

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 scoleophidians 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 scoleophidians are basal snakes and that all known fossil snakes are either scoleophidians 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 (aniiloids 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

YURLUNGUR Scanlon, 1992
YURLUNGUR 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 basiptyergoid processes is 7.3 mm; the same, immediately anterior to ossified portions of trabeculae is 5.0 mm; the maximum width across the basiptyergoid processes is 10.7 mm; the length of the canal for the abducens nerve is 6.4 mm; the length of the articular surface of the basiptyergoid 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 basiptyergoid 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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