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## 1. Character List

Characters 1-154 and codings are taken directly from Zaher and Scanferla (2012) with minor edits (see section 2); the following 84 characters are added for this study, primarily on the basis of study of specimens and CT scans, but also with additions from Tchernov et al. (2000), Lee and Scanlon (2002), Scanlon (2005, 2006), Scanferla and Canale (2007) and Gauthier et al. (2012).

### TEETH

155. Teeth, implantation: interdental ridges absent (0), or interdental ridges present (1). In squamates ancestrally, the teeth implant in a pleurodont fashion with their bases set into a shallow trough, the dental gutter. In Scolecophidia, the teeth are separated by low, bony ridges that define shallow, medially open sockets, as the dental parapet is not extended to the same level as the interdental ridges (Zaher and Rieppel, 1999). This condition is also seen in *Najash rionegrina* (Zaher et al., 2009) and *Coniophis precedens*. In *Dinilysia patagonica*, Madtsoiidae, and Alethinophidia, teeth attach to deep sockets (Alethinophidian implantation of Zaher and Rieppel, 1999) that are formed by interdental ridges and a medial dental parapet that approaches the level of the lateral dental parapet.
156. Teeth, replacement: replacement teeth lie vertically (0) or lie horizontally in the jaws (1) (Lee, 1998; Gauthier et al., 2012). Primitively in lizards and Scolecophidia, replacement teeth erupt with their crowns lying vertically. In crown alethinophidian snakes, the replacement teeth develop in the jaw lying horizontally, then rotate into position when the teeth attach to the jaw. This character could not be scored for any fossil taxa.
157. Teeth, replacement: single replacement tooth per tooth position (0) or two or more replacement teeth per tooth position (1). Primitively in squamates, no more than one replacement tooth is present per tooth position, although as a replacement tooth implants, its successor may begin to develop before attachment is completed. This condition is retained in Anilioidea and the basal macrostomatans *Loxocemus bicolor* and *Xenopeltis unicolor*. Henophidia are characterized by having two replacement teeth per tooth position, with the exception of *Ungaliophis continentalis*. Again, this character could not be scored for any fossils.
158. Teeth, attachment: ankylosed to jaws (0) teeth loosely attached to jaws by connective tissue (1). Primitively in snakes and other squamates, bone of attachment is deposited around the base of the tooth and fuses the tooth to the tooth-bearing elements of the skull. In both *Xenopeltis unicolor* and *Loxocemus bicolor* the base of the tooth is not ankylosed, and is instead anchored by connective tissue to the theca of the tooth-bearing elements (dentary, maxilla,

palatine, and pterygoid). Hinged teeth are seen in a range of snakes (Savitsky, 1982) but *Uropeltis* was the only other taxon we studied to exhibit this character. The primitive condition was clearly evident in many fossil species but the derived condition is difficult to assess because teeth tend to break away from the jaw soon after death.

159. Teeth, size: crowns isodont or enlarged at the middle of the tooth row (0) crowns large anteriorly, and decrease in size posteriorly (1) (Lee and Scanlon, 2002; Scanlon, 2006); anterior teeth conspicuously elongate, length of crown significantly exceeds height of dentary at midlength (2) (Gauthier et al., 2012: 416.3). ORDERED. Tooth crowns terminate at roughly the same level in squamates ancestrally; in Varanoidea the tallest teeth lie in the middle of the tooth row. In most snakes, the teeth are larger and taller-crowned anteriorly and progressively decrease in size posteriorly. This condition is taken to the extreme in Boinae, Pythoninae, and Erycinae, in which the crowns at the tip of the dentary are significantly taller than the height of the dentary. *Coniophis precedens* and *Najash rionegrina* appear to be primitive in having more isodont dentition, as judged from the size of the alveoli, but this coding remains tentative given that the dentition is not completely known in either species. Anilioids (e.g., *Anilius scytale*, *Cylindrophis ruffus*, *Uropeltis melanogaster*, *Anomochilus leonardi*) are unusual in that the anterior teeth are relatively small, and the tallest teeth lie near the middle of the maxillae and dentaries, as in Varanoidea.

## SKULL

160. Premaxilla: teeth borne medially on premaxilla (0) or teeth absent from midline of premaxilla (1). In snakes, teeth may be present or absent from the maxilla, but teeth are invariably absent from the middle of the premaxilla. This character is typically associated with strong arching of the premaxilla in anterior view, and the acquisition of a diastema and arched premaxilla morphology is presumably related to the evolution of tongue-flicking, creating a gap in the toothrow that allows the tongue to be extended and retracted without opening the jaws.
161. Premaxilla: ascending process transversely expanded, partly roofing external nares (0) or ascending process mediolaterally compressed, blade-like or spine-like (Lee and Scanlon, 2002; Scanlon, 2006). Primitively in lizards and scolecophidians, the ascending process of the maxilla is mediolaterally expanded. In Alethinophidia, the premaxilla is mediolaterally compressed and forms a vertical blade or a spine.
162. Premaxilla: premaxilla medial to maxillae (0) or located anterior to maxillae (1). In lizards and basal Alethinophidia (including Simoliophiidae) the transverse processes of the premaxillae lie medial to the maxillae. In

- Macrostomata, the premaxillae and the transverse processes of the premaxillae are displaced anteriorly.
163. Prefrontal: prefrontal socket for dorsal peg of maxilla absent (0) or present (1). The anilioids *Anilius scytale*, *Cylindrophis ruffus*, and *Uropeltis melanogaster* are characterized by a unique prefrontal-maxilla articulation in which the ventral margin of the premaxilla bears a socket that receives a short, peg-like dorsal process of the maxilla; in lateral view the premaxilla appears to be notched. This joint is further reinforced by a long anteroventral process of the prefrontal that extends medial to the prefrontal. The peg-and-socket morphology is absent from *Anomochilus leonardi*, however. *Yurlunggur* has been described as having an interlocking joint between the maxilla and prefrontal (Scanlon, 2006) but appears to lack the distinct peg-and-socket of anilioids.
  164. Prefrontal: prefrontal extends medially across frontal for more than 75% of the width of the frontal: absent (0) or present (1) (modified from Gauthier et al., 2012:132). Primitively in Alethinophidia, the prefrontal extends medially across the frontal and overlaps the frontal for 50% or more of its width. In Pythoninae and Boinae, the prefrontals extend medially across the frontal and almost contact along the midline. The same condition is also seen in *Xenopeltis*.
  165. Prefrontal: anterior margin concave, bounding an expanded narial aperture: absent (0) or present (1). In *Loxocemus bicolor* and *Xenopeltis unicolor*, the anterior margin of the prefrontal is strongly concave, bounding the caudal and caudoventral margins of an expanded narial aperture.
  166. Frontal: nasal processes of frontal project between nasals (0), or nasal processes absent (1) (modified from Gauthier et al., 2012: 30). Primitively in squamates, the naso-frontal joint is V-shaped or W-shaped, with the frontals bearing a pair of nasal processes that project between the nasals. In all known snakes, the nasal processes of the frontals are lost and a hinge joint is typically developed between the nasals and frontals. In Henophidia, the nasals do not articulate with the frontals dorsally, with the exception of Pythoninae.
  167. Frontals: frontals taper anteriorly, distinct interorbital constriction (0) or frontals broad anteriorly, interorbital region broad (1). A similar character is used by Lee and Scanlon (2002) and Scanlon (2002). Primitively in lizards, the frontals are subtriangular in dorsal view, being broad posteriorly and distinctly constricted anteriorly between the orbits, with the interorbital region being about half the width of the frontal at the frontoparietal suture. In Serpentes, the anterior width of the frontals is comparable to the posterior width at the frontoparietal suture.
  168. Frontal: subolfactory process abuts prefrontal in an immobile articulation (0) or subolfactory process articulates with prefrontal in a mobile joint (1) or subolfactory process with a distinct lateral peg or process that clasped dorsally and ventrally by the prefrontal (2). ORDERED. Primitively in lizards, the

- prefrontal simply abuts the frontal laterally in an immobile joint. In Scolecophidia, the subolfactory process articulates with the prefrontal via a kinetic joint. In *Dinilysia*, Madtsoiidae, and most crown Alethinophidia, there is a prominent lateral process clasped dorsally and ventrally by the prefrontal.
169. Frontals and parietals: do not contact ventrally (0) or descending wings of frontals and parietals contact ventrally to enclose the optic foramen (1) (Scanlon, 2005, 2006). Primitively in lizards the frontals and parietals do not enclose the optic foramen. In *Dinilysia patagonica*, *Yurlunggur* sp. and *Wonambi naracoortensis*, the frontals and parietals bear descending processes that partly enclose the brain but fail to enclose the optic foramen ventrally (Scanlon, 2005, 2006). In Anilloidea, Booidea, Bolyeriidae, Tropidophiidae and basal Caenophidia, the descending wings of the frontals and parietals contact ventrally and enclose the optic foramen. The optic foramen becomes ventrally open again in some members of the Colubroidea. The optic foramen is fully enclosed in Scolecophidia and therefore coded as state 1, but the foramen is enclosed by the frontal rather than the frontal and parietal which raises the possibility that this condition is not homologous.
  170. Parietal, sagittal crest: absent (0), present posteriorly but not anteriorly, and extending for no more than 50% of parietal midline length (1), or present anteriorly and posteriorly, and extending more than 50% of parietal midline length (2) (modified from Gauthier et al., 2012). This character combines two characters from Gauthier et al. (2012): state (1) tracks the simple presence vs. absence of a parietal sagittal crest; state (2) indirectly tracks the shape of fossa from which temporal muscles originate. A parietal sagittal crest is absent primitively in Anguimorpha. Parietal sagittal crests are variably developed in snakes, and may be absent, developed posteriorly, or developed along the length of the parietal. Primitive snakes including *Dinilysia patagonica*, Madtsoiidae, Aniliidae, and *Cylindrophis ruffus* have an extensive parietal crest. The parietal crest is restricted to the posterior of the skull in Bolyeriidae, Tropidophiidae, and Caenophidia.
  171. Parietal: narrow (0) or inflated (1). Primitively in snakes, including *Dinilysia patagonica*, Madtsoiidae, *Anilius scytale* and *Cylindrophis ruffus*, the parietal is narrow in dorsal view. An inflated parietal is seen in all macrostomatans, as well as Scolecophidia, *Anomochilus leonardi*, and Uropeltinae. Although crushed, the postorbital region of the parietal in *Haasiophis terrasanctus* appears to have been expanded to a degree comparable to that seen in the basal macrostomatan *Loxocemus bicolor* and it is coded as exhibiting the derived state.
  173. Skull, postorbital region relative length: (0) short, less than half the length of the skull; (1) elongate, half or more the length of the skull. In anguimorphs and other lizards, the postorbital region (as measured from the frontoparietal suture to the occipital condyle) is typically less than half the overall length of the skull. In all

- snakes examined except *Typhlops*, the postorbital region is elongated, with the distance from the frontoparietal suture to the occipital condyle representing 50% the skull length or more.
174. Supraoccipital region of skull, nuchal crests absent (0) or present (1) (Gauthier et al., 229:2). Primitively in snakes the temporal muscles attach to a sagittal crest. In Macrostromata (excepting *Lichanura* and *Acrochordus*), a nuchal crest extends laterally across the supraoccipital or supraoccipital/parietal for attachment of the parietal muscles, giving the ridges for temporal muscle attachment a Y or forked configuration.
  175. Supratemporal: supratemporal short, does not extend posterior to paroccipital process (0) or elongate, extending well beyond the paroccipital process (1). Primitively the supratemporal is short and does not extend project beyond the paroccipital process. In *Loxocemus*, *Xenopeltis*, booids, Bolyeriidae, Tropidophiidae, and most Caenophidia, the supratemporal is elongate and projects beyond the paroccipital process, but the condition is lost in *Acrochordus*. Simoliophiids have a free supratemporal, but in *Haasophis terrasanctus* (Rieppel et al., 2003) a free but short left supratemporal ends near the end of the paroccipital process; thus the two characters (elongate supratemporal, and free supratemporal) appear to be distinct. The supratemporal appears to be longer in *Pachyrhachis problematicus* but the skull roof is poorly preserved making its position relative to the other elements unclear.
  176. Maxilla: palatine process short, weakly developed, (1); palatine process long, strongly projecting medially (1) (Lee and Scanlon, 2002; Scanlon, 2006). Primitively the palatine process of lizards is an anteroposteriorly broad, mediolaterally narrow flange. A long, medially projecting palatine process is unique to *Dinilysia patagonica*, Madtsoiidae, and crown Alethinophidia. The highly modified skull of Scolecophidia complicates comparisons, but a stubby process of the maxilla abuts the palatine in *Leptotyphlops dulcis* and scolecophidians are therefore scored as 0. *Xenopeltis unicolor* is unique among the alethinophidians examined here in lacking a distinct palatine process. Zaher and Scanferla (2012:152) discuss a related character but as coded for *Dinilysia* this character describes the reduced maxillary process of the palatine, rather than the enlarged palatine process of the maxilla.
  177. Maxilla: facial process projects up strongly, caudal margin inclined steeply relative to maxilla (0) or facial process weakly projecting, caudal margin of facial process lies at an angle of 30° to the horizontal or less (1). Primitively in lizards and in *Coniophis precedens*, the posterior margin of the maxilla rises up at a steep angle relative to the suborbital process of the maxilla; typically in those snakes that retain a facial process (*Dinilysia patagonica*, Madtsoiidae, Aniliidae) it slopes forward at a low angle. *Leptotyphlops dulcis* and *Anomochilus leonardi* among Serpentes exhibit state 0.

