THE BASICRANIAL MORPHOLOGY OF MADTSOIID SNAKES (SQUAMATA, OPHIDIA) AND THE EARLIEST ALETHINOPHIDIA (SERPENTES)

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Snakes of the extinct family Madtsoiidae are known from early Late Cretaceous to Eocene deposits in Madagascar, western and northern Africa, southwestern Europe (Spain and possibly France), and South America (reviewed by Rage, 1998; Rage and Werner, 1999). Two genera occur in both the Campanian or Maastrichtian of Argentina and the early Eocene of Australia (*Patagoniophis* and *Alamitophis*, Albino, 1986; Scanlon, 1993; see Boles, 1999, for recent discussion and confirmation of the Eocene date), and Australia is the only region in which madtsoiids are known later than the Eocene. *Wonambi naracoortensis* Smith, 1976, occurs in Pleistocene and Pliocene deposits (Scanlon and Lee, 2000), and large species of *Yurlunggur* Scanlon, 1992, also range from late Oligocene to late Pleistocene (Mackness and Scanlon, 1999). The highest known diversity and some of the best-preserved material of madtsoiids are from the late Oligocene and Miocene of Riversleigh, northwestern Queensland, including *Wonambi barriei*, one or more unnamed species of *Yurlunggur*, two small species of *Nanowana*, and at least one additional new taxon (Scanlon, 1996, 1997; Scanlon and Lee, 2000).

Cranial remains of *Wonambi naracoortensis* from Naracoorte, South Australia (Barrie, 1990; Scanlon and Lee, 2000), provide the best evidence of the morphology and affinities of any madtsoiid (though the family as currently recognized may not be monophyletic; see below). These specimens were originally interpreted as supporting the inclusion of Madtsoiidae in Alethinophidia (Barrie, 1990; Scanlon, 1992), but reinterpretation of the morphology and more comprehensive phylogenetic analyses placed this lineage outside a clade including all living snakes, including scolecophidians as well as alethinophidians (Scanlon, 1996; Scanlon and Lee, 2000; Lee and Scanlon, 2002). These results confirm the interpretations of Hoffstetter (1961:155) and McDowell (1987) regarding the primitive features of madtsoiid vertebrae relative to those of all living snakes, and conflict with the widespread assumptions that scolecophidians are basal snakes and that all known fossil snakes are either scolecophidians or alethinophidians (e.g., Underwood, 1967; Rage, 1984, 1987; Rieppel, 1988; Zaher and Rieppel, 1999; Tchernov et al., 2000).

Part of the braincase of a second Australian madtsoiid, similar to that of *Wonambi* but differing conspicuously in proportions, has been recognized from a late Oligocene or early Miocene deposit at Riversleigh, northwestern Queensland. This deposit contains vertebrae, ribs, and jaw elements representing several taxa of madtsoiids including *Nanowana godthelpi*, *N. schrenki*, and *Wonambi barriei* (Scanlon, 1996, 1997; Scanlon and Lee, 2000). However, the only vertebrae consistent in size with the braincase fragment are similar to those of *Yurlunggur camfieldensis* Scanlon, 1992, allowing the braincase fragment to be referred to the same genus (Scanlon, 1996). All *Yurlunggur* vertebrae known from Riversleigh have relatively higher neural spines than the somewhat later *Y. camfieldensis*, so are considered specifically distinct, but taxonomic treatment of vertebrae is deferred pending study of recently discovered articulated remains.

As well as *Wonambi*, comparisons are made with extant snakes of some basal lineages (anilioids and booids) and with *Dinilysia patagon-ica* Woodward, 1901 (?Coniacian, Late Cretaceous; Estes et al., 1970; Caldwell and Albino, 2001), which has been interpreted as a basal alethinophidian or a pre-alethinophidian snake of similar grade to madtsoiids (reviewed by Scanlon and Lee, 2000). I also make some comparisons with a putative madtsoiid braincase fragment from the Cenomanian of Wadi Abu Hashim, Sudan (Rage and Werner, 1999), and comment on its significance.

Comparisons with recent taxa are based on collections of the Queensland Museum, Australian Museum, Macleay Museum, South Australian Museum, M. Archer, D. J. Barrie, and the author (details available on request).

