

Skull of the large non-macrostromatan snake *Yurlunggur* from the Australian Oligo-Miocene

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Understanding the origin and early evolution of snakes from lizards depends on accurate morphological knowledge of the skull in basal lineages, but fossil specimens of archaic snakes have been rare, and either fragmentary or difficult to study as a result of compression by enclosing sediments^{1–6}. A number of Cenozoic fossil snakes from Australia have vertebral morphology diagnostic of an extinct group, Madtsoiidae, that was widespread in Gondwana from mid-Cretaceous (Cenomanian) to Eocene times, and also reached Europe in the late Cretaceous period^{3,7–11}. Despite this long history, only about half the skull is known from the best-known species *Wonambi naracoortensis*^{7,11–13}, and the few known cranial elements of other species have added little further evidence for phylogenetic relationships^{10,14–19}. Conflicting hypotheses have been proposed for their relationships and evolutionary significance, either as basal ophidians with many ancestral (varanoid- or mosasaur-like) features, or advanced (macrostromatan) alethinophidians of little relevance to snake origins^{3,4,7,11–15,20}. Here I report two partial skeletons referred to *Yurlunggur*⁸, from the late Oligocene and early Miocene of northern Australia, which together represent almost the complete skull and mandible. The exceptionally preserved skulls provide new evidence linking *Yurlunggur* with *Wonambi* and other madtsoiids, falsifying predictions of the macrostromatan hypothesis, and supporting the exclusion of Madtsoiidae from the clade including all extant snakes.

Freshwater carbonate deposits of the Riversleigh World Heritage Area, northwestern Queensland, preserve rich samples of successive vertebrate local faunas from about 25–12 Myr ago²¹. Riversleigh fossils are rarely articulated but usually undistorted, can be completely freed from matrix with acid, and include the most diverse known assemblages of Madtsoiidae^{8,10,11,16}. This group comprises small to very large snakes (total adult length estimated to range from 0.5 to 6.5 m in Australian forms, and to more than 9 m elsewhere), presumed to be constrictors ecologically analogous to living pythons and boas^{3,7–13,22,23}.

Squamata Oppel, 1811
Ophidia Brongniart, 1800
Madtsoiidae Hoffstetter, 1961
Yurlunggur Scanlon, 1992

Stratigraphic and geographic range. Late Oligocene to Late Pleistocene; northeastern and central Australia (Queensland, Northern Territory, South Australia, New South Wales^{8,16–18,23}).

Remarks. Madtsoiid monophyly is only weakly supported as long as most included taxa are inadequately known^{13,18,19}; their taxonomy has been based on vertebrae, and the single named species of *Yurlunggur* (*Y. camfieldensis*) is known only from postcranial remains^{8,23}. Revised diagnoses of Madtsoiidae and *Yurlunggur* are provided in Supplementary Information; in the Riversleigh faunas, vertebrae attributable to *Yurlunggur* are readily distinguished from

other co-occurring madtsoiids (including species of *Wonambi* and *Nanowana*), pythons, typhlopids and elapids by numerous shape characters as well as much larger adult size^{8,10,11,16,24,25}. Some isolated skull elements can also be referred to this taxon on the basis of their large size^{16–18}. More than one new species may be represented in the material reported here, but pending further study of vertebrae the new skeletons are simply referred to *Yurlunggur* sp. or spp.

Referred material. Hiatus A Site (Late Oligocene²¹): disarticulated remains of two different-sized adults in blocks collected in 2002, the larger including more than 40 cervical, trunk, cloacal and caudal vertebrae, ribs, fragments of the right maxilla (Queensland Museum F45217), dentary (QMF45073) and frontal (QMF45388), and articulated partial braincase (QMF45111, Fig. 1i–m) comprising prootics, exoccipital–opisthotics, basioccipital, partial supraoccipital and part of the parietal. Smaller individual represented by right frontal (QMF45389) and exoccipital–opisthotic (QMF45390) as well as several trunk vertebrae inconsistent (in combination of size and regional features) with the rest of the material. CS Site (Early Miocene²¹): associated and partly articulated skeleton (QMF45391) of a small adult in several contiguous blocks collected in 2000, including most of the skull (premaxilla, nasals, septomaxillae, vomers, maxillae, palatines, pterygoid, ectopterygoids, frontals, prefrontals, postorbitofrontals, jugals, parietal, supraoccipital, parabasisphenoid, quadrates, splenials and dentary; Fig. 1a–h) and more than 60 vertebrae including atlas, axis and several successive cervicals, articulated series of mid-trunk vertebrae with ribs, and additional preloacal, cloacal and caudal vertebrae. Disarticulated vertebrae of several other (larger and smaller) *Yurlunggur* individuals were recovered from the same blocks.