178. Maxilla, premaxillary process: medial projection articulating with vomers present (0); premaxillary process does not contact vomers (1). In squamates ancestrally the maxilla's premaxillary process bears a prominent medial process that contacts the vomer. *Coniophis precedens* retains a large process with an expanded distal end bearing an articular surface, indicating that the maxilla retained a contact with the vomers. The process is reduced or absent, and vomer-maxilla contact is lost, in all Serpentes. A prominent medial projection of the premaxillary process does occur in *Anilius scytale* and *Uropeltis melanogaster*, but it fails to touch the vomers.
179. Maxilla, number of mental foramina: 5 or more (0); 4 or fewer (1). Primitively in lizards the maxilla bears a large number of mental foramina. Although the number is highly variable and can vary between the left and right maxillae, there are typically 5 or more mental foramina. In all extant snakes examined, there are 4 or fewer mental foramina on the maxilla. Among fossil snakes, *Coniophis precedens* retains more than five mental foramina, and Madtsoiidae appear to have five foramina on the maxilla.
180. Maxilla, supradental shelf development: extending the full length of the maxilla (0); reduced anterior to palatine process (1). Primitively in squamates, the toothrow is separated from the maxilla by a distinct horizontal shelf extending along the medial surface of the maxilla. *Coniophis precedens* retains the primitive condition. In *Dinilysia* and all more crownward snakes, the supradental shelf is reduced anterior to the palatine process. A shelf-like medial structure is also present in *Leptotyphlops dulcis* but in the absence of teeth it is unclear whether this structure represents a supradental shelf or simply the ventral margin of the dentary. *Typhlops jamaicensis* and *Liotyphlops albirostris* clearly lack a supradental shelf and so Scolecophidia are scored with state 0.
181. Maxilla: medial surface of facial process with a distinct naso-lacrimal recess demarcated dorsally by an anteroventrally trending ridge: (0) present; (1) absent. In autarchoglossan lizards ancestrally, there is a distinct naso-lacrimal recess on the medial surface of the maxilla (Gauthier, 1982). The dorsal border of this recess is marked by a ridge that descends anteroventrally from just above the lacrimal duct to the dorsal surface of the supradental shelf of the maxilla. The lacrimal duct exits here to join the vomeronasal organ further anteriorly. The dorsal ridge and associated naso-lacrimal recess are absent from all known snakes, including *Coniophis precedens*. A distinct medial fossa is found on the posterodorsal end of the facial process in both *Dinilysia patagonica* (Zaher and Scanferla, 2012) and *Wonambi naracoortensis* (Scanlon, 2005), but this fossa continues onto the prefrontal in *Dinilysia* and so it is interpreted as the fossa for the lateral recess of the nasal capsule, rather than the lacrimal fossa. The medial surface of the maxilla is broadly concave in *Leptotyphlops*, but lacks a distinct ridge and so the nasolacrimal recess is interpreted as being absent here.

182. Maxilla: medial surface of the facial process with a well-defined fossa for the lateral recess of the nasal capsule: present (0); reduced and present as a small fossa on the back of the facial process (1); absent, fossa for the lateral recess developed entirely on the prefrontal (2) (ORDERED). In anguimorphs, the dorsal end of both the facial process and the prefrontal are concave medially to receive the lateral recess of the nasal capsule. *Coniophis precedens* retains the primitive condition of having a broad, concave depression on the facial process. In *Dinilysia patagonica* (Zaher and Scanferla, 2012) and *Wonambi naracoortensis* (Scanlon, 2005) the maxilla bears a small fossa posterodorsally. In *Dinilysia* this fossa is confluent with the medial fossa of the premaxilla, indicating that this depression accommodated the lateral recess. In all higher snakes, the maxilla lacks a fossa for the nasal capsule; instead the fossa for the nasal capsule is developed exclusively on the prefrontal. A broad fossa is present on the medial surface of the ascending process in *Leptotyphlops*. It remains unclear whether this fossa is homologous or not given the highly derived nature of the skull, but we tentatively consider *Leptotyphlops* as exhibiting state 2. The maxilla lacks a medial fossa in typhlopids and anomolepidids, and so we code Scolecophidia as 0 & 2.
183. Maxilla: extensive contact of dorsal margin of maxilla with nasal (0) or nasal-maxilla contact lost (1) (Estes et al., 1988; Gauthier et al., 2012). Primitively in lizards the maxilla articulates with the nasal. This condition is retained in Anguillidae and *Xenosaurus* but lost in *Shinisaurus* and Varanoidea. Maxilla-nasal contact is lost in all snakes.
184. Maxilla: maxilla overlaps prefrontal laterally in a tight sutural connection (0) overlap reduced, mobile articulation (1). Primitively in lizards the maxilla contacts the premaxilla by overlapping it laterally to form a tight lap joint. In snakes, lateral overlap of the maxilla is limited or absent, and the contact is loose, permitting kinesis. The posterodorsal margin of the facial process is extremely thin and platelike in *Coniophis precedens*, indicating an immobile maxilla-premaxilla overlap.
185. Maxilla: excluded from anteroventral margin of the orbit by jugal (0), or maxilla forms anteroventral margin of orbit (1). Primitively, the jugal slots into a narrow, V-shaped recess on top of the posterior process of the maxilla and forms the anteroventral margin of the orbit. This V-shaped suture is clearly present in *Coniophis precedens* and so it is scored as state 0. In all other known snakes, the maxilla alone forms the anteroventral and ventral margin of the orbit. Scanlon (2006) has argued that the postorbital bar in *Yurlunggur* is composed of the jugal; but assuming that this element is the jugal, *Dinilysia* and *Yurlunggur* still resemble other snakes in that the jugal is excluded from the anteroventral margin.
186. Maxilla: palatine process of maxilla projects medially (0) or palatine process of maxilla is downturned (1). Primitively in anguimorphs, the palatine process of the maxilla is small and projects medially. Although the palatine process resembles



- crown Alethinophidia in being enlarged in both *Dinilysia patagonica* (Zaher and Scanferla, 2012) and *Wonambi naracoortensis* (Scanlon, 2005), the palatine process retains the primitive, lizard-like orientation and projects medially. In Alethinophidia, the palatine process is pendant and is projected downward or has its medial end turned down. Exceptions include *Uropeltis melanogaster* and *Xenodermus javanicus*, in which the process projects medially.
187. Maxilla, superior alveolar foramen: positioned near the middle of the palatine process, and opening posterodorsally (0) or positioned near the anterior margin of the palatine process, and opening medially (1). Primitively in anguimorphs, the superior alveolar foramen is centered in the palatine process and opens back and up, such that it is not visible in medial view. This primitive condition is retained in *Coniophis precedens* and the scolecophidian *Leptotyphlops dulcis* (the superior alveolar foramen is absent in anomalepidids and typhlopids). In *Dinilysia patagonica*, *Wonambi naracoortensis*, and all Alethinophidia in which the foramen is present, the superior alveolar foramen is located at the anterior margin of the palatine process and opens posteromedially or medially.
  188. Maxilla, accessory foramen posterior to palatine process: absent (0) or present (1). Primitively in anguimorphs, the maxilla is pierced posteriorly by a single opening above the palatine process, the superior alveolar foramen. This condition is retained in *Dinilysia patagonica* (Zaher and Scanferla, 2012) and as illustrated, in *Wonambi naracoortensis* (Scanlon, 2005). In crown Alethinophidia, a small second foramen is present posterior to the palatine process. CT data show that this foramen is connected internally by a channel to the superior alveolar foramen. The accessory foramen is lost in Bolyeriidae and *Acrochordus javanicus*.
  189. Maxilla, ectopterygoid process absent (0) or present (1) (Lee and Scanlon, 2002; Scanlon, 2006; Gauthier et al., 2012). In a number of alethinophidians, the posterior dentigerous process of the maxilla is expanded medially at, or slightly ahead of, the contact with the ectopterygoid. This feature appears to diagnose the clade containing Bolyeriidae, Tropidophiidae, and Caenophidia but an ectopterygoid process also occurs in Boinae, *Xenopeltis unicolor*, and *Cylindrophis ruffus*.
  190. Maxilla: articulates with distally expanded postorbital element to form a complete postorbital bar: present (0), absent (1) (Lee and Scanlon, 2002; Scanlon, 2006). Primitively in squamates the maxilla is connected to the skull roof by a postorbital bar formed by the jugals and postfrontal. In all extant snakes, postorbital elements are either absent, or fail to articulate with the maxilla. A complete postorbital bar is retained in *Dinilysia patagonica* and *Yurlunggur*, however, in which there is an elongate postorbital element, variously interpreted as a jugal (Scanlon, 2006) or a postorbital (Zaher and Scanferla, 2012), with an expanded distal end for articulation with the maxilla. The homology of the postorbital elements in snakes is disputed, but in the absence of definitive evidence one way or the other, we elect to code the character as a potential homology shared by lizards, *Dinilysia*,

- and Madtsoiidae, rather than assume *a priori* that the structures are nonhomologous.
191. Maxilla: 15 or more maxillary teeth (0), fewer than 15 maxillary teeth (1) (Lee, 1998). A reduced number of maxillary teeth is seen in Scolecophidia and among all members of the Anilioidea.
  192. Postfrontal: anterior and posterior processes clasping frontals and parietals (0), anterior and posterior processes present, but postfrontal abuts frontals and parietals (1) anterior and posterior processes absent (2) ORDERED. Lee and Scanlon (2002); Scanlon, (2006). Primitively in lizards the postfrontal bears distinct anterior and posterior processes that wrap around the frontal anteriorly and the parietal posteriorly. In *Dinilysia* and Madtsoiidae, the postfrontal retains a distinct triradiate shape with anterior and posterior processes, but abuts the frontal/parietal complex rather than embracing it. In those Alethinophidia that retain a postfrontal, the anterior and posterior processes are absent.
  193. Supratemporal: free caudal end of supratemporal projects posteroventrally (0) posteriorly or posterodorsally (1). In the basal macrostomates *Loxocemus* and *Xenopeltis*, Ungaliophiidae, Bolyeriidae, and Tropidophiidae, the caudal end of the supratemporal projects ventrally in lateral view. In Erycinae, Boinae, Pythoninae, and Caenophidia, the caudal end of the supratemporal projects horizontally or slightly dorsally.
  194. Quadrate, lateral conch present (0) or absent (1) (Gauthier et al., 2012). Primitively in lizards the lateral surface of the quadrate is concave and bears a prominent anterior crest, a feature associated with the tympanum. The lateral conch of the quadrate is absent in all known snakes.
  195. Quadrate, maximum length relative to proximal width: quadrate elongate, maximum length at least 125% of maximum width of quadrate head (0), or quadrate short, length less than 125% of width of quadrate head (1). The quadrate is relatively long in squamates ancestrally. It shortens in basal snakes, and becomes long again in Simoliophiidae and crown Macrostromata (with the exception of *Xenopeltis*). The scolecophidian *Typhlops* appears to have a short quadrate shaft with a long posterior process, whereas *Leptotyphlops* has a long, splint-like quadrate, although this may be derived from a *Typhlops*-like quadrate by reducing the width of the head; Scolecophidia are scored as polymorphic for this character. Lee and Scanlon (2002) and Scanlon (2006) also incorporate a character for quadrate length, but it is defined differently.
  196. Quadrate, proximal end platelike: absent (0) or present (1). In lizards and basal snakes, the proximal end of the quadrate has a robust head, or a splint-like end in Scolecophidia. In Simoliophiidae and crown Macrostromata, the proximal end of the quadrate is anteroposteriorly expanded and mediolaterally compressed to produce a spatulate shape.

