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Cranial morphology of the Plio-Pleistocene giant madtsoiid snake *Wonambi naracoortensis*

JOHN D. SCANLON



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New material and additional morphological details of a rare and phylogenetically significant large fossil snake, *Wonambi naracoortensis* Smith, 1976, are described from Pleistocene and Pliocene cave deposits in southern South Australia. The new data refute some previous interpretations of the morphology of this species, and have implications for the phylogenetic position of *Wonambi* relative to extant snakes and other fossils, including other Madtsoiidae. The nature of contacts among palatal, braincase, snout, and mandibular elements imply similar functional attributes to those of extant anilioid snakes: maxillae from multiple individuals show corrugated contact surfaces for the prefrontal, implying a tight suture; structures on the anterior and medial surfaces of the palatine choanal process are interpreted as forming extensive contacts with the vomer and parasphenoid; and the distinctly bounded facets on the basiptyergoid processes and pterygoid imply little or no capacity for anteroposterior sliding of the palatopterygoid arch, hence absence of the macrostomatan “pterygoid walk”. On the frontal, interolfactory pillars were either absent or very slender, and a deep, sculptured contact surface for the nasal implies a prokinetic joint was also absent. Margins of the frontal and parietal indicate broad entry of the sphenoid into the ophthalmic fenestra, as in *Dinilysia*. Similarity of elements and features of the braincase (trigeminal foramen, ear region, and basiptyergoid processes) with both lizards and extant snakes show that differences between snakes and other squamates have sometimes been overstated. The case for macrostomatan affinities of *Wonambi* is not supported by new evidence.

Key words: Ophidia, *Wonambi*, anatomy, braincase, palate, mandible, Plio-Pleistocene, Australia.

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Introduction

Snake fossils with relatively complete skulls are rare, and in most cases occur in aquatic sediments that impose crushing and other damage, making interpretation of their morphology difficult. Thus, despite the spectacular preservation of a number of Cretaceous and early Tertiary snakes [such as *Pachyrhachis problematicus* Haas, 1979; *Eupodophis descouensi* (Rage and Escuillié, 2000); *Haasiophis terrasanctus* Tchernov et al., 2000; *Dinilysia patagonica* Woodward, 1901; *Archaeophis proavus* Massalongo, 1859; *A. turkmenicus* Tatarinov, 1963; and *Rottophis atavus* (von Meyer, 1860)], the identity and morphology of many of their cranial bones are either undocumented or subject to conflicting interpretations (Janensch 1906; Auffenberg 1959; Estes et al. 1970; Haas 1980a, b; Tatarinov 1988; Szyndlar and Böhme 1996; Lee and Caldwell 1998; Zaher 1998; Rage and Escuillié 2002; Lee and Scanlon 2002; Caldwell and Albino 2002; Rieppel et al. 2003). Madtsoiidae, another extinct snake group already widespread in Gondwana during the Cretaceous, and hence of comparable phylogenetic interest to those mentioned above, has not yet produced such fully articulated skeletons but is represented by associated and fully three-dimensional cranial remains from several Tertiary and

Quaternary deposits in Australia. Descriptions of some of this material have appeared (Barrie 1990; Scanlon 1997; Scanlon and Lee 2000, 2002; Scanlon 2003) but the evidence for a relatively basal phylogenetic position of Madtsoiidae among snakes, and unusually good preservation of the Australian material, justify more detailed documentation.

The description of *Wonambi naracoortensis* by Smith (1976) was the first report of an extinct snake species in Australia. When first described this species was represented by eight large vertebrae and a jaw fragment from the Main Fossil Chamber, Victoria Fossil Cave, Naracoorte, south-eastern South Australia; Smith referred *Wonambi* to Boidae (as diagnosed by Hoffstetter and Gasc 1969) and considered it to have probable affinities to *Madtsoia* and *Gigantophis*, although she did not formally include it in Madtsoiinae (erected for the latter two genera by Hoffstetter 1961; spelt incorrectly by Smith 1976 as “Madtsoiinae”). In subsequent popular works Smith (1983, 1985) referred to *Wonambi* as a “giant python”, but this was apparently only meant as an informal characterisation of this large and presumably constricting snake, not a change of systematic assignment to a particular modern boid lineage.

Merrillees (1968) and Archer (1972) had previously mentioned large snake vertebrae from Pleistocene cave deposits

in the south-west of Western Australia (Mammoth Cave and Koala Cave, Yanchep); initially unidentified or thought to be from pythons, this material was subsequently referred to *W. naracoortensis* (Merrilees 1979; Molnar 1984; Smith 1985) but has never been fully described.

During a salvage excavation by volunteers at Naracoorte in the early 1980s, many disarticulated elements representing two different-sized individuals were found mingled together in the lower fissures of Henschke's Quarry Fossil Cave (Barrie 1990). D. John Barrie assembled bones attributed to the larger individual as a partly rearticulated display specimen and presented it to the South Australian Museum in 1989 (Barrie 1990: fig. 2; Vickers-Rich and Rich 1993: fig. 292; cover of *Nature*, 27 January 2000). Barrie (1990) attempted to interpret the affinities of *Wonambi* within the context of a broadly defined Boidae (*sensu* Underwood 1976), and supported Smith's suggestion that it was close to *Madtsoia*, and thus a Gondwanan relict with a long history independent of extant lineages including pythonines. From Barrie's work until very recently, *W. naracoortensis* was the most completely known fossil snake in this continent.

Further vertebral remains referable to this species have since been identified from additional Pleistocene cave deposits at Naracoorte (Grant Hall in Victoria Fossil Cave, Wet Cave, and Haystall Cave; Reed and Bourne 2000), Wellington Caves, New South Wales (Scanlon 1995), and Tight Entrance Cave, southern Western Australia (Gavin Prideaux, personal communication 2002). Skeletal material referred to *W. cf. naracoortensis* is also known from the Curramulka Local Fauna, obtained from a cave on the Yorke Peninsula, South Australia, and is considered to be early Pliocene in age (or perhaps latest Miocene; Pledge 1992). Based on a figure published by Pledge (1992: fig. 3a), I earlier suggested (Scanlon 1995) that the Curramulka fauna might include a species of *Yurlunggur* Scanlon, 1992; however, subsequent examination of the material indicates that *Wonambi* is the only large snake present. On the other hand, a vertebra from the Pleistocene Wyandotte Local Fauna of northern Queensland (Qld), initially referred to *Wonambi* by G. McNamara (1990), is excluded from that genus and referred to *Yurlunggur* sp. (Scanlon 1995, 1996; Mackness and Scanlon 1999). A vertebra from the Pliocene Kanunka Local Fauna, South Australia, referred to *W. naracoortensis* by Pledge (1992), also belongs to a species of *Yurlunggur* (personal observations).

Although some cranial bones of other madtsoiid species are known, almost all of these are elements also known from *W. naracoortensis* (Scanlon 1996, 1997; Rage 1998; Scanlon and Lee 2000; personal observations). The late Oligocene to mid-Miocene deposits at Riversleigh contain abundant and taxonomically diverse remains of this group, but until recently only a single braincase fragment was recognized (a sphenoid of *Yurlunggur* sp. identified in 1990; Scanlon 1993b, 2003). For comparison among madtsoiid taxa and resolution of phylogenetic relationships with other squamate lineages, more detailed description of the cranial morphology of *Wonambi* is required than that given by Barrie (1990), especially as

Barrie's material was only partly prepared and additional elements have since been identified. Scanlon and Lee (2000) reported some of this new material of *W. naracoortensis* as well as a smaller, Oligo-Miocene species from Riversleigh described as *W. barriei* Scanlon in Scanlon and Lee, 2000, and provided revised diagnoses for the genus and both species.

Rieppel et al. (2002) have given some additional description of the Henschke's Quarry display specimen, which they interpret as a macrostomatan snake of uncertain affinities. They did not refer to any of the additional specimens from the same locality reported by Barrie (1990), or any material identified after 1987, or from other deposits including the type locality, but state incorrectly that of the two species of *Wonambi*, "P30178 ... is ... the only specimen with preserved parts of the skull" (Rieppel et al. 2002: 824). Due to limited representation of material as well as numerous errors and questionable interpretations in their work (some mentioned by Scanlon 2003: 975–976, and others below), a full description of this extinct snake is no less necessary than before.

The reconstruction and interpretation of the cranial morphology of *Wonambi* presented by Scanlon and Lee (2000) is slightly modified by new observations and more detailed description in this work. Postcranial morphology and comparisons with *W. barriei* will be discussed elsewhere. Recently discovered partial skeletons of *Yurlunggur* from the Oligocene and Miocene of Riversleigh, Qld, currently being prepared and studied, provide additional tests of many of the interpretations in this work.

Institutional abbreviations.—AMS, Australian Museum, Sydney (R, Herpetology); AR, Michael Archer reference collection, University of New South Wales (also used as temporary registration for some Riversleigh fossils); FU, Flinders University, Department of Zoology, Adelaide; QM, Queensland Museum, Brisbane (F, Palaeontology, J, Herpetology); SAM, South Australian Museum, Adelaide (P, Palaeontology, R, Herpetology); UNSW, University of New South Wales, Sydney.

Other abbreviations.—CL, Corra-Lynn Cave, Curramulka, Yorke Peninsula; CQ, Curramulka Quarry, Yorke Peninsula; HQ, lower fissures of Henschke's Quarry Fossil Cave, Naracoorte; VF, Main Fossil Chamber, Victoria Fossil Cave, Naracoorte.

Materials and methods

The description below is based on all known cranial material of *Wonambi naracoortensis*, which comes from four localities (see previous section), all in South Australia: VF (Pleistocene; Smith 1976; Reed and Bourne 2000), HQ (Pleistocene; Barrie 1990, 1997), CL (?early Pliocene; Pledge 1992), and CQ (fissure RF 95, probably Pleistocene based on associated mammals, James McNamara, personal communication 2002). All of this material is registered in the SAM P or FU collections. Reference is also made to QM F specimens of other madtsoiid

taxa studied at UNSW as part of a PhD project (Scanlon 1996), and other Riversleigh material identified subsequently and currently being studied. Recent comparative material has been consulted in the AMS R, QM R, SAM R, and AR collections.

VF material represents at least two skeletons, currently very incomplete (as careful excavation of the deposit initiated by R.T. Wells is still in progress) but showing excellent preservation of teeth and bone surfaces. Smith (1976) reported a jaw fragment (SAM P16170c), and Barrie (1990) a near-complete parietal (SAM P27777) from this deposit, but did not publish detailed illustrations or descriptions of either. Scanlon and Lee (2002) described features of the dentition based on a partial maxilla of a very large individual (FU1762). Another partial maxilla from a smaller individual is also described below.

Material from HQ (registered under the single number SAM P30178) comprises two partial skeletons, referred to below with suffixes A and B for the larger and smaller respectively (HJD2:84Wi and HJD1:83Wi of Barrie 1990). Although the fissure containing the deposit no longer exists, processing and sorting of the excavated material has been continued by John Barrie, and he has made additional elements of both skeletons available for study and lodgement in the SAM (Scanlon and Lee 2000); more may remain to be identified. Most of the cranial elements are attributed to SAM P30178A; Barrie reported a complete right maxilla from the smaller SAM P30178B, and some other fragments may be attributed to the same individual. At the time of recovery the surfaces of most of the cranial elements were hardened with a PVA wash (Barrie 1990), which consolidated a layer of “terra rossa” cave-earth, in places overlying a calcite patina, so that much surface detail remained obscured. This was the condition of the material when first described (Barrie 1990), but I cleaned parts of the braincase in 1991, revealing some additional features (Scanlon 1993b, 1996; Scanlon and Lee 2000; see also Rieppel et al. 2002: 814). Further preparation of all cranial elements was carried out either in 1999 (on specimens that were held by D.J. Barrie since collection, then studied at the University of Queensland before lodgement in the SAM) or July 2001 (subsequent to examination of some SAM material by O. Rieppel and A.G. Kluge): I removed most of the superficial calcite with the aid of dilute acetic acid, and also separated some of the braincase elements and cleaned their contact surfaces, but was unable to safely separate the sphenoid, basioccipital and left opisthotic-exoccipital, and some foramina and canals remain blocked. The right basipterygoid process and posterior part of the sphenoid were unfortunately damaged during handling (present condition shown in Fig. 8). Parts of the calcitic encrustation also remain on the left maxilla and right dentary; some of these resistant areas appear to form internal moulds of tubes several millimetres in diameter, consistent with Barrie’s (1990) inference of termite damage to (and partial destruction of) some postcranial elements. None of the other identified cranial elements shows similar damage, but some have cracks or breaks con-

sistent with crushing or impacts. In attempting to correct Rieppel et al.’s (2002) mis-statement of SAM P30178’s origin as “Victoria, Australia”, I made a similar but smaller lapse (Scanlon 2003: 975) in attributing it to VF rather than HQ (the two sites are about 15 km apart).

Jaw remains known from CL (previously unreported) include a maxilla and a pterygoid described below, which are fragmentary but show fine preservation of bone surfaces and teeth. Another partial maxilla, more severely worn, is the only cranial fragment of *Wonambi* from CQ. The further preparation of the HQ specimens, and study of less complete material not previously described or illustrated, thus allow description of surface details hitherto unreported, and comparison of one cranial element (maxilla) from multiple individuals.

For purposes of comparisons discussed here, I assume the relationships found by Lee and Caldwell (2000) and Lee and Scanlon (2002). Thus, phylogenetically relevant comparisons are made with other madtsoiids, other extinct snake taxa such as *Dinilysia*, *Pachyrhachis* and *Haasiophis*, “anilioids” (basal alethinophidians *Anilius*, *Cylindrophis* and *Anomochilus*, but not the more derived uropeltines), macrostomatans (*Xenopeltis*, pythonines and others), and “lizard” outgroups (particularly, extant varanoids and extinct mosasauroids) based on examination of specimens or descriptions in the literature. For all comparisons involving extinct species, the criterion of primary homology is topographic similarity of ossified structures, and does not depend on hypothetical soft-tissue relationships or ontogenetic trajectories (this corresponds to the principle espoused, though not always practiced, by Rieppel and Zaher 2000). Perceptually “similar” states, i.e. those amenable to identical partial descriptions in different species, are regarded provisionally as historically identical effects of common ancestry (Hennig 1966; Kluge 2004), and testing of such homologies by character congruence takes place in (and subsequent to) simultaneous analyses of many characters and taxa (e.g., Lee and Scanlon 2002).

Terminology for cranial structures follows Oelrich (1956) unless stated otherwise; other valuable sources for terminology and comparisons include Estes et al. (1970), Rieppel (1979, 1985), Bellairs and Kamal (1981), Kluge (1993), Cundall and Rossman (1993), Norell and Gao (1997), and Rieppel and Zaher (2000). I use “sphenoid” for the element representing indistinguishably fused basi-sphenoid and parasphenoid (“parabasisphenoid” of many authors); “exoccipital” may include opisthotic where reference is made to the fused (dorsal) parts of these bones.

Systematic palaeontology

Squamata Opperl, 1811

Ophidia Brongniart, 1800

Madtsoiidae Hoffstetter, 1961

Diagnosis.—Snakes of small to very large size; hypapophyses present only in anterior trunk; middle and posterior

trunk vertebrae with moderately or well developed haemal keel (except a few near the cloacal region), often with short laterally paired projections on the posterior part of the keel. All trunk and caudal vertebrae with a parazygantral foramen (or sometimes several foramina) in a more or less distinct fossa lateral to each zygantral facet; prezygapophyseal processes absent; paracotylar foramina present; diapophyses relatively wide, exceeding width across prezygapophyses at least in posterior trunk vertebrae (Scanlon in press, modified from Rage 1998).

Remarks.—Polarity of some characters listed above remains uncertain. Additional apomorphies have been identified in phylogenetic analysis but may not apply to all included taxa (Lee and Scanlon 2002: table 2; see remarks on diagnosis in Scanlon in press). Monophyly of Madtsoiidae is accepted provisionally while there is insufficient contradictory evidence, but remains weakly supported as long as any of the included taxa are poorly known (Rage 1998; Rage and Werner 1999; Scanlon 2003). Due to the inferred phylogenetic position of this group outside the clade containing all extant snakes (Scanlon 1996; Scanlon and Lee 2000; Lee and Scanlon 2002), it is referred to Ophidia (defined as in Lee 1998) but not to Serpentes Linnaeus, 1758; the latter is restricted to “crown clade” snakes, i.e., the least inclusive clade containing all extant snake taxa (Scolecophidia+Alethinophidia, collectively referred to as “modern snakes”).

Wonambi Smith, 1976

Type species: *Wonambi naracoortensis* Smith, 1976.

Referred species: *Wonambi barriei* Scanlon in Scanlon and Lee, 2000.

Diagnosis.—Neural spines of vertebrae high, sloping posterodorsally, with sharp-edged anterior lamina extending to near anterior edge of zygosphenes; transverse processes extending laterally beyond zygapophyses in most trunk vertebrae, diapophyses with concave dorsal edge in lateral view; zygosphenes relatively narrow, with steep facets (20–30° from vertical); zygapophyses inclined 20° or more above horizontal; haemal keel in middle and posterior trunk region narrow and weakly defined laterally, but often distinctly bifid or trifid on the posterior third of the centrum. Pterygoid tooth row near middle of bone, away from medial edge, and basipterygoid facet narrow and facing medially as much as dorsally; ectopterygoid process of pterygoid triangular in palatal view. Maxilla and dentary relatively elongate and depressed; maxilla with deep, anterolaterally directed trough on sub-orbital surface (Scanlon and Lee 2000).

Remarks.—All characters in the generic diagnosis are observed directly in both species except for the shape of the ectopterygoid process in *W. naracoortensis*, which is inferred below to be similar to that of *W. barriei* (and unlike the other madtsoiids where this structure is known). Diagnoses of both species are given in Scanlon and Lee (2000). All *Wonambi* material from the Pliocene and Pleistocene (southern Western Australia and South Australia, and central New South Wales) is referred to *W. naracoortensis*; the smaller *W. barriei* is

known only from Early Miocene and possibly Late Oligocene deposits at Riversleigh, Qld.

Postcranial variation will not be described fully here, but I add some remarks on two points: (A) the relative indistinctness of parazygantral foramina in *W. naracoortensis*, and (B) the nature and preservation of haemal arches on caudal vertebrae in madtsoiids.

(A) When *Wonambi* was represented by just a handful of vertebrae, it was referred to Madtsoiidae provisionally or doubtfully, because its parazygantral foramina (not in all vertebrae, but in some including the holotype; Smith 1976: fig. 2E) were smaller or less distinct than in the few giant species of *Madtsoia* and *Gigantophis* then known (Smith 1976; Rage 1984). According to Rieppel et al. (2002: 812), “the association of *Wonambi* with madtsoiids was considered tentative by Rage (1984; see also Smith 1976), and it still is.” This ambiguous phrasing either attributes to J.C. Rage a view which he does not actually hold (e.g., Rage 1998), or asserts that the grounds for earlier doubt are still valid. In fact we now know rather more about variation of parazygantral foramina in Australian members of this group, and three independent components of variation can be identified. Many *W. naracoortensis* vertebrae have one or more of the following features: (1) subdivision of the large, single foramen on each side usual in other madtsoiids; (2) shallowness of the depression (“fossette”, Hoffstetter 1961) containing the foramina; and (3) presence of numerous smaller additional foramina or pits in the parazygantral area, beyond the depression. These features (1–3) have a restricted distribution within Australian Madtsoiidae and are potentially useful as taxonomic characters, as they vary independently within and between some species (particularly those of *Wonambi* and *Yurlunggur*), while others (including species of *Alamitophis*, *Patagoniophis*, and *Nanowana*) have bilaterally single, relatively large, usually distinctly recessed foramina and no additional pits (Scanlon 1992, 1993a, 1995, 1996, 1997, in press).