Measurements of overlapping parts of the skulls (frontal, supraoccipital, parietal–prootic contacts) show that QMF45111 has linear dimensions about 1.3-fold those of QMF45391. Maximum vertebral sizes show a similar ratio of width across prezygapophyses (41.0 mm:33.2 mm \approx 1.2), and a simple proportionality method^{9,23} gives total length estimates of 5.7 and 4.7 m respectively. The description below is based principally on the two most complete skeletons, but other referred cranial material from Riversleigh includes the posterior part of the parabasisphenoid (MM Site QMF23041) and articular region of the mandible (BSE Site QMF23060) as well as jaw elements represented in QMF45391 (refs 13, 16–19).

Most significant new morphological information. The premaxilla of QMF45391 lacks teeth or alveoli and has concave lateral facets indicating tight contact with the maxillae, consistent with a mobile articulation but not the loose ligamentous connection found in most modern snakes¹⁵. The maxilla, palatine, pterygoid and dentary resemble those of *Nanowana* spp. more than those of *Wonambi*^{10,11,13,19}; the complete maxilla has 22 alveoli, palatines 10/11, pterygoid 7 (but 9 in QMF51378; WH Site), and dentary

¹Riversleigh Fossil Centre, Outback at Isa, PO Box 1094, Mount Isa, Queensland 4825, Australia. ²South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia.

(incomplete posteriorly) at least 20. The maxillary dentition is nearly isodont, dentary is slightly proterodont, and radial infolding of the tooth bases ('placidine'^{11,17}) is observable on broken or detached teeth in both new specimens. The nasals, septomaxillae and vomers are similar to those of *Cylindrophis* except that the nasals are narrow and separated from the prefrontals by posterior extensions of the external nares reaching the frontals, as in varanoid and mosasauroid lizards but not *Dinilysia* or any basal modern snakes¹⁵. Posteriorly, the nasals extend slightly between the frontals mesially and overlap them dorsally, probably forming a somewhat mobile prokinetic articulation as in basal alethinophidians, not a strong suture as inferred in *Wonambi*^{11,13,26}. The prefrontal has interlocking but potentially mobile articulations with both the frontal and the distinct dorsal process of the maxilla, possibly permitting rocking motions but little or no sliding at the prefrontal–maxillary contact, and thus resembles anilioids but neither macrostomatans nor *Wonambi*^{11,13,15,26,27}. The orbital lamina of the prefrontal has two deep, ventrally open notches representing the foramina of the single lacrimal duct (between prefrontal and maxilla) and palatine nerve (between prefrontal and palatine); there is no horizontal lamina roofing the lacrimal duct, as present in macrostomatans apart from some booids¹⁵. The frontals

have descending interolfactory processes, their anterior surfaces forming a clasping contact with the nasals, but the undamaged subolfactory laminae have no ascending projections and hence the interolfactory pillars are incomplete; complete (sutured or fused) pillars are synapomorphic for Alethinophidia, with no instances of reversal known^{1,13,15,20}. The parietal is relatively both shorter and narrower than in *Wonambi* and *Dinilysia*, and the transverse anterior margin and anterolateral (postorbital) processes extend further anteriorly to underlap and clasp the frontals, thus forming supra-orbital processes as in anilioids, xenopeltids and *Haasiophis*^{1,5,6,13,15}. The postorbital bar is complete, with two triradiate elements each forming about half of the posterior border of the orbit, unlike all modern snakes¹⁵ but similar to *Dinilysia*⁵. The stepped, oblique overlap of the upper and lower elements is comparable to the plesiomorphic postorbital–jugal contact retained in many lizards²⁸, suggesting that the bones can be identified respectively as postorbito-frontal (fused postfrontal and postorbital, contacting the frontal and prefrontal, and clasping the anterolateral margin of the parietal supraorbital process) and jugal (forming an elongate, narrow contact with a dorsal facet on the maxilla); this raises questions concerning homology of the 'postorbital' in modern snakes, which might

