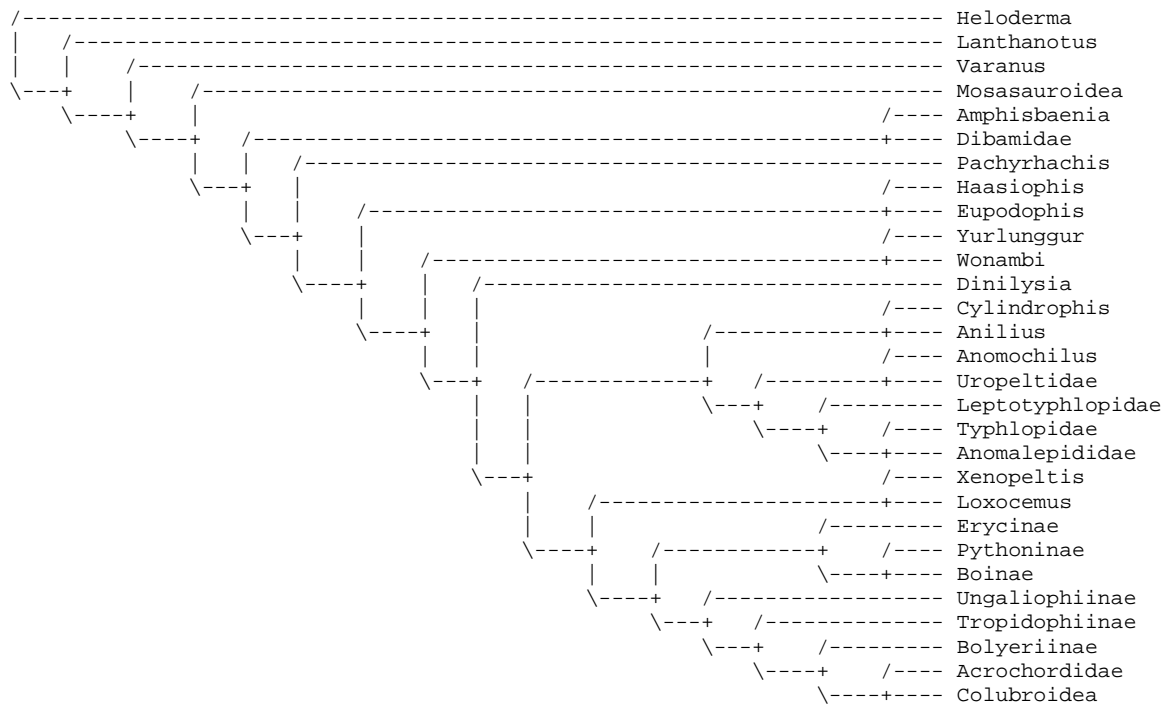



Bipartitions found in one or more trees and frequency of occurrence (bootstrap support values):