(B) Extant snakes have the caudal haemal arches (haemapophyses, corresponding to chevron bones in most other amniotes), if present, fused to the centra proximally, and forming laterally paired projections which are unfused and usually separated distally (Hoffstetter and Gasc 1969; Lee and Scanlon 2002, characters 204–206). Paired ventral projections of caudal centra in madtsoiids were thus initially identified as “haemapophyses”, despite having flat or concave facets rather than finished bone distally (e.g., Scanlon 1993a; Rage 1998). However, one caudal vertebra of *W. naracoortensis* is known (part of SAM P30178, HQ) that retains a complete chevron (V-shaped element, open proximally and fused distally) partially fused to the distal facets of the “haemapophyses”, indicating that the latter are actually pedicels for the chevron like those in varanoid lizards (Scanlon and Lee 2000: fig. 2g). This lizard-like condition in *Wonambi* unambiguously supports a phylogenetic position outside the clade of modern snakes characterized by typical haemapophyses. Rieppel et al. (2002: 813, 824) raise several objections to this interpretation: (1) Barrie (1990: fig. 11) il-

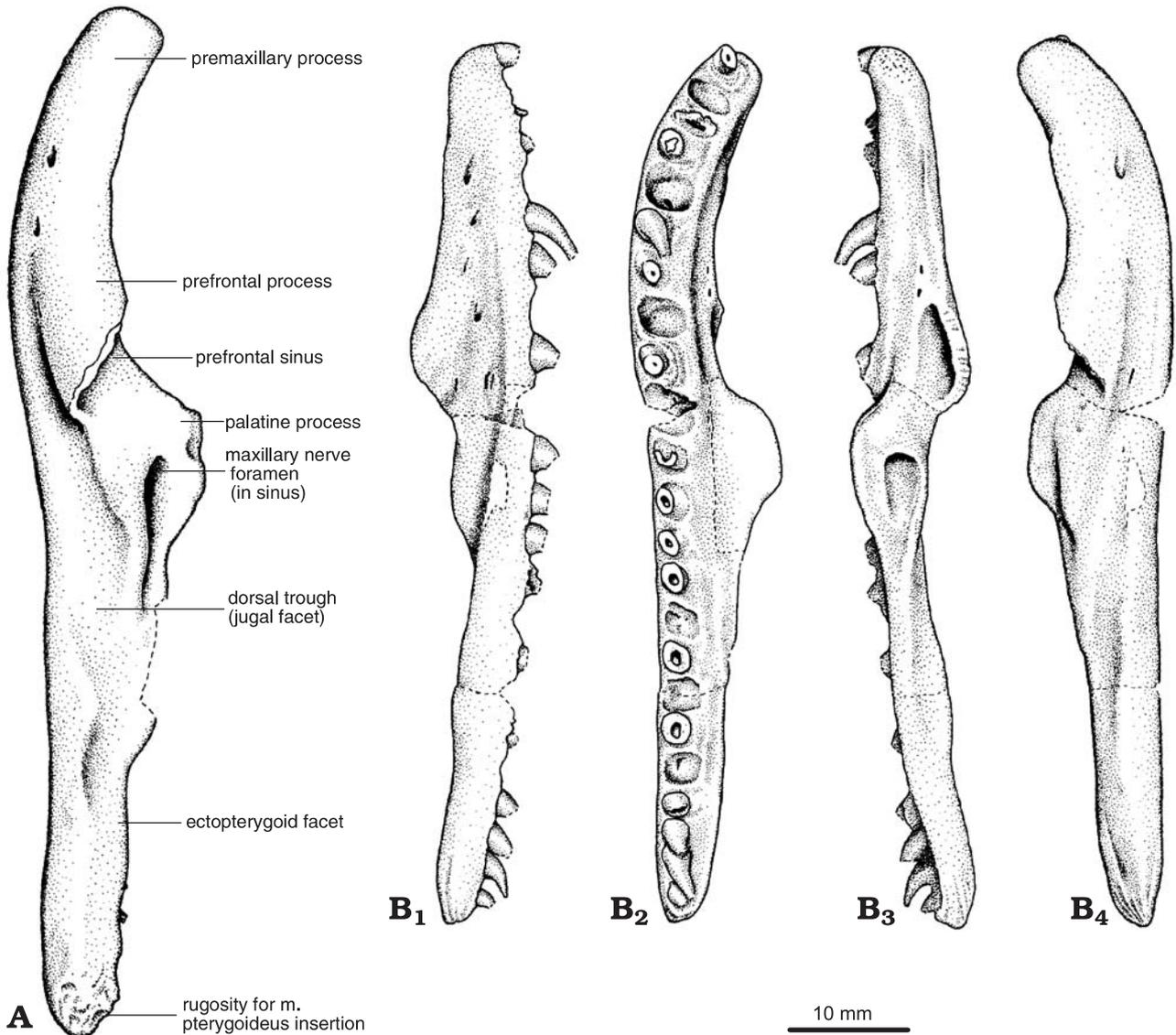


Fig. 1. *Wonambi naracoortensis*. A. Left maxilla of SAM P30178A in dorsal view. B. Right maxilla of SAM P30178B in lateral (B₁), ventral (B₂), medial (B₃), and dorsal (B₄) views.

illustrated a considerably larger caudal vertebra of P30178 which lacks a chevron; (2) the vertebra with attached chevron was not among the material examined by Rieppel and Kluge; (3) the suggestion was made (attributed to M. Hutchinson, SAM Herpetology) that the specimen illustrated by Scanlon and Lee was from a different locality and age; and (4) “it seems that chevrons are a plesiomorphic trait at the level of Serpentes, and hence cannot be used in an argument supporting the basal position of *Wonambi*.” These are answered briefly below. (1) The large caudal figured by Barrie is from immediately posterior to the cloacal region (it is almost the same size as the cloacal vertebra figured adjacent to it) and lacks any sign of an ossified haemal arch or pedicels; the presence of at least one such “pygal” vertebra is typical of squamates and has also been demonstrated in *W. barriei* (Scanlon 1996; Scanlon and Lee 2000). More posterior vertebrae of the same caudal series are, not surprisingly,

smaller; but it is also possible that the caudal with chevron comes from the smaller of the two skeletons comprising SAM P30178. (2, 3) The vertebra in question was not in the display cabinet (donated in 1989) that Rieppel et al. (2002) examined; it remained with the collector and donor (D.J. Barrie) until positively identified as *Wonambi* in 1998. The final objection (4, repeated by Rieppel et al. 2003: 538) represents a basic misunderstanding of the principles of phylogenetic inference: synapomorphy is evidence for monophyly, while symplesiomorphy is not (Hennig 1966). All modern snakes either have fixed, paired haemapophyses in place of chevrons (Macrostomata, with few exceptions), fixed median “caudal hypapophyses” (Uropeltinae), or lack any such structures (Scolocophidia, *Anilius*, *Cylindrophis*) (Hoffstetter and Gasc 1969; Lee and Scanlon 2002, characters 204–206; Szyndlar and Rage 2003). Whether these represent separate derivations from the plesiomorphic state or

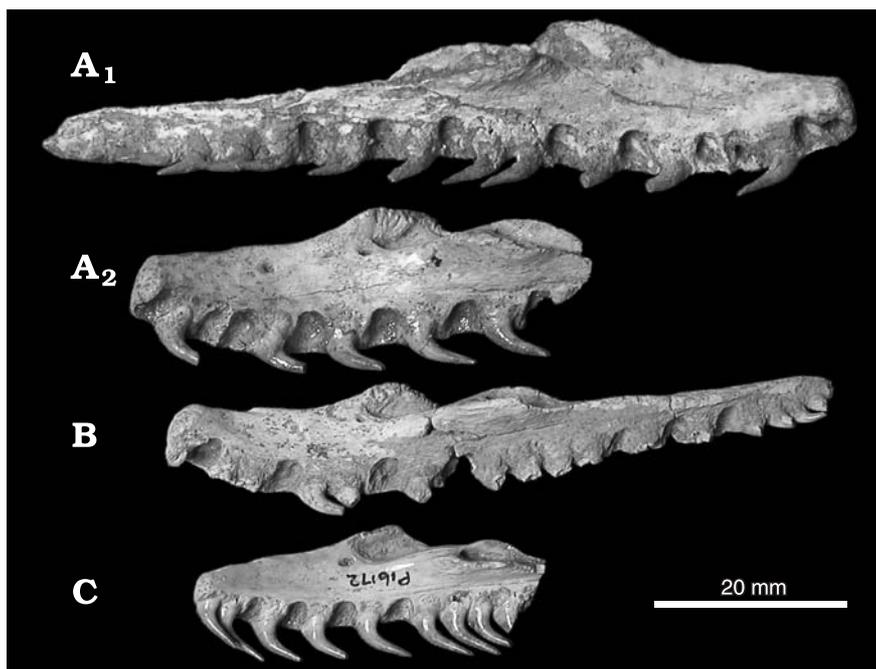


Fig. 2. Maxillae of three individuals of *Wonambi naracoortensis* in medioventral view. A. SAM P30178A, left (A₁) and right (A₂) sides. B. P30178B. C. P16172.

(as it may be more parsimonious to assume) true chevrons were lost only once in an ancestor of modern snakes, these synapomorphies are indeed evidence for grouping modern snakes to the exclusion of *Wonambi*, and thus for the relatively basal phylogenetic position of the latter (and of *Eupodophis*, Rage and Escuillié 2000).

Description of cranial elements of *Wonambi naracoortensis*

Maxilla (Figs. 1, 2; for measurements see Table 1).—Partial to complete maxillae from VF, HQ, and CL provide an indication of the number and size range of individual skeletons represented; the single maxilla from CQ (SAM P40158) lies within the size range of the other material but is omitted from Table 1 because it is too worn for comparably precise measurements. SAM P16172 was not mentioned by Smith (1976), despite the registration number (very close to those of the type material) suggesting it was collected at about the same time; the “anterior left maxilla” fragment reported by Smith (P16170c) is here identified as part of a right dentary (see below). The unidentified “maxillary fragment” shown in lateral view by Rieppel et al. (2002: fig. 2) is not consistent with any material that they reported examining; comparison with all SAM *Wonambi* material indicates it is actually the dentary fragment P16170c (Fig. 12B).

There are 22–23 alveoli in complete maxillae, and alveoli (numbered from anterior) are used below to indicate the relative positions of other features. Prefrontal (= ascending, nasal, or facial) and palatine (medial) processes are level with the 7th–10th and 10th–12th alveoli respectively (Fig. 1; note that

Hoffstetter 1939 and Szyndlar 1984 applied the term “prefrontal process” to the anterior medial process in colubroids, here considered equivalent to the palatine process of the maxilla). In overall shape, including relatively great length of the bone and correspondingly high tooth number, and also shape of the palatine process, the maxilla is similar to those of some macrostomatan snakes, particularly *Loxocemus* and some pythons (species of *Liasis* sensu lato); but the prefrontal process is quite different from these extant taxa and more closely resembles that of anilioid snakes (e.g., *Cylindrophis*). Comparison with maxillae of other madtsoiids (complete in *Nanowana godthelpi* Scanlon, 1997, partially known in *N. schrenki* Scanlon, 1997, *Yurlunggur* sp. or spp. [Scanlon 1996], *Madtsoia camposi* Rage, 1998, and *Wonambi barriei* Scanlon in Scanlon and Lee, 2000) reveals variation in proportions and details, but all possess a high (lizard-like or anilioid-like) prefrontal process; it is relatively lower in *Wonambi* than the other madtsoiids, but unlike any macrostomatan.

In lateral view, the bone is long and low, the alveolar margin nearly straight. The apex of the prefrontal process (above 9–10) and a lower rise above 17–18 define three concave sections of the dorsal margin corresponding to the preorbital, suborbital and postorbital regions. The suborbital concavity is the deepest, formed by a broad and deep trough passing obliquely across the dorsal surface. Anterolaterally this trough is bounded fairly distinctly by a ridge parallel to the alveolar margin, extending anteriorly to the level of the 5th alveolus (Fig. 1B; not previously described, and unknown in other snakes). The prefrontal process is rounded dorsally, but falls off sharply posteriorly at the 10th, then continues as another dorsally convex ridge until obscured by the posterolateral rise. Seven small lateral foramina (alveolar foramina, for branches of the trigeminal nerve) are present in the

Table 1. Measurements (mm) of jaw elements of *Wonambi naracoortensis*. HQ1, HQ2 etc. = single individuals from Henschke's Quarry Fossil Cave (HQ), Victoria Fossil Cave (VF), Corra-Lynn Cave, Curramulka (CL); L = left, R = right. Where possible, measurements are defined in the same way as for *Nanowana godthelpi* (Scanlon 1997: table 1); values in brackets are minima for measurements affected by damage. No precise measurements could be obtained from the other known maxilla, SAM P40158. Maxilla: max alv = total number of alveoli; mtl = total length; map = length from anterior tip to posteromedial angle of palatine process; m7-12 = length from anterior edge of 7th to anterior edge of 13th alveolus; mpw = total width across palatine process; mph = total depth at prefrontal process (excluding teeth, from ventrolateral margin of alveoli to crest of process, not projected in parasagittal plane); m12-p = length from anterior edge of 12-last alveolus to posterior tip. Palatine (ventral view): pal alv = total number of alveoli; ptl = length of palatine from anterior tip of dentigerous process to posterior tip of tooth row spine or choanal process; pcl = base length of choanal process from intersection of anterior edge with dentigerous process to apex of posterior notch; pl-11 = length from anterior tip to anterior edge of 11th alveolus; ptw = width across choanal and maxillary processes; pcw = width (in same line as preceding) of choanal process; prw = width (in same line as preceding) of tooth row bar; pmw = width (in same line as preceding) of maxillary process. Pterygoid (ventral view): pte alv = total number of alveoli; tl5 = length across most posterior five alveoli (5–9); lbp = length of basipterygoid facet; wbp = maximum width of facet; taw = width between near-parallel edges anterior to ectopterygoid process. Dentary: den alv = total number of alveoli; mff = number of mental foramina; dtl = total straight-line length; dl-15 = length to anterior edge of 15th alveolus; dlf = length to lateral fossa; d4t = posterior edge of 4th alveolus to posterior extremity; d4-15 = posterior edge of 4th to anterior edge of 15th; d4f = posterior edge of 4th to lateral fossa; dl-7 = anterior tip to anterior edge of 7th alveolus; dmd = depth from dorsolateral to ventromedial edge in middle part of bone; dpp = depth of upper posterior process.

Mus. cat. no.	SAM P30178A		SAM P30178B	FU1762	SAM P16172	SAM P31801	SAM P31785
Specimen	HQ1L	HQ1R	HQ2R	VF1L	VF2R	CL1R	CL?L
max alv	22	(12)	23	(13)	(14)	–	(7)
mtl	81.0	–	69.8	–	–	–	–
map	38.9	40.5	34.85	–	31.3	–	–
m7-12	22.2	24.0	21.7	–	17.1	–	–
mpw	14.0	12.9	10.9	–	9.5	–	(10.5)
mph	15.0	14.5	(9.2)	–	10.0	–	12.4
m12-p	46.0	–	35.5	47.9	–	–	–
pal alv	–	(12)	–	–	–	–	–
ptl	–	(33.45)	–	–	–	–	–
pcl	–	15.4	–	–	–	–	–
pl-11	–	(26.2)	–	–	–	–	–
ptw	–	(17.4)	–	–	–	–	–
pcw	–	8.0	–	–	–	–	–
prw	–	6.5	–	–	–	–	–
pmw	–	(2.1)	–	–	–	–	–
pte alv	–	–	(7)	–	–	(5)	–
tl5	–	–	9.1	–	–	12.0	–
lbp	–	–	8.0	–	–	–	–
wbp	–	–	2.4	–	–	–	–
taw	–	–	(6.7)	–	–	7.1	–
den alv	25	25	–	–	–	–	–
mff	1	1	–	–	–	–	–
dtl	75.2	74.5	–	–	–	–	–
dl-15	41.2	40.6	–	–	–	–	–
dlf	43.3	43.1	–	–	–	–	–
d4t	65.1	64.6	–	–	–	–	–
d4-15	30.0	30.0	–	–	–	–	–
d4f	34.6	33.9	–	–	–	–	–
dl-7	16.8	16.8	–	–	–	–	–
dmd	14.6	15.0	–	–	–	–	–
dpp	4.9	5.1	–	–	–	–	–

dorsolateral concavity; most of these form a single longitudinal row (almost in one-to-one association with the alveoli), with the remainder more dorsal. The tips of the first 13 teeth lie almost in a single plane parallel to that of the alveoli (Fig. 2C); the few most anterior teeth are somewhat more erect but not much longer, while posterior teeth are shorter, and more strongly inclined posteriorly and medially. The maxillary dentition is thus not really proterodont (as described by Scanlon 1997) but nearly isodont.

In dorsal view the general outline is approximately as shown by Barrie (1990: fig. 5), but additional features are now visible: a longitudinal crest overhanging a sinus and foramina on the palatine process; the posterolateral (as well as anteromedial) boundary of the dorsal trough; and lateral and medial grooves for the ectopterygoid (above the last four alveoli) converging at a short dorsoposterior crest. The anterior tip is not smoothly rounded (as shown by Barrie 1990; Rieppel et al. 2002: 814) but somewhat square in all specimens, with angles defining a distinct, slightly convex anteromedial margin; in this it resembles anilioids and xenopeltids rather than “core” macrostomatans. The posterior end is also not rounded (as previously described) but bluntly angular, with ridges and grooves presumably for ligamentous or tendinous attachments (to the ectopterygoid, and apparently also the *m. pterygoideus*).

In ventral view the alveoli and tooth bases are somewhat rectangular in shape, with an anterolateral ridge on each tooth forming a bluntly acute angle; distinct anterior and posterolateral cutting ridges are present on the more complete crowns. A concave medial face of the bone is visible up to about the 6th tooth, defined above by the dorsomedial ridge. Between the 7th and 8th alveoli this ridge bifurcates around a medial sinus, forming the edges of the (dorsal) prefrontal process and (medial) palatine process. The medial ridge remains distinctly dorsal to the alveolar row from the 8th to 10th, converging with it more posteriorly. The palatine process has a relatively symmetrical, bluntly square profile in ventral view, slightly longer than wide (very similar in outline to some pythonines including *Liasis olivacea* Gray, 1842, but without the strongly downturned medial edge typical of pythons); its posterior edge converges gradually toward the tooth row until a distinct inflexion between the 15th and 16th alveoli (indicating the anterior extent of the ectopterygoid, see below). The bone then tapers in width from the 16th to 21st alveolus, then more steeply from inner and outer edges. There is a shallow longitudinal groove medial to the tooth row from the 14th alveolus to the posterior extremity, the medial edge of the bone projecting as a low ventral crest from 17 to 20. The extent of bone posterior to the last alveolus varies, being relatively greatest in the largest specimen (FU1762) where there is a medioventral outgrowth with a strongly pitted surface (Scanlon and Lee 2002: fig. 3a), inferred to be for part of the tendinous anterior insertion of *m. pterygoideus*.

In medial view, the blunt anteromedial tip of the premaxillary process is roughened and pitted above the first

tooth; this has been interpreted as the attachment surface for a robust premaxillary ligament (Scanlon 1996). This flattened area is more distinctly demarcated and relatively larger in successively larger maxillae (Fig. 2); that the ligament was very short (as well as thick) is suggested by the squared-off shape of the maxillary tip (cf. *Cylindrophis*) suggesting near-contact with the premaxilla, although the latter element remains unknown. The concave medioventral surface of the anterior part of the maxilla is bounded ventrally by a blunt ridge adjacent to the alveoli, and dorsally by the sharper crest leading up to the prefrontal process; the crest is interrupted above the 4th alveolus by a narrow oblique notch resembling that in pythonines (Scanlon 2001), but not containing a foramen. Two foramina occur above the 7th (a small followed by a larger foramen); immediately posterior to the foramina, above the 8th to 10th alveoli, the prefrontal process is strongly concave, forming a deep sinus within the prefrontal process similar to that in lizards, but apparently unmatched in modern snakes (anilioids and leptotyphlopids being the only ones with an equivalent medial surface of the process). The dorsomedial “lip” of the process (above the sinus) faces medially and somewhat posteriorly, and bears vertical grooves and ridges implying an interdigitating suture with the prefrontal; this sutural surface is similar in all maxillae but increases in relative depth, and extent of digitation, in successively larger specimens (three individuals represented in Fig. 2), refuting the suggestion of Rieppel et al. (2002: 814) that the sculpture was artefactual in SAM P30178. The prefrontal sinus is floored by the anterior part of the palatine process. A separate, large, posteromedially directed sinus on the dorsal face of the process encloses a small medially-directed foramen and a larger, deeper one facing posteriorly (two similar foramina are separated by more or less flat bone in the booids examined, and separated by a prominent, oblique dorsal ridge in anilioids). The lateral margin of this sinus forms a posterior extension of the prefrontal process, the two dorsally convex crests separated by a dorsal concavity or saddle. These crests form the medial margin of the oblique dorsal trough, which continues posteriorly as a shallow dorso-medial concavity as far as the 18th alveolus.

As reported by Scanlon and Lee (2000, 2002), breaks through some teeth reveal a basal zone of curtain-like infolding affecting both the outer (enamel) and inner (dentine) surfaces. This condition is considered comparable to the “plicidentine” of varanoid lizards, but in *Wonambi* (and *Yurlunggur*) it is normally hidden by bone of attachment in ankylosed teeth, and has been revealed fortuitously in only a few cases (e.g., FU1762). Hence, failure to observe infolding on teeth with intact bone of attachment does not provide evidence of its absence in any snake taxon, and it is difficult to exclude the possibility that the condition occurs more widely in extant snakes (Scanlon and Lee 2002).

Palatine (Fig. 3).—The nearly complete right palatine of SAM P30178A is the only one known from this species, and can be compared with practically complete palatines of

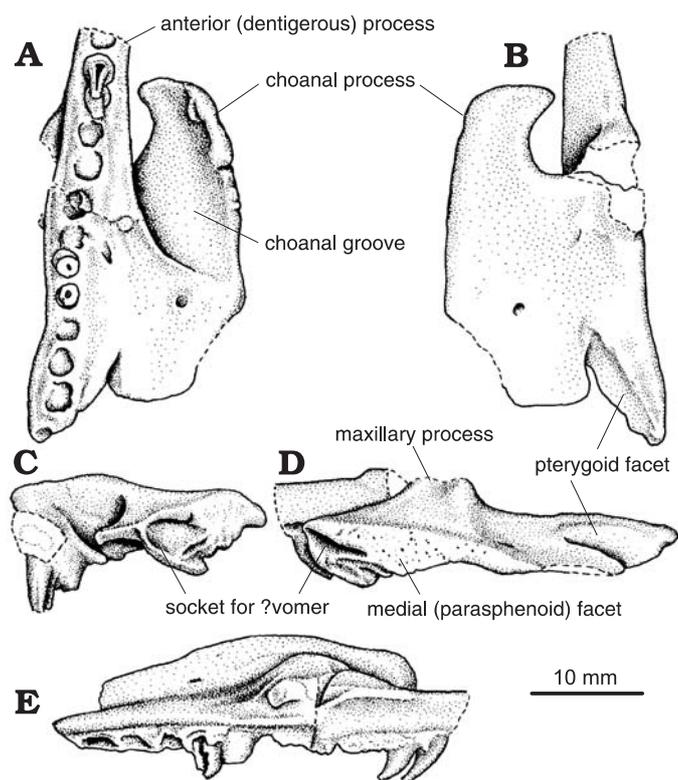


Fig. 3. Right palatine of *Wonambi naracoortensis* SAM P30178A in ventral (A), dorsal (B), anterior (C), medial (D), and lateral (E) views.