Riversleigh fossils are prepared using acetic acid (e.g., Archer et al., 1991) and the specimen described here is completely free of carbonate matrix. The course of canals and foramina was determined visually under a binocular microscope, using a hair as a probe.

Terminology for cranial anatomy either follows that in Rieppel's (1979) review of snake basicranial evolution, or Rieppel's terms are noted parenthetically when different ones are preferred.

Institutional Abbreviations—QM F, Queensland Museum (Palaeontology), Brisbane.

SYSTEMATIC PALEONTOLOGY

REPTILIA
SQUAMATA
OPHIDIA
YURLUNGGUR Scanlon, 1992
YURLUNGGUR sp.

Material—QM F23041.

Locality—Mike's Menagerie Site (Mike's Menagerie Local Fauna), Godthelp Hill, Riversleigh World Heritage Fossil Property, northwestern Queensland.

Age—The deposit forms part of 'Tertiary System B,' interpreted to be late Oligocene or early Miocene in age (Archer et al., 1989, 1997).

Description—A fragment 22.0 mm in length comprises most of the co-ossified basisphenoid and parasphenoid (Fig. 1), here referred to as 'sphenoid' for brevity; the width of the cultriform process immediately anterior to the basipterygoid processes is 7.3 mm; the same, immediately anterior to ossified portions of trabeculae is 5.0 mm; the maximum width across the basipterygoid processes is 10.7 mm; the length of the canal for the abducens nerve is 6.4 mm; the length of the articulatory surface of the basipterygoid process (right) is 7.5 mm; the length of the vidian canal is greater than 6.6 mm.

The dorsal surface (Fig. 1A) bears an oval, bowl-like hypophysial pit (sella turcica) centered just anterior to a line joining the posterior ends of the basipterygoid processes. It is not recessed below the posterior dorsum sellae (crista sellaris); the posterior and lateral walls are nearly vertical, while the anterior wall is more oblique but demarcated anteriorly by a shallowly overhanging crest approximately 2 mm across. This crest is interrupted by three small troughs probably accommodating blood vessels (one to the left of the midline, two smaller ones to the right). A similar pattern of three anterior troughs is seen in *Calabaria reinhardti*, and a slightly less similar condition in *Xenopeltis unicolor* and *Loxocemus bicolor* (Rieppel, 1979:figs. 5, 7), where they represent the anterior course of the ramus cranialis of the cerebral carotid.

In the midline within the hypophysial pit, 0.7 mm posterior to the transverse anterior crest, is a small foramen opening posteriorly, re-