197. Palatine, palatine teeth small relative to lateral teeth (0) or enlarged, palatine teeth at least half the diameter of posterior maxillary teeth (1). Primitively in lizards (e.g., *Shinisaurus*) and the basal snake *Dinilysia*, the palatine teeth are small. In Madtsoiidae and Alethinophidia, the palatine teeth are enlarged in diameter and length.
198. Palatine, elongate lateral process projecting to lateral edge of orbit to articulate with the caudal margin of the prefrontal: absent (0) or present (1) (Lee and Scanlon, 2002; Scanlon, 2006). *Xenopeltis unicolor* and *Loxocemus bicolor* are unique among the species examined here in having an elongate lateral process of the palatine that projects laterally almost to the edge of the orbit, bracing the prefrontal caudally. Although the palatine also extends towards the orbit and underlies the prefrontal in anguimorphs (e.g., *Celestus enneagrammus*, *Heloderma horridum*) the configuration is different; in *Loxocemus* and *Xenopeltis* the palatine is expanded into a spur lateral to the foramen for the maxillary branch of the trigeminal nerve, whereas it is the medial part of the palatine that is expanded in anguimorphs.
199. Epipterygoid: present (0), or absent (1) (Estes et al., 1988; Lee, 1998; Gauthier et al., 2012). The epipterygoid is absent in all known snakes.
200. Ectopterygoid clasps pterygoid anteromedially (0), ectopterygoid overlaps pterygoid (1), ectopterygoid abuts pterygoid medially (2) (UNORDERED) (Tchernov et al., 2000). Ancestrally in anguimorphs, the ectopterygoid articulates with the pterygoid anteromedially and wraps around the pterygoid lateral process dorsally and ventrally. In Anilioidea, *Loxocemus bicolor*, *Xenopeltis unicolor*, Bolyeriidae, Tropidophiidae, and Caenophidia, the ectopterygoid has a simple, dorsally overlapping contact with the pterygoid. In Booidea, the ectopterygoid abuts the ectopterygoid, but contacts it medially, rather than dorsally.
201. Vidian canals: enclosed in sphenoid (0) or open intracranially (1). Scanlon and Lee (2002), Scanlon (2006). Primitively the vidian canals are enclosed in the sphenoid throughout their length. In Scolecophidia, Anilioidea, and most Henophidia, the canal is broadly open inside the braincase. The vidian canal is enclosed in the sphenoid in *Dinilysia*, Madtsoiidae, *Loxocemus*, *Xenopeltis*, and Caenophidia, although the vidian canal communicates with the interior of the braincase via a small foramen.
202. Vidian canals: posterior openings symmetrical (0) or asymmetrical, opening on either the left or right side distinctly enlarged (1). (Lee and Scanlon, 2002; Scanlon, 2006; Gauthier et al., 2012). The posterior openings of the vidian canal are distinctly asymmetrical in a number of macrostomatans, with an enlarged opening on either the left (*Loxocemus bicolor*, *Python molurus*) or right (*Boa constrictor*, *Eryx colubrinus*).

203. Exoccipitals, separated ventral to foramen magnum (0) or contact below foramen magnum (1) (Lee and Scanlon, 2002; Scanlon 2006). Primitively in lizards and snakes the exoccipitals do not contact below the foramen magnum. In *Wonambi* (Scanlon, 2005), *Yurlunggur* (Scanlon, 2006) and Uropeltidae, the exoccipitals contact below the foramen magnum and exclude the basioccipital from the dorsal surface of the occipital condyle.
204. Exoccipital-opisthotic: horizontal, winglike crista tuberalis absent (0) or present (1). In *Wonambi* (Scanlon, 2005) and *Yurlunggur* (Scanlon, 2006) the posterior margin of the exoccipital bears a broad, winglike crest that is oriented horizontally. A similar crest appears to be present in *Sanajeh* (Wilson et al., 2010)
205. Otoccipitals, do not project posteriorly to level of occipital condyle (0) or project posteriorly to conceal the occipital condyle in dorsal view (1). The occipital condyle is visible in dorsal view in anguimorphs, Scolecophidia, *Dinilysia patagonica*, Anilioidea, and the basal macrostomatans *Loxocemus bicolor* and *Xenopeltis unicolor*. The otoccipital shelf obscures the occipital condyle in all Henophidia examined here, with the exception of *Acrochordus*. This character appears to relate to a shorter occipital condyle, rather than to an elongate otoccipital shelf.
206. Sclerotic ring: present (0) or absent (1) (Lee, 1998). The sclerotic ring is lost in all known snakes.

#### MANDIBLE

207. Dentary: enlarged mental foramen absent (0) or present (1). Primitively in lizards the mental foramina are relatively small. In snakes, there is an enlarged mental foramen near the tip or middle of the jaw, which may or may not be accompanied by a smaller mental foramen posteriorly. This character is distinct from the enlarged mental foramen at the back of the toothrow in Varanoidea.
208. Dentary, depth of Meckelian groove anteriorly: deep slot (0); shallow sulcus (1). In *Coniophis precedens* and the stem snakes *Najash rionegrina* and *Dinilysia patagonica*, Meckel's groove just behind the symphyseal region forms a relatively deep, parallel-sided slot, similar to the condition in anguimorphs. In Scolecophidia, Madtsoiidae, and crown Alethinophidia the Meckelian groove is reduced to a shallow sulcus.
209. Dentary, angular process shape: (0) posteroventral margin of the dentary angular process is weakly wrapped around the underside of the jaw; (1) the dentary angular process projects more nearly horizontally to wrap beneath the jaw. Primitively in squamates, the posteroventral margin of the dentary (angular process) is weakly wrapped around the underside of the jaw. Although the back of

- the dentary is broken in *Coniophis precedens* and *Najash rionegrina*, the preserved parts of the dentary indicate that they retain the ancestral squamate condition. In *Dinilysia patagonica*, Madtsoiidae, and crown snakes, however, the angular process is strongly curled under the mandible, such that the angular process lies in a more or less horizontal position.
210. Dentary, angular process length relative to coronoid process: angular process distinctly shorter than coronoid process, the former terminating well anterior to the latter (0), or subequal in length posteriorly (1) (Lee and Scanlon, 2002; Scanlon, 2006). The angular process is distinctly shorter than the coronoid process in *Dinilysia* (a long coronoid process was present but has been broken off, as inferred by the presence of a dentary facet on the lateral surface of the coronoid), Scolecophidia, Madtsoiidae, *Cylindrophis* among the Anilioidea, Tropidophiidae, and Caenophidia. The angular process extends to the back of the dentary in *Anilius*, *Anomochilus*, Booidea, and Bolyeriidae.
  211. Dentary, symphysis weakly projecting medially (0) or hooked inward and strongly projecting medially (1) (Gauthier et al., 2012). In anguimorphs and scolecophidians, the dentary symphysis projects weakly medially or not at all. In *Najash*, *Dinilysia*, *Wonambi* and all Alethinophidia examined here except for *Uropeltis*, the the dentary symphysis is strongly hooked inwards and projects medially in dorsal view. This character is modified from Gauthier et al. (2012), who describe the dentary symphysis as hooked down and in. If the mandible is oriented with the bases of the teeth vertical, then the symphysis does indeed appear to be hooked down, but when the dentary is in life position in the skull (and the teeth project dorsolaterally), the symphysis is hooked inward, not down.
  212. Dentary, ventral margin unexpanded, medial margin of dentary straight in ventral view (0), ventral margin of dentary expanded, medial margin crescentic in ventral view (1). Scanlon (2005) describes a ‘medioventral crest’ on the dentary of *Wonambi naracoortensis* in which the ventral margin of the dentary has a broad, convex margin that wraps underneath the Meckelian groove. The medioventral crest is absent in anguimorphs as well as basal snakes including *Coniophis precedens*, *Najash rionegrina*, *Dinilysia patagonica*, and Scolecophidia. A medioventral crest is especially well-developed in *Wonambi* but this feature is widely distributed (albeit not as well-developed) among alethinophidians, including *Pachyrhachis problematicus*, *Loxocemus bicolor*, Ungaliophiidae, Bolyeriidae, Tropidophiidae, and Caenophidia.
  213. Dentary, coronoid process wraps around surangular laterally and medially (0), broad and sits atop surangular (1). Primitively in lizards, the coronoid process of the dentary wraps over the top of the surangular, extending medial and lateral to the dentary process of the surangular. In Scolecophidia, *Dinilysia patagonica*, and higher snakes, the dentary sits atop the surangular process, sometimes in a shallow trough. This feature is absent in the anilioids *Anilius scytale* and *Uropeltis melanogaster*.

214. Dentary, coronoid process with a slot for medial tab of surangular: absent (0) or present (1). A surangular slot is absent from the dentary in *Dinilysia patagonica* and Scolecophida. In *Cylindrophis ruffus* and most Macrostromata, the coronoid process of the dentary bears a distinct slot beneath the subdental shelf, which receives a medial tab of the surangular. *Wonambi naracoortensis* closely resembles macrostomatans here (Scanlon 2005), and appears to share this feature. Among anilioids, the surangular slot is absent in *Anilius scytale*, *Uropeltis melanogaster*, and *Anomochilus leonardi*. It is present in all of the macrostomatans studied except for *Xenopeltis unicolor* and *Xenodermus javanicus*.
215. Dentary, subdental ridge, depth anteriorly: shallow anteriorly (0); deep (1). In lizards ancestrally, the subdental surface above Meckel's canal forms a thin lip along the length of the dentary. In *Coniophis precedens* and more crownward snakes, however, the subdental surface is markedly deeper anteriorly, and is typically half the height of the dentary or more. Scolecophidians are the only snakes to have a shallow subdental ridge at the tip of the jaw.
216. Dentary, subdental ridge, depth posteriorly: shallow posteriorly (0); deep (1). In lizards ancestrally, and in *Coniophis precedens*, the subdental surface above Meckel's canal forms a thin lip from just anterior to the articulation of the splenial posteriorly. In *Najash rionegrina* and more crownward snakes, however, the subdental surface is deepened posteriorly as well as anteriorly.
217. Dentary, enlarged mental foramen position: near tip of dentary (0); displaced from tip of jaw (1); displaced further to lie halfway between the symphysis and the surangular notch (2) (Gauthier et al, 2012). ORDERED. The mental foramen starts out at the tip of the dentary in basal snakes, including *Coniophis precedens* and *Najash rionegrina*. This character has a complicated distribution among higher snakes, but the Tropidophiidae - Caenophidia clade is characterized by state (2).
218. Surangular, dentary process with a distinct triradiate cross-section: absent (0) or present (1). In anguimorphs the dentary process of the surangular is a simple blade. This condition is retained in *Dinilysia patagonica*, and Scolecophidia also have a simple anterior process of the dentary. In *Wonambi naracoortensis*, *Cylindrophis ruffus*, *Anilius scytale*, and Macrostromata, the dentary process of the surangular has a triradiate or T-shape, with a medial blade and dorsal and ventral blades. The bolyeriid *Casarea dussumieri* lacks the triradiate dentary process, but it is present in *Xenophidion acanthognathus*. This character may be associated with the development of a surangular slot of the dentary (character 193) although a number of species have triangular dentary processes that do not insert into a dentary slot.