Nanowana godthelpi and *N. schrenki*, *Yurlungur* sp., and (?)*Wonambi barriei* (Scanlon 1996, 1997; Scanlon and Lee 2000), as well as one from *Madtsoia camposi* (Rage 1998; also mentioned by Rage 1984) that, if originally comparable in morphology, must be very incomplete posteriorly and medially. The following points can be noted in addition to the information given by Barrie (1990: fig. 6) and Rieppel et al. (2002: fig. 3; note that their figure is reversed and thus appears to show a badly encrusted left palatine instead of a right).

There are 11 complete alveoli preserved (ventral view Fig. 3A), and part of one anterior to these, through which the bone is broken; the complete alveoli are referred to here as 2–12, but it is possible that one or even several more are missing anteriorly. Ankylosed stumps of teeth are present in 2, 3, 8, and 9. The alveoli are close to the lateral margin of the bone, which forms two slightly convex arcs separated by a concavity level with the 10th (an apparently minor feature, but not insignificant as similarly inflected tooth rows are seen in other madtsoiid taxa; Scanlon 1996, 1997). The dentigerous process has a sloping dorsomedial surface partly flooring the choanal passage (dorsal view Fig. 3B), bounded by a dorsolateral ridge that becomes higher posteriorly, expanding above the middle of alveolus 4 into a raised surface that branches laterally (forming the maxillary process) and medially (forming the anterior edge of the choanal process). The maxillary process, mostly broken away, extends posteri-

only as far as the middle of the 7th alveolus. The anterior edge of the choanal process crosses above the medial edge of the dentigerous bar at the rear of the 4th, curving anteriorly and laterally to define the “sub-circular perforation” mentioned by Barrie, and extends anteriorly as far as the rear of the 2nd alveolus; its narrow separation from the dentigerous process is best seen in anterior view (Fig. 3C). The choanal groove occupies the anterior half of the ventral surface of the choanal process, divided from a flatter posterior area by a curved ridge continuous with the medial margin of the dentigerous process, the ridge extending to the medial edge at the palatine’s broadest point, between the 7th and 8th alveoli. The anterior part of the choanal process forms distinct lateral, dorsomedial and medioventral flanges, the hollow between the two medial ridges further divided by a ridge into two distinct concave “sockets” (Fig. 3C, D). The deep anteromedial socket was presumably for articulation with the vomer (cf. *Anomochilus*, Cundall and Rossman 1993: fig. 5B), while the shallow posteroventral one might have received an interchoanal process of the parasphenoid; however, in *Anomochilus* and *Cylindrophis* the interchoanal process is dorsal to the vomerine articulation and does not form a distinct groove on the palatine. Barrie (1990) reported presence of a foramen within the anterior socket, but this is not confirmed after cleaning of the specimen. The rest of the medial face, dorsal and posterior to the sockets, is sculptured and pitted rather than smoothly finished bone (similar in appearance to the facet of the basiptyergoid process, or the anterior tip of the maxilla), suggesting that it formed an articulating surface or tight fibrous connection. Similar sculpture and pitting of the medial palatine surface is seen in *Cylindrophis* (SAM R36779) where the palatine abuts the interchoanal keel of the parasphenoid. The transverse posterior margin of the choanal process is unusually blunt and almost square, but close inspection reveals that this shape is natural, with no transverse break (previously regarded as probable; Scanlon 1996; Rieppel et al. 2002), and damage is limited to the posteromedial margin (shown dashed in Fig. 3A, B).

Because the maxillary process is broken there is no evidence of a foramen or groove piercing it for the palatine nerve in *W. naracoortensis*; other known madtsoiids lack such a foramen but sometimes have a shallow groove (Scanlon 1996, 1997; Rage 1998; multiple losses of the foramen are known among modern snakes; Lee and Scanlon 2002, character 98). Cleaning of the specimen has revealed two foramina piercing the choanal process, one close to the tooth row level with alveoli 7–8 (its dorsal opening facing medially), and a larger one closer to the medial edge, level with the 9th alveolus, which opens posteriorly. Similar foramina are common in lizards, and known in other Australian madtsoiids (Scanlon 1996, 1997); among extant snakes they have been reported in *Acrochordus* (Hoffstetter and Gayraud 1965; Underwood 1967) and illustrated in *Tropidophis* (McDowell 1975: fig. 4), and are also present in *Cylindrophis ruffus* (Laurenti, 1768) (single foramen piercing each palatine of SAM R36779). These are also among the few

modern snakes with large, plate- or scroll-like choanal processes as in madtsoiids, which is presumably the ancestral condition (see Lee and Scanlon 2002, character 82, which refers to shape but omits relative size).

Presence of an anterior dentigerous (or subvomerine) process has been considered one of the few “core” alethinophidian synapomorphies (Estes et al. 1970; McDowell 1975; Rieppel 1988; Scanlon 1992, 1993b; Cundall et al. 1993), but the absolute reliability of this character was put in doubt when other evidence suggested that *Pachyrhachis*, madtsoiids and (in later analyses) *Haasiophis*—which all have the process well developed—lay outside the modern snake clade (Scanlon 1996; Scanlon and Lee 2000; Lee and Scanlon 2002, character 94). These analyses imply that absence of the process in *Dinilysia* and *Scolecophidia* results from secondary losses. Reduction or loss of palatine teeth (as in the latter taxa) has occurred independently in numerous alethinophidian lineages, some of which also reduce the anterior process but do not lose it completely (e.g., *Anomochilus*, Cundall and Rossman 1993).

Pterygoid (Fig. 4).—Interpretation of fragmentary pterygoid specimens has been facilitated by comparison with more complete pterygoids of *Nanowana godthelpi*, *Wonambi barriei*, and *Yurlunggur* sp. (Scanlon 1996, 1997; Scanlon and Lee 2000), as well as other squamates. A fragment of this element from HQ was mentioned by Barrie (1990); it is part of the right pterygoid (greatest length 15.0 mm) retaining the posterior part of the tooth row (not the anterior part as Barrie thought) and part of the medial edge with the complete, though worn, basiptyergoid articular facet (Fig. 4B). The facet is slightly smaller than those on the basiptyergoid processes of SAM P30178A (8.0 × 2.4 mm, versus 8.7 × 5.6 mm); moreover, the disparity in size between palatine and pterygoid alveoli (remarked on by Barrie 1990) is not matched in associated palatal elements of *Wonambi barriei* (Scanlon 1996), *Nanowana godthelpi* (Scanlon 1997) or *Yurlunggur* sp. (personal observations), so is best explained by referring the pterygoid fragment to the smaller individual, SAM P30178B. The tooth row is incomplete anteriorly, broken through the seventh alveolus from the rear; the 2nd to 6th alveoli show signs of bone of attachment but the teeth themselves are absent. The tooth row is slightly concave medially, with the last alveolus displaced further in the same direction; the alveoli are separated by one to two times their diameter from the medial edge. The alveoli lie on a ridge, which is more sharply defined on the lateral side; a shallow longitudinal trough is present between this ridge and the basiptyergoid facet. The facet extends from between the 4th and 5th to about one alveolus-length behind the 7th, and faces dorsomedially and somewhat posteriorly (relative to the long axis of the fragment). The surface of the facet is pitted and slightly worn, apparently unfinished bone similar in appearance to those of the vertebral synapophyses, suggesting an original cartilaginous covering (consistent with possible retention of a synovial basiptyergoid joint; see Irish 1989 and Discussion below), and about four times as long as deep. The dor-

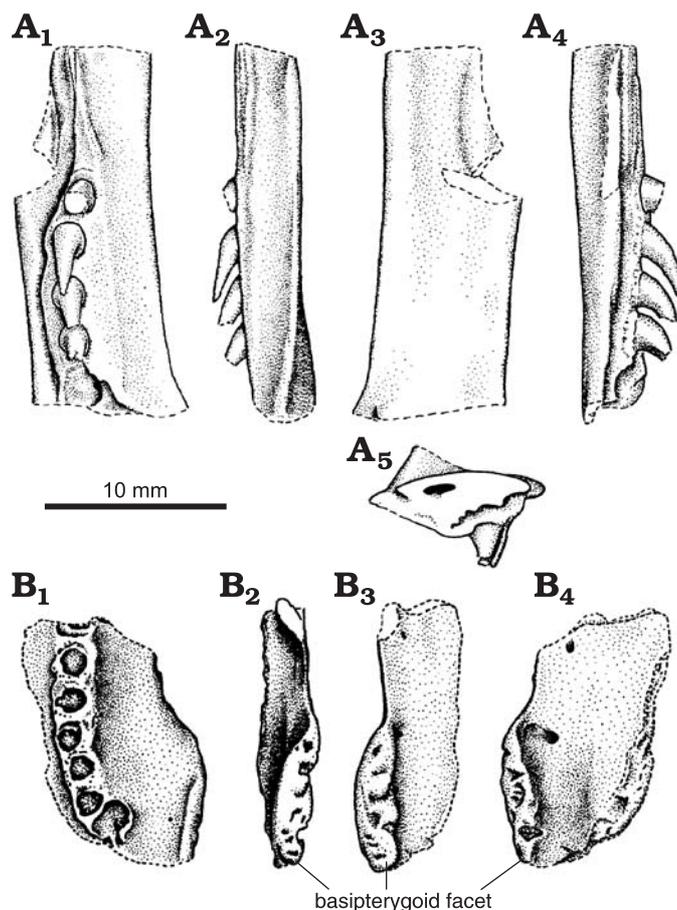


Fig. 4. Right pterygoid fragments of *Wonambi naracoortensis*. A. SAM P31801 in ventral (A₁), medial (A₂), dorsal (A₃), lateral (A₄), and posterior (A₅) views. B. SAM P30178B in ventral (B₁), medial (B₂), dorsomedial (B₃), and dorsal (B₄) views.

sal surface of the bone is transversely concave lateral to the facet, this concavity corresponding in position with the collumellar fossa of lizards. A small round foramen is present about half way between the last alveolus and the medial edge; two larger foramina are present within the dorsal concavity about one alveolar diameter from the medial edge level with the second (opening anteriorly) and fifth alveoli (the latter largest and opening medially).

A more extensive right pterygoid fragment from CL (SAM P31801, Fig. 4A) retains a curved row of 5 complete alveoli and part of a 6th (1–4 with teeth) and an edentulous anterior portion about as long as the first three alveoli. The medial and lateral edges are nearly straight and parallel, apart from damage to the lateral margin anteriorly; the most anterior and posterior alveoli (1 and 6) are in the middle of the bone, but the others are much closer to the lateral edge. The teeth are strongly curved, similar to posterior maxillary teeth but directed posteriorly rather than posteromedially; the second is nearly complete and its distal part nearly parallel to the bone, and in contrast to marginal teeth there are no visible “cutting ridges” adjacent to the tip. The alveoli lie on a ridge, which is moderately distinct on the medial side but quite sharply de-

finned laterally; the ridge narrows in front of the alveoli, continuing as a distinct crest to the anterior margin of the fragment. The dorsal surface is slightly convex transversely at the posterior end, becoming concave anteriorly as the medial edge expands to form a dorsal crest. A curved groove within the dorsolateral hollow is interrupted by the transverse anterior break (similar features of the anterior pterygoid are seen in *Nanowana godthelpi*; Scanlon 1997).

Both of these pterygoid fragments, and the two pieces referred to *W. barriei*, differ from other madtsoiids (*N. godthelpi* and *Yurlunggur*) in the wide separation of the tooth row from the medial edge of the bone (Scanlon and Lee 2000; see generic diagnosis above); polarity of this character is uncertain due to the extent of variation among other basal snakes. Based on the small size of the alveoli relative to the width of the pterygoid in the HQ specimen, I previously estimated that there were about 12 alveoli in the tooth row of *Wonambi* (Scanlon 1996; Scanlon and Lee 2000: fig. 1b). With a second partial pterygoid now available, there are still insufficient shared landmarks to positively assess their relative sizes and extent of overlap, but two likely identifications provide an estimate of tooth numbers closer to those of other madtsoiids. In the CL specimen there is a slight medial expansion at the posterior end, and the transverse posterior break passes through a dorsal foramen close to this margin (Fig. 4A₅); if these correspond to the projection bearing the basipterygoid facet and the larger of the two dorsal foramina in the HQ specimen, there would be an overlap of about 3 alveoli between the two fragments. This leads to an estimated total of 9 alveoli in *W. naracoortensis*, which is equal to the number in complete pterygoid tooth rows of *Nanowana godthelpi* and *Yurlunggur* sp. (Scanlon 1996, 1997). Given that the most posterior alveolus is similarly located in each taxon relative to the basipterygoid facet, the relatively smaller size of the alveoli in the *Wonambi* pterygoid is compensated by the greater relative length of its edentulous anterior region.

The narrow, subcylindrical form and apparently unfinished surface of the facet in *Wonambi* also differs from *N. godthelpi* and *Yurlunggur* where the pterygoid facet is broader, flatter and formed of compact bone, similar to *Cylindrophis*. The *Wonambi* condition may be derived (synapomorphic for the two species), but the corresponding surface is not well known in Cretaceous fossil snakes so polarity remains uncertain.

The lateral (ectopterygoid) process has not been identified in material of *Wonambi naracoortensis*, but is known in *W. barriei*, *Nanowana godthelpi*, and *Yurlunggur* sp. or spp. (Scanlon 1996, 1997; personal observations); in each case the process is large, distinct, and projects strongly laterally and somewhat ventrally from the pterygoid shaft, unlike most modern snakes but comparable to those of *Anilius*, *Cylindrophis* and many lizards, including mosasauroids (Lee and Scanlon 2002, character 101). The ectopterygoid process of *W. barriei* differs from the other two taxa in forming a triangular lateral prominence, with a weakly curved postero-

lateral margin, rather than having a strongly concave posterior margin with a distinct, rugose posterior process presumably for attachment of the m. pterygoideus. The reconstruction of the process in Scanlon and Lee (2000: fig. 1) is based on the observed morphology of *W. barriei*; evidence for variation in muscle-attachment patterns is described further below in reference to the ectopterygoid. As pointed out by Lee and Scanlon (2002), published photographs of *Pachyrhachis* and *Haasiophis* (Haas 1979, 1980a; Tchernov et al. 2000; Rieppel et al. 2003) indicate that both these taxa have surprisingly large ectopterygoid processes comparable to those of madtsoiids and anilioids, although they were not recognised in previous studies of the Cretaceous fossils. The quadrangular shape of the process in both these snakes appears more like the condition in *Nanowana*, *Yurlunggur* and the anilioids, so the triangular *Wonambi* state is considered apomorphic; *Dinilysia*, *Scolecophidia* and most alethinophidians have the processes further reduced or absent, inferred to be convergent.

Just behind the basipterygoid facet and ectopterygoid process, the pterygoid expands into a curved sheet bounded by dorsolateral and medioventral longitudinal ridges in *W. barriei*, *N. godthelpi*, and *Yurlunggur*, similar to *Dinilysia* and *Cylindrophis*. The complete posterior (quadrate) process of the pterygoid remains unknown in any madtsoiid, but in snakes other than scolecophidians this element shows the usual squamate condition of extending posteriorly and laterally to terminate just medial to the quadrate-articular joint, to which (in extant forms) it is connected by ligaments and the m. pterygoideus (usually a separate posterior portion with relatively short fibres, the m. pterygoideus accessorius); its extent thus depends mainly on the position of the jaw joint relative to the palate (which can be reconstructed by anatomical interpolation, see Discussion below) but its detailed morphology is uncertain as this is quite variable among basal snakes and many modern lineages.

Ectopterygoid (Fig. 5).—An ectopterygoid referred to SAM P30178A (listed, and used in a reconstruction, but not fully described by Scanlon and Lee 2000) was the second example known from a madtsoiid; it was identified by comparison with an isolated but slightly more complete specimen from the Miocene of Riversleigh, referred to *Yurlunggur* sp. (QM F19740; Scanlon 1996). Also, an associated skull of *Yurlunggur* collected in 2000 includes both ectopterygoids (one of them perfectly preserved and articulating with the maxilla and pterygoid; personal observations), so that there is no doubt concerning the previous identification of this element (*contra* Rieppel et al. 2002: 827). The bone is roughly L-shaped in dorsal and ventral view, consisting of a medial and a lateral expanded portion joined by a constricted and twisted transverse shaft. The medial (pterygoid) expansion has broken margins but its posterodorsal surface retains part of the facet for attachment to the pterygoid. This facet is bounded by a low ridge anteriorly and a stronger one posteriorly; a groove continuous with the facet extends across the dorsal surface of the shaft

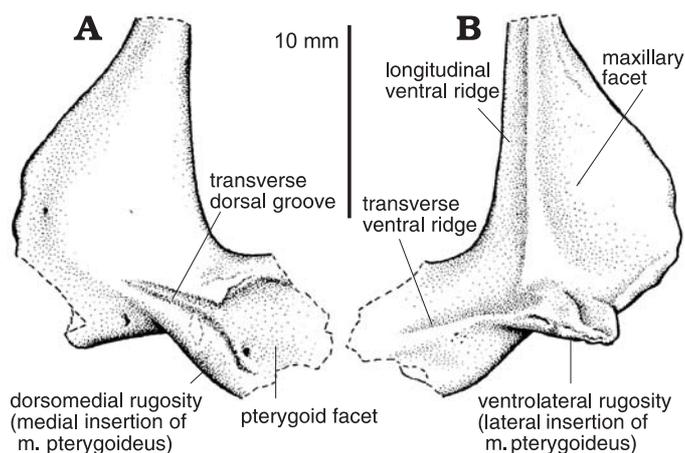


Fig. 5. Left ectopterygoid of *Wonambi naracoortensis* SAM P30178A in dorsal (A) and ventral (B) views.

onto the lateral (maxillary) expansion. The anteromedial margin of the bone is smooth and parabolic, and although both are broken it is likely that both the medial and main anterior portions of the bone extended into acute pointed processes (as in QM F19740). The posterior edge (smoothly concave in the *Yurlunggur* specimen) is here angular in dorsal or ventral view due to the more strongly developed dorsomedial and ventrolateral ridges, which cross each other at an angle. The long anterior spine extended along the medial margin of the maxilla (complete maxillae show an inflection marking the limit of its extent, see Fig. 1), while the lateral part of the ectopterygoid is smoothly convex except for a shallow concavity, containing a foramen, near its lateral margin. As in *Yurlunggur* the lateral edge is smoothly sinuous, concave anteriorly where it arched over the maxilla and convex more posteriorly; the margin is damaged posterolaterally.

In ventral view there is a strong transverse ridge intersecting the dorsal one (running posterolaterally rather than anterolaterally), and a straight longitudinal ridge beginning where they intersect and extending to the most anterior point of the bone. This ridge separates a concave medioventral surface (bordering the parabolic edge of the infraorbital fenestra) from the wide ventrolateral surface, which formed a facet receiving the posterior end of the maxilla. Unlike *Yurlunggur*, where the corresponding surface is strongly arched and bounded by a lateral (as well as posterior and medial) ridge, here the maxillary facet is only weakly concave and relatively much broader, and the bone tapers laterally to a blade-like edge. This difference corresponds to those of maxillary morphology in each genus: in *Yurlunggur* the maxilla has a rod-like or triangular cross-section posteriorly (e.g., QM F23046 and F39330 [= AR 10775]; Scanlon 1996), while in *Wonambi* the posterior part of the bone is somewhat wider than deep, though with a dorsal ridge just anterior to the ectopterygoid facet (a similar divergence is seen between *Nanowana godthelphi*, with a flat maxilla, and *N. schrenki* where it is rod-like posteriorly, though the ectopterygoids of both these species remain unknown; Scanlon 1997).

On the posterior surface of the *Wonambi* ectopterygoid there are two distinct areas of rugosity presumably for muscular or tendinous insertion: medially, on the dorsal ridge adjacent to the pterygoid contact, and laterally, on the ridge that projects ventrally behind the posterior tip of the maxilla (as noted above, the adjacent portion of the maxilla also bears indications of tendinous attachment, strongest in FU 1762). The only major muscle attaching in this area in modern snakes or lizards is the m. pterygoideus (e.g., Haas 1973, McDowell 1986), which varies in having either a single or double insertion (fleshy, or via round or sheet-like tendons). The condition in *W. naracoortensis* suggests that there were two separate anterior insertions of the m. pterygoideus, separated by a smooth portion of the ectopterygoid shaft (this may be convergent, as a double insertion appears to be derived within modern snakes; McDowell 1986). Two such insertion sites are also distinct in *Yurlunggur*, but both are located more medially; the medial one is on the lateral process of the pterygoid (AR13901) rather than the ectopterygoid, while the lateral one is mainly on the transverse shaft of the ectopterygoid (QM F19740) and relatively faintly marked on the posterior tip of the maxilla (QM F39330; Scanlon 1996). The presence of two muscle-insertion structures on the ectopterygoid of *W. naracoortensis* makes it unlikely that there was also a distinct posterior rugosity on the lateral process of the pterygoid, so it is inferred (or predicted) that the ectopterygoid process was similar in form to that of *W. barriei* (Scanlon 1996, Scanlon and Lee 2000; see above).

The ectopterygoid overlapped (or loosely clasped) the posterior end of the maxilla on its dorsal and posterior aspects. The smooth, concave surface of the ventrolateral facet indicates a mobile, fibrous connection with the maxilla as in most other snakes (e.g., Frazzetta 1966). The ventral ridge along the medial margin of the maxillary portion is similar to that in booids such as *Liasis olivacea* and probably extended as a long, spinelike anteromedial process (as preserved in the ectopterygoid of *Yurlunggur*, Scanlon 1996) where the elements were more tightly connected by ligaments (also as in booids).