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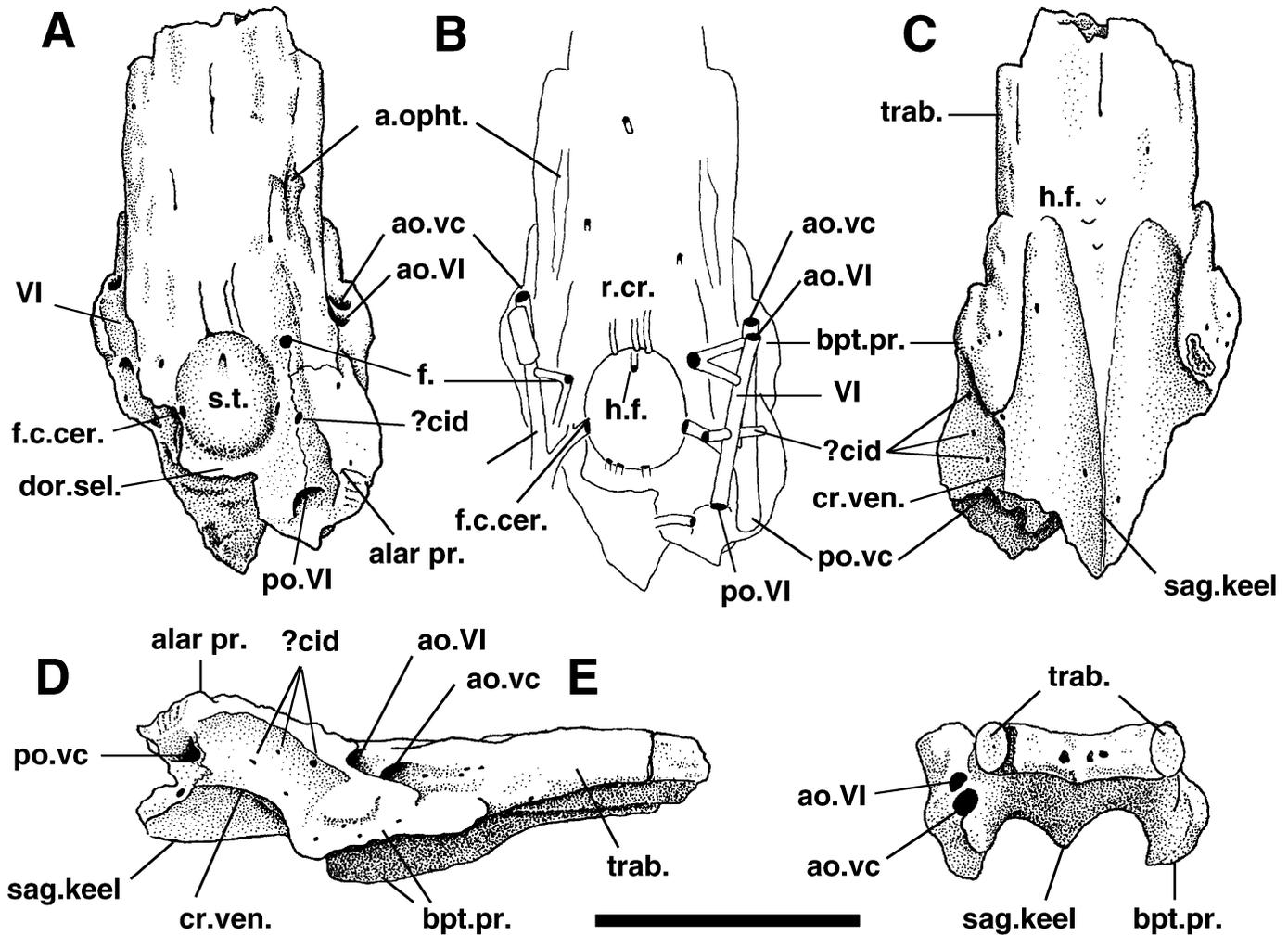
FIGURE 1. Sphenoid fragment referred to *Yurlunggur* sp. (QM F23041), in (**A**) dorsal, (**B**) schematic dorsal, (**C**) ventral, (**D**) right lateral (slightly ventral), and (**E**) anterior views. **Abbreviations**: **a.opht**., trough probably for ophthalmic artery; **alar pr**., alar process; **ao.vc**., anterior opening of vidian canal; **ao.VI**, anterior (extracranial) opening for abducens nerve; **bpt.pr**., basipterygoid process; **?cid**, foramina possibly for branches of trigeminal (V4) innervating constrictor internus dorsalis musculature; **cr.ven**., crista ventrolateralis of basisphenoid; **dor.sel**., dorsum sellae; **f**., unidentified foramen; **f.c.cer**., cerebral carotid foramen; **h.f**., hypophysial foramen; **po.vc**., posterior opening of vidian canal; **po.VI**, posterior (intracranial) opening for abducens nerve; **r.cr**., troughs for ramus cranialis of cerebral carotid artery; **sag.keel**, sagittal keel of sphenoid; **s.t**., sella turcica (hypophysial pit); **trab**., trabecula cranii; **vc**., vidian canal; **VI**, canal for abducens nerve. Scale bar equals 10 mm.

garded as the hypophysial foramen (reported as 'cerebral foramen' in *W. naracoortensis*; Barrie, 1990).

A large cerebral carotid foramen opens into each side of the hypophysial pit, just posterior to its midpoint, from the medial branch of the vidian canal. The bifurcation of the canal is exposed by breakage on the left and is visible through its posterior opening on the right (shown schematically in Fig. 1B), the medial branch being somewhat smaller than the main anterior branch.

The posterior wall of the pit is pierced by three small foramina, one just to the right of the midline and two smaller ones farther to the left. These communicate with a cavity within the dorsum sellae, exposed posteriorly by breakage. Their identity is unknown, unless they indicate an extracranial course of the basilar artery as in mosasaurs (cf. Russell, 1967).