219. Surangular, adductor fossa small (0) or extended caudally towards jaw articulation (1). Primitively in *Dinilysia patagonica*, *Wonambi naracoortensis*, and uropeltids, the adductor fossa is relatively small. It is enlarged in *Anilius*, *Pachyrhachis problematicus*, and all macrostomates studied except for *Acrochordus*.
220. Surangular: ventrolateral surface of surangular bearing a distinct crest for attachment of adductor muscles: absent (0) or present (1). The ventrolateral surface of the mandible is smooth in basal snakes. In many henophidians, the ventrolateral surface of the mandible bears a distinct crest or ridge which marks the insertion of the jaw adductors.
221. Coronoid, lateral overlap of coronoid onto dentary absent (0) or present (1). (Gauthier et al. 2012: 394). Primitively in anguimorphs, the coronoid extends anteriorly to overlap the lateral surface of the dentary. This overlap is absent in all known snakes, fossil and extant.
222. Splenial attachment to dentary above Meckel's canal: close throughout length (0); loose, with dorsal dentary suture confined to posterodorsal corner of splenial (1) (Pregill et al., 1986); (2) contact with subdental shelf reduced to a small spur of bone or contact lost entirely (ORDERED). Ancestrally in squamates, the splenial articulates along the base of the subdental shelf above Meckel's canal. In snakes, the splenial may extend well forward along the jaw, but in *Dinilysia* and basal Alethinophidia, the splenial only contacts the back of the subdental ridge. *Coniophis* appears to share this condition on the basis of the development of a splenial facet at the back of the subdental ridge. Contact between the splenial and subdental ridge is further reduced or lost entirely in a number of taxa, including *Xenopeltis unicolor*, Erycinae, Ungaliophiinae, Bolyeriidae, Tropidophiidae, and Caenophidia. Both derived states are also present in Varanoidea.
223. Splenial – angular articulation: splenial overlaps angular (0); splenial abuts against angular to form a hinge joint (1) (Pregill et al., 1986). The splenial of squamates projects caudally to overlap the medial surface of the angular. In Serpentes, however, medial overlap is eliminated and the splenial forms a butt joint with the angular which creates a hinge between the two bones. This hinge joint is retained in some scolecophidians, e.g. *Leptotyphlops dulcis*, but is absent in others, e.g. *Typhlops jamaicensis*. Although the derived state is often attributed to *Lanthanotus borneensis* (e.g., McDowell and Bogert, 1954), and the angular is notched medially for reception of the splenial, the bones still overlap one another (Gauthier et al., 2012).
224. Splenial, size: splenial elongate, extends more than half of the distance from the angular to the dentary symphysis (0) or splenial short, extends less than half the distance from the angular to symphysis (1) (Lee; 1998; Lee and Scanlon 2002;

- Scanlon, 2006; Gauthier et al., 2012). Shortened splenials are found in Scolecophidia and crown Alethinophidia.
225. Splenial, anterior mylohyoid foramen present (0) or absent (1) (Lee and Scanlon, 2002; Scanlon, 2006). The anterior mylohyoid foramen is primitively present in snakes, and is lost in a number of lineages. The absence of the foramen may diagnose a *Loxocemus-Xenopeltis* clade.
226. Angular, lateral exposure (with coronoid region pointing dorsally): the angular is broadly exposed laterally along its length (0); the angular is only narrowly exposed laterally, if at all (1). In squamates ancestrally, the angular is broadly visible in lateral view. That condition appears to have been retained in Scolecophidia. In *Dinilysia patagonica* and Alethinophidia, however, the angular is borne mainly on the medial surface of the surangular, so that little if any of the element is visible in lateral view.
227. Angular, length posteriorly relative to glenoid (quadrate articulation): relatively long, extends more than half the distance from the anterior end of the angular to the glenoid; (0) relatively short, half or less of the distance to the glenoid (1); very short, one third or less of distance to the glenoid (2). ORDERED. In Anguimorpha ancestrally (except *Lanthanotus borneensis*), the angular bone is elongate, extending more than half the distance from the splenial to the quadrate articulation. That condition is retained in *Leptotyphlops* but not in *Typhlops*. In other basal snakes, including *Dinilysia patagonica* and *Wonambi naracoortensis*, as well as in *Loxocemus bicolor* and Pythonidae, the angular is reduced, and extends about 50% the length of the surangular. In most other Alethinophidia, the angular is further reduced, and is less than a third of the length of the surangular in ventral view.
228. Surangular, enlarged anterior surangular foramen: absent (0); or present (1). In squamates ancestrally, there is a small foramen on the external surface of the surangular near the surangular-dentary articulation, the anterior surangular foramen. In Serpentes this foramen is greatly enlarged.
229. Coronoid eminence: (0) well-developed; (1) weakly developed or absent (Gauthier et al., 1988). The coronoid eminence is here regarded as a well-developed convex protrusion on the anterodorsal margin of the surangular just behind the dentary. It can be composed of the coronoid alone (the ancestral squamate condition), the coronoid and surangular (common among basal alethinophidians), or the surangular alone (e.g., *Ungaliophis continentalis*). In the latter two cases, the surangular always rises steeply to just behind the dentary, whether or not a discrete coronoid bone is present (Gauthier et al., 2012). In other Serpentes the surangular is not so developed, and instead there is a prominent medial process (e.g. *Tropidophis haetianus*). That structure presumably arises from the prearticular bone, and not the surangular (the two bones are fused



- indistinguishably in all snakes). This character therefore emphasizes the shift in the adductor musculature from an insertion on the coronoid/surangular complex to insertion on the angular, seen in the Tropidophiidae-Caenophidia clade. Reduction of the coronoid eminence also occurs in the bolyeriid *Casarea dussumieri* (but not in *Xenophidion acanthognathus*) and *Xenopeltis unicolor*.
230. Glenoid, shape: quadrate cotyle shallow (0), anteroposteriorly concave and transversely arched, ‘saddle shaped’ (1). In squamates ancestrally, the articular bone bears a shallow glenoid with a pair of cotyles that articulate with the condyles of the quadrate. In Serpentes, the articulation for the quadrate is formed by a single articular surface, which is concave in lateral view and arched transversely, to create a distinctively saddle-shaped joint that apparently facilitates opening of the jaw and rotation about the long axis of the mandible. Some variant of this saddle-shaped articulation is seen in all snakes examined, with only two exceptions. *Anilius scytale* is unusual among snakes in that the jaw joint is cupped about the quadrate cotyles and strongly concave in lateral view, but not arched mediolaterally, creating a simple hinge rather than a saddle-shaped joint. However the jaw morphology is closer to that of snakes than to other squamates and so *Anilius* is scored as a 1. *Liotyphlops* has a rudimentary jaw joint rather than a saddle-shaped articulation, but *Leptotyphlops* and *Typhlops* have a saddle-shaped joint.
231. Retroarticular process: retroarticular process elongate (0) or shortened (1) (Lee and Scanlon, 2002; Scanlon, 2006, Gauthier et al., 2012). The retroarticular process is shortened relative to the condition in anguimorphs in all of the snakes examined here except *Xenodermus javanicus*.
232. Ventral projections (pedicles) of anterior precloacals: short, about 50% the length of the centrum (0) or long, subequal to or longer than centrum (1). In primitive snakes, including *Najash*, *Dinilysia*, and *Coniophis*, ventral projections of the anterior precloacal vertebrae are very short and are roughly half the length of the centrum of the vertebra. In Scolecophidia, Madtsoiidae, and Alethinophidia, ventral projections approach or exceed the length of the associated centrum.
233. Vertebrae, ridgelike or bladelike ventral keels developed posterior to pedicles: (0) absent; (1) present. In *Coniophis precedens* and basal crown snakes, the anterior pedicles grade nearly imperceptibly into low, narrow ridges. Posteriorly these ridges typically develop into a broad, ventrally rounded haemal keel.
234. Vertebrae, dorsolateral ridges of neural arch: (0) absent; (1) present (Scanferla and Canale, 2007). In squamates ancestrally, the dorsolateral surface of the neural arch is smooth. In basal snakes, including *Dinilysia patagonica*, *Najash rionegrina*, and Madtsoiidae, there are a pair of conspicuous mounds on the posterior margin of the neural arch to either side of the neural spine that continue forward as low ridges, which Scanferla and Canale termed “arqual ridges” (Scanferla and Canale, 2007). Similar ridges are also found in pythons. *Coniophis*

- precedens* bears a pair of low knobs in this region that are presumably homologous to the arqual ridges, but they do not extend forward to form ridges.
235. Vertebrae, vertebral centrum narrow in ventral view (0), or broad and subtriangular in shape (1). In primitive anguimorphs (e.g., *Shinisaurus*) and *Coniophis precedens*, the centrum is relatively elongate in ventral view. In a number of snakes, including *Najash*, *Dinilysia*, Madtsoiidae, *Loxocemus bicolor*, Boinae, and Pythoninae, the subcentral ridges extend anterolaterally to give the centrum a distinctly triangular shape in ventral view.
236. Vertebrae, arterial grooves absent in neural arch (0) or present (1). In squamates ancestrally, the neural arch forms an arch about the spinal cord, U-shaped in outline and flat on top of the centrum. *Coniophis precedens* and higher snakes are characterized by paired channels at the ventrolateral corners of the neural canal. These give the neural canal a distinctive inverted trefoil shape. The neural arch may be more U-shaped in some snakes (e.g. *Tropidophis*) but distinct arterial grooves are still present.
237. Vertebrae, posterior condyle confluent with the centrum ventrally (0) distinctly separated from centrum by a groove/constriction between the centrum and the condyle (1) (Lee and Scanlon, 2002; Scanlon, 2006). In anguimorphs and basal snakes, including *Coniophis precedens*, *Najash rionegrina*, and *Dinilysia patagonica*, the posterior condyle of the vertebra is confluent with the centrum ventrally. In Madtsoiidae and crown Alethinophidia, the edge of the condyle has a distinct rim separating it from the centrum and may also have a distinct groove running between the condyle and centrum, such that the vertebra appears to have a notch when viewed laterally.
238. Vertebrae narrow, width across zygapophyses not significantly greater than distance from prezygapophyses to postzygapophyses (0) or vertebrae wide, width across zygapophyses 150% of length or more. In primitive snakes, including *Coniophis*, *Najash*, and Scolecophidia, the neural arch is about as wide as long. In a number of snakes, including *Dinilysia*, Madtsoiidae, and Erycinae, Pythoninae, and Boinae, vertebrae are transversely expanded and the neural arch is much broader than long.

## 2. Edits to characters and codings

In adding characters to the matrix, we noticed that a number of characters (both new and previously identified) conflicted with previous hypotheses of tree topology put forward by Wilson et al. (2010), Zaher and Scanferla (2012) and Gauthier et al. (2012) and supported alternative placements for several key taxa, including (1) placement of *Dinilysia patagonica* on the alethinophidian stem (Tchernov et al., 2000; Conrad, 2008), (2) a basal position of Madtsoiidae relative to Anilioidea (Scanlon, 2000, 2006; Lee and Scanlon, 2002; Conrad, 2008), and (3) a *Loxocemus-Xenopeltis* clade (Scanlon, 2000, 2006; Lee and Scanlon, 2002; Gauthier et al., 2012). There are also disagreements over (4) the relationships of the Simoliophiidae with crown Macrostromata. We concur with recent studies that Simoliophiidae are related to macrostomatans (Tchernov et al., 2000; Apesteguía and Zaher, 2006; Wilson et al., 2010; Zaher and Scanferla, 2012; Gauthier et al., 2012), but recent analyses variously place Simoliophiidae on the stem of Macrostromata (Zaher and Scanferla, 2012), on the stem of Henophidia (Wilson et al., 2010; Gauthier et al., 2012) or unresolved with respect to *Loxocemus* and *Xenopeltis* (Apesteguía and Zaher, 2006).

In light of these conflicts, we carefully reexamined character codings relevant to these four problems to test the hypothesis that apparent character conflict might result in part from differences in interpretation of morphology. A complete list of our edits to the Zaher and Scanferla (2012) matrix, with discussion, is provided below.