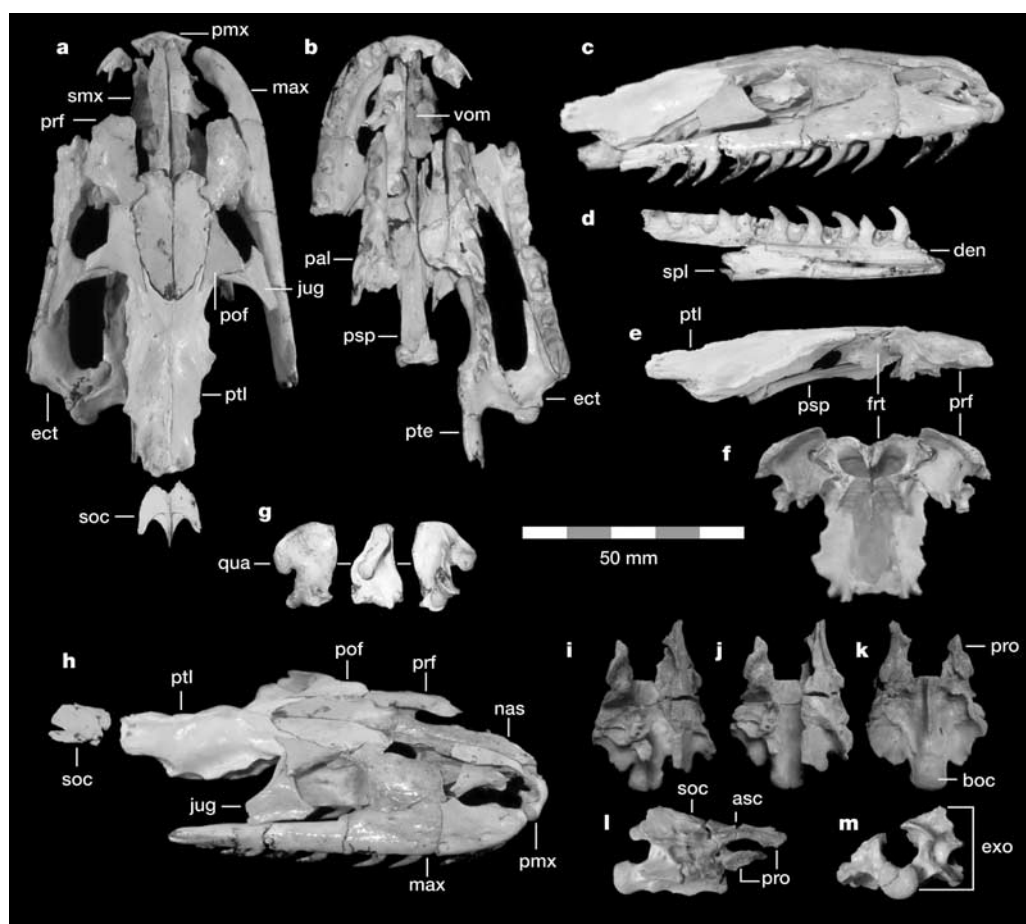


Figure 1 | *Yurlunggur* sp. or spp. (Madtsoiidae), parts of two skulls from Riversleigh, Queensland, Australia. **a–h**, QMF45391 (CS Site, Early Miocene); **i–m**, QMF45111 (Hiatus A Site, Late Oligocene). **a–c**, Dorsal (**a**), palatal (**b**) and right lateral (**c**) views of rearticulated cranial bones; supraoccipital shown in **a** only; parietal and posterior part of right maxilla omitted in **b**. **d**, Medial view of left dentary (omitting anterior portion) and splenial. **e**, **f**, Right lateral (**e**) and anteroventral (**f**) views of parietal, parasphenoid, frontals and prefrontals (same elements partly obscured in **a–c**). **g**, Right quadrate in lateral, posterior and medioventral views. **h**, The same elements as **a**, in right dorsolateral and slightly anterior view.

i–m, Braincase elements in left dorsolateral (**i**), dorsal (**j**), ventral (**k**), right lateral (**l**) and posterior (**m**) views (parts of left prootic and parietal omitted). Abbreviations: asc, furthest extent of anterior semicircular canal (exposed in repaired crack); boc, basioccipital; den, dentary; ect, ectopterygoid; exo, exoccipital–opisthotic; frt, frontal; jug, jugal; max, maxilla; nas, nasal; pal, palatine; pmx, premaxilla; pof, postorbitofrontal; prf, prefrontal; pro, prootic; psp, parasphenoid; pte, pterygoid; ptl, parietal; qua, quadrate; smx, septomaxilla; soc, supraoccipital; spl, splenial; vom, vomer. Scale bar, 50 mm.