Posterolateral to the hypophysial pit on the right side, near the broken posterior edge, is a large foramen, opening posterolaterally, which communicates by a long canal with a similar-sized foramen just posterodorsal to the anterior opening of the vidian canal. The position of the posterior opening is typical for n. abducens (VI) (e.g., Rieppel, 1979; Bellairs and Kamal, 1981). In most squamates the abducens nerve traverses a very short tunnel through the dorsum sellae and the anterior opening is on the anterior-facing wall lateral to the hypophysial pit,

while a more anterolateral (but still intracranial) position is usual in snakes. While it is intersected by some narrower passages which may have conveyed smaller nerves or vessels (see below), the canal and anterior opening are here considered as primarily for the abducens nerve. On the left side the bone has broken along the canal and it is preserved only as a short trough facing dorsolaterally, directly above, but at a slight angle to, the vidian canal.

The bone is incompletely fused dorsal to the abducens canal, leaving a T-shaped hairline suture connecting the dorsal margins of both openings (Fig. 1A); a similar feature has been illustrated in *Anilius* and *Cylindrophis* (Rieppel, 1979:fig. 4). Two smaller foramina lie on this suture lateral to the hypophysial pit (only the anterior one of the pair is preserved on the left side, and it is smaller than the corresponding one on the right). The narrow canal from the more posterior foramen intersects the abducens canal and exits the braincase laterally above the rear of the basipterygoid process. The more anterior bifurcates immediately within the bone, sending an anterior branch (preserved on both sides) ventrolaterally to join the vidian canal, and a posterior branch (complete on the right side) to the abducens canal. This anterolateral pair occupies the same position relative to the hypophysial pit as do the internal carotid foramina of anilioids (cf. Rieppel, 1979), though such a role seems unlikely in this case as their connections with the vidian

canal are less direct. Each branch apparently ramifies further within the bone, resulting in four groups of smaller foramina on the external surface; these are mostly too small to probe successfully, so that only three external openings can be identified confidently (?cid in Fig. 1C, D). It seems likely that some or all of these foramina provide egress for branches of the cid-nerve (V4 levator bulbi, innervating the constrictor internus dorsalis musculature), but no detailed similarity to this arrangement has been found in other taxa. A similar-sized canal enters the dorsum sellae in a medioventral direction from the posterior opening for nerve VI; this is truncated by breakage, and its identity is unclear.

Immediately lateral to the posterior opening of the abducens canal and dorsal to the posterior opening of the vidian canal, i.e., at the lateral edge of the dorsum sellae, is an angular dorsal prominence of the sphenoid element (somewhat worn), which corresponds topographically to the alar process of lizards (Oelrich, 1956; Russell, 1967; Bellairs and Kamal, 1981; = 'clinoid process' in Rieppel and Zaher, 2000). The posterior face of this prominence has several low transverse corrugations, and a compact appearance (in contrast to the rest of the element which appears more chalky) suggesting endochondral bone.

The vidian canal opens anteriorly above the center of the basipterygoid process on each side, and the similar-sized abducens canal just posterodorsal to it; however, the processes are located asymmetrically, about 1 mm more anterior on the left than right, so that the foramina are also asymmetrical in position. Distortion is absent, as in most Riversleigh fossils, so the asymmetry was present in life, but it is not known whether this represents individual or taxic variation. The original posterior opening of the vidian canal is not preserved on either side, but on the more complete right side the canal is exposed by breakage about 4 mm posterior to the basipterygoid process, which may have been very close to its natural position (Fig. 1D).

The anterior part of the fragment is bounded laterally by the vertically oval, cylindrical trabeculae cranii (cristae trabeculares); these are seen in anterior view (Fig. 1E) to be ossified separately from the broad plate joining them (basisphenoidal rostrum), which is the same depth as the trabeculae laterally, gently concave dorsally, and bears a low midventral ridge. The cristae trabeculares must have formed the dorsal surfaces for contact with the lower edge of the parietal, but (as in *Wonambi*) do not show any distinctly bounded facet-like structures, implying an abutting or weakly clasping (syndesmotic) contact rather than a suture. There are only irregular and asymmetrical traces of longitudinal grooves on the dorsal surface just medial to the cristae (Fig. 1A), whereas *Wonambi* has more distinct grooves here, possibly for the ophthalmic arteries (Barrie, 1990). The anterior ends of the ossified trabeculae, level with each other, have concave surfaces whence they extended forward as cartilaginous rods (indicating a platytrabic condition as in *Dinilysia* and alethinophidians).