Frontal (Fig. 6).—The left frontal of *Wonambi* from HQ, identified subsequent to Barrie's description and attributed to the same skeleton as the rest of the braincase (SAM P30178A), was the first frontal known from any madtsoiid (several examples now also known in *Yurlunggur*; personal observations). The ventral part of the element was somewhat fragmented and disarranged when found and consolidated with PVA glue, but on reassembly of the fragments it proved to be nearly complete. The specimen was listed, and used in a reconstruction, but not fully described by Scanlon and Lee (2000).

In dorsal view (Fig. 6A) the bone is roughly rectangular in outline, about twice as long as wide (maximum dimensions 23.20 × 11.95 mm), but several more or less distinct areas of the surface can be recognized. The main part is trapezoidal, bounded medially by the line of the median suture

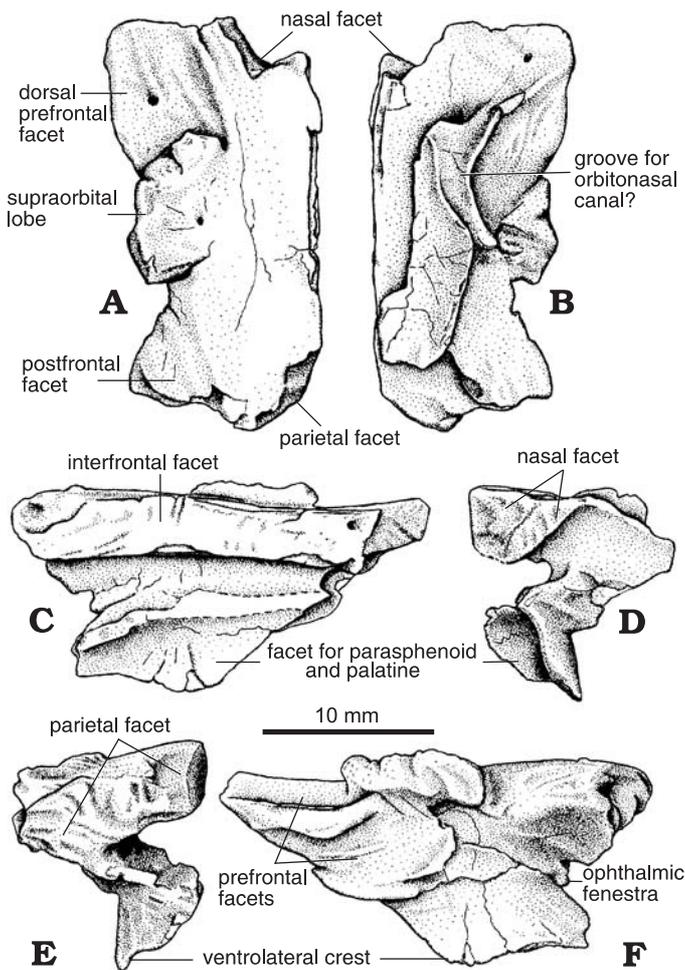


Fig. 6. Left frontal of *Wonambi naracoortensis* SAM P30178A in dorsal (A), ventral (B), medial (C), anterior (D), posterior (E), and lateral (F) views.

with the right element, posteriorly for the full width of the element by the parietal suture (an irregular curve matching that of the parietal, see below), and narrowing anteriorly to a sutural contact surface for the nasal, about one third the total anterior width of the frontal. This main dorsal surface is smooth and flat, but for approximately the middle third of its length it is continuous laterally with a roughly semicircular supraorbital lobe, which has a mainly convex but irregularly thickened, upturned dorsolateral edge. This lobe is fully co-ossified with the main body of the frontal, with no trace of a suture, but there is a single foramen at its medial edge (compare the row of six or seven tiny foramina paralleling the orbital margin in *Dinilysia*, Estes et al. 1970). The posterolateral corner of the bone is at a slightly lower level and set off by a step-like groove, indicating that the frontal was overlapped here by either the postfrontal (if discrete as in *Dinilysia*) or anterior part of the postorbitofrontal. The anterolateral part of the dorsal surface is recessed below both the supraorbital lobe and the rest of the frontal roof, and presumably formed a contact surface for the prefrontal. This sur-

face is smooth and concave, roughly rectangular in outline, with both long edges and low longitudinal ridges aligned slightly anterolaterally relative to the midline. There is a foramen about 1 mm in diameter near the centre of this facet, probably providing blood supply to connective tissue between the two bones. Together with the smooth contours, this suggests a mobile sliding articulation between the frontal and prefrontal, effectively a ball-and-socket joint with its centre of rotation somewhat dorsal to the skull roof.

In posterior view (Fig. 6E), the dorsal part of the frontal is the deep, irregularly interdigitating sutural surface for the parietal. This is generally concave in its lateral portion, but divided medially by a horizontal ridge into dorsal and ventral concave facets where the frontals were clasped between external and internal anterior projections or “tabs” of the parietal. The angle between the dorsal surface and median sutural surface indicates that the interorbital region was arched across the midline, so the supraorbital lobes would not project above the middle of the skull roof. Overall, the frontal is slightly deeper than wide; the subolfactory process projects medioventrally from the lateral part of the frontal roof, and (at least in its posterior part) extends medially to reach the midline, and thus its opposite member. From this point the subolfactory process flares ventrolaterally to a considerable extent, as seen in some modern snakes such as *Cylindrophis*, *Tropidophis*, and large pythons.

Laterally (Fig. 6F), the dorsal region of the frontal shows the dished prefrontal facet, raised shelf-like supraorbital lobe, and the more rounded posterolateral shelf with its dorsal surface recessed for the postorbitofrontal overlap. These three lobes are separated by distinct grooves (accentuated by cracks), the supraorbital lobe distinctly overhanging the posterior edge of the prefrontal facet. The dorsal lobes are also undercut more or less distinctly, and the orbital surface of the subolfactory process is not smoothly concave but features several ridges and grooves. The subolfactory process is deeply notched posteriorly for the ophthalmic fenestra (optic foramen), and forms an angular posteroventral prominence below the notch (but somewhat anterior to the posterior edge of the frontal roof). The ventral edge (ventrolateral crest of the subolfactory process) is approximately horizontal but slightly concave from this point forward to below the middle of the frontal, then generally angles dorsally to be occluded before the anterior edge of the prefrontal process. The anteroventral edge is sinuous, with a convex middle lobe defined below by a groove (the bone has broken horizontally at this level and been rejoined), which continues onto the anteroventral face of the bone (see below). There is an irregular ridge in the middle of the lateral face, with a pit just above it, below the supraorbital lobe; this ridge probably formed the posterior limit for the prefrontal within the orbit (similar to the condition in *Cylindrophis*, and pythons such as *Morelia* spp.; personal observations).

In medial view (Fig. 6C) the dorsal part of the frontal forms a somewhat sculptured, rather deep, rectangular surface for sutural contact with the opposite member. Below it,

the smooth-walled olfactory canal is of similar depth posteriorly, tapering anteriorly. The horizontal break through the subolfactory process has resulted in loss of bone along its medioventral edge, so it is not clear whether it reached the midline along most of its length, or only posteriorly. Below this broken edge is the deep medioventral face that formed a curved "roof" for the space occupied by the cultriform process of the sphenoid, the cartilaginous trabeculae cranii, and the choanal process of the palatine. This surface is slightly concave both transversely and longitudinally, with greater curvature posteriorly, rather than showing a cylindrical form as in most snakes; this ellipsoidal curvature suggests that the cultriform process was quite constricted at the rear of the frontal (also implied by the ventral view of the parietal, Fig. 7D) but may have expanded in the middle of its length. Together with the fact that the preserved posterior part of the cultriform process increases in width anteriorly (see below), the frontal shape implies a constriction and possible second expansion of the cultriform process anterior to the part preserved (see below). Also possible is a condition similar to *Cylindrophis*, where the cultriform process is narrow below the frontals and forms an interchoanal keel abutted by the dorsal and medial surfaces of the palatines, although the latter element appears too flat to form a close contact with the ventral surface of the frontal in *Wonambi*.

The anterior view (Fig. 6D) shows what is perhaps a unique feature of *Wonambi*: a distinctly digitate, roughly vertical sutural surface, rather than signs of either a dorso-ventral overlap or a hinge or ball joint for the nasal. The sutural surface is divided by a groove into an anterolateral-facing medial portion and a dorsomedial-facing lateral part, each of which is somewhat digitate, and just as deep as the interfrontal and frontoparietal sutures. This clearly implies a strong and practically immobile contact with the nasal (and/or, possibly, the premaxilla as in mosasaurs). An oblique ridge separates the dorsomedial sutural surface from the smooth, flared antero-internal surface of the frontal ventrolateral to it. The latter surface, surrounding the olfactory canal, expands laterally on the underside of the prefrontal process, and continues ventrally onto the subolfactory process. A ridge extending dorso-medially from the lateral edge of the prefrontal process demarcates the anterior from the orbital surface, but just below the level of the olfactory canal this ridge turns onto the lateral face. A second, similar ridge extends from near the midline below the olfactory canal, separating the anterolateral and medioventral surfaces of the subolfactory process and forming its flared ventrolateral edge. The space between the two ridges is wide anterodorsally where it is continuous with the interior surface of the canal, narrowing posteroventrally to emerge on the lateral surface as the groove below the mid-lateral ridge. The smooth trough bounded by these ridges possibly indicates the course of the orbitonasal canal.

The ventral view (Fig. 6B) shows four distinct surfaces: the medioventral one to clasp the trabecula, cultriform process and/or palatine, the anterolateral concave triangle (roof of orbitonasal canal?), the concave lateral surface bounding

the orbit (including the presumed ventral part of the prefrontal facet), and the smooth internal surface of the olfactory canal (anterior extension of the braincase). We also see the posteromedial sutural surface for the parietal, the antero-medial one for the nasal, and two small areas of breakage anteromedially: adjacent to the nasal suture, and on the anteromedial corner of the subolfactory process. In extant alethinophidians these two points are joined by a more or less robust bridge of bone, the interolfactory pillar, while such a structure is absent in scolecophidians, *Dinilysia* and lizards. Finding fresh breaks at both points may suggest that the pillar was present in *Wonambi*, but is consistent with either state since there could easily have been two distinct points of damage. The small size of both broken areas implies that a pillar, if present at all, was very slender in comparison to most alethinophidians.

Most of the features of the frontal correspond topographically to those of non-ophidian squamates, as well as other snakes. For example, in a moderately large *Varanus varius* (White, 1790) (AR 5378), there is a distinct posterolateral facet for the postorbitofrontal; a small supraorbital process or rugosity (present on only one side) above the main lateral facet for the prefrontal and at the posterior end of a narrow dorsolateral extension of the facet; the dorsal prefrontal facet is separated from the nasal facet by a longitudinal ridge; the anterior margin is formed by the rounded (though narrow) prefrontal lobe laterally, and two pointed extensions bounding the dorsally exposed nasal facet.

Parietal (Figs. 7, 8, 10A).—*W. naracoortensis* was until recently the only madtsoiid in which the parietal was known, from one almost complete specimen and another more fragmentary (Barrie 1990; Scanlon 1996); that of *Yurlunggur* has now also been identified (personal observations). SAM P27777 (VC, Fig. 7; reported by Barrie 1990 and used as a basis for his reconstruction figs. 5 and 8, but not mentioned by Rieppel et al. 2002) is nearly complete, unworn and free of matrix, requiring almost no extra preparation for this study. It is about twice as long as wide, broadest across the transversely directed, anterolateral postorbital processes. The anterior surface (Fig. 7C) has a rounded median prominence flanked by concave facets for the frontals, about 2.25 mm deep and each 5.0 mm wide, and less distinct facets for the circumorbital elements laterally. The anterior border is thus scolloped, similar in dorsal view (Fig. 7A) to those in *Dinilysia* and *Pachyrhachis*, but relatively broader and less jagged. Haas (1979: 57) said of the parietal in *Pachyrhachis* that "the pair of hollow sockets for the articulation of a pair of anterior bones (frontals) is not snake-like at all..."; while many morphological details of *Pachyrhachis* are still subject to varying interpretations, we can state that *Wonambi*, at least, is a snake that does have such a pair of sockets (Fig. 7A, C). Adjacent to the frontal facets is a slightly concave, pentagonal parietal table, defined laterally and posterolaterally by crests for muscle attachment (for m. adductor externus superficialis, and possibly the deeper m. pseudotemporalis)

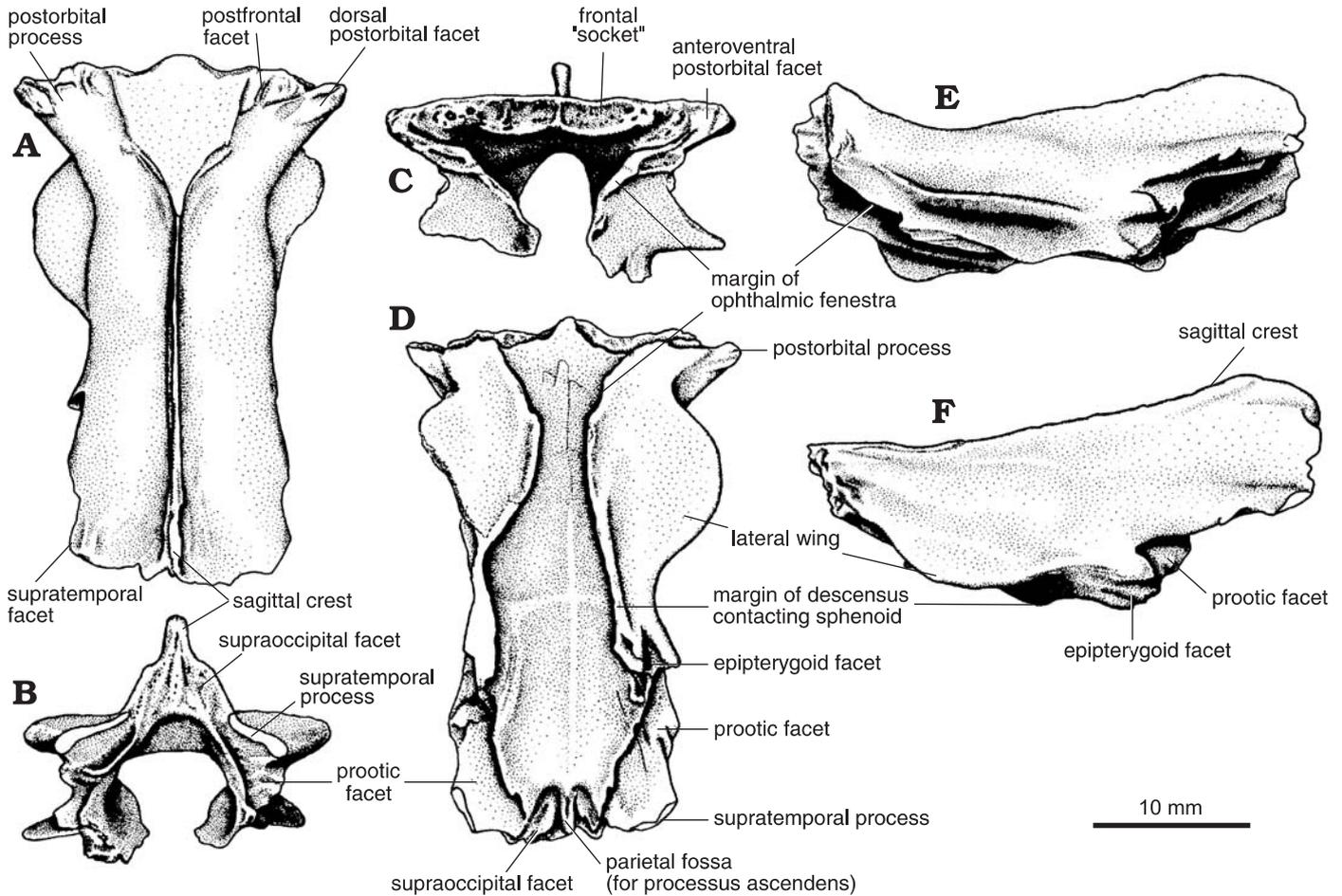


Fig. 7. Parietal of *Wonambi naracoortensis* SAM P27777 in dorsal (A), posterior (B), anterior (C), ventral (D), ventrolateral (E), and lateral (F) views.

and continuous posteriorly with a strong sagittal crest, which extends to the posterior margin of the parietal and increases steadily in height for most of this length. On the anterior part of the dorsal surface to either side of the parietal table, ridges and rugosities define facets for contact with the postorbitals and postfrontals. There are distinct facets on the posterodorsal and anteroventral surfaces of the anterolateral processes where presumably, as in *Dinilyisia* and booids, they were clasped by the postorbitals. Medially adjacent to the dorsal facets for the postorbitals, and abutting the parietal table, are separate facets corresponding to the areas overlapped by the postfrontals in *Dinilyisia*; this suggests that the postorbital and postfrontal were probably discrete as in that taxon.

The smooth dorsolateral surface of the parietal is slightly constricted just posterior to its mid-length, as well as behind the postorbital processes, thus defining a cerebellar swelling (more distinct than in *Dinilyisia* but less than in booids); cerebral and cerebellar lobes are also marked by smooth ridges on the internal surface (ventral view, Fig. 7D). Most distinctively, in both *Wonambi* and *Dinilyisia* there is a prominent, shelf-like lateral crest (lateral wing; Barrie 1990), rounded laterally in dorsal view and angled somewhat below horizon-

tal, at a level below the postorbital process and extending almost half the total length of the parietal. Posteriorly, the lateral wing contracts smoothly in lateral extent but continues as a low ridge onto the projecting posterolateral lobe that underlaps the alar process of the prootic (lateral view, Figs. 7F, 8C, 10A). While lateral ridges of similar length occur in some large boines (*Eunectes* and *Boa*; Bellairs and Kamal 1981; Rieppel et al. 2002) and a rather dissimilar dorsolateral crest in *Acrochordus* (bounding a uniquely enlarged supra-temporal facet; Hoffstetter and Gayrard 1965; Rieppel and Zaher 2001), the only other snake with comparably broad lateral crests on the parietal is *Dinilyisia* (Estes et al. 1970; Caldwell and Albino 2002).

In dorsal view, the posterior edge of the parietal seems to lack a median projection over the supraoccipital (as present in *Dinilyisia*), but a posterior view (Fig. 7B) shows that the contact with the supraoccipital was expanded dorsally, and a median process was indeed present in the form of a vertical ridge, further divided by a groove containing several small foramina (see Discussion).

SAM P27777 retains considerable portions of the borders of the ophthalmic fenestrae on both sides (contrary to Barrie 1990, who considered this area damaged); these are bounded

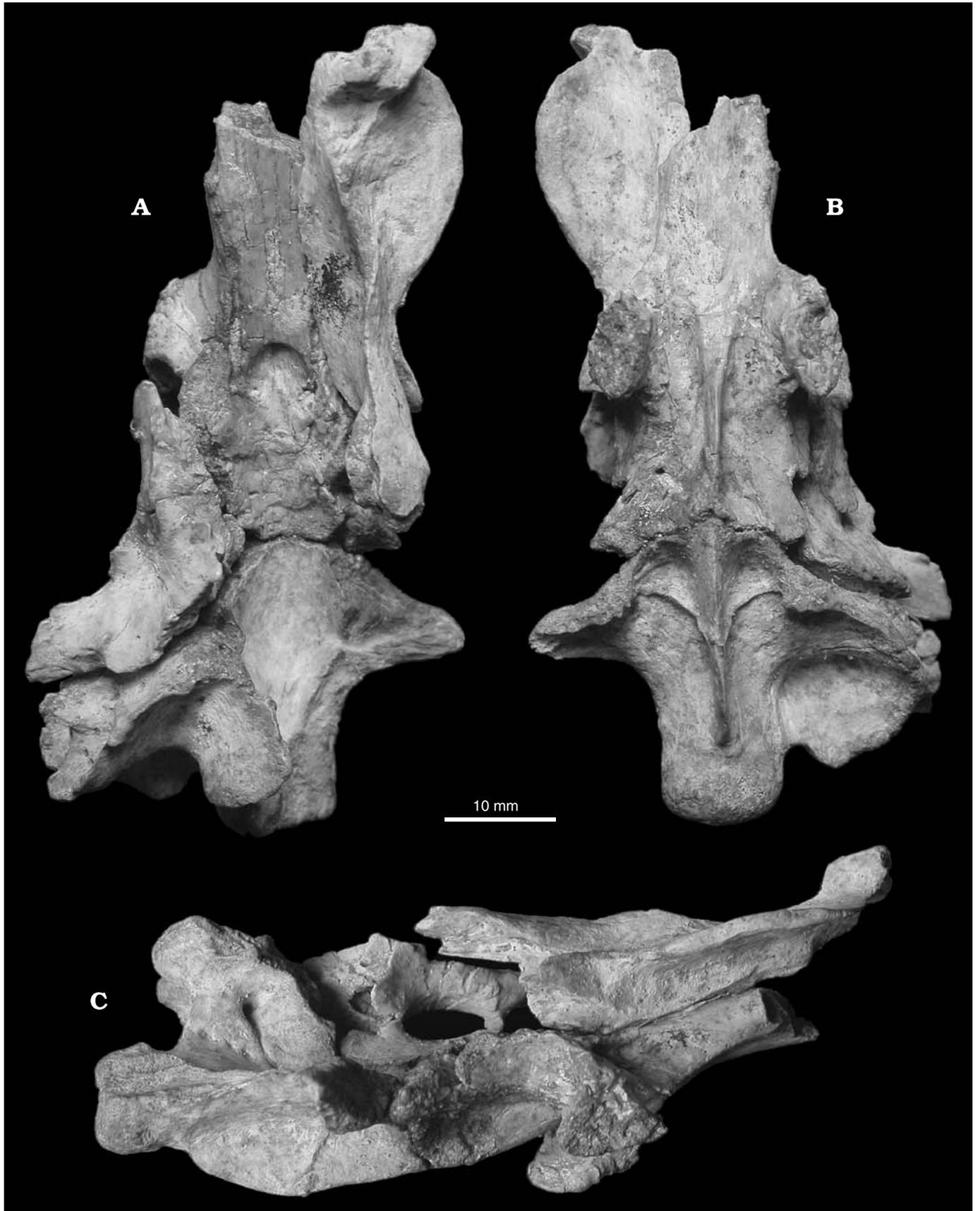


Fig. 8. Braincase elements of *Wonambi naracoortensis* SAM P30178A in dorsal (A), ventral (B), and right lateral (C) views. Sphenoid and basioccipital with (right) part of parietal, left prootic and exoccipital-opisthotic. See also Figs. 9 and 10.

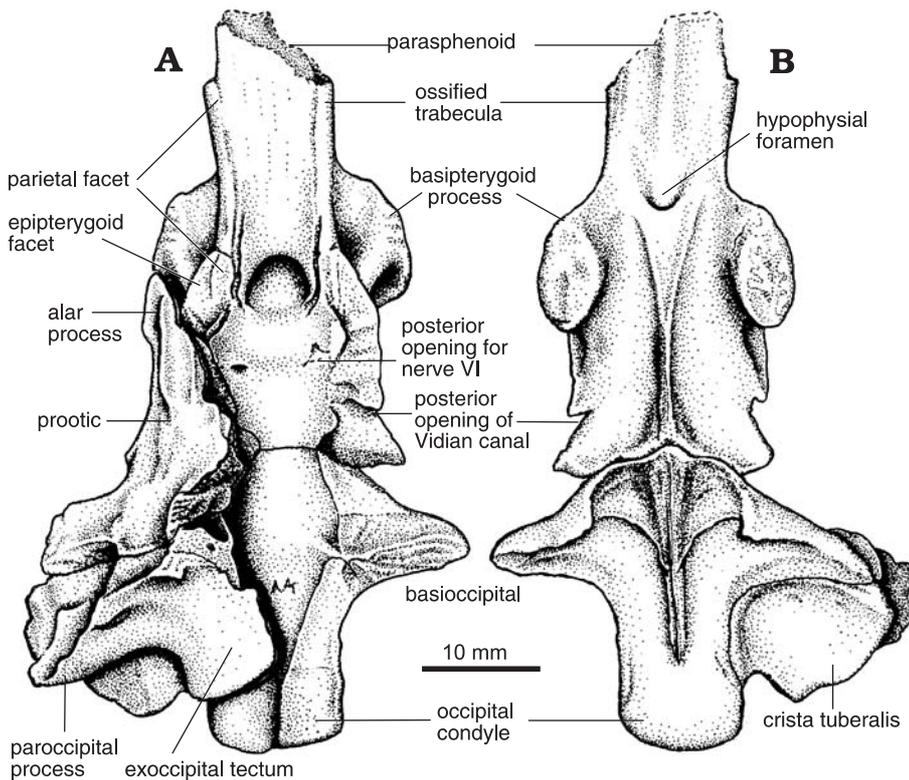


Fig. 9. Braincase elements of *Wonambi nara-coortensis* SAM P30178A in dorsal (A) and ventral (B) views. Slight displacement of prootic and opisthotic-exoccipital corrected graphically in A, prootic omitted in B.

posteriorly by small anteroventral (suboptic) processes showing no sign of a contact surface for the frontal descensus, implying that the fenestra was probably extensively bordered below by the sphenoid. This state also occurs in *Dinilysia* (Estes et al. 1970) and most colubroids, but few other snakes; the character has not yet been used in published phylogenetic analyses at this level, and the condition in *Pachyrhachis* and *Haasiophis* is uncertain, but it can be predicted that the contacts of frontal and parietal with the sphenoid were either similar or less extensive in these taxa (symplesiomorphic, or transitional between lizards and the *Wonambi–Dinilysia* condition; exclusion of the sphenoid from the fenestra synapomorphic for modern snakes and reversed in colubroids). The rest of the ventrolateral margin is well-preserved on one side each in SAM P27777 (Fig. 7E) and SAM P30178A (Figs. 8, 10A), representing surfaces for extensive but apparently non-sutural (i.e., syndesmotic) contact with the dorsolateral margins of the sphenoid. In the posterior third of its length, strong crests on the ventral surface demarcate the intracranial face from the contact surfaces for the prootics; the latter surfaces face mainly ventrally and posteriorly, but also laterally where the anterodorsal (alar) process of the prootic would overlap the parietal above a posterolateral projection. The parietal thus formed an extensive but non-interdigitating contact between two dorsal ridges on the prootic (Figs. 7–10), as in other snakes (and comparable in mosasaurs, see Discussion). The supratemporal processes (suspensorial rami) of the parietal are partly broken off in SAM P27777; the remaining lateral and posterior margins, together with the braincase of SAM

P30178A, indicate that the processes were at least somewhat acute and better developed than in booids, but not flared laterally to the extent seen in *Dinilysia* and some anilioids (which are closer to varanoids in this respect). Low longitudinal ridges near the posterolateral corners of the dorsal surface are interpreted as the medial boundaries of facets for the supratemporals, indicating that an overlap did exist (as in lizards, *Dinilysia* and *Cylindrophis*); this was recognized only recently, whereas the supratemporals were shown as separated from the parietals in the reconstruction of Scanlon and Lee (2000: fig. 1). The relationship of the supratemporal process to the triple junction of prootic, exoccipital and supraoccipital is uncertain, so it is not known whether or not small “islands” of the prootics were exposed behind the parietal-supratemporal contacts as in *Dinilysia* and some anilioids.

Less than half of the parietal has previously been described in SAM P30178A, a fragment comprising much of the right side but not reaching the midline or the anterior or posterior margin (shown articulated with the sphenoid in Fig. 8). Fig. 10A (drawing used in Scanlon and Lee 2000: fig. 2a) is a composite of views from left and right sides, so that the parietal fragment is accurately articulated with the sphenoid, but mirror-reversed to also illustrate the interlocking contact it would have made with the prootic. The assumption of approximate bilateral symmetry in a nearly undistorted skull seems reasonable, but it is regrettable that mention of the graphical transposition was cut from the *Nature* paper due to space restrictions. Rieppel et al. (2002: 813) claim that this procedure is misleading (“...creates the illusion of characters for which there is no empirical basis...”), but it is not respon-

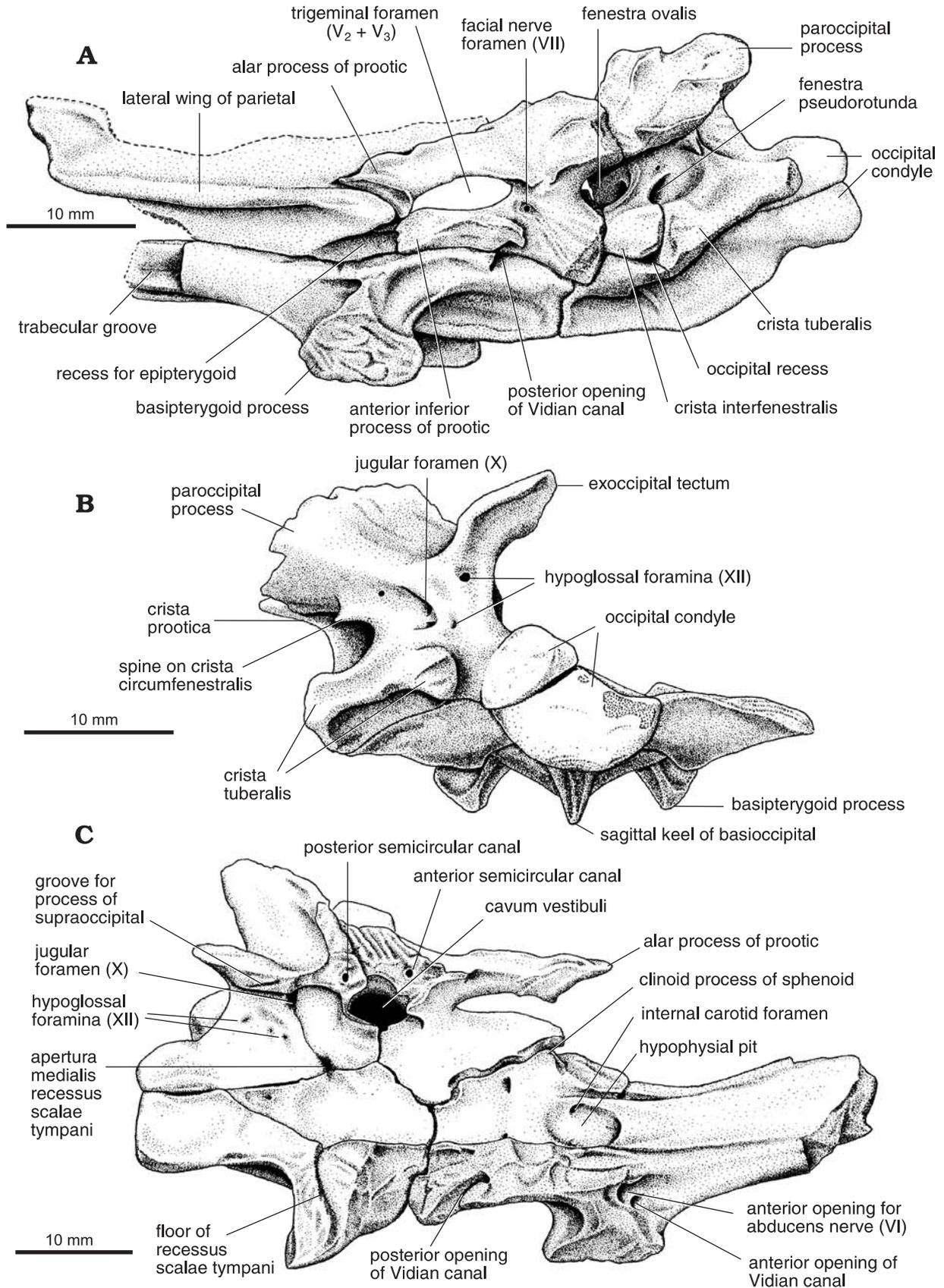


Fig. 10. Braincase elements of *Wonambi naracoortensis* SAM P30178A in left lateral (A), posterior (B), and right dorsolateral (C) views. Sphenoid, basioccipital, left prootic and left exoccipital shown in articulation; in A the right side of the parietal is shown reversed as if articulated with the left side elements. Drawings in A and C published previously in Scanlon and Lee (2000). Scale approximate, varies with perspective.

sible for their erroneous statements that the parietal specimen retains a “severely abraded” sagittal crest and that the posterior part of the lateral wing is missing due to abrasion (p. 815). The smoothly curved border of the lateral wing is virtually complete on the right side of SAM P30178A, as on the left side of SAM P27777. No trace of sagittal crest (or other midline structures) is preserved on the specimen they examined, but another non-adjointing piece from HQ (“posterior part of parietal” attributed to the smaller individual by Barrie 1990: 140; not seen by Rieppel et al. 2002) is here also considered part of SAM P30178A. This specimen (19.5 mm long, 9.7 mm wide when laid flat but approximately 8.5 mm in natural orientation; not figured) does include parts of the sagittal crest as well as the posterior end of the lateral crest, and the ventrolateral and posterior contact surfaces for the prootic and supraoccipital on the left side, but due to abrasion the original and broken margins are partly indistinct (identified only by direct comparison with SAM P27777). There appear to be differences in proportions from SAM P27777, though they have not been quantified due to the incompleteness and wear of the parietal in SAM P30178A. Since the parietal bears crests for major jaw adductor muscles (expected to show positive allometry) and also encloses the brain (with negative allometry), this element shows significant ontogenetic shape changes in many vertebrates including most snakes. Consistent with these expected trends, the larger specimen (SAM P30178A) has a relatively longer and broader lateral wing; it also appears that its contact surface on the prootic is closer to the midline than would be consistent with isometry (compare Figs. 7A, 8A), indicating the larger parietal was relatively narrower posteriorly. In the reconstruction of Scanlon and Lee (2000: fig. 1), drawn before examination of SAM P27777, the parietal is shown inaccurately as excessively broad.

Sphenoid (Figs. 8–11).—The sphenoid complex (fused basi-sphenoid and parasphenoid) of SAM P30178A is similar to that of *Yurlunggur* (Scanlon 2003) in general morphology, but differs to some extent in proportions and in the arrangement of foramina; these are the only madtsoiids where the element is known, and the anterior part (parasphenoid rostrum or cultriform process) is missing in both.

In ventral view the element consists of two roughly rectangular portions; the narrower anterior portion (mainly formed by the parasphenoid) is the base of the cultriform process, partly bounded laterally by the ossified trabeculae cranii (trabecular processes). The latter are slightly divergent anteriorly rather than being parallel, and the part of the lateral margin preserved anterior to them angles slightly anteromedially, so that this part of the sphenoid is somewhat kite-shaped rather than rectangular; the ventral margin of the parietal (Fig. 7D) indicates that the parasphenoid continued to taper anteriorly at least as far as the ophthalmic fenestrae. The larger posterior portion (corresponding approximately to the basisphenoid) contacts the basioccipital posteriorly; the posterolateral corners form acute projections, and contribute marginally to the

large speno-occipital tubercles (Fig. 10A). The lateral margins are notched, just anterior to the basioccipital contact, for the posterior Vidian canal openings, and bounded anterolaterally by the prominent basiptyergoid processes. There is a strong median crest on the posterior part (more or less continuous with that on the basioccipital), but it widens and becomes flat anteriorly between the basiptyergoid processes, disappearing level with their anterior ends. At this point there is a wide but shallow opening (seen ventrally as an anteriorly open parabola) for the hypophysial foramen (“cerebral foramen” in Barrie 1990; not shown by Rieppel et al. 2002: fig. 6B), and in front of it a low, blunt median ridge that increases in depth up to the broken edge, suggesting there was a distinct ventral keel further anteriorly on the cultriform process.

The basiptyergoid processes are considerably more prominent laterally and ventrally than in any other snake known (including *Dinilysia patagonica* and *Yurlunggur* sp.; Estes et al. 1970; Scanlon 2003). The pedicels project ventrolaterally, and are prolonged parallel to the midline by strong anterior and posterior ridges; there is also a distinct ascending ridge on the lateral face of each process with a flat, triangular dorsolateral surface adjacent to the distal facet. The expanded distal facets are roughly elliptical (with long axes parallel to the midline) and slightly convex, facing ventrolaterally and very slightly anteriorly. The hollow between the anterior and lateral ridges on each side contains two large foramina (only one shown by Barrie 1990), the lower and more anterior being interpreted as the opening of the Vidian canal. Rieppel et al. (2002: 816) regard both openings as for the Vidian canal (separate exits for the palatine nerve and artery) but there is no evidence for this view, as the canals remain blocked by matrix in this specimen. The upper, slightly more posterior foramen is here identified based on its correspondence to that in *Yurlunggur*, which is the anterior opening of the tunnel for the abducens nerve (VI) (Scanlon 2003).

In dorsal view, the smooth, transversely concave intracranial surface is flanked by poorly marked contact surfaces for the parietal (on and adjacent to the dorsal surfaces of the cristae trabeculares), and distinct, dorsolateral sutural surfaces for the prootics. The oval hypophysial pit (sella turcica) is level with the posterior halves of the basiptyergoid processes. The pit is partly overhung anteriorly and laterally by a strong, smoothly curved crest, which hides the median hypophysial foramen and posterolateral cerebral carotid foramina from dorsal view, but it is more weakly defined posteriorly, sloping up to the low transverse swelling representing the dorsum sellae. The posterior foramina for the abducens nerves (not identified by Barrie 1990; margin damaged on right side) are at the rear of this low ridge, facing directly posteriorly (while slightly laterally in *Yurlunggur*). To each side, the lateral part of the dorsum sellae projects dorsally as a low pyramidal prominence (broken on the right side), which thus corresponds topographically to the clinoid (or alar) process of lizards (Lee and Scanlon 2002, character 119; Scanlon 2003); as in other snakes but in contrast to most lizards (e.g., *Ctenosaura*, *Varanus*, mosasaurs; Oelrich 1956; Rieppel and

Zaher 2000), it does not form part of the external braincase wall, as its lateral face is covered by the anteroventral process of the prootic. Just anterior to the clinoid process and the prootic suture, the dorsolateral contact surface on each side is divided into lateral and medial portions by a low, longitudinal ridge. Only the medial portion could have contacted the posterior end of the parietal descensus; the identity of the inferred lateral element is considered below (Discussion).

Close on either side of the hypophysial pit, and extending well beyond it anteriorly, are deep, narrow but dorsally open channels. These were originally identified as for the arteria ophthalmica (Barrie 1990, based on a suggestion by Oliver Rieppel's personal communication 1987); Rieppel et al. (2002: 817) rejected this hypothesis due to the channels extending posteriorly beyond the cerebral carotid foramina (and implicitly, lack of connection to the latter), and thought they were instead either canals for nerve VI exposed by abrasion, or somehow related to the suture with the parietal descensus (the latter suggestion attributed to John Barrie). Both the anterior and posterior openings for nerve VI can be identified based on comparison with *Yurlunggur* (Scanlon 2003), and the open channels, following an almost parallel but more dorsomedial course, are apparently unconnected with these. There are matrix-filled exit foramina within the longitudinal channels on both sides anterolateral to the pit; a dorsally open transverse branch (shown bilaterally by Barrie 1990: fig. 9) is actually present on the left side, while the corresponding channel on the right is partly roofed by the sphenoid (Fig. 9A), but both exit foramina would have appeared externally identical, lying on the sphenoid-parietal border. The *Yurlunggur* sphenoid has shallow and irregular grooves on the anterior part of the sphenoid (Scanlon 2003; labelled as "probably for ophthalmic artery" following Barrie 1990) but no distinct open channels on either side of the hypophysial pit as in *Wonambi*; instead there are broader, smooth concave surfaces, pierced by several foramina connecting with the Vidian canal, nerve VI canal, and the outside of the braincase. These foramina (and by extension the longitudinal canals in *Wonambi*) are therefore tentatively associated with the cid-nerve, which often ramifies intracranially and has been reported as exiting through a variable number of distinct narrow openings in both the sphenoid and prootic (e.g., Rieppel 1979; Rieppel et al. 2002).

Rieppel et al. (2002) state that *Wonambi* has the alethinophidian character of "lateral wings" on the sphenoid, but the proposal of the "best way to ascertain the presence of 'lateral wings'" (Rieppel et al. 2002: 817) based on appearance of the disarticulated sphenoid (without regard to its contacts in the braincase wall) does not provide an explicit criterion, and in particular cannot be applied to taxa such as *Dinilyisia* or *Anomochilus* where no disarticulated sphenoid has been described (Scanlon 2003: 976). The reality and reliability of this character of Alethinophidia has been generally accepted since identified by McDowell (1967) and Underwood (1967), but it has been variously and never very satisfactorily defined; the homology of the "lateral wing" is a partly sepa-

rate matter and has also been much discussed (e.g., Rieppel 1979; Kluge 1991; Cundall et al. 1993; Lee and Scanlon 2002; Scanlon 2003). The operational definition I have used, based on the shape of the external dorsolateral margin of the sphenoid, is perhaps simplistic, but readily applicable, and optimizes as an unambiguous and unreversed synapomorphy of Alethinophidia, excluding the madtsoiids *Wonambi* and *Yurlunggur* as well as *Dinilyisia* (Lee and Scanlon 2002, character 119). It is probably also accurate to say that in (extant) Alethinophidia the lateral (usually dorsolateral) projections of the sphenoid form sutural contacts with the parietal descensus. These "wings" are usually considered to be homologues of the basiptyergoid processes of other squamates, and even in those alethinophidians where "basiptyergoid processes" (possibly secondarily re-evolved analogues in booids, see e.g., Kluge 1991) project strongly below the basicranium, the parietal extends ventrally to form a suture with the anterodorsal surface of the sphenoid wing. In *Wonambi* (like *Yurlunggur*) the dorsolateral margin of the sphenoid is straight in the region of the parietal and prootic sutures, and the basiptyergoid process projects ventrolaterally, entirely free of the parietal; in these respects the madtsoiids differ from all alethinophidians and resemble *Dinilyisia* (Scanlon 2003).

Prootic (Figs. 8–11).—The prootic, opisthotic-exoccipital and basioccipital of *W. naracoortensis* (SAM P30178A; Barrie 1990; Scanlon and Lee 2000) are the only ones to have been described from madtsoiids (these elements have recently been identified in *Yurlunggur* sp. from Riversleigh; personal observations). Only the complete left prootic is known; it is basically tetradial in form, with long, shallow upper and lower anterior processes almost completely enclosing the single trigeminal foramen, and short, deep upper and lower posterior processes expanding laterally and diverging around the fenestra ovalis and juxtastapedial recess. There are contact surfaces for the parietal (anterior and dorsomedial), sphenoid (anterior, medioventral), basioccipital (posterior, medioventral), supraoccipital (posterior, dorsomedial), supratemporal (posterior, dorsolateral), and transversely broad posterior contacts with the opisthotic-exoccipital, both dorsal and ventral to the cavum vestibuli and juxtastapedial recess.