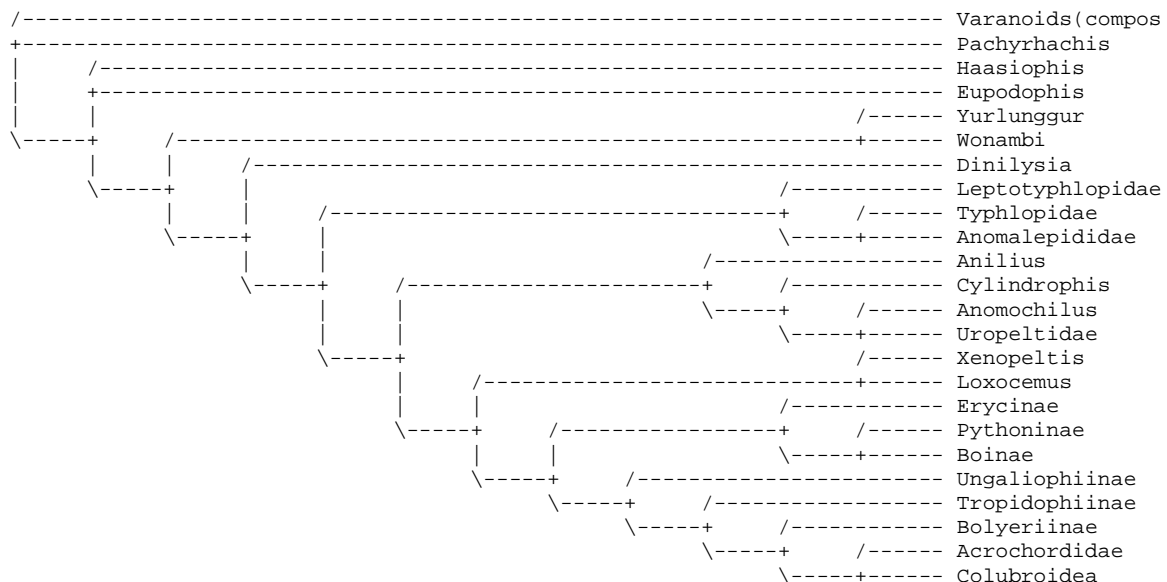
11111111112222222223 58912345678901234567890	Freq /10000	%	compatible (*) with shortest tree
.....***.....	9999.71	100.0%	*
.....**.....	9993.83	99.9%	*
.....**.....	9992.17	99.9%	*
.....*****	9987.17	99.9%	*
.....***.....	9949.54	99.5%	*
.....*****	9944.58	99.4%	*
.....*****	9840.33	98.4%	*
.....*****	9131.61	91.3%	*
.....**.....	9072.07	90.7%	*
.....*****	8628.90	86.3%	*
.....**.....	8469.13	84.7%	*
.....***	8389.54	83.9%	*
.....**.....	8241.88	82.4%	*
.....****	7742.26	77.4%	*
.....*****	7196.75	72.0%	*
.....*****	6737.61	67.4%	*
.....*****	6184.78	61.8%	*
.....**.....	5838.56	58.4%	*
.....***	4830.90	48.3%	*
.....*****	3634.93	36.3%	*
.....***	3564.81	35.6%	*
.....**.....	3491.72	34.9%	*
.....*****	3422.87	34.2%	*
.....*****	3028.77	30.3%	*
.....*****	1423.54	14.2%	(+other groups omitted, all incompatible)

6. Other analyses

6.1. All taxa, excluding only the varanoid composite. Only character 239 is parsimony-uninformative, and excluded. Again a single tree is found: length = 894.0, CI = 0.4083, HI = 0.5917, RI = 0.6857, RC = 0.2799. Compared to the previous analysis, the only topological changes within Ophidia are that *Cylindrophis* is sister to *Anilius*, and Scolecophidia is sister to the (*Anomochilus*, Uropeltidae) clade. There is no effect on the lower nodes within Ophidia, i.e. using an alternative outgroup of fossorial limb-reduced lizards (which might be expected to force scolecophidians and/or anilioids into a more basal position) does not alter the positions of *Pachyrhachis*, *Haasiophis* and (*Yurlunggur*, *Wonambi*) as basal to all extant snakes. *Eupodophis* groups with *Haasiophis* in this analysis, but only weakly (see below).



6.2. Varanoid composite outgroup (no Dibamidae or Amphisbaenia), *Eupodophis* included; three characters excluded as uninformative, as in main analysis. Two equally parsimonious trees of length 783 are found, differing in the position of the least well-known taxon, *Eupodophis*. The strict consensus is shown; all other relationships are the same as in Fig. 2.



6.3. Bootstrap analysis (1000 x 100 random addition sequence replicates, heuristic) of same taxon and character set as preceding. Most values are similar to those in Fig. 2; again *Eupodophis* groups with *Haasiophis*, but with low support. Relative to the main

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