represent or incorporate the actual jugal (usually considered absent^{5,10–13,15,28}). The parasphenoid broadly enters the optic fenestra, as in *Dinilysia* and *Wonambi* but no modern snakes except colubroids, which are deeply nested within Macrostromata^{1,13,20}. The strongly arched choanal process of the palatine wraps around the posterior process of the vomer, and abuts the frontal descensus and a sagittal keel (interchoanal process) of the parasphenoid rostrum, consistent with slight kinesis (lateral rotation) of the palatine relative to the braincase, as in anilioids^{26,27}. The ectopterygoid clasps the large lateral process of the pterygoid both dorsally and ventrally, as in most lizards but unlike any modern snake (this region is poorly known in other fossil snakes)^{11,15,16}. The quadrate is similar in shape to those of *Dinilysia* and some basal alethinophidians (particularly *Cylindrophis* and *Xenopeltis*): nearly vertical and relatively short dorsoventrally, with a prominent and downcurved suprapedial process^{1,5,15,26}. There is a distinct stapedial facet on the posteroventral surface of the process, but as in *Dinilysia* and *Xenopeltis* the extracolumella of the stapes (stylohyal) is not fused either to the process as in anilioids or to the shaft of the quadrate as in other macrostromatans.

The prootic (QMF45111) has a large, undivided trigeminal notch, without damage indicating that a laterosphenoid bridge was ever present on either side (as in *Wonambi* and *Dinilysia*, most simply interpreted as absence of the alethinophidian synapomorphy^{1,5,11–13,15,20}). As in the latter fossils the anterodorsal (alar) process is elongate and shallow, but here it is confirmed to extend far beyond the anterior semicircular canal, unlike in all modern snakes, that have the crista alaris greatly reduced and the labyrinth extending close to the anterior margin of the prootic^{13,15,29}. The left and right exoccipitals meet broadly on the dorsal surface of the occipital condyle (as in *Wonambi*, *Dinilysia*, *Cylindrophis* and *Anomochilus*; separated in most other squamates^{1,13,15,27}), and narrowly above the foramen magnum. In QMF45111, the exoccipital–opisthotics are partly fused with the basioccipital and supraoccipital, whereas the supraoccipital (QMF45391) and exoccipital–opisthotic (QMF45390) are unfused in both smaller specimens, suggesting that fusion occurred in late ontogeny (rare in modern squamates).

The dentary (most complete in QMF45391) is relatively narrow but widest posteriorly, with two elongate mental foramina on the

lateral face below alveoli 3–4 and 7–8. The large splenial has a long interlocking contact with the medioventral crest of the dentary, a concave posterior articular surface for the angular (intramandibular joint) and a dorsoposterior facet for an anterior process of the coronoid.

Yurlunggur, hitherto known only from few isolated elements^{10,16–19}, is now more completely known than *Wonambi naracoortensis*^{7,11–13}. Almost every cranial element is now represented in one or both of these taxa; only the supratemporal, stapes, angular, coronoid and epipterygoid (if present¹³) have not yet been identified. Of 212 osteological characters used in a recent phylogenetic analysis¹⁵, *Yurlunggur* can now be scored for 182, *Wonambi* (including *W. barriei*^{11,16}) for 143, and either or both for 188.

Previous analyses inferring Madtsoiidae to be archaic, non-alethinophidian snakes^{11,15,18,20} are further supported by characters newly discovered in *Yurlunggur*, many of which have never previously been observed in fossil snakes. The competing hypothesis, that *Wonambi* and related taxa belong to the extant clade Macrostromata^{4,7,12}, would predict the presence of apomorphies including complete interolfactory pillars, laterosphenoid dividing trigeminal notch, crista alaris of prootic reduced relative to semicircular canals, extracolumella of stapes fusing to the quadrate, prefrontal roofing lacrimal duct, parasphenoid excluded from optic fenestra, and reduced ectopterygoid process overlapped only dorsally or laterally by ectopterygoid^{5,6,12,13,15,20}. *Yurlunggur* possesses ancestral or intermediate states for each of these characters, previously unobserved in madtsoiids or disputed in *Wonambi*. These two Australian snakes differ in many details but are related (forming a clade with bootstrap support of 82%; Fig. 2) and apparently more distant from modern snakes than is *Dinilysia* (72%). There is strong support for monophyly of the nested clades Serpentes, Alethinophidia and Macrostromata (98%, 62% and 99%, respectively) as excluding both of the Cenozoic madtsoiids as well as the three best-known Cretaceous ophidians. These long-jawed or 'macro-stomate' fossils are thus excluded from Macrostromata (which is diagnosed by numerous characters, not all related to the jaw apparatus¹⁵), and collectively represent the ancestral morphology of the diverse modern snake radiation.