### Edits to Zaher and Scanferla (2011) characters

46. *Original*. Ascending process of the maxilla present (0), absent (1).
46. *Revised*. Ascending process of the maxilla tall and extending as far dorsally as the dorsal margin of the prefrontals (0), short, ascending process terminates well below dorsal margin of the prefrontal (1), or absent (2) ORDERED

(Gauthier et al., 2012). *Coniophis* and other basal snakes, including Scolecophidia, *Dinilysia*, Madtsoiidae, Anilioidea, and Simoliophiidae, are characterized by reduction of the ascending process of the maxilla.

### Edits to Zaher and Scanferla (2011) character codings.

3. *Dinilysia* 1=>2.  
The replacement tooth figured for *Dinilysia patagonica* by Zaher and Scanferla (2012) has a long, thin, needle-shaped tip (state 2).
4. *Haasiophis* 1=>?

- Only the midline of the premaxilla is exposed in *Haasiophis terrasanctus*, making it impossible to determine whether teeth are present laterally or not; this character is therefore scored as missing data.
6. Uropeltidae 1=>1&0  
Palatal teeth are absent in *Uropeltis melanogaster* (state 1) but present in *Cylindrophis ruffus* (state 0).
  7. Uropeltidae 1=>0&1.  
The premaxilla is firmly sutured to the maxilla in *Uropeltis melanogaster*.
  10. Uropeltidae 0=>1&0; *Xenopeltis* 0=>1.  
The nasals are broad anteriorly (state 0) in *Uropeltis melanogaster* but narrow anteriorly in *Cylindrophis ruffus* (state 1). In *Xenopeltis unicolor* the nasals are broader anteriorly than posteriorly but this results from the narrow nasals being constricted posteriorly, rather than expansion of the nasals anteriorly, and so *Xenopeltis* is rescored as state 1.
  13. Boinae 0=>1, Ungaliophiinae 0=>1, Erycinae 0=>1.  
The articulation between the anterodorsal margin of the frontals and the nasals is reduced in booids (state 1), with the exception of pythons.
  35. Uropeltidae 1=>0&1  
A postorbital element is absent in *Uropeltis melanogaster* (state 1) but present in *Cylindrophis ruffus* (state 0).
  36. Outgroup 0=>1, Bolyeriidae 0=>1, *Anilius* 0=>?  
If the postorbital element in snakes is the jugal, then the elongate postorbital element (state 1) in snakes and anguimorphs would be homologous. In the absence of definitive evidence of homology we choose to code them as showing the same state, i.e. potentially homologous. The postorbital of *Casarea* is elongate (state 1); *Anilius* lacks a postorbital and is therefore coded as “?”
  38. *Dinilysia* 1=>0, *Wonambi* 1=>0, *Yurlunggur* 1=>0, *Pachyrhachis* 1=>?  
We consider this character to relate to a distinct shelf posterior to the orbit, which projects lateral to the frontals and which is oriented about 45° to the horizontal, a character that is restricted to Henophidia.
  40. *Sanajeh* 0=>?  
As preserved (Wilson et al., 2010) the parietal margin suggests a U-shaped frontal-parietal contact (state 1), but because the skull is damaged we code this feature as missing data.
  41. *Loxocemus* 1=>0  
The parietal is not notched for the optic foramen in *Loxocemus bicolor*, and instead closely resembles the primitive condition seen in *Xenopeltis unicolor* (state 0).

48. Uropeltidae 1=>1&2  
The posterior process of the maxilla is moderately long in *Uropeltis melanogaster* (state 1) but long and flat in *Cylindrophis ruffus* (state 2).
50. *Loxocemus* 1=>0 *Xenopeltis* 1=>0 Bolyeriidae 1=>0 Tropidophiidae 0=>1  
*Loxocemus bicolor*, *Xenopeltis unicolor*, and Bolyeriidae have a large superior alveolar foramen (state 1) but the foramen is reduced in Tropidophiidae (state 1).
53. *Sanajeh* 1=>?  
The element identified as a free supratemporal (state 1) by Wilson et al. (2010) does not lie atop the skull as expected for a supratemporal, and we consider its identity uncertain.
58. *Wonambi* 1=>0 *Yurlunggur* 1=>0.  
In anguimorphs, the pterygoid and palatine articulate in the horizontal plane and have an interlocking articulation (state 0). In extant Alethinophidia, the palatine has a tongue-and-groove articulation with the pterygoid: the posterior margin of the palatine bears a slot that accommodates a vertical flange from the pterygoid (state 1). In *Wonambi naracoortensis* (Scanlon, 2005) the caudal margin bears a weak notch but clearly lacks a vertical slot, similar to the condition in Varanidae and Anguinae. The figured pterygoid of *Yurlunggur* sp. (Scanlon, 2006) is identical to that of *Wonambi* and we therefore code it as "0" as well.
62. *Anilius* 0=>1 Uropeltidae 0=>1.  
CT scans show that a well-defined gap exists between the palatine and maxilla in anilioids (state 1), rather than a tight suture (state 0).
65. *Wonambi* 1=>0, *Yurlunggur* 1=>0; *Eupodophis* 65 :1=>? Tropidophiidae 0=>1, Pythoninae 0=>1, Erycinae 0=>1, *Acrochordus* 0=>1.  
*Wonambi* and *Yurlunggur* both have short internal articulations of the pterygoid and palatine (state 0). We could not assess this character for *Eupodophis descouensi* from the figures provided by Rieppel and Head (2004) and score it as missing data. Tropidophiidae, Python, Erycinae, and *Acrochordus* all have long posteromedial processes of the palatine that broadly overlap the pterygoid (state 1).
70. Uropeltidae, 0=>0&1.  
The ectopterygoid overlies the maxilla (state 1) in *Cylindrophis ruffus*.
74. *Loxocemus* 1=>0  
The quadrate of *Loxocemus bicolor* has a short, posteriorly projecting suprastapedial process (state 0) as in *Xenopeltis unicolor*.
78. Bolyeriidae 0=>1

- The stapedial shaft is short (state 1) in both *Casarea dussumerieri* and *Xenophidion acanthognathus*.
90. *Sanajeh* 1=>?, *Wonambi* ?=>0.  
*Sanajeh* is poorly preserved here and scored as missing data; *Wonambi naracoortensis* (Scanlon, 2005) appears to resemble *Dinilyisia* in that the prootic is exposed medial to the supratemporal facet (state 0).
91. *Loxocemus* 1=>0  
The exit for the hyomandibular branch of the facial nerve is located in a separate opening from the mandibular branch of the trigeminal nerve (state 0) in *Loxocemus bicolor*.
96. Uropeltidae 0=>0&1.  
A pterygoideus crest is absent (state 0) in *Uropeltis melanogaster*, but a low pterygoideus crest (state 1) is present on the ventral surface of the skull in *Cylindrophis ruffus*.
99. *Loxocemus* 1=>0; *Anilius* 1=>0  
Distinct basiptyergoid processes articulate with the pterygoids (state 0) in *Loxocemus bicolor*. Basiptyergoid processes are also present in *Anilius scytale*, being massively constructed but short and poorly differentiated from the base of the skull.
103. *Sanajeh* 0=>?  
The parabasphenoid is damaged in *Sanajeh indicus* (Wilson et al., 2010) and the shape of its rostroventral surface cannot be determined, and therefore this character is coded as missing data.
107. Uropeltidae 1=>1&2, *Dinilyisia* 1=>2  
Teeth do not extend to the back of the mandible in *Uropeltis melanogaster* (state 1) but *Cylindrophis ruffus* has a well-developed surangular notch with an elongate posterior dentary process bearing teeth along its length (state 2). The dentigerous process is broken caudally in *Dinilyisia patagonica*. Assuming the posterior process contacted the coronoid ascending process as occurs in anguimorphs and basal snakes, and as indicated by the presence of a dentary facet on the coronoid, the dentigerous process of *Dinilyisia* would have been elongate (state 2).
109. *Dinilyisia patagonica*, ?=>1; *Acrochordus* 0=>1.  
As described by Zaher and Scanferla (2012) the anterior end of the dentary in *Dinilyisia patagonica* bears a single, enlarged mental foramen (state 1).
- 110: *Haasiophis* 0=>1  
Although *Haasiophis terrasanctus* lacks the unique tall, recurved coronoid process seen in *Pachyrhachis problematicus* and *Eupodophis descouensi*, the distal end of the coronoid (as seen in figured radiographs) is distinctly expanded

- anteroposteriorly (state 1) as in the other Simoliophiidae (Rieppel et al., 2003) and therefore coded as "1" to emphasize its similarity in this feature to the other Simoliophiidae.
127. *Dinilysia* 1=>0&1  
As figured by Rage and Albino (1989) anterior trunk vertebrae of *Dinilysia patagonia* have subcircular condyles (state 1) but posterior trunk vertebrae appear to have ovoid condyles (state 1).
132. Anguimorph root, 0 => 0&1.  
Anguimorphs are polymorphic for this character, with xenosaurs having medially positioned synapophyses (Conrad, 2005).
154. Scolecophidia 1=>0&1.  
The coronoid lies medial to the compound bone in some scolecophidia (e.g. *Liotyphlops albirostris*) but it sits on the dorsal and dorsomedial surface of the compound bone (state 0) in *Leptotyphlops dulcis*.

### 3. Materials Examined

Coding of extant snakes was conducted using CT scan data from Gauthier et al. (2012), through examination of osteological specimens, and using publications for fossil taxa.

#### Fossil snakes

*Najash rionegrina*: Apesteguía and Zaher (2006); Zaher et al. (2009).

*Dinilysia patagonica*: CT scans, MACN-RN 1013, 1014, MUCP v38; Rage and Albino (1989), Scanferla and Canale (2007), Zaher and Scanferla (Zaher and Scanferla, 2012).

*Yurlunggur* spp.: Scanlon (2006), Mackness and Scanlon (1999).

*Eupodophis descouensi*: Rieppel and Head (2004)

*Haasiophis terrasanctus*: Rieppel et al. (2003)

*Pachyrhachis problematicus*: Polcyn et al. (2005), CT scans.

*Sanajeh indicus*: Wilson et al. (2010)

*Wonambi naracoortensis*: Scanlon(1995), Scanlon (2000).

#### Anilius

*Anilius scytale* MCZ R-5478, MCZ R-19537, MCZ R-2984, MCZ R-5479, skeletons

#### Scolecophidia

*Leptotyphlops dulcis*: CT scans, TNHC 60638

*Leptotyphlops macrorhynchus*: MCZ R-184114, skeleton

*Typhlops jamaicensis*: CT scans, USNM 12378

*Liotyphlops albirostris*: CT scans, FMNH 216257

#### Pythoninae

*Python molurus*: CT scans, TNHC 62769, YPM R 10871, skeleton

*Aspidites melanocephalus*: CT scans, FMNH 97055

#### Boinae

*Epicrates striatus*: CT scans, USNM 59918

*Boa constrictor*: CT scans, FMNH 31182; YPM R 10866, skeleton

#### Ungaliophiinae

*Ungaliophis continentalis*: CT scans, UTA 50569

*Ungaliophis panamensis*: MCZ 56051, skeleton



*Exiliboa placata*: CT scans, FMNH 207669

### **Tropidophiidae**

*Tropidophis haetianus*: CT scans, TNHC 64040; YPM R13585, skeleton  
*Trachyboa boulengeri*: CT scans, FMNH 131266

### **Bolyeriidae**

*Casarea dussumieri*: CT scans, UMMZ 190285; MCZ 49135, skeleton  
*Xenopheidion acanthognathus*: CT scans, FMNH 235170

### **Uropeltidae**

*Plectrurus aureus*: Comeaux et al. (2010)  
*Plectrurus perroteti*: MCZ 3875, skeleton  
*Uropeltis melanogaster*: CT scans, FMNH 167048-167051  
*Anomochilus leonardi*: CT scans, FRIM 0026  
*Cylindrophis ruffus*: FMNH 60958

### **Xenopeltis**

*Xenopeltis unicolor*: CT scans, FMNH 148900; MCZ 188760, 3114, 188759, 5483, skeletons