Three small foramina on the ventral surface, close to the midline between the anterior ends of the basipterygoid processes (Fig. 1C) appear to be multiple openings of the hypophysial foramen, but they are too narrow (especially dorsoventrally) to demonstrate this directly by probing. As in *Wonambi*, clearly bounded concave surfaces (presumably for muscle origin) are present on the posterior part of the sphenoid, separated posteriorly by a median keel that broadens gradually between the basipterygoid processes, and extending to a line between the anterior tips of the processes. However, the posterior keel is sharp-edged rather than thickened ventrally as in *Wonambi*, and also less prominent. Such a mid-ventral keel (extending onto the basioccipital) is not present in *Dinilysia* or lizards, and may be present or absent in alethinophidians. When present in extant snakes, the median keel separates the areas of origin of the mm. protractor pterygoidei, whereas in lizards these muscles do not extend farther medially than the basipterygoid process. The crest extending posteriorly from the basipterygoid process in *Yurlunggur* (crista ventrolateralis; Oelrich, 1956) is also sharper than the equivalent structure in *Wonambi*. The similarly concave surface lateral to this crest (posterior and partly dorsal to the basipterygoid process) is unlikely to provide the origin of an entirely different muscle since the m. levator pterygoidei in snakes typically originates more dorsolaterally, on the parietal; the division by a longitudinal crest might indicate a division of the protractor pterygoidei into separate medial and lateral heads, as in some extant snakes, but it is the lateral one that would resemble that of lizards such as *Varanus*.

The basipterygoid processes, slightly asymmetric in position as noted above, are elongated almost parallel to the midline and face ventrolaterally and slightly anteriorly. Their distal surfaces are convex and bumpy, like the cartilage-invested basipterygoid processes of lizards,

not smooth facets of dense bone as in the corresponding structures of booid snakes. The articulating surfaces are roughly triangular; the convex apical part of the facet is demarcated by a longitudinal groove and a notch in the anterodorsal edge, and is continuous with a crest extending posterodorsally (lateral margin of the sphenoid unit) which, at least posteriorly, was in sutural contact with the prootic.

Comments—The *Yurlunggur* fragment has been compared with a slightly more complete sphenoid of *Wonambi naracoortensis* that is associated with other braincase and jaw elements (Barrie, 1990; Scanlon and Lee, 2000). The two madtsoiids are similar in most respects, but the present specimen provides additional information as most of the canals within the bone have not been observed directly in *Wonambi*. Other phylogenetically relevant comparisons are with *Dinilysia* (see above) and extant snakes such as anilioids and booids; also relevant are the likely nearest outgroups to snakes, represented by terrestrial varanoid lizards and mosasauroids (Lee, 1998; Caldwell, 1999; Rieppel and Zaher, 2000). Some information from the present specimen has already been incorporated in phylogenetic analyses (Scanlon and Lee, 2000; Lee and Scanlon, 2002).

As in many other snakes the dorsum sellae of madtsoiids is low and saddle-shaped, not overhanging anteriorly, and there are no retractor pits or a median crest within the hypophysial pit. The abducens canal emerges anterolateral to the hypophysial pit rather than within it; the basisphenoid rostrum is broad and well ossified between the trabeculae, which remain separate and parallel into the orbital region of the skull. These are differences from typical lizards such as *Varanus* and (in most cases) from mosasaurs (e.g., Rieppel and Zaher, 2000).

The vidian canals give off an interior branch for the cerebral carotid that emerges in the posterolateral wall of the hypophysial pit, and the main anterior opening lies on the anterodorsal face of the basipterygoid process, entirely within the sphenoid complex, as in *Dinilysia* and lizards. There is thus no secondary anterior opening on the sphenoid-parietal boundary as seen in anilioids and most other alethinophidian snakes (Underwood, 1967; Estes et al., 1970; Rieppel, 1979).

Immediately above and behind the anterior vidian foramen is the similar-sized anterior opening of the abducens canal. The anterior abducens foramen thus occupies a similar (extracranial) position, relative to the vidian canal and basipterygoid process, as in typical lizards (Rieppel, 1979) and mosasauroids (Russell, 1967). Its position in extant snakes is lateral or anterolateral to the hypophysial pit, which results from two likely apomorphies of snakes: greater length of the canal, and the formation of a distinct anterolateral margin of the hypophysial pit (weakly or not defined in lizards); these are also present in the madtsoiids. However, the anterior abducens foramen in modern snakes also differs from that in the madtsoiids in being intracranial, i.e., medial to the secondary braincase wall (parietal-sphenoid contact).