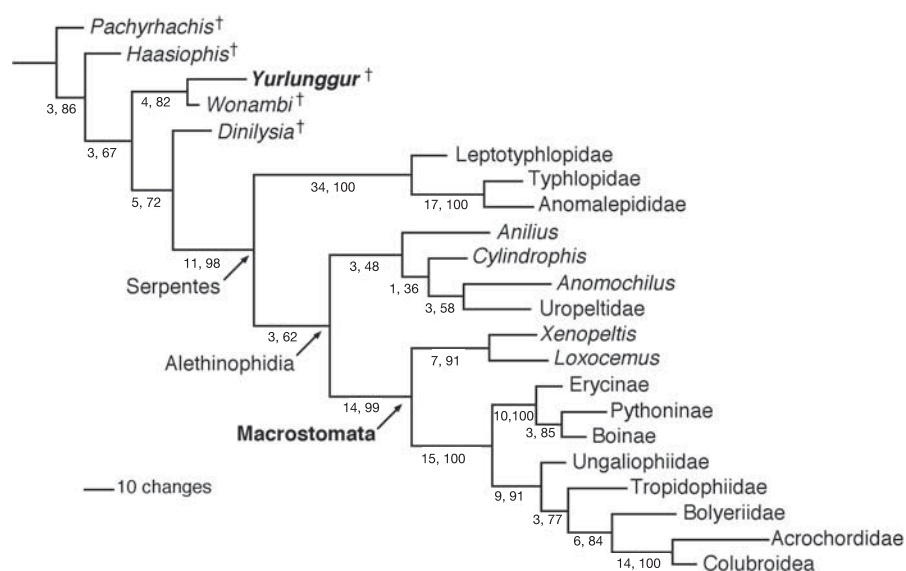


Figure 2 | Phylogenetic relationships of extant and extinct snakes (Ophidia). The cladogram is based on a recent phenotypic data matrix¹⁵, modified as explained in Supplementary Information. The single most parsimonious cladogram was found by using PAUP³⁰ (with multistate characters treated as numerically or topologically ordered where reasonable, and a composite 'varanoid' outgroup¹⁵), and is shown with branch lengths

proportional to the minimum number of changes; cladistically uninformative characters are excluded, so only homoplastic changes are shown on terminal branches. Measures of clade support (Bremer decay index, bootstrap percentage) are shown on branches. Extinct taxa are marked (†), and clade names Serpentes (crown group of 'modern snakes'), Alethinophidia and Macrostromata are placed at their basal nodes.