### **Loxocemus**

*Loxocemus bicolor*: YPM R13879, CT scans; YPM R13879, MCZ 31570, 31654 skeletons

### **Erycinae**

*Lichanura trivirgata*: CT scans, YPM R12869, YPM R17918, skeletons  
*Eryx colubrinus*: CT scans, FMNH 63117

### **Acrochordus**

*Acrochordus javanicus*, YPM R 10874, skeleton  
*Acrochordus granulatus*, FMNH 201350, 202059E

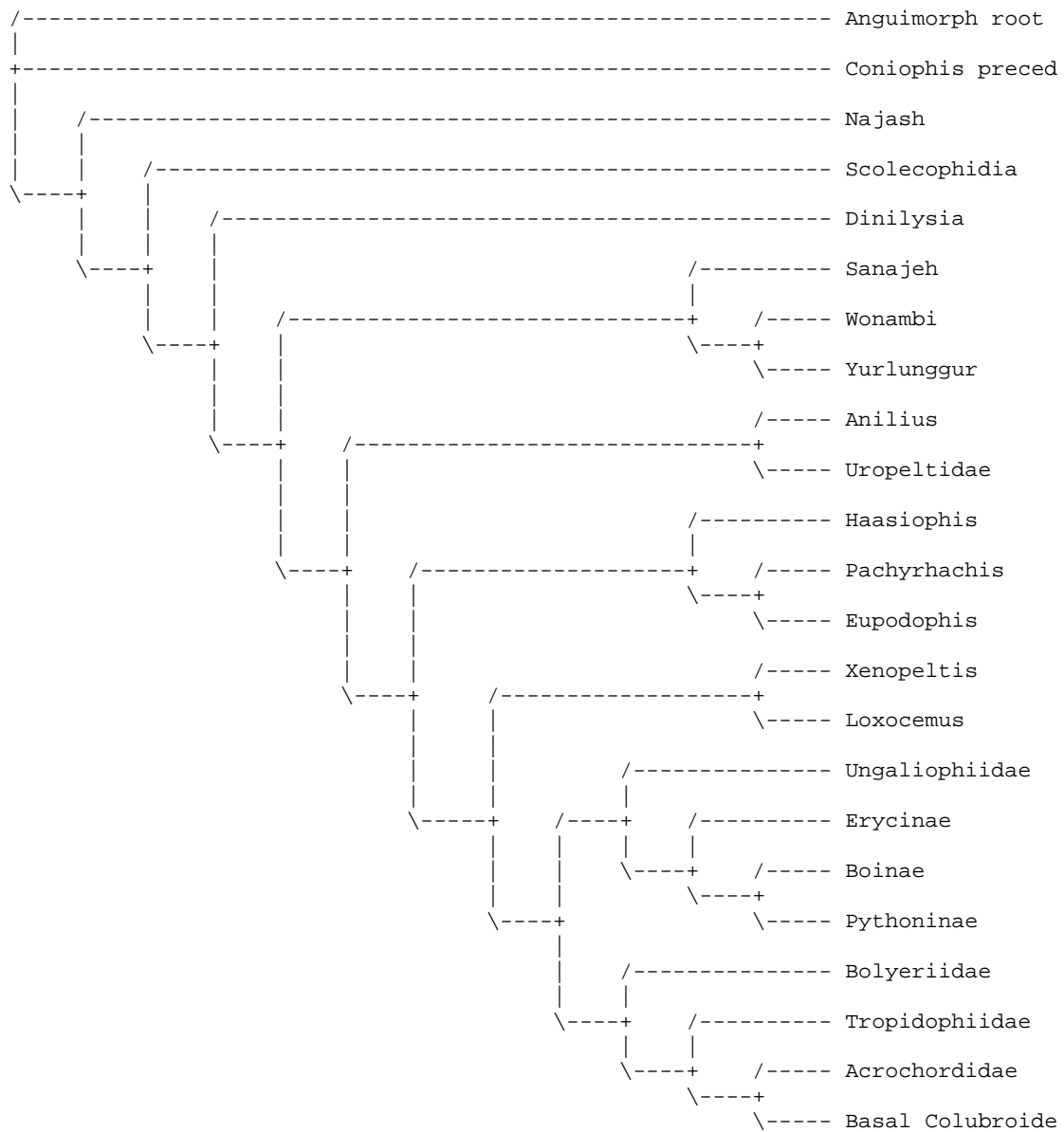
### **Basal Colubroidea**

*Xenodermus javanicus*: FMNH 158613, 222889; YPM HERR 017634, 017642, 017643

## 4. Results

### Anguimorph outgroup

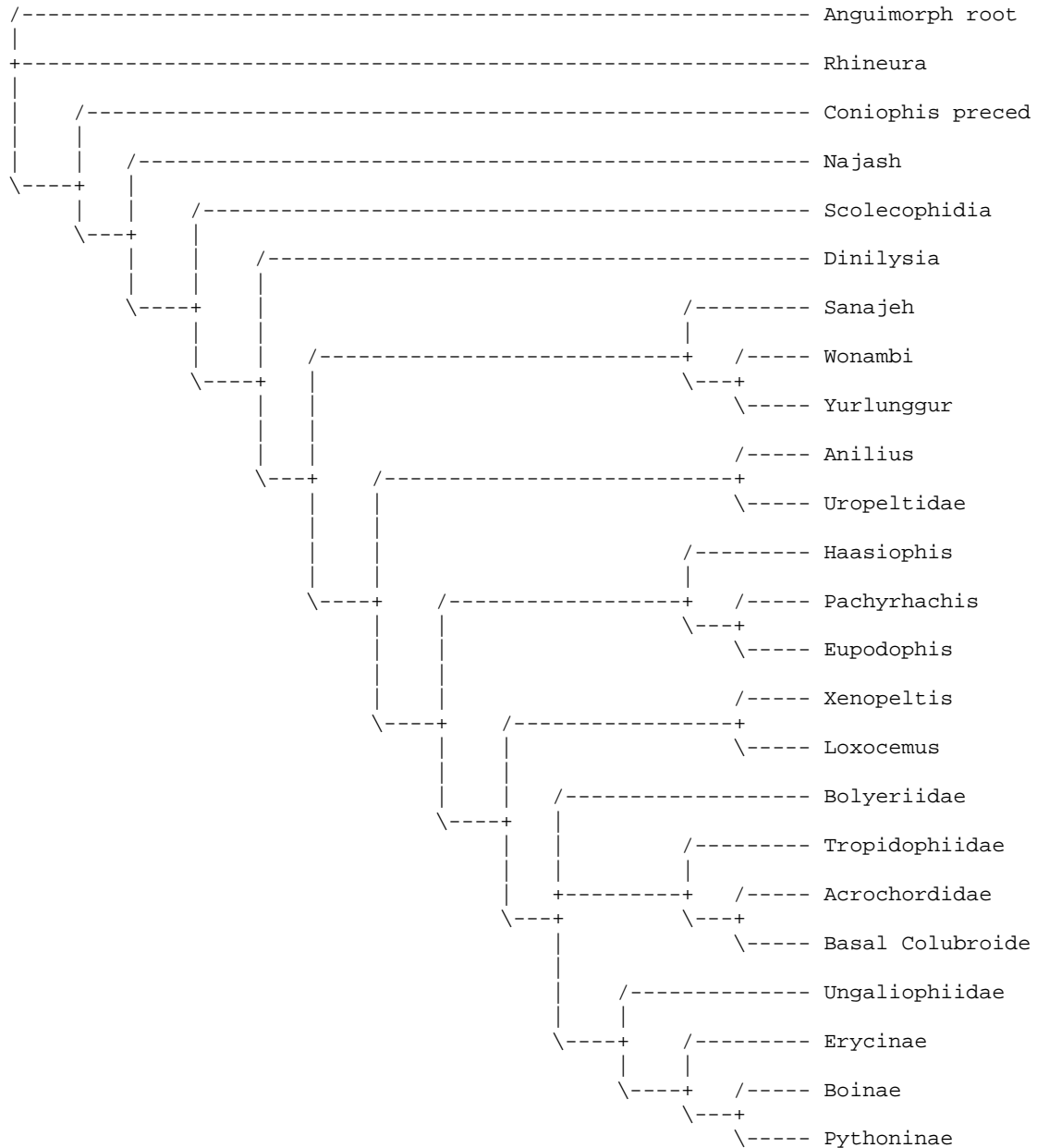
Tree length = 506  
 Consistency index (CI) = 0.5395  
 Homoplasy index (HI) = 0.4605  
 CI excluding uninformative characters = 0.5021  
 HI excluding uninformative characters = 0.4979  
 Retention index (RI) = 0.6958  
 Rescaled consistency index (RC) = 0.3754





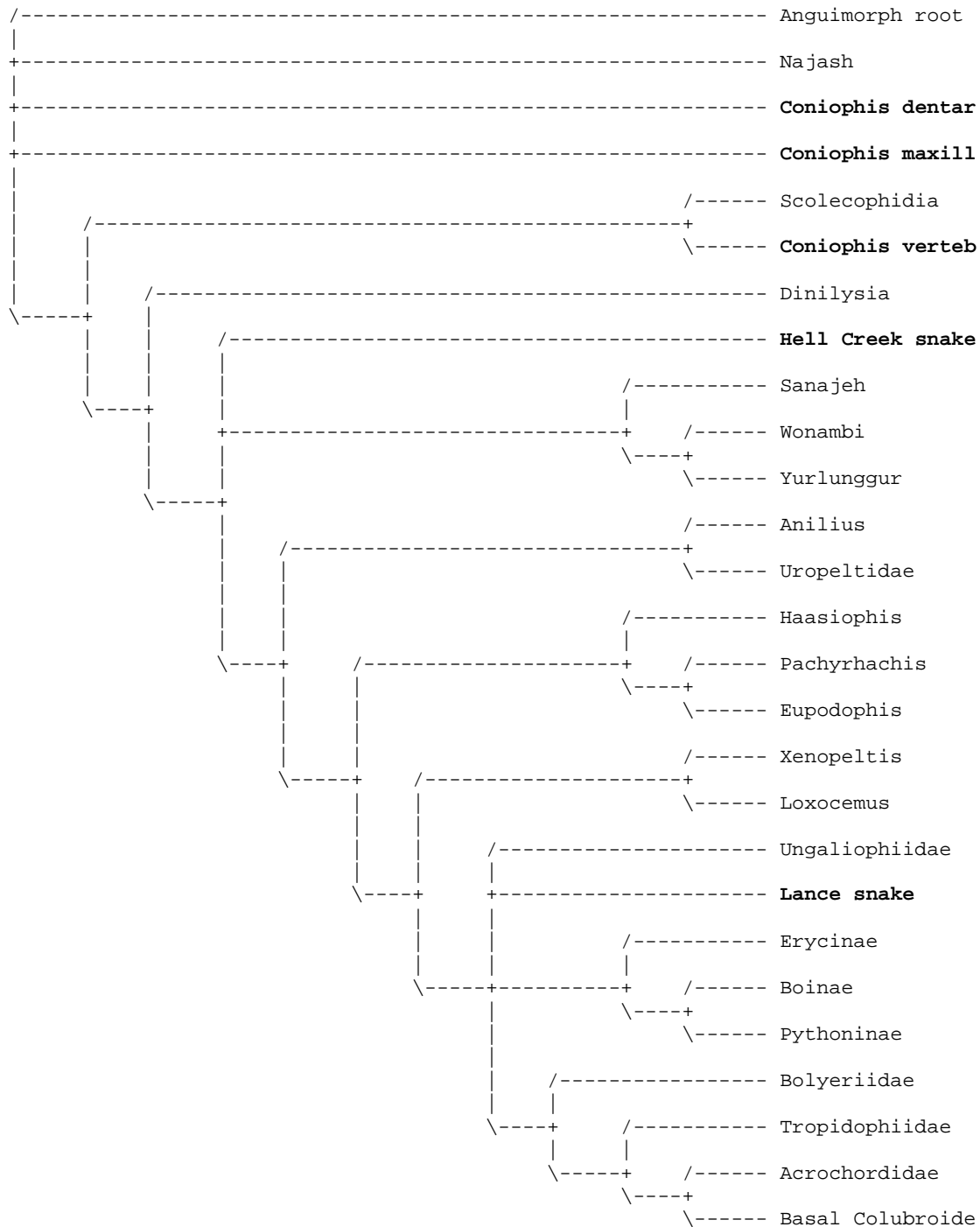
**Results: Amphisbaenia included in outgroup**