A large foramen in the extracranial, 'supra-vidian' position was reported in *Dinilysia patagonica* by Estes et al. (1970), but not identified. Rieppel (1979) and McDowell (1987) interpreted it as the exit of the cid-nerve (=V4 levator bulbi) from the cavum epiptericum, but separate channels, likely to be for the cid-nerve, are present in *Yurlunggur* (see above). Estes et al. (1970:fig. 5) partially excavated the vidian canal and the canal dorsal to it in *Dinilysia*, and though they did not expose the intracranial opening, they show the posterior part of the upper canal extending to a position dorsomedial to the posterior vidian canal opening. This is precisely the same situation as in *Yurlunggur* (Fig. 1B) and as inferred in *Wonambi*. In *Dinilysia* there is also a small branch joining or intersecting both of the two longitudinal canals posterior to the basipterygoid process, which is similar if not identical to the (tentatively identified) cid-nerve canal in *Yurlunggur*. The similarity of position of the abducens openings in the madtsoiid and lizards, and the similarity of these canals and their anterior openings in *Yurlunggur* and *Dinilysia*, indicate that the 'unknown foramen' of *Dinilysia patagonica* is also for the abducens nerve.

It might be significant that the mosasaur *Platecarpus* also has a large foramen immediately above and behind the anterior vidian canal opening, the function of which is also uncertain (exit for basilar artery according to Russell, 1967; 'dorsal anterior opening of Vidian canal' in Rieppel and Zaher, 2000:499 and fig. 2C). An intracranial anterior opening for nerve VI is also reported in *Platecarpus* by Rieppel and Zaher (2000:fig. 4), but it is not clear from their descriptions whether the identities of these foramina have been assumed, or actually demonstrated by tracing internal canals.

Rieppel (1979) regards the anilioid and primitive booid condition of an intracranial primary anterior opening of the vidian canal to be prim-

itive for snakes as a whole, and contrasts this with the condition in *Dinilysia* and advanced booids (some members of both Boinae and Pythoninae) in which the primary opening is extracranial, as in lizards. Rieppel suggests (1979:427) that "... elongation of the braincase relative to the facial region of the skull together with the enclosure of the brain within frontal and parietal downgrowths in snakes makes complex changes necessary before the lacertilian type of Vidian canal was reestablished," and that the condition in *Dinilysia* was derived in parallel to that of advanced booids. This comparison depends partly on Rieppel's interpretation of the 'unidentified foramen' of *Dinilysia* (Estes et al., 1970) as an exit for the cid-nerve.

But if, as argued here, this foramen in *Dinilysia* is the opening of the abducens canal as in *Yurlunggur* sp., the *Dinilysia* condition is distinct from that in derived booids and similar in both respects to that of lizards (where the anterior abducens opening is almost directly dorsal to that of the vidian canal, albeit 'intracranial'). Following this interpretation, the enclosure of the brain by the parietal in primitive snakes took place medial to the anterior openings of both the vidian and abducens canals. This does not affect the polarity for changes within Alethinophidia (Rieppel's conclusion is supported by the distribution of character states among extant forms; see also Underwood, 1967:15–18), but implies that the state seen in anilioids and basal booids originated subsequent to the enclosure of the brain, and after the origin of lineages leading to *Dinilysia* and madtsoiids. The phylogenetic position of *Dinilysia* (and where included, madtsoiids) as basal to Alethinophidia has been supported by almost all analyses (reviewed in Scanlon and Lee, 2000).

A sphenoid fragment of a snake from the Cenomanian of Sudan (Rage and Werner, 1999) was considered comparable in some respects to *Wonambi* and hence possibly referable to the madtsoiid (indeterminate genus and species) represented by vertebrae in the same deposit, although a number of other snake taxa were also present. Some comparisons are therefore made here between Australian madtsoiids and the much older African specimen (Technical University of Berlin—Special Research Project 69, Vb-690) based on the published illustrations (Rage and Werner, 1999:fig. 22).