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- Estes, R., Frazzetta, T. H. & Williams, E. E. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part 1. Cranial morphology. *Bull. Mus. Comp. Zool. Harvard* **140**, 25–74 (1970).
- Lee, M. S. Y. & Caldwell, M. W. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. *Phil. Trans. R. Soc. Lond. B* **353**, 1521–1552 (1998).
- Rage, J.-C. & Werner, C. Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: The earliest snake assemblage. *Palaeontol. Afr.* **35**, 85–110 (1999).
- Coates, M. & Ruta, M. Nice snake, shame about the legs. *Trends Ecol. Evol.* **15**, 503–507 (2000).
- Caldwell, M. W. & Albino, A. Exceptionally preserved skeletons of the Cretaceous snake *Dinilysia patagonica* Woodward, 1901. *J. Vertebr. Paleontol.* **22**, 861–866 (2002).
- Rieppel, O., Zaher, H., Tchernov, E. & Polcyn, M. J. The anatomy and relationships of *Haasiophis terrasanctus*, a fossil snake with well-developed hind limbs from the mid-Cretaceous of the Middle East. *J. Paleontol.* **77**, 536–558 (2003).
- Barrie, D. J. Skull elements and associated remains of the Pleistocene boid snake *Wonambi naracoortensis*. *Mem. Queensl. Mus.* **28**, 139–151 (1990).
- Scanlon, J. D. A new large madtsoiid snake from the Miocene of the Northern Territory. *Beagle Rec. N. Territory Mus. Arts Sci.* **9**, 49–60 (1992).
- Scanlon, J. D. Madtsoiid snakes from the Eocene Tingamarra Fauna of eastern Queensland. *Kaupia: Darmst. Beitr. Naturgeschichte* **3**, 3–8 (1993).
- Scanlon, J. D. *Nanowana* gen. nov., small madtsoiid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Mem. Queensl. Mus.* **41**, 393–412 (1997).
- Scanlon, J. D. & Lee, M. S. Y. The Pleistocene serpent *Wonambi* and the early evolution of snakes. *Nature* **403**, 416–420 (2000).
- Rieppel, O., Kluge, A. G. & Zaher, H. Testing the phylogenetic relationships of the Pleistocene snake *Wonambi naracoortensis* Smith. *J. Vertebr. Paleontol.* **22**, 812–829 (2002).
- Scanlon, J. D. Cranial morphology of the Plio-Pleistocene giant madtsoiid snake *Wonambi naracoortensis*. *Acta Palaeontol. Pol.* **50**, 139–180 (2005).
- Rage, J.-C. Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata* **27**, 109–144 (1998).
- Lee, M. S. Y. & Scanlon, J. D. Snake phylogeny based on osteology, soft anatomy and behaviour. *Biol. Rev.* **77**, 333–402 (2002).
- Scanlon, J. D. *Studies in the Palaeontology and Systematics of Australian Snakes* Thesis, Univ. New South Wales (1996).
- Scanlon, J. D. & Lee, M. S. Y. On varanoid-like dentition in primitive snakes (Madtsoiidae). *J. Herpetol.* **36**, 100–106 (2002).
- Scanlon, J. D. The basicranial morphology of madtsoiid snakes (Squamata, Ophidia) and the earliest Alethinophidia (Serpentes). *J. Vertebr. Paleontol.* **23**, 971–976 (2003).
- Scanlon, J. D. Australia's oldest known snakes: *Patagoniophis*, *Alamitophis*, and cf. *Madtsoia* (Squamata: Madtsoiidae) from the Eocene of Queensland. *Mem. Queensl. Mus.* **51**, 215–235 (2005).
- McDowell, S. B. in *Snakes: Ecology and Evolutionary Biology* (eds Seigel, R. A., Collins, J. T. C. & Novak, S. S.) 1–50 (Macmillan, New York, 1987).
- Archer, M., Hand, S. J., Godthelp, H. & Creaser, P. Correlation of the Cainozoic sediments of the Riversleigh World Heritage fossil property, Queensland, Australia. *Mém. Trav. École Prat. Hautes Études Inst. Montpellier* **21**, 131–152 (1997).
- Simpson, G. G. A new fossil snake from the *Notostylops* beds of Patagonia. *Bull. Am. Mus. Nat. Hist.* **67**, 1–22 (1933).
- Scanlon, J. D. First known axis vertebra of a madtsoiid snake (*Yurlunggur camfieldensis*) and remarks on the neck of snakes. *Beagle Rec. N. Territory Mus. Arts Sci.* **20**, 207–215 (2004).
- Scanlon, J. D. *Montypythonoides*: the Miocene snake *Morelia riversleighensis* (Smith and Plane, 1985) and the geographical origin of pythons. *Mem. Assoc. Australas. Palaeontol.* **25**, 1–35 (2001).
- Scanlon, J. D., Lee, M. S. Y. & Archer, M. Mid-Tertiary elapid snakes (Squamata, Colubroidea) from Riversleigh, northern Australia: early steps in a continent-wide adaptive radiation. *Geobios* **36**, 573–601 (2003).
- Cundall, D. Feeding behaviour in *Cylindrophis* and its bearing on the evolution of alethinophidian snakes. *J. Zool. (Lond.)* **237**, 353–376 (1995).
- Scanlon, J. D. & Rossman, D. S. Cephalic anatomy of the rare Indonesian snake *Anomochilus weberi*. *Zool. J. Linn. Soc.* **109**, 235–273 (1993).
- Estes, R., de Queiroz, K. & Gauthier, J. A. in *Phylogenetic Relationships of the Lizard Families* (eds Estes, R. & Pregill, G.) 119–281 (Stanford Univ. Press, Stanford, California, 1988).
- Rieppel, O. & Zaher, H. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. *Zool. J. Linn. Soc.* **129**, 489–514 (2000).
- Swofford, D. L. *PAUP* Version 4—Phylogenetic Analysis Using Parsimony (*and Other Methods)* (Sinauer, Sunderland, Massachusetts, 1999).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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