Tree length = 537  
 Consistency index (CI) = 0.5158  
 Homoplasy index (HI) = 0.4842  
 CI excluding uninformative characters = 0.4951  
 HI excluding uninformative characters = 0.5049  
 Retention index (RI) = 0.7039  
 Rescaled consistency index (RC) = 0.3631



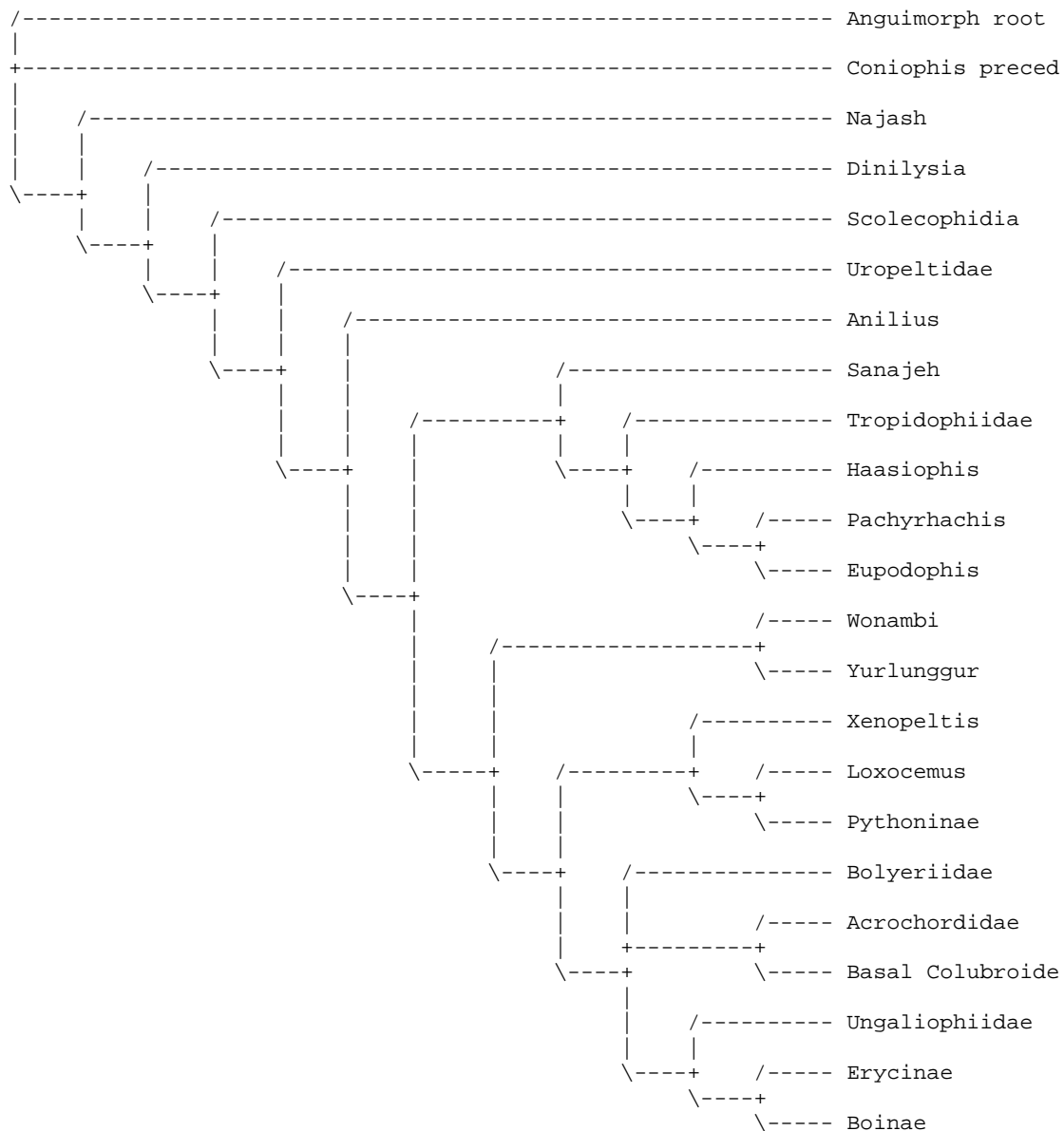
**Results: individual elements**

Tree length = 505  
 Consistency index (CI) = 0.5406  
 Homoplasy index (HI) = 0.4594  
 CI excluding uninformative characters = 0.5032  
 HI excluding uninformative characters = 0.4968  
 Retention index (RI) = 0.6999  
 Rescaled consistency index (RC) = 0.3783  
 Strict consensus of 75 trees:



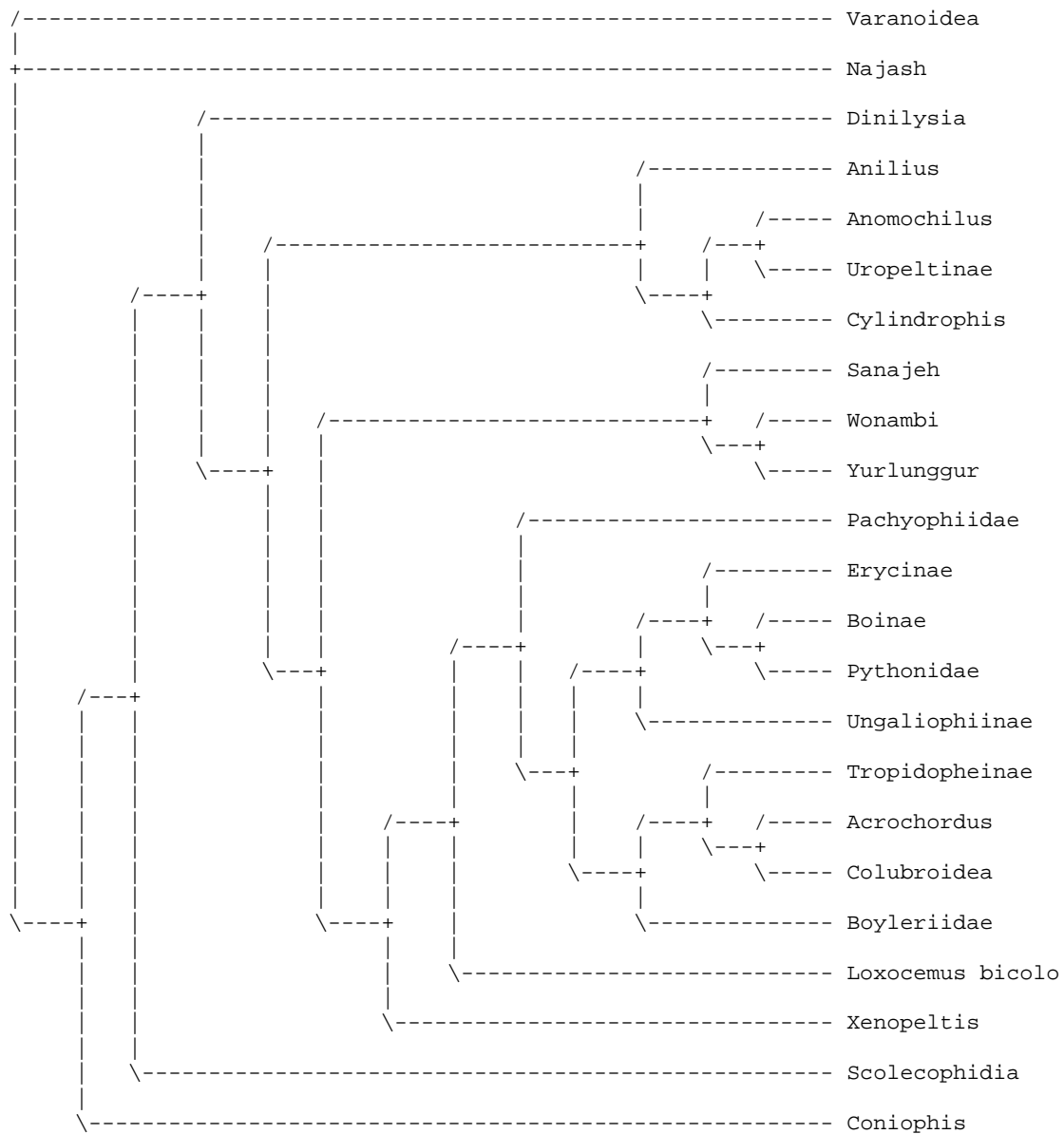
**Results: molecular topology constraint (Amerophidia + Afrophidia topology)**

constraints amerophidia (backbone) =  
 (1,4,((19,5),((13,(18,14)),(17,15,16),6,20,(21,22))))))  
 Tree length = 601  
 Consistency index (CI) = 0.4542  
 Homoplasy index (HI) = 0.5458  
 CI excluding uninformative characters = 0.4174  
 HI excluding uninformative characters = 0.5826  
 Retention index (RI) = 0.5718  
 Rescaled consistency index (RC) = 0.2597  
 Strict consensus of 2 trees:



### Results for Wilson et al. (2010) matrix

Tree length = 285  
 Consistency index (CI) = 0.5158  
 Homoplasy index (HI) = 0.4842  
 CI excluding uninformative characters = 0.4851  
 HI excluding uninformative characters = 0.5149  
 Retention index (RI) = 0.7019  
 Rescaled consistency index (RC) = 0.3621



## 5. Characters supporting referral of *Coniophis* to Ophidia and characters supporting major clades

Unambiguous synapomorphies are listed below:

### *Coniophis* + Serpentes

#### A. Maxillae

- |      |       |                                       |
|------|-------|---------------------------------------|
| 46.  | 0==>1 | Reduced ascending process of maxilla  |
| 155. | 0==>1 | Teeth separated by interdental ridges |
| 181. | 0==>1 | Lacrimal fossa of maxilla reduced     |

#### B. Dentaries

- |      |       |   |
|------|-------|---|
| 155. | 0==>1 | Interdental ridges                                |
| 205. | 0==>1 | Enlarged mental foramen.                          |
| 211. | 0==>1 | Dentary sits atop surangular                      |
| 213. | 0==>1 | Dentary subdental ridge deep anteriorly           |
| 220. | 0==>1 | Splenic articulates along back of subdental ridge |

#### C. Vertebrae

- |      |       |  |
|------|-------|--|
| 120. | 0==>1 | Subcentral perilymphatic fossae                  |
| 125. | 0==>1 | Neural spine a low ridge                         |
| 231. | 0==>1 | Narrow ventral ridge in anterior trunk vertebrae |
| 234. | 0==>1 | Vertebrae with trefoil-shaped neural canal       |

### *Najash* + Serpentes

- |      |         |                                  |
|------|---------|----------------------------------|
| 216. | 0 ==> 1 | Deep subdental ridge posteriorly |
|------|---------|----------------------------------|

### Serpentes

- |      |         |                                      |
|------|---------|--------------------------------------|
| 84.  | 0 ==> 1 | Otoccipitals contact dorsally        |
| 106. | 0 ==> 1 | Mobile dentary symphysis             |
| 119. | 0 ==> 1 | Prezygapophyseal accessory processes |
| 130. | 0 ==> 1 | Three lymphapophyses                 |
| 131. | 0 ==> 1 | Sacral vertebrae absent              |
| 138. | 0 ==> 1 | Tibia, fibula, hindfoot absent       |
| 140. | 0 ==> 1 | Pelvis internal to ribs              |

### *Dinilysia* + Madtsoiidae + crown Alethinophidia

- |     |         |   |
|-----|---------|---|
| 1.  | 0 ==> 1 | Alethinophidian tooth implantation      |
| 59. | 0 ==> 1 | Palatine does not contact ectopterygoid |