The alar (upper anterior) process is elongate and pointed anteriorly, with two low, approximately parallel dorsal crests (bounding the contact surface for the lateral part of the parietal) and a sharply defined, wedge-shaped lateral thickening of the anteroventral margin. The anterior tip of the process would overlap the lateral surface of the parietal just above the posterior end of the longitudinal crest (lateral wing, Fig. 9A), as is easily confirmed by comparison of the left and right sides of SAM P30178A (Fig. 8C; *contra* Rieppel et al. 2002). More posteriorly, the parietal overlaps the prootic dorsally, so that their surface of contact is effectively "twisted", as it is in most snakes. The trigeminal foramen or notch in the prootic resembles the single medial opening of the

“trigemino-facialis chamber” of anilioids and booids (Rieppel 1979; Rieppel et al. 2002: 818) rather than their lateral openings for V_2 and V_3 ; it is also very like the same region in varanoids, including mosasaurs (e.g., *Clidastes*; Russell 1967: figs. 12, 13), except that the alar process extends horizontally (anteriorly rather than anterodorsally), and the notch is consequently nearly closed anteriorly. The wedge-shaped anteroventral thickening of the alar process was partly involved in the interlocking contact with the parietal, but is not simply a “facet” (Rieppel et al. 2002: fig. 6A). It is strikingly similar in form and position to a structure in the mosasaur *Platecarpus* (Rieppel and Zaher 2000: fig. 2B, C), but does not appear to be matched in other squamates, including *Clidastes* (Russell 1967: fig. 12). It is not similar in either form or position to the supratrigeminal process or spine of lower squamates, which is usually considered either absent (Estes et al. 1988) or “virtually lost” (Norell and Gao 1997) in all anguimorphans, and has not been observed in snakes or mosasaurs; Rieppel and Zaher (2000: 492) refer to the supratrigeminal process in *Varanus* as “weakly developed”, while I have detected none in Australian *Varanus* material.

There are several cracks through the alar process (containing some matrix) and the prootic was also separated and rejoined through the facial nerve foramina, which may slightly affect its shape, so that it is uncertain whether the two anterior projections contacted to exclude the parietal; probably they were originally narrowly separated (as in *Dinilysia*; Estes et al. 1970), but certainly not sutured or fused as in some modern snakes (variation mentioned by Rieppel et al. 2002: 818). The trigeminal foramen was reconstructed by Barrie (1990) as divided laterally by the ventrolateral projection of the alar process contacting the inferior process of the prootic, but this appears highly unlikely. Barrie interpreted the laterally open space below the posterolateral lobe of the parietal as the exit for V_2 , its shape possibly affected by breakage of the inferior process. However (assuming approximate bilateral symmetry), this space is bounded medially as well as dorsally by the parietal, posterolaterally by the inferior process of the prootic, and posteromedially by the upturned lateral flange of the inner face of the basisphenoid, interpreted above as the clinoid process. The small crack, if any, remaining medially is too insignificant and irregularly shaped to be a passage for a major branch of the trigeminal. Moreover, cleaning of the parietal and prootic surfaces reveals no significant damage, and the separated surfaces have sculpture consistent with digitate sutural contacts rather than the borders of a foramen. Hence (contrary to Barrie 1990) both V_2 and V_3 passed through the single large opening or “trigemino-facialis chamber” (Scanlon 1993b; Scanlon and Lee 2000; Rieppel et al. 2002).

On first examining the specimen in 1991 I investigated the possibility that lack of a laterosphenoid bridge was due to pathology or post-mortem damage by cleaning the external surface of the prootic, revealing that (apart from the cracks mentioned above) the surface of the bone is excellently pre-

served, smooth and compact, and there is no indication that any part of the bone is missing. Rieppel et al. (2002: 818) also found no evidence of a laterosphenoid bridge, but nevertheless coded it as present based on the assumption that its lack was a preservational artifact (their character 28). Absence of this structure in madtsoiids is independently confirmed by a recently discovered braincase of *Yurlunggur* sp. preserving both prootics (personal observations).

The lateral surface of the inferior process is “bevelled” anterodorsally, suggesting the anteroventral course of V_2 adjacent to it (or perhaps an additional contact with the epipterygoid, see below); similarly, a wide and deep lateral groove continues the trigeminal notch posteriorly (for V_3), and also contains the external facial nerve foramen (VII), which is apparently single (the existence of a small, matrix-filled second opening is possible if it lay within the ventrolateral hollow near the sphenoid border). The crest above this groove forms two slightly separated portions, one continuous with the dorsal margin of the trigeminal notch, the other with the ventrolateral crest of the paroccipital process and dorsal margin of the juxtastapedial recess. Below the wide groove, a separate crest (prootic flange, Rieppel et al. 2002) forms a lateral projection undercut posteriorly by a narrower groove leading to the posterior opening of the Vidian canal on the prootic-basisphenoid suture. Apart from being interrupted behind the trigeminal notch as in other snakes, these crests are partly comparable with the crista prootica of lizards such as *Varanus*.

The dorsal surface posterior to the trigeminal notch expands laterally to form the anterior part of the paroccipital process, and is excavated medially for the (missing) supraoccipital. The dorsolateral crest on the alar process (lateral margin of the parietal facet) continues more weakly on the posterior portion, meeting the transverse crest (probable anterior margin of the supratemporal facet) just anterior to the suture with the opisthotic-exoccipital. This interpretation of facet boundaries differs from both the reconstruction in Scanlon and Lee (2000: fig. 1) and the interpretation of Rieppel et al. (2002: 819, fig. 6A); it was not known until recently that the supratemporal overlapped the parietal (this work, see above), but Rieppel et al. (2002) apparently did not consider that the parietal might overlap the prootic (as it normally does in snakes and mosasaurs).

The lower posterior process meets the crista interfenestralis and lateral process of the basioccipital, and its ventrolateral edge forms the anterior part of the sphenoccipital tubercle (= basal tuber). The posterior margin of the prootic is notched between the upper and lower processes, the embayment forming the anterior and anterodorsal part of the crista circumfenestralis (lateral rim of the juxtastapedial recess).

The medial face bulges inward posteriorly, forming the anterior part of the tympanic bulla (this term, used for lizards by Oelrich 1956, should not be taken to imply the existence of an external tympanum), and there is a single medial opening into the cavum vestibuli in the anteroventral quadrant of the bulla,

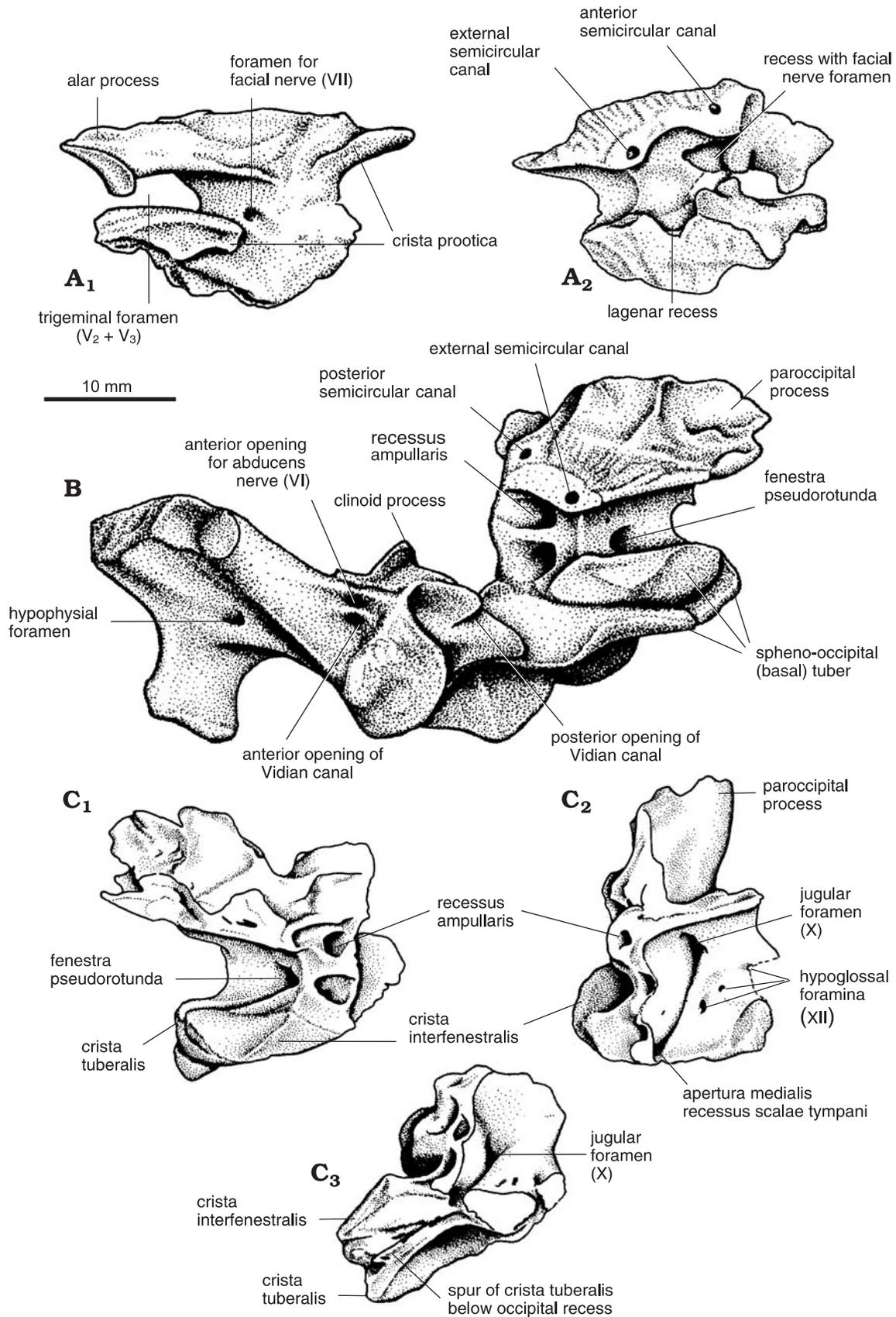


Fig. 11. Braincase elements of *Wonambi naracoortensis* SAM P30178A. **A.** Left prootic in anterolateral (A₁) and posteromedial (A₂) views. **B.** Sphenoid, basioccipital, and left exoccipital-opisthotic in anterolateral view. **C.** Right exoccipital-opisthotic in anterolateral (C₁), dorsomedial (C₂), and medioventral (C₃) views. Scale approximate, varies with perspective.

bordered about equally by the prootic, opisthotic-exoccipital, and (missing) supraoccipital. There is a notch located ventrally in the anterior edge of the fenestra adjacent to a shallow recess within the prootic containing the single medial foramen for the facial nerve (VII; Figs. 8C, 10C, 11A); the medial opening can thus be called an acoustico-facial fenestra. When the prootic is separated from the other cranial elements and viewed in posteromedial aspect (Fig. 11A₂), the anterior part of the cavum vestibuli is seen, with anterior ampullar recess (dorsal to the recess containing the medial facial nerve foramen, which has been damaged), ventral lagenar recess (on the suture with the basioccipital, but mainly within the prootic), and the curved crest defining the fenestra ovalis (for the footplate of the missing stapes) separating the cavum vestibuli from the juxtastapedial recess. The posteroventral surface below the canal has a sutural contact with the lateral wing of the basioccipital and the crista interfenestralis of the opisthotic-exoccipital; the posterodorsal surface, with foramina for the anterior and external (lateral) semicircular canals, forms sutures with the exoccipital-opisthotic laterally, and supraoccipital medially. The endochondral bone adjacent to the auditory capsule is clearly differentiated from the more superficial parts of the sutural surfaces, which are digitate, with radiating ridges and grooves (Figs. 10C, 11A, B). This distinction of cartilaginous medial and digitate distal parts of the sutures around the ear region is commonly seen in large lizards and snakes (e.g., *Varanus* and *Liasis*; personal observations), with the most extreme differentiation in mosasaurs (e.g., *Clidastes*, Russell 1967: fig. 13; *Platecarpus*, Rieppel and Zaher 2000: fig. 5).

Opisthotic-exoccipital (Figs. 8–11).—The complete left opisthotic-exoccipital of SAM P30178A is preserved in contact with the basioccipital (Barrie 1990), slightly rotated from its natural position, and it has not yet been possible to separate these elements. The right element from the same specimen, found separately and identified later (Scanlon and Lee 2000) is somewhat damaged but has been more completely cleaned, revealing the contact surface for the basioccipital in addition to structures visible on the left. This complex element comprises the opisthotic and exoccipital, which are partly fused as in other squamates; it forms the posterior part of the lateral wall of the braincase, with five major processes, contacts with five or six other bones (prootic, supraoccipital, supratemporal, exoccipital of the opposite side, basioccipital, and possibly parietal), and numerous canals and recesses for the cranial nerves and otic capsule. The dorsomedial process (exoccipital tectum, with posterior atlanteal crest) reaches the midline where it would narrowly contact its opposite member, excluding the supraoccipital from the dorsal border of the foramen magnum. The posteromedial process forms the dorsolateral part of the occipital condyle, and also reaches the midline so that the foramen magnum was completely enclosed by the exoccipitals. Dorsolaterally, the large paroccipital process bears a facet for the supratemporal and forms most of the roof of the juxtastapedial recess. There are two separate but adjacent

ventrolateral processes, which both rest on the lateral wing of the basioccipital and floor the juxtastapedial recess: the nearly horizontal, platelike crista tuberalis (with a broad posterior projection beside the occipital condyle, and anterolateral portion forming the posterior end of the spheno-occipital tubercle) and smaller crista interfenestralis (separating the crista tuberalis from the prootic, and with an expanded lateral portion forming the dorsal part of the spheno-occipital tubercle). Buttress-like, concave ridges connect several of these processes: a vertical, posteromedial ridge forming the lateral margin of the foramen magnum; a transverse dorsal ridge from the occipital arch across the rear of the paroccipital process; and a vertical, lateral ridge from the paroccipital process to the crista tuberalis, separating the juxtastapedial recess from the hollow containing the jugular and hypoglossal foramina; and adjacent to it, a low curved ridge on the dorsal surface of the crista tuberalis, forming the posterolateral limit of the juxtastapedial recess. Rieppel et al. (2002: 820) confirm the weak posterior definition of the recess, but their suggestion that the “jagged lateral edge of the crista tuberalis indicates some degree of damage” is not supported by close examination of the cleaned specimen. Rieppel et al. (2002: fig. 6B) also show and label the crista tuberalis erroneously, in ventral view, as part of the basioccipital.

The medial (intracranial) surface of the element is bounded most extensively by the basioccipital ventrally, and by the missing supraoccipital dorsally. It bulges inward anterodorsally as part of the tympanic bulla. The sutural surface for the supraoccipital is triradiate, with extensions posterolaterally (along the dorsal crest of the paroccipital process; this may have been partly for the supratemporal process of the parietal), posteromedially (in the skull roof), and anteroventrally (in the thin wall of the tympanic bulla, reaching the margin of the acoustico-facial fenestra). At the confluence of these three branches is the foramen for the posterior semicircular canal, and as on the prootic the bone texture differs between the auditory capsule and more superficial parts of the sutures. Rieppel et al. (2002: 822) claim to detect “extensive damage to the medial wall of the otic capsule” and that this is indicated by Scanlon and Lee’s (2000) fig. 2b (Fig. 10C here); in fact, apart from the absence of the supraoccipital, the only slight damage is to the prootic border of the fenestra directly posterior to the trigeminal foramen (Figs. 8C, 11A); this occurred in 1991, but subsequent to the drawing in Fig. 10C, when the prootic was separated through the facial nerve foramina.

The internal jugular foramen (for the vagus nerve X, most likely accompanied by the posterior cerebral vein and occipital artery), opening posterolaterally, is in a dorsal position close to the overhanging tectum (contrasting with a more ventral position in most lizards and snakes, but similar to that in *Clidastes propython* Cope, 1869 and *Python molurus* [Linnaeus, 1758]; Russell 1967: fig. 13; Rieppel 1979: fig. 6). The apertura medialis recessus scalae tympani, slightly smaller than the jugular foramen, lies on the border with the

basioccipital as in most squamates (but not *Platecarpus*, Rieppel and Zaher 2000: fig. 5). These two openings are connected by a deep, oblique groove on the medial face of the exoccipital, representing the embryonic fissura metotica (= occipito-capsular fissure; see Bellairs and Kamal 1981: fig. 50) and the sutural boundary of the opisthotic and exoccipital components, which are indistinguishably fused dorsal to the jugular foramen. Posterior to this fissure is a row of three smaller foramina for roots of the hypoglossal nerve XII. The internal jugular foramen is not subdivided (Rieppel 1979: 413), and no distinct internal glossopharyngeal foramen is detected (nerve IX passing through either the recessus scalae tympani or jugular foramen). The external jugular foramen opens posterolaterally within a dorsoventrally elongated depression between the two vertical and two transverse ridges described above (Fig. 10B); one of the three external hypoglossal foramina is immediately ventral to the jugular within this depression, the other two lie outside it, closer to the foramen magnum. Another small external foramen lateral to the depression is unidentified, but may be comparable to several small foramina on the posterior face of the paroccipital process in *Varanus*. As in most lizards (e.g., *Varanus*) and some other snakes (Rieppel et al. 2002: 821), the external jugular foramen is hidden from lateral view by an ascending branch of the crista tuberalis.

The occipital condyle is slightly wider than the foramen magnum, and the atlanteal crest (dorsoposterior margin of the exoccipital, which overlaps the atlas neural arch to form the dorsal part of the occipito-vertebral articulation) wider again, with a distinct lateral margin where a concave transverse crest links it to the paroccipital process. In dorsal view, the shape of the posterior margin thus resembles that of *Lanthanotus* (Estes et al. 1970: fig. 9e), contrasting with the condition in *Dinilysia* (Estes et al. 1970: fig. 9b) and many lizards (e.g., *Ctenosaura*, Oelrich 1956: fig. 12; *Varanus*, personal observations; *Platecarpus*, Russell 1967: fig. 83) where the atlanteal crest is smoothly continuous with the paroccipital process posteriorly, and also with most anilioids and booids where there is a constricted notch (Estes et al. 1970; the latter difference may be due to the small size of the paroccipital process in modern snakes). The atlanteal crest is oblique posteriorly (even allowing for slight clockwise rotation of the element relative to the basioccipital), indicating it met its opposite member at an angular median concavity rather than forming a smooth transverse margin (both of these states are widespread in modern snakes). The dorso-medial process apparently contacted its opposite member only narrowly between this concavity and a triangular, median posterior process of the supraoccipital. There is an oblique notch in the (undamaged) medial edge of the exoccipital (Figs. 8C, 10C), which suggests a clasping (tongue-in-groove) contact with the process of the supraoccipital. Complete but narrow separation of the exoccipitals by such a process is seen in a specimen of *Cylindrophis* figured by Estes et al. (1970), but this is an unusual and probably juvenile condition in that taxon (Jean-Claude Rage, per-

sonal communication 1994); the condition of narrow midline contact in *Wonambi* is more similar to that of *Dinilysia* (as noted by Barrie 1990). In some macrostomatans the median exoccipital contact may be hidden in dorsal view by an overlap, or reduced or eliminated by a broadly angular posterior margin of the supraoccipital (e.g., Zaher and Rieppel 2002; Rieppel et al. 2002: 822), but the intact anterior and medial margin of the exoccipitals readily distinguish such conditions from the one here.

The median contact of the exoccipitals on the occipital condyle, broadly excluding the basioccipital from the foramen magnum, is shared with *Dinilysia*, *Anomochilus* and *Cylindrophis*, but few other snakes or lizards (Estes et al. 1970; Cundall and Rossman 1993; Cundall 1995; Lee and Scanlon 2002, character 142); this is parsimoniously considered a synapomorphy reversed in Scolecophidia and within Alethinophidia, but has also converged within the typhlopoid genus *Ramphotyphlops* (Greer 1997).

The paroccipital process is more prominent and expanded than in any modern snakes, but not as elongate posteriorly as in *Dinilysia* or most lizards. Prominent ridges outline a concave facet for the supratemporal on the dorsolateral face of the process (extending narrowly onto the prootic); a ridge also divides the facet into a long dorsal and shorter ventral portion, structurally similar to the bipartite facet of *Varanus* and mosasaurs (e.g., Rieppel and Zaher 2000: fig. 2). The posterior part of the facet does not curve inward to face somewhat posteriorly as it does in *Dinilysia* and anilioids (Estes et al. 1970; Cundall and Rossman 1993); in shape (but certainly not size) the process is more similar to that of some booids (e.g., *Liasis*, personal observations). The free dorsal and posterior margin of the process is irregularly scolloped, a condition unknown in other taxa, but which probably indicates that the supratemporal extended some distance in both directions beyond the facet. The transverse ridge on the posterior surface of the process is similar to that in lizards (e.g., *Ctenosaura*, Oelrich 1956; *Varanus*, personal observations), which separates dorsal and ventral concave surfaces for insertion of the obliquus capitis and longissimus cervicis muscles, respectively (Oelrich 1956).

The ventral surface of the element is broad and shallowly concave, bounded medially and anteriorly by its nearly semi-circular contact with the condylar process and lateral wing of the basioccipital, and posterolaterally by the oblique, slightly sinuous crista tuberalis. The margin of the latter crest is thickened ventrally for its whole length, but especially at the ends where it forms obtusely angular projections, the anterolateral one forming the posterior part of the spheno-occipital tubercle, and the posterior one (apparently for tendinous insertion of deep epaxial muscles, most likely m. longissimus cervicis) separated from the condyle by a narrow notch.

The posterior wall of the cavum vestibuli (Fig. 11B, C) is mainly occupied by two large pocket-like recesses opening medially, the posterior recessus ampullaris dorsally (just below the prootic suture) and below it the perilymphatic foramen (or foramen cochleae), immediately dorsal to the lagenar re-

cess in the prootic. The perilymphatic duct passes under the constricted, posteromedial part of the crista interfenestralis, connecting the medial perilymphatic foramen with the lateral opening within the large juxtastapedial recess (dorsomedial part of the subdivided apertura lateralis recessus scalae tympani or occipital recess). I have used the term “fenestra pseudorotunda” for this lateral opening, following Rieppel’s (1979) use of the term for the more medial of two lateral openings in anilioid snakes (see Discussion).

The fenestra ovalis is horizontally elliptical and directed posterolaterally, defined by a low ridge on the prootic (as described above) and opisthotic-exoccipital (mainly on the crista interfenestralis); the fenestra is relatively much larger than in *Varanus* or mosasaurs, somewhat larger than in pythons, similar to anilioids, and smaller than *Dinilysia* (see Rieppel et al. 2002: 820, who point out an error in the data matrix of Scanlon and Lee 2000: character 125; not used in Lee and Scanlon 2002). There is apparently a small (matrix-filled) foramen just dorsal to the fenestra pseudorotunda, where the crista interfenestralis joins the main body of the element; this might be a separate exit for the glossopharyngeal nerve (IX), whose course is so variable in reptiles that it is unlikely to be of phylogenetic significance (e.g., Rieppel 1979, 1980, 1985), but is also said to exit from the jugular (vagus) foramen in “snakes” (Rieppel and Zaher 2000: 506). The crista interfenestralis and crista tuberalis are in tight contact (at their dorsal margins) lateral to the fenestra pseudorotunda, but diverge slightly again on the lateral face of the sphenoccipital tubercle, just above their contacts with the basioccipital. On the left side of the specimen this lower opening is blocked by matrix, but on the right side (Fig. 11C₃) the two cristae of the opisthotic-exoccipital are seen to be slightly separated for their full width, except for an anterior spur of the crista tuberalis that floors a short section of the canal. This continuous canal joining medial and lateral openings on the suture with the basioccipital (completed ventrally by the narrow transverse groove on the basioccipital lateral wing; Fig. 10C) is the recessus scalae tympani (= occipital recess of lizards, Oelrich 1956; Rieppel 1985). While an occipital recess is sometimes said to be absent in snakes (Rieppel 1979, 1985; Rieppel and Zaher 2000), the state in *Wonambi* (topologically identical to that of lizards except that the apertura lateralis is subdivided into two openings by contact, but not fusion, between the crests) is apparently also present in several extant booids (figures in Rieppel 1979). In some other booids, indeed, the crests remain separated ventrally as in lizards, and the lateral aperture is single and wide open, differing (topologically) in no way from the occipital recess of lizards (e.g., *Liasis olivacea*, personal observations; apparently also shown in *Python sebae* [Gmelin, 1789] by Rieppel and Zaher 2000: fig. 6B).

The laterally concave vertical ridge bounding the juxtastapedial recess posteriorly, and forming a buttress for the paroccipital process, bears an anteroposteriorly compressed spine projecting ventrolaterally; it seems likely that this spine closely approached the shaft of the stapes, but its significance

is unclear as I do not know of an equivalent structure in other squamates. This vertical ridge separates the fenestra pseudorotunda (medial part of apertura lateralis recessus scalae tympani) from the shallow recess surrounding the jugular foramen.

The crista circumfenestralis (external margin of the juxtastapedial recess) is thus formed by various distinct structures of the prootic (its concave, vertical posterolateral edge and dorsal, horizontal part of the crista prootica) and opisthotic-exoccipital (ventral edge of the paroccipital process, the dorsomedial buttress on the crista tuberalis and the spine projecting from it, and the lateral part of the crista interfenestralis). Almost all of these structures have clear topographic equivalents in both lizards (e.g., *Varanus* and mosasaurs, Rieppel and Zaher 2000) and alethinophidian snakes. Unlike the crista circumfenestralis of most modern snakes, the crests extend laterally forming a partial tube rather than tending to close up external to the stapedial footplate (Lee and Scanlon 2002, character 135), but this is a difference of relative growth only, and does not obscure the topological continuity or identity of this region between lizards, *Wonambi*, and modern snakes.

Basioccipital (Figs. 8–11).—The basioccipital forms the median, ventral part of the posterior braincase and of the occipital condyle. A deep, narrow midventral keel extends from the anterior border (in continuity with the sphenoid keel) to just anterior to the condylar process. The anterior part of the basioccipital is expanded into triangular lateral processes, bearing posteriorly concave ventral ridges overlapping and diverging from the median keel (Fig. 8B). The rugose anterolateral parts of these processes form the ventral parts of the large sphenoccipital tubercles (or basal tubera), and are in broad contact with the ventral surface of the exoccipital and the posteroventral surface of the prootic (the two dorsal contact surfaces demarcated by a nearly linear crest on the basioccipital; Figs. 9A, 10C). A narrow groove on the dorsal surface of the lateral process extends anterolaterally to emerge at the basioccipital-opisthotic-prootic junction, forming the floor of the occipital recess (see above). There is an extensive trapezoidal contact between basioccipital and sphenoid, narrowing dorsally, but these surfaces have not been separated in SAM P30178A.

The generally concave, pentagonal dorsal face of the basioccipital floors the posterior part of the cranial cavity. A low transverse ridge defines a posterior depression in this surface, near the posterior apex of which there is a small foramen; such foramina are not known in other snakes, but a pair is present in some lizards (e.g., *Ctenosaura*, Oelrich 1956) and there is a much larger opening in this position in some mosasaurs (Russell 1967; see below).

Mandibles (Figs. 12, 13).—The general shape and features of the dentary and compound are shown by Barrie (1990), but additional details can be noted after further preparation and comparison with other taxa. Partial or complete dentaries are known in *Madtsoia* sp. cf. *M. bai* (Hoffstetter 1960), *M.*

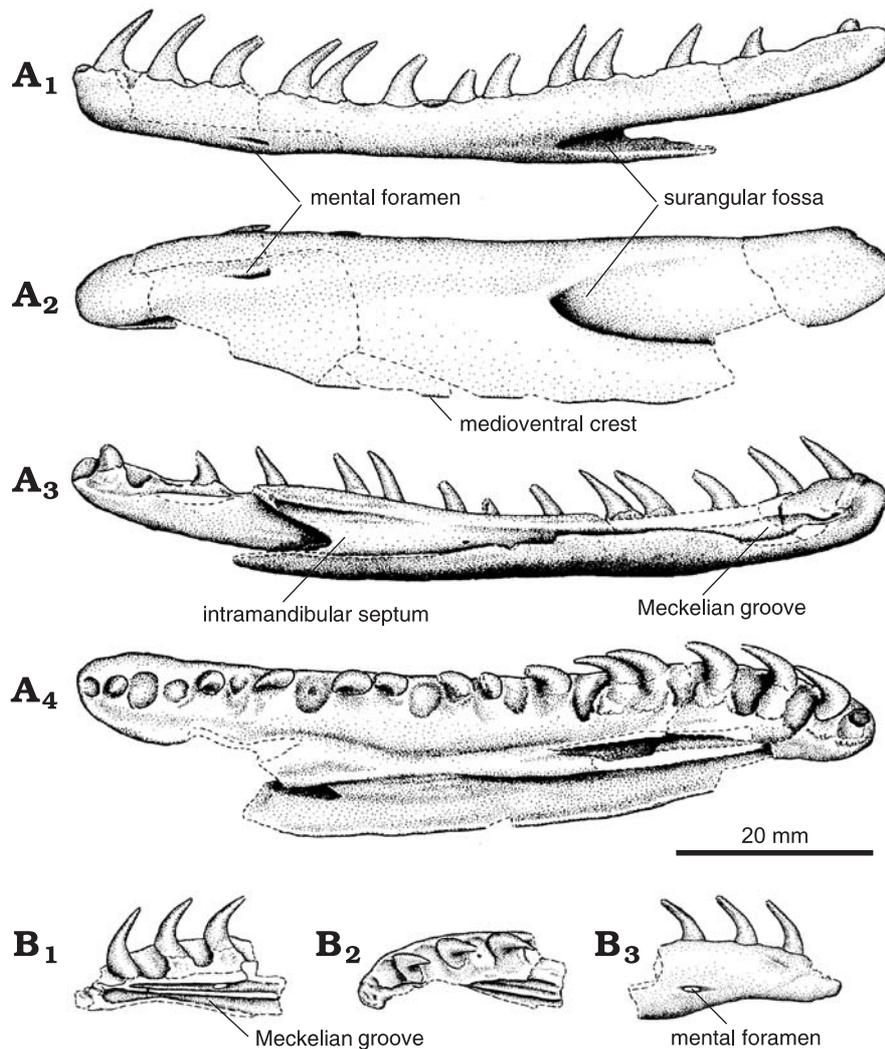


Fig. 12. Dentaries of *Wonambi naracoortensis*. A. SAM P30178A, left dentary in lateral (A₁), ventrolateral (A₂), medial (A₃), and dorsomedial (A₄) views. B. SAM P16170c, right dentary fragment in dorsomedial (B₁), dorsal (B₂), and ventrolateral (B₃) views. Anterior direction to left in A₁, A₂, B₁ and B₂.

camposi (Rage 1998), *Nanowana godthelpi*, *N. schrenki* (Scanlon 1997), *Wonambi barriei* (Scanlon and Lee 2000), and species of *Yurlunggur*, *Alamitophis*, and *Patagoniophis* (Archer et al. 1991; Scanlon 1996, in press). A jaw fragment from VF (P16170c), reported by Smith (1976) as the anterior part of a left maxilla, is actually part of a right dentary (Fig. 12B; see also Rieppel et al. 2002: fig. 2); three teeth are well preserved but the bone is broken medial to the alveoli, and in medial view both the Meckelian groove and internal mental canal are exposed. Most features of the dentary are best represented by the near-complete specimens from HQ (SAM P30178A), particularly the left element (Fig. 12A), which has well preserved, and now relatively clean, bone surfaces and dentition.

There are 25 alveoli (complete row) on each dentary of SAM P30178A (Barrie 1990). The medioventral crest of the dentary (flooring the Meckelian groove) is very broad, even more so than in other madtsoiids; it does not appear to have had a distinctly widest point as in other madtsoiid dentaries

(Scanlon 1996, 1997, in press), but is slightly convex medially for almost its full length. Rieppel et al. (2002: 822–823) report the presence of a “splenial” partly blocking the Meckelian groove, and interpret its morphology in some detail, but the fragments concerned are actually parts of the medioventral crest that had been broken and displaced dorsally (shown reattached in Fig. 12A); the splenial remains unknown. Medial to the 1st to 3rd alveoli, the Meckelian groove is overhung by a slightly expanded surface for muscular or tendinous attachment between the mandibles, but it does not form a distinct “bulb” as in some other madtsoiids (Scanlon 1997, in press). The ridge defining the upper edge of the Meckelian groove (partly damaged on the left element figured, but nearly intact on the right) is sharp for most of its length but indistinct at the level of the 12th–13th (probably representing the position of the foramen between dentary and splenial for the lingual branch of the inferior alveolar nerve; Rieppel et al. 2003: 550), and a distinct facet for the dorsal margin of the splenial extends from the 15th to end as a

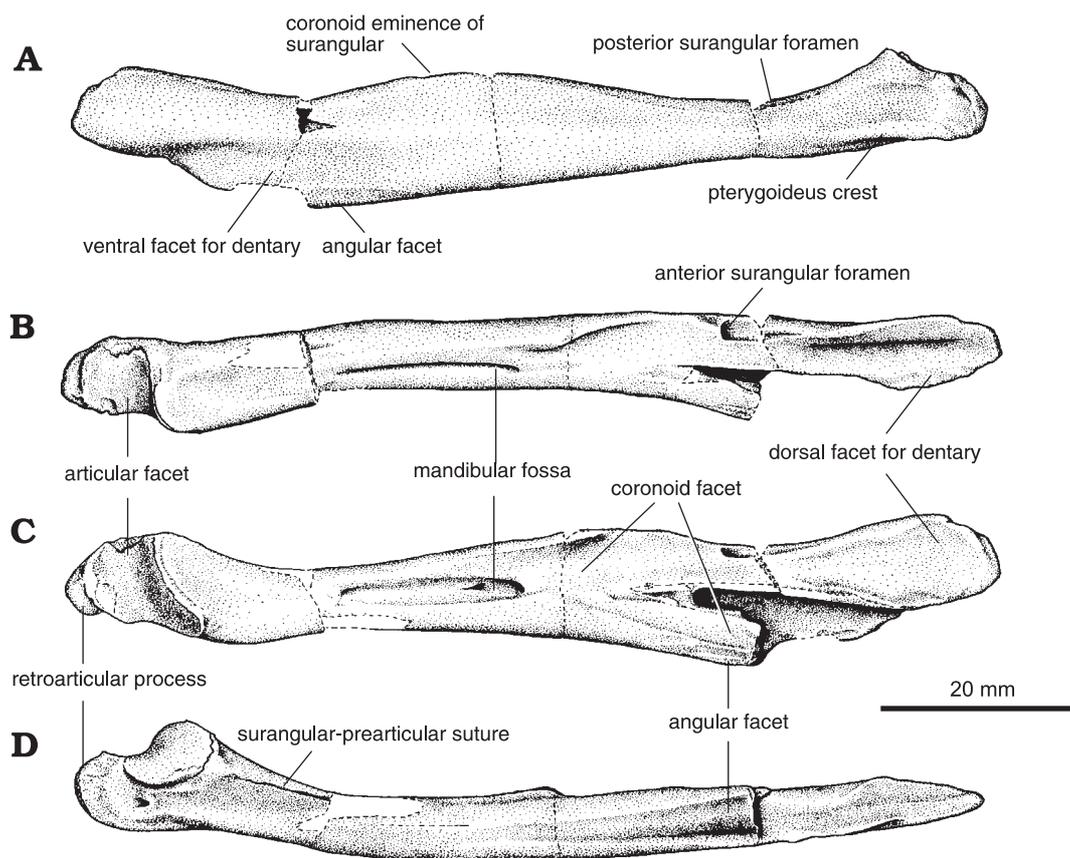


Fig. 13. Compound mandibular element of *Wonambi naracoortensis* (SAM P30178A; Pleistocene, Naracoorte) in ventrolateral (A), dorsal (B), dorsomedial (C), and medial (D) views. Images reversed (element from right side shown as if left) for ease of comparison with Fig. 12. Anterior direction to left in A only.

rounded posterior process (preserved on right only, not shown) at the 20th, separated from the dentigerous posterior process by an acute notch. The upper posterior process ends bluntly, the tooth-row occupying its middle third rather than the lateral edge. The lateral fossa for the surangular extends forward to between the 15th and 16th alveoli, not far behind the midpoint of the dentary; the lower posterior process (preserved on left side only) is only half as long as the upper. The vertical intramandibular septum joins the two processes for half the length of the lower (a well-developed septum is typical of snakes; Lee and Scanlon 2001). The upper process in lateral view is almost as deep as the anterior end of the dentary, and for most of its length is shallow medially, roughly triangular in section; but posteriorly it is also deep medially, a ventromedial process being defined by an oblique crest visible ventrally. The lateral fossa for the surangular is shallow dorsoventrally but exceptionally broad in ventral view. The “subdental shelf” is damaged on the left side, but complete posteriorly, with a free-ending posterior process (forming contacts with the splenial and sometimes coronoid in modern snakes).

In a reconstruction of the *W. naracoortensis* skull in Scanlon and Lee (2000: fig. 1c), I drew the dentary with two mental foramina. At the time I had not closely examined this

element of SAM P30178A, but a photograph of the left dentary provided by John Barrie showed it to have several cracks and thick encrustation that could have prevented identification of a second, smaller foramen, and I predicted its presence based on the fact that all other known madtsoiid dentaries (representing two South American and six Australian species, including material referred to *W. barriei*) possessed either 2 or 3 mental foramina (Scanlon 1996, 1997; Rage 1998). However, cleaning of the specimen revealed that there is indeed only a single mental foramen in both the left and right dentaries of SAM P30178A (Fig. 12A), and Madtsoiidae was therefore recoded as polymorphic for this character in Lee and Scanlon (2002, character 148). It is not clear whether the single foramen (known in only one specimen) characterizes the species or represents individual variation, but (contrary to Rieppel et al. 2002: 812–813) it does not cast serious doubt on *Wonambi*’s relationship with other madtsoiids. Some comparisons among dentaries of eight madtsoiid taxa are tabulated and discussed elsewhere (Scanlon in press).

The nearly complete right compound (largely fused articular, prearticular and surangular) can be compared with those of *Nanowana godthelpi* (Scanlon 1997), and fragmentary specimens referred to *Gigantophis garstini* (Andrews 1901),

Yurlunggur sp. (Scanlon 1996), and *Wonambi barriei* (Scanlon 1996; Scanlon and Lee 2000). The images in Fig. 13 are reversed, showing the specimen as if from the left mandible to facilitate comparison with Fig. 12. Rieppel et al. (2002: fig. 12) show the compound in two separated pieces, the images also reversed (but perhaps not intentionally), with the main anterior portion upside-down in lateral view. In addition to the features described by Barrie (1990), there is a low, curved crest on the anteromedial surface, bounding the facet for an extensive coronoid; this is relatively much larger than in *Nanowana* or most other snakes with a coronoid (the overlapping portions of dentary and compound are expanded mediolaterally relative to the other parts; see below). The surangular lamina is low, forming two dorsally concave sections separated by the low “coronoid process” (probably only a small part of the complete process formed mainly by the coronoid itself), just anterior to the middle of the bone. Dorsomedially, a distinct partial suture extends longitudinally anterior to the articular facet; this incomplete fusion of prearticular and surangular differs from the state normally found in snakes (Lee and Scanlon 2002, character 169); in *Nanowana godthelpi* and *W. barriei* there is also a distinct transverse fissure or partial suture between the surangular and articular (Scanlon 1997; Scanlon and Lee 2000: fig. 2c), and neither of these partial sutures should be confused with the boundary of finished bone adjacent to the articular facet (Rieppel et al. 2002: 823). There is a short, blunt longitudinal crest ventrolaterally below the articular facet, for the posterior attachment of the m. pterygoideus (often more prominent in other snakes, similar here to *N. godthelpi* and *W. barriei*). The shaft of the compound is nearly cylindrical just in front of this crest (so that reattaching the broken pieces required attention to small details of the incompletely preserved margins), and a small posterior surangular foramen is present dorsolaterally in this region (relatively larger in *N. godthelpi*). The mandibular (adductor) fossa is narrow and relatively short, beginning anterior to the level of the foramen, and extending just posterior to the margin of the coronoid facet (contrasting with *N. godthelpi* where the coronoid facet is adjacent to and partly surrounds the fossa, which also extends farther posteriorly). The surangular lamina does not overhang the mandibular fossa; anterior to the low coronoid eminence, it reduces in height and then again expands dorsally, the two sections about equal in length. The large anterior surangular foramen opens anteriorly at the lowest point of this dorsolateral crest, and is hidden in lateral view. The facets for coronoid and angular do not appear to meet, but may have done so beyond the broken anteromedial edge of the compound.

In general, the mandibles of *Wonambi* are broad and relatively shallow, and the most unusual aspect of their morphology is that this overall shape is attained not simply by proportional changes in cross-sectional dimensions, but by deformation of major elements so that the anatomically medial and lateral surfaces come to face (respectively) mainly dorsally and ventrally, while the articular facet, tooth row, and

(by inference) intramandibular joint retain their normal orientations. This is apparent not only in comparison with alethinophidians, but also with other madtsoiids (dentaries of *Madtsoia camposi* and *Nanowana schrenki*, and complete dentaries and compounds of *N. godthelpi*; Scanlon 1997; Rage 1998), and even with lizards such as *Varanus*. This major set of morphological changes in the *Wonambi* lineage (possibly including *Yurlunggur*, in which the dentary is incompletely known but also relatively broad posteriorly; Scanlon 1996 and personal observations) would presumably have significant functional correlates. For example, the wide and long, but dorsoventrally shallow region of overlap between dentary and surangular might still allow considerable mediolateral flexion at the intramandibular joint (as in anilioids, see Cundall 1995), but would apparently impose quite strict limits on dorsoventral flexion.

Discussion

Remarks on undiscovered elements

Reconstruction (i.e., prediction) of the complete skeletal morphology in *Wonambi naracoortensis* is constrained most importantly, but still only partially, by the elements and features already known from one or more adequately preserved specimens of this species. There are several less direct approaches to further restricting the class of logically possible morphologies to a subset that is scientifically defensible, based on both interpolation and extrapolation (e.g., Bryant and Russell 1992). In phylogenetic interpolation, morphology of the object taxon is inferred from that of other taxa based on parsimonious character optimisation applied to a (provisionally accepted) hypothesis of phylogenetic relationships; this may be more or less precise, depending on the stability of the feature in question across the taxa being compared. In the case of features not preserved in fossils, this approach corresponds to use of the “extant phylogenetic bracket” (Witmer 1995). Anatomical interpolation, where features of unknown elements are inferred based on those of known elements when arranged in their (hypothesized) natural spatial relationships, depends on prior phylogenetic interpolation—at least to a very rough level—so that approximately correct skeletal anatomy is assumed. Extrapolation, based on hypotheses of convergent function and correlation of parts, is less direct again. Other things being equal, the appropriate null hypothesis for testing by further observation would be to predict the absence of any structure that is currently unknown in a fossil taxon; the “other things” include parsimonious interpretations of phylogeny and character evolution, other known structures, and biomechanical regularities and constraints. Of course, hypothetical but unobserved structures do not constitute evidence for phylogenetic relationships (*contra* Rieppel et al. 2002, character 28).

The maxilla, palatine, pterygoid, ectopterygoid, frontal, parietal, prootic, opisthotic-exoccipital, sphenoid, basioccipi-

tal, dentary and compound of *W. naracoortensis* are more or less completely known, as described above (accounting for 9 paired and 3 median elements). The premaxilla, nasal, septomaxilla, vomer, prefrontal, postorbital, supraoccipital, stapes, supratemporal, quadrate, coronoid, angular and splenial (11 paired and 2 median elements) remain undiscovered, but the presence of these highly stable elements in this species can be inferred, with high to extreme confidence, by phylogenetic and anatomical interpolation. The skull is thus approximately half known, but the known “half” includes all the largest elements, and much can be reliably inferred about the morphology of the remainder by anatomical interpolation based on preserved contact surfaces and the spatial relationships of known elements. While all the elements just listed can be expected based on comparison with macrostomatan (e.g., booid) snakes, a consequence of the more basal phylogenetic position inferred for Madtsoiidae (Scanlon 1996; Scanlon and Lee 2000; Lee and Scanlon 2002) is that the presence of additional elements (lacrimals, jugals, postfrontals, epipterygoids) cannot be ruled out without discussion, and might be predicted.