Yurlunggur, *Wonambi* and Vb-690 are similar in having a well-defined, ellipsoidal hypophysial pit (circular in Vb-690) pierced by posterolateral carotid foramina (their connection with the vidian canals not confirmed in Vb-690, but hardly to be doubted) and an anterior, median hypophysial foramen that emerges on the ventral midline somewhat anterior to the internal foramen. There is a sagittal ventral keel that divides anteriorly below the hypophysial pit, enclosing a flat triangular space within which the hypophysial foramen emerges. The foramen interpreted as the anterior opening of the abducens canal also lies directly behind and above the anterior vidian canal opening, in a common concavity or trough. Each of these shared features is matched in some extant snakes, but in combination they appear to distinguish these three from all other snakes and indeed all squamates (cf. Rieppel, 1979; Rage and Werner, 1999). However, there are also a number of differences. For instance, the dorsum sellae is less prominent in Vb-690; the posterior openings of the abducens canals relatively smaller and closer to the hypophysial pit; the posterior openings of the vidian canals farther anterior and more distant from the borders with the prootics; and the element strongly 'arched' in the sagittal dimension rather than conspicuously flat as in the Australian forms. These proportional and shape differences might be explained as correlates of size difference (Vb-690 is roughly half as large as the *Yurlunggur* specimen) or indicating a low level of phylogenetic divergence, but others seem more significant.

I disagree with Rage and Werner's interpretation (1999:106–107) that neither a lateral wing nor basipterygoid processes are present in Vb-690. In fact the specimen shows the typically alethinophidian condition (McDowell, 1967, 1987; Rieppel, 1979) of an upturned lateral wing projecting between the prootic and parietal, directly lateral to the hypophysial pit, with the anterior opening of the vidian canal (in a channel on the dorsal surface of the wing) medial to the parietal contact and thus intracranial. This lateral wing has both a thickened dorsolateral edge, interpreted as contacting the parietal (with no counterpart in the Australian material, at least not lateral to the vidian canal), and a distinctly bounded, 'corrugated' ventral surface corresponding in position to the basipterygoid facet of the madtsoiids. The corrugated areas are interpreted by Rage and Werner as muscle attachment areas for m. protractor pterygoidei; however, in extant snakes with a sagittal keel on the posterior sphenoid, this muscle reaches the keel and extends anteriorly to just behind or between the basipterygoid articulations (e.g., *Python*, Frazzetta, 1966; *Casarea*, Cundall and Irish, 1989). Thus, I

interpret the corrugated areas as basipterygoid 'facets' (functionally at least), and their sessile (i.e., non-pedicellate) nature suggests the sphenoid-pterygoid attachment may have been formed by short ligaments as reported in anilioids or bolyeriids, in contrast to the discrete sliding or hinge joints formed by the prominent, pedicellate processes in the madtsoiids or booids (which in these respects resemble *Dinilysia* and lizards).

The formation of a lateral wing, apparently by the upturned ventrolateral part of the sphenoid (i.e., basipterygoid process) meeting the parietal lateral to the vidian canal, has long been regarded as a significant and reliable alethinophidian synapomorphy (Underwood, 1967; McDowell, 1967, 1974, 1987; Rieppel, 1979, 1988), and this view is supported by several recent analyses (Scanlon, 1996; Scanlon and Lee, 2000; Lee and Scanlon, 2002). Hence, Vb-690 can be referred to Alethinophidia based on its possession of the derived condition. By the same criterion, the Australian madtsoiids are not alethinophidians (Scanlon and Lee, 2000).

The snake fauna of Wadi Abu Hashim is diverse, including at least nine species and at least seven families (Werner and Rage, 1994; Rage and Werner, 1999). All of these families have been referred to Alethinophidia in widely accepted classifications (e.g., Rage, 1987), and some even to the highly advanced clade Colubroidea, previously unknown before the Eocene (Rage and Werner, 1999). Together with phylogenetic analyses (Cundall et al., 1993; Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon, 2002), these identifications have the surprising implication that nearly all of the major ('superfamily' level) lineages of modern snakes would have originated by the Cenomanian (Rage and Werner, 1999). However, while the taxonomy of fossil snakes necessarily depends mainly on vertebrae, these present a very restricted set of phylogenetically informative features compared to certain bones of the skull. Hence the proposed relationships of most of the extinct families, presently known only from vertebrae, stand in need of testing by discovery and analysis of associated cranial remains.

Rage and Werner (1999) remained uncertain as to the affinities of the only snake cranial element recognized from Wadi Abu Hashim, concluding from its relatively large size compared to most of the vertebral remains that "Vb-690 may belong to the Madtsoiidae, to a lapparentophiid-grade family, or to a still unknown family" (Rage and Werner, 1999:107). If it is accepted that Madtsoiidae as presently defined is monophyletic, Vb-690 can now be excluded by possession of a 'definitive' alethinophidian character that is absent in both madtsoiids where it can be evaluated. The same apomorphy would also be unexpected in a lapparentophiid-grade snake, as *Lapparentophis* and similar forms (known only from vertebrae) have always been considered to occupy an even more basal phylogenetic position (Hoffstetter, 1959; Rage, 1984, 1987; McDowell, 1987; Rage and Werner, 1999). However, there is an additional possibility that seems at least as plausible as the presence of an additional large snake taxon in the fauna, none of whose vertebrae have yet been found: Vb-690 may indeed belong to the same taxon as the 'madtsoiid' vertebrae, if their combination of vertebral features actually characterises a paraphyletic stem-group to Alethinophidia, rather than a clade. Support for monophyly of all madtsoiids is weak (a single apomorphy, presence of parazygantral foramina and fossae; e.g., Rage, 1998), they encompass considerable diversity in other aspects of vertebral form, and indeed the possibility of paraphyly has been suggested before (Scanlon, 1996; M. K. Hecht, pers. comm.).

It can at least be inferred that the Cenomanian snake represented by Vb-690 was more closely related to extant alethinophidians than to *Yurlunggur* or *Wonambi*, thus providing a good minimum date for the divergence of these Australian madtsoiids from all extant alethinophidian lineages. Confirmation of alethinophidian skull characters adds support to Rage and Werner's (1999) interpretation that at least some of the vertebrae from the same site represent alethinophidian families. However, it remains to be seen how many, and which, of the Cenomanian taxa will find a permanent place within Alethinophidia.

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Note added in proof.

In a paper appearing while this one was in press, Rieppel et al. (2002) redescribed the skull of another madtsoiid, *Wonambi*. In their paper they give the locality of SAM P30178 as [the State of] ''Victoria, Australia'' (p. 812), whereas it comes from Victoria Fossil Cave, Naracoorte, in the State of South Australia (Barrie, 1990). They also suggested that a caudal vertebra with chevron figured by Scanlon and Lee

(2000:fig. 2g) is from a different locality and age (pp. 813, 824); however, it was collected by John Barrie from the same deposit as the rest of P30178. Rieppel et al. (2002) also consistently misspell the specific epithet of *Wonambi barriei* as 'barrei.'

Rieppel et al. also give a number of interpretations of *Wonambi naraacoortensis* differing from those in Scanlon and Lee (2000) and this work. Their statement (p. 816, and their character 18) that "the anterior opening of the Vidian canal is bipartite in *Wonambi*" is rendered unlikely by the observations on *Yurlunggur* in this paper. Their coding of a laterosphenoid as persent (their character 28) in *Wonambi* is based on the idea that its absence is due to damage (p. 819). Most relevant to the present paper, they also state (2002:817) that '[t]he "lateral wings" of the basisphenoid are present in *Wonambi* . . . Comparing the disarticulated basisphenoid of *Typhlops* (Rieppel, 1979b:fig. 3) with that of alethinophidians (Rieppel, 1979a) and with *Wonambi* is the best way to ascertain the presence of "lateral wings" of the basisphenoid in the latter genus.' As used in the present paper, the alethinophidian character "presence of lateral wings" involves the lateral margins of the basi-

sphenoid (usually considered to be homologues of the lizard basipterygoid processes; McDowell, 1967) extending dorsolaterally to form sutural contacts with the parietal and prootic, thus producing a triangular dorsal prominence between the latter elements in lateral view. In *Wonambi* (as in *Dinilysia* and *Yurlunggur*) the corresponding parts of the sphenoid are indeed present, but they form basipterygoid processes projecting ventrolaterally, are entirely free of the prootic and parietal, and the external dorsolateral margin of the basisphenoid is straight. Rieppel et al. code *Wonambi* with a different state from *Dinilysia* (character 21 in appendix 3, p. 828), but their suggestion of the 'best way' to evaluate this character is not applicable to Dinilysia, where no disarticulated basisphenoid has been described.

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