107.	0 ==> 2	Elongate posterior dentigerous process
168.	1 ==> 2	Frontal lateral processes clasped by prefrontal.
176.	0 ==> 1	Elongate palatine process of maxilla
177.	0 ==> 1	Caudal margin of facial process lies at an angle
187.	0 ==> 1	Maxilla superior alveolar foramen opens medially
226.	0 ==> 1	Angular borne on inside of mandible
227.	0 ==> 1	Angular short

#### Madtsoiidae + crown Alethinophidia

31.	0 ==> 1	Median frontal pillar
32.	0 ==> 1	Weak overlap of frontals by nasals
55.	0 ==> 1	Anterior dentigerous process of palatine
62.	0 ==> 1	Loose overlap of maxilla/palatine
64.	0 ==> 1	Articular facet between vomer/palatine
95.	0 ==> 1	Lateral wings of basisphenoid present
152.	0 ==> 1	Reduced maxillary process of palatine
197.	0 ==> 1	Large palatal teeth
218.	0 ==> 1	T-shaped dentary process of surangular
237.	0 ==> 1	Centrum and condyle separated by groove

#### crown Alethinophidia

23.	0 ==> 1	Prefrontal articulates with frontal anterolaterally
34.	0 ==> 1	Supraorbital ossification absent
37.	0 ==> 1	Postorbital element articulates primarily with parietal
58.	0 ==> 1	Pterygoid-palatine tongue and groove
65.	0 ==> 1	Long internal articulation of palatine with pterygoid
88.	0 ==> 1	Laterosphenoid absent
116.	0 ==> 1	Hemapophyses present
145.	0 ==> 1	Preorbital ridge absent
150.	0 ==> 1	Subolfactory processes close olfactory tract
169.	0 ==> 1	Optic foramen enclosed
182.	1 ==> 2	Fossa for nasal capsule entirely on prefrontal
186.	0 ==> 1	Maxilla palatine process curves down
188.	0 ==> 1	Maxilla accessory foramen
190.	0 ==> 1	Postorbital bar absent
200.	0 ==> 1	Ectopterygoid lies atop palatine

#### Simoliophiidae + crown Macrostromata

3.	1 ==> 2	Needle shaped teeth
43.	0 ==> 1	Supratemporal processes reduced

45.	1 ==> 0	Parietal-supraoccipital contact straight
53.	0 ==> 1	Supratemporal hinged
56.	0 ==> 1	Choanal process finger-like
68.	0 ==> 1	Lateral process of pterygoid reduced
76.	1 ==> 2	Stylohyal fuses to quadrate
79.	0 ==> 1	Paroccipital process of otoccipital reduced
90.	0 ==> 1	Prootic ledge underlaps trigeminal foramen
130.	1 ==> 2	More than three lymphapophyses
171.	0 ==> 1	Parietal inflated
195.	1 ==> 0	Quadrate secondarily elongate
196.	0 ==> 1	Platelike quadrate head
220.	0 ==> 1	Surangular with posterolateral crest

#### crown Macrostromata

24.	0 ==> 1	Orbital margin of prefrontal vertical
46.	1 ==> 2	Maxilla ascending process absent
67.	0 ==> 1	Quadrate ramus of pterygoid with groove
112.	0 ==> 1	Coronoid posteroventral process absent
142.	1 ==> 2	Pelvic elements fused
162.	0 ==> 1	Premaxilla displaced anteriorly
170.	2 ==> 1	Parietal sagittal crest reduced anteriorly
175.	0 ==> 1	Supratemporal elongate

#### *Xenopeltis* + *Loxocemus*

4.	1 ==> 0	Premaxillary teeth present
14.	0 ==> 2	Nasals interlock with prefrontals
124.	0 ==> 1	Axis intercentrum fused to centrum
158.	0 ==> 1	Teeth not fused to dentigerous elements
165.	0 ==> 1	Anterior margin of prefrontal concave
198.	0 ==> 1	Elongate lateral process of pterygoid
225.	0 ==> 1	Splenic mylohyoid foramen absent

#### Henophidia (Boidae + Colubridae)

13.	0 ==> 1	Lateral flanges of nasals do not contact frontals
29.	0 ==> 1	Reduced prefrontal-maxilla contact
38.	0 ==> 1	Lateral wings of parietal
40.	1 ==> 0	Frontoparietal joint lacks U shape
41.	0 ==> 1	Parietal notched for optic foramen
60.	0 ==> 1	Dentigerous process does not meet vomer/septomaxilla
80.	1 ==> 2	Juxtastapedial recess closed posteriorly

- |      |         |  |
|------|---------|--|
| 91.  | 0 ==> 1 | hyomandibular nerve exit inside trigeminal nerve opening |
| 108. | 0 ==> 1 | Medial margin of adductor fossa with crest               |
| 125. | 1 ==> 0 | Tall neural spine  |
| 126. | 0 ==> 1 | Notched neural spine                                     |
| 157. | 0 ==> 1 | Two replacement teeth per tooth position                 |
| 205. | 0 ==> 1 | Occipital condyle obscured by otoccipitals               |

## 6. Discussion

### A. Relationships of *Coniophis*.

Placement of *Coniophis* relative to *Najash* is complicated by the fact that there is limited overlap between the two in terms of skull material; the only skull element shared by both is the dentary, which is incomplete in both. Furthermore, many of the features that differentiate *Coniophis* from *Najash* (medially placed synapophyses, undivided synapophyses, absence of dorsolateral ridges of neural arch) occur in Scolecophidia, complicating attempts to optimize them. As a result, only a single feature- a posteriorly thin subdental ridge- optimizes as an unambiguous synapomorphy of the *Najash* + Serpentes clade. We concede that future finds might conceivably show that *Coniophis* lies elsewhere in the tree, but emphasize that (1) we feel the evidence is compelling that *Coniophis* lies outside of the Serpentes, and (2) whether or not *Coniophis* occupies the basalmost node or not is somewhat beside the point; even assuming it lies above *Najash* as the sister taxon to Serpentes, it would still provide critical information on the evolution of cranial kinesis in snakes, and bolster the argument that fossoriality is primitive for snakes.

That *Coniophis* lies outside Serpentes is strongly supported by the analysis; indeed the fossils are sufficiently un-snakelike that the identity of the AMNH maxillae as ophidian was not recognized, either during initial sorting of the AMNH collections or our initial examinations of these collections. We assert that this “un-snakelike” appearance is precisely what is expected for a stem form (e.g. the skeleton of *Archaeopteryx* looks like a non-avian theropod, not a crown bird). A stem form it will inevitably lack many of the characters that diagnose the crown, and so stem snakes are expected to look more like lizards in many respects. The important factors to consider are that the *Coniophis* specimens (1) exhibit features that are unique to snakes among squamates (e.g., claw-like teeth, interdental ridges), (2) possess features that are consistent with placement on the snake stem (e.g., absence of lacrimal fossa, low facial process) and (3) lack features that would argue for referral to any other squamate clade.

### B. Relationships within Serpentes

The phylogeny is also of interest in light of debates over the relationships within Serpentes. Notably, the phylogeny recovered here combines elements of a number of previously published snake phylogenies. In particular, this study differs from recently published phylogenies (Wilson et al., 2010; Zaher and Scanferla) in (1) recovering *Dinilysia patagonica* as the most basal member of Alethinophidia, a result previously published by Tchernov et al. (2000) and Conrad (2008); (2) recovering Madtsoiidae outside of crown Alethinophidia, as previously argued by Scanlon (2005, 2006); (3) recovering a clade consisting of the primitive macrostomates *Loxocemus* and *Xenopeltis* (a result previously found by Scanlon 1995, 2006, and Gauthier et al., 2012). Support for the first conclusion is relatively weak, but the available data strongly support the second two hypotheses.

Placement of *Dinilysia* along the stem of Alethinophidia has weak bootstrap support (51%) and only three additional steps are required to place *Dinilysia* outside of Serpentes. In light of the extreme modification seen in the skull of all extant

Scolecophidia, it seems entirely possible that some of the features optimized as diagnosing a *Dinilysia*-Alethinophidia clade actually arose outside of Serpentes. Perhaps the most compelling evidence for placement of *Dinilysia* with Alethinophidia, however, is the shape of the tooth alveoli, which form deep sockets (Zaher and Scanferla, 2012) a condition absent in Scolecophidia, but present in all Alethinophidia (Zaher and Rieppel, 1999). Furthermore, the clasping of the frontals by the prefrontals is characteristic of Alethinophidia. We do not regard the placement found here as the final word and emphasize that more fossils of stem snakes are required to better understand the placement of *Dinilysia*.

Placement of Madtsoiidae outside of the alethinophidian crown has much better bootstrap support (77%), and eight additional steps are needed to place Madtsoiidae inside of Alethinophidia. Madtsoiids exhibit a number of strikingly primitive features, notably the retention of a postorbital bar contacting the maxilla, a triangular supraorbital element, weak median frontal pillars, the lizard-like, clasping articulation of the ectopterygoids and pterygoids, and the interlocking (rather than tongue-and-groove) articulation between pterygoids and palatines. The data therefore support Scanlon's (2005, 2006) conclusion that Madtsoiidae lie outside the crown of Alethinophidia.

Another unusual feature of this study is the recovery of a *Loxocemus-Xenopeltis* clade. Some of the characters supporting this clade are highly homoplastic (e.g., absence of mylohyoid foramen) or may in fact represent plesiomorphies that are incorrectly optimized as synapomorphies (presence of premaxillary teeth is optimized as a synapomorphy). However, these snakes exhibit a number of striking features not found in any of the other snakes we studied. These include the interlocking prefrontal-nasal joint, the elongate lateral process of the pterygoid, and the concave anterior margin of the prefrontal. In addition, the bases of the teeth are not ankylosed to the dentigerous elements in either taxon.

Furthermore, this study corroborates placement of Simoliophiidae as the sister to Macrostromata. Simoliophiidae exhibit a number of primitive characters- notably the unfused pelvic elements and retention of a coronoid posterior process- that would not be expected in a crown macrostromatan, however, the long quadrates suggest that they could be more derived than *Loxocemus* and *Xenopeltis*. A better understanding of simoliophiid anatomy is required to help resolve this issue. Much of the disagreement over their placement seems to stem from differering interpretations of the fossils, rather than the characters used.

*Coniophis* provides surprisingly little insight into the relationships of snakes to other squamates, which remain poorly understood (Gauthier et al., 2012). The maxillae and dentaries resemble platynotans and mosasauroids in having relatively large, widely spaced, posteriorly curved teeth. These features could simply reflect the carnivorous habits of snakes, however, rather than common ancestry. We found no other derived features in the skull elements of *Coniophis* to support referral to any particular group of lizards.

### C. Implications for molecular analyses.

The topology presented here broadly agrees with previous morphological phylogenetic analyses, but contrasts markedly with previously published snake phylogenies using molecular data (Lee et al., 2007; Vidal et al., 2009; Wiens et al., 2010),

notably in recovering tropidophiids with Caenophidia and in placing *Loxocemus* and *Xenopeltis* as the basalmost macrostomatans. Never the less, when using a molecular backbone based on Lee et al. (2007) *Coniophis* still comes out as the basalmost snake.

The incorporation of additional characters into the Zaher and Scanferla (2012) matrix and revisions to that matrix do not help resolve the conflict but instead highlight the degree to which the morphological data consistently support a different tree. We approached this project expecting that we might find morphological support for at least one the controversial relationships posited on the basis of molecular data, given that some have argued that such morphological characters may exist in the soft tissue (Siegel et al., 2011) but character recodings and additional characters have largely supported previous morphology-based hypotheses concerning the interrelationships of Serpentes. Previously published morphological analyses have therefore accurately predicted the results of further research, which would seem to imply that the morphology is providing real signal, rather than only noise.

Finally, it is worth noting that *Coniophis precedens* has been used as a calibration point in molecular analyses (Noonan and Chippindale, 2006) based on the assumption that it represents a member of the Aniliidae. The erroneous assumption that *Coniophis* represents an anilioid leads to erroneous dating of the snake radiation, in which boas and pythons appear to radiate in the late Cretaceous, a conclusion that is at odds with the fossil evidence.

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