Circumorbital elements: jugal, postorbital, postfrontal.—

The number and arrangement of bones surrounding the orbit are variable and have been considered important in many classifications of primitive snakes, but their homologies are contentious. Different authors have referred to the anterior dorsal ossification as a postfrontal (presumptive homologue of that in some lizards, as in *Dinilysia*) or a supraorbital (supposed neomorph of some alethinophidian snakes, attributed to pythoines, *Loxocemus* and *Calabaria*; see Estes et al. 1970; McDowell 1975; Kluge 1993a, b; Tchernov et al. 2000). Thus, information on these elements in madtsoiids might be very useful, but they are presently unknown. I have previously reconstructed the skull with discrete postfrontal, postorbital, and jugal (Scanlon 1996; Scanlon and Lee 2000: fig. 1) based on the structural similarity of the braincase to that of *Dinilysia*, in which the same elements had been described. This interpretation is consistent with, but not fully determined by, phylogenetic and anatomical interpolation. It was partly confirmed by the discovery of the frontal (recognized in 1998), since the posterolateral corner of this element is recessed below the interorbital plane, consistent with its being covered by a post-orbitofrontal or, if there were two dorsal elements, the post-frontal as in *Dinilysia*.

The presence of a complete postorbital bar can be expected in a basal snake, but the condition in some extant macrostomatan snakes, where this is formed more or less entirely by the postorbital, is derived. Most lizards, including all varanoids, have well-developed jugals that form at least the ventral half of the posterior orbital margin. In varanoids the jugal overlaps the posterior end of the maxilla dorsally, extending more posteriorly lateral to the ectopterygoid,

which abuts or clasps only the posterior end of the maxilla¹. In all varanoids except some *Varanus*, the jugal's overlap on the maxilla also extends anteriorly beyond the orbit, ventrolateral to the prefrontal and lacrimal (Russell 1967; Estes et al. 1988: character 31).

The lacrimal is absent as a discrete element in all snakes where this region is observable, including *Pachyrhachis* and *Haasiophis* (Lee and Scanlon 2002). It seems unclear whether it is truly lost or can be regarded as indistinguishably fused to the prefrontal (and perhaps identifiable with the “lateral foot process” which occupies a similar position on the orbital margin in snakes), because intermediate stages of reduction or partial fusion have not been described in extant forms, fossils, or early ontogenetic stages. In any case a distinct lacrimal is expected (by phylogenetic interpolation) to be absent in *Wonambi*.

No extant snakes are considered to possess jugals; their presence was reported in anomalepidid scolecophidians by List (1966), but these elements were more plausibly identified as postorbitals (i.e., homologous to the postorbitals in alethinophidians) by Haas (1964, 1968). On the other hand, the suborbital ossifications of bolyeriids (Cundall and Irish 1989) are distinct from the postorbitals and structurally comparable to jugals, although parsimonious character optimisation indicates they are actually neomorphic structures (Scanlon 1996; Lee and Scanlon 2002). Given that jugals have been considered present in *Pachyrhachis*, *Haasiophis*, and *Dinilysia* (Estes et al. 1970; Scanlon 1996; Lee and Caldwell 1998; Lee and Scanlon 2002), their presence in madtsoiids would be consistent with phylogenetic interpolation, and hence unsurprising, if these fossil snake taxa all lie outside Serpentes (Scanlon 1996, 1997; Scanlon and Lee 2000; Lee and Scanlon 2002).

A large proportion of the dorsal surface of the maxilla in *Wonambi* is occupied by a moderately deep and distinct “trough” (Barrie 1990; and see above). This feature has been interpreted as a facet for a large jugal forming the ventral margin of the orbit (Scanlon 1996, 1997), based on Estes et al.'s (1970) identification of a flattened ellipsoidal bone lying in a longitudinal dorsal channel on each maxilla in *Dinilysia*. Similarly located, though less distinct, troughs or facets are also present in other Australian madtsoiids (*Yurlunggur* and *Nanowana*), and I have also argued (Scanlon 1996, 1997) for the presence of a bone in this position based on the relative mechanical weakness of the elongate maxilla in these taxa, especially *N. godthelpi* (anatomical interpolation and extrapolation). The longitudinal symmetry of the facet (straight in *Dinilysia* and *Nanowana*, oblique and helically twisted in *Wonambi*) and its lack of discrete anterior or posterior boundaries in these taxa, suggest the presence of a functional sliding joint between the maxilla and the jugal, leading to the interpretation that the latter formed a more or

¹ Polcyn et al. (1999: fig. 7) show an apparently different arrangement of bones below the orbit in a basal mosasauroid, *Haasiasaurus gittelmani*, but it seems more plausible that the actual jugal is the element labelled “?pf” and the ectopterygoid is their “j”, in which case *Haasiasaurus* would possess precisely the same condition as terrestrial varanoids and some mosasaurs (see Polcyn et al. 2003 for replacement of the preoccupied name *Haasia*).

less rigid extension of the postorbital bar (Scanlon 1996). In *Wonambi* the trough extends further forward as a shallow concavity, defined below by a ridge, onto the preorbital lateral surface of the maxilla; this anterior extension recalls that of the jugal in varanoids, but may have accommodated ligamentous attachments (comparable to the circumorbital ligaments in *Casarea* described by Cundall and Irish 1989) rather than the jugal bone itself.

To the extent that this interpretation depends on the presence of a discrete jugal in *Dinilyisia*, it conflicts with Caldwell and Albino's (2002) interpretation of new material of *D. patagonica*, in which the "jugal" of Estes et al. (1970), in contact with the maxilla, is seen to be indistinguishably co-ossified with the more posterior of the two upper orbital ossifications. There is almost unanimous agreement that the single element forming the postorbital bar of snakes (when present) is a postorbital, and that the jugal is absent in modern snakes. However, the postorbital bar of *Dinilyisia* can not simply be equated with that of any modern snake: the dorsal extremity has topographic relationships consistent with a postorbital (in a lizard or snake), while the ventral end has an expanded contact with the maxilla (typical of a squamate jugal, as in the interpretation of Estes et al. 1970). Thus, there are at least two ways of describing the postorbital bar of *Dinilyisia*: (1) the jugal is absent, but the postorbital has replaced it by gaining an expanded distal contact with the dorsal surface of the maxilla, or (2) the postorbital and jugal are fused into a single element. Hypothesis (2), loss of a suture within the postorbital bar, is a relatively simple change but may be difficult to falsify by observation; on the other hand, it would tend to be confirmed (and the alternative falsified) by finding specimens of *Dinilyisia* or similarly primitive snakes retaining a complete or partial suture within the postorbital bar. Some extant booids have long, distally expanded postorbitals approaching or abutting the maxilla or ectopterygoid (e.g., Frazzetta 1966; Kluge 1991, 1993; Zaher and Rieppel 2002), but this "complete" postorbital bar may not be homologous to conditions in lizards or *Dinilyisia*; consequently, we must be cautious in using booids as a guide to interpretation of morphology in *Dinilyisia* or madtsoiids. Despite this reservation, there is currently no justification for differentiating fundamentally between *Dinilyisia* and these booids with respect to the jugal and postorbital (Tchernov et al. 2000 in the parallel cases of the supraorbital/postfrontal and basiptyergoid process; see remarks in Lee and Scanlon 2002, characters 47, 117). By phylogenetic and anatomical interpolation, therefore, *Wonambi* can now be reconstructed with a dorsal orbital ossification (postfrontal or supraorbital homologous to that of *Dinilyisia*) adjacent to a complete postorbital bar formed by a single element having a long distal contact on the dorsal surface of the maxilla. It seems to be an open question whether this hypothetical element (or the one observed in *Dinilyisia*) should be considered a "postorbital", "jugal", or as comprising both.

Prefrontal.—The sculptured dorsomedial surface of the dorsal process of the maxilla indicates an interdigitating su-

ture with the prefrontal (anatomical interpolation), which differs from conditions in all extant snakes (or at least all alethinophidians: a suture may be formed in *Leptotyphlops*, but is relatively small and apparently simple in form; e.g., List 1966). In anilioids there is a rocking joint between maxilla and prefrontal formed by interlocking saddle-shaped surfaces (*Cylindrophis* and *Anomochilus*; Cundall 1995; Cundall and Rossman 1993), whereas most macrostomatans have nearly flat or broadly convex contact surfaces allowing sliding as well as transverse and/or anteroposterior rocking motions (e.g., Frazzetta 1966; a highly mobile saddle joint is regained in solenoglyphous colubroids, e.g., *Atractaspis*; Deufel and Cundall 2003). Estes et al. (1970) report that in *Dinilyisia* the "prefrontals have a wide, firm, interlocking contact with both frontals and maxillae, much as in *Anilius* and *Cylindrophis*", while Frazzetta (1970) inferred that the maxillary-prefrontal joint "is certainly much tighter than in booids, and it seems likely that little separation between the bones was possible. But the form of the joint suggests that the maxilla could slip relative to the prefrontal by slight rotation about its own longitudinal axis, and by transverse rotation in a horizontal plane". Because the opposing surfaces of the maxilla and prefrontal are not exposed in described material of *Dinilyisia* (Caldwell and Albino 2002), it seems uncertain whether their "interlocking" contact was a saddle joint (like anilioids) or an immobile suture. In *Wonambi*, in contrast, the evidence is sufficient to infer a practically rigid suture rather than a joint, whereas the contact surfaces for the prefrontal on the frontal (concave dorsal and lateral facets bounded by ridges) are consistent with mobility. Hence, the prefrontal was functionally part of the maxillary unit, with kinesis mostly or entirely restricted to the prefrontal-frontal contact. The posteroventral margin of the prefrontal probably also had fairly close and tight connections with the palatine, as the latter has a well developed transverse dorsal ridge on the choanal process (more distinct in *Nanowana* spp. and *Yurlunggur*; Scanlon 1996, 1997). Thus *Wonambi* shows similar conditions to *Dinilyisia* and anilioids, in which palatal mobility appears to be quite minor (e.g., Cundall 1995). The separation of nasal and prefrontal facets on the frontal suggests, but does not prove, that there was a fissure between these elements (posterior extension of the external naris) extending to the frontal border, as in most varanoids and some (non-basal) extant snakes. Apart from the "free" anteromedial border, the general shape of the prefrontal can be inferred from its functional role and associated elements of the palate and braincase (reconstruction, Scanlon and Lee 2000: fig. 1).

Snout unit: premaxilla, nasal, septomaxilla, and vomer.—

No remains of these elements have yet been recognized. The premaxilla presumably bore teeth in ancestral snakes (and most retain a functional egg-tooth in neonates), but parsimonious character optimization implies there have been several losses within Serpentes, and it can even be inferred that adult premaxillary teeth re-evolved after loss at least once (Kluge 1993b; Lee and Scanlon 2002, character 173); hence, phylo-

genetic interpolation is inconclusive for this character. However, as ankylosed teeth and alveoli of snakes are distinctive and easily recognized among fragmentary remains, and all other tooth-bearing elements have been represented by one or more specimens, a probability argument would suggest that the madtsoiid premaxilla lacked teeth. The “negative evidence” for this inference is statistically weak in the case of *W. naracoortensis* alone, where samples remain very small, but is stronger when considered in conjunction with madtsoiid taxa from Riversleigh, where larger numbers of well-preserved tooth-bearing elements are known (especially from *Nanowana godthelpi*, Scanlon 1997); the only toothed premaxillae of snakes yet identified in the Australian fossil record are referable to the pythonine genus *Morelia* ($n = 2$; Scanlon 2001 and personal observations). Somewhat more direct evidence of premaxillary morphology is available by interpolation from the anterior tips of maxillae, which are somewhat squared-off and with an elliptical pitted surface, suggesting that the maxilla was closely connected to the lateral process of the premaxilla by a short and tough ligament (or possibly syndesmosis), not sutured as in “lizards” nor as freely mobile as in extant booids. In this respect, *Wonambi* was possibly equivalent to *Anilius* or *Cylindrophis*, though comparison is made difficult by the difference in absolute size. A similarly “square” posterolateral margin of the premaxilla can therefore be expected. The rounded anterolateral margins of the maxillae suggest a smoothly rounded snout with the body of the premaxilla lying in the arc of the maxillary tooth rows; however, a modified premaxilla (e.g., enlarged and projecting outside the maxillary arc in the manner of *Loxocemus* or *Aspidites*) cannot be ruled out on present evidence.

Evidence for nasal morphology is provided by the frontal (see above), which indicates an extensive, digitate sutural contact: the posterior end of the nasal is thus inferred to be relatively massive and apparently rigidly attached to the braincase. This condition is unlike any extant squamate, and particularly unlike most alethinophidian snakes where there is usually a functional prokinetic joint between frontal and nasal (Frazzetta 1966; Cundall 1995; Cundall and Shardo 1995). An alternative anatomical possibility is that the suture involved a massive posterior process of the premaxilla, as in mosasaurs, but such a state does not occur in other basal snakes (*Dinilysia*, *Pachyrhachis*, *Haasiophis*; Estes et al. 1970; Lee and Caldwell 1998; Tchernov et al. 2000; *contra* Haas 1979) and there seems no reason to expect convergence on functional grounds. Secondary solidification of the fronto-nasal joint occurs in some fossorial snakes (e.g., *Atractaspis*, Deufel and Cundall 2003), but such habits are unlikely in *Wonambi* and it is therefore parsimonious to suppose that immobility is retained from “lizard” ancestors. The anterior (rather than dorsal) orientation and digitate structure of the suture are thus considered apomorphic; it is presently unclear whether these features characterize Madtsoiidae or a less inclusive lineage.

The vomer is similarly represented only by a putative contact surface on the palatine (see above), implying an in-

terlocking joint similar to that of extant anilioids (e.g., *Anomochilus*, Cundall and Rossman 1993). Considering the inferred absence of prokinesis, if the vomers were involved in kinesis of the palate they probably had little or no mobility against the ipsilateral septomaxillae (to which they were probably sutured as in extant squamates) but more freedom relative to the nasals and the contralateral vomer and septomaxilla (mediated by the cartilaginous nasal septum, see Cundall and Shardo 1995).

Epipterygoid.—As noted in the description above, the parietal, prootic and sphenoid of *Wonambi* apparently do not meet in a simple triple junction as in most extant snakes, but sutural surfaces define a recess in the external braincase wall. Several explanations have been considered for this “slot” at the posteroventral corner of the parietal. After rejecting Barrie’s (1990) interpretation as the foramen for V_2 , the first hypothesis I considered was that it was filled by the inferior process of the prootic, but that the skull was asymmetric in SAM P30178A, with the process shorter on the left (where the prootic is known) than the right side (represented by the parietal). Asymmetry in this region is not unknown in snakes (the basiptyergoid processes are slightly asymmetric in position in a specimen of *Yurlunggur* sp., Scanlon 2003; and the Vidian canals are asymmetric in size in some extant snake lineages, Underwood 1967). However, except for the difference in the ?cid-nerve canals (dorsally open on one side) the dorsolateral contact surfaces on the sphenoid are similar on both sides in SAM P30178A, each divided into inner and outer portions by low longitudinal ridges (Figs. 9A, 10C), and only the inner portion matching a contact surface on the parietal. Further, the left side of the parietal SAM P27777 is similar to the right side in SAM P30178A (Figs. 7, 8), so there is no evidence for such asymmetry in *Wonambi*.

The alternative explanation here considered most likely (by anatomical interpolation, not contradicted by phylogenetic interpolation) is that the space was filled by a separately ossified element wedged between the parietal, basisphenoid, and prootic. This inferred element, in immediate contact or close association with the basiptyergoid process and clinoid process of the sphenoid, both anterior processes of the prootic, and parietal descensus, can be identified topographically with the epipterygoid of non-ophidian squamates. Presence of a distinct epipterygoid, partly incorporated in the braincase wall, may represent a transitional stage in the evolutionary origin of both the “parasphenoid wing” and the “laterosphenoid” of alethinophidians, as discussed further below.

Supraoccipital.—The boundaries of this median dorsal element are fairly precisely defined by the sutural surfaces on the surrounding elements; some uncertainty pertains to the posterolateral processes of the parietal (which probably overlapped the lateral parts of the supraoccipital as well as the rest of its anterior margin), and the supratemporal (which overlapped the parietal laterally, and may also have contacted this element). Externally, the supraoccipital was probably most similar to those of *Dinilysia* and *Cylindrophis*. It would cer-

tainly have had a sagittal dorsal crest continuing that on the parietal, and the whole dorsal surface including the crest must have sloped down steeply posteriorly, as the exoccipitals are much lower than the posterior margin of the parietal, but lack an extension of a median crest. There may well also have been a transverse nuchal crest (as in *Dinilysia* and most other snakes), separating attachment areas for jaw adductors (anteriorly) and epaxial trunk muscles posteriorly. Intracranially, the supraoccipital formed the dorsal part of the tympanic bulla (pierced by the endolymphatic foramen in lizards and snakes), and contributed to the margin of the acoustico-facial fenestra (as defined above). Dorsolateral to the endolymphatic foramen, in the medial part of the roof of the cavum vestibuli on each side, would be the recessus crus communis (Oelrich 1956: fig. 54), giving rise within the body of the supraoccipital to the anterior and posterior semi-circular canals. See also below (“The relation of the parietal to the supraoccipital”).

Suspensorium and stapes.—It can be presumed that, as in most other snakes, the supratemporal and quadrate formed the link between the braincase (parietal and paroccipital process, each with indications of contact surfaces) and mandible (articular facet). The combined extent of these elements (in resting position, with jaws closed) can thus be estimated by interpolation, after reconstruction of the links between the braincase and upper jaw elements. Phylogenetic interpolation is hardly applicable to details or proportions of these elements because of their extensive variation among basal snakes and varanoids, including whether and how far the supratemporal extends beyond the paroccipital process, presence or absence of a suprastapedial process of the quadrate, and the nature and position of the connection between the stapes and quadrate.

As noted above, the supratemporal facet on the exoccipital and posterior part of the prootic comprises several concave areas bounded and divided by crests. It is unknown whether the inner face of the supratemporal was correspondingly sculptured; if so, it would apparently have been firmly attached (“intercalated”) to the braincase, and unable to slide or rotate against the skull, as is also the case in *Dinilysia* and extant anilioids (*Cylindrophis*, *Anilius*). The supratemporal facet appears to be contiguous anteromedially with the surface overlapped by the parietal, as defined by diverging ridges on the prootic and exoccipital consistent with the preserved portions of the posterolateral processes in SAM P27777; this supports the evidence from the latter specimen for an extension of the supratemporal facet on the parietal (contrary to the reconstruction of Scanlon and Lee 2000: fig. 1). If the parietal reached or closely approached the transverse ridge on the exoccipital (continuation of the inferred transverse ridge on the missing supraoccipital), the dorsal edge of the prootic would not be isolated as a separate dorsal exposure as it is in *Dinilysia* and anilioids (Estes et al. 1970). It may be unreasonable to expect a clear indication of the extent of the parietal on the other braincase elements; in a suffi-

ciently primitive snake a contact of parietal and supratemporal need not leave any impression on the braincase because a narrow slit might be retained as a vestige of the post-temporal fenestra (e.g., in *Cylindrophis*, SAM R36779, the medial margin of the supratemporal is not in tight contact with the posterior part of the prootic, which it overlaps). Similarly, it is not clear how far the supratemporal extended posterior to the paroccipital process. The reconstruction of the skull by Barrie (1990: figs. 5, 6) is certainly somewhat telescoped (with proportions approaching those of the caenophidian *Acrochordus*), and the jaw elements should be located more anteriorly relative to the braincase. Even allowing for this effect, the length of the mandibles implies that either the supratemporal extended well posterior to the paroccipital process, or the quadrate shaft was angled posteriorly, or both (as reconstructed in Scanlon and Lee 2000: fig. 1). Rieppel et al. (2002: fig. 6A) identified the supratemporal facet as extending almost the entire length of the prootic; while the actual anterior extent of the supratemporal is unclear, it is certain that most of the surface they label “f.st.” was directly overlapped by the parietal.

Accessory mandibular elements: coronoid, angular and splenial.—Contact surfaces for these elements can be recognized on the compound and dentary, and indicate their approximate extent and form; details of the angular-splenial contact (intramandibular joint) and dorsally free extent of the coronoid are potentially significant for systematic and functional interpretation, but still unknown. The coronoid eminence of the surangular is well-defined and angular in outline, but low, and directed more laterally than dorsally relative to the occlusal plane of the tooth row when the compound-dentary joint is reconstructed. This is consistent with the overall “flattening” of the major mandibular components, but the same set of autapomorphic changes make it hard to predict the shape of the missing elements.

The Braincase: continuity between lizards and snakes

Braincase structures in *Varanus* and the mosasaur *Platecarpus* have recently been discussed in connection with the relationships of snakes (Rieppel and Zaher 2000). Throughout that paper, Rieppel and Zaher emphasized the differences between snakes and other squamates (repeatedly using terms such as “fundamentally different” and “not comparable”). Here I will reverse that emphasis to highlight continuity (i.e., similarity, or the relative absence of evidence for evolutionary change; see Kluge 2004), with comments on the interpretation and significance of madtsoiid braincase structures, following the sequence of subheadings in Rieppel and Zaher (2000).

The relation of the parietal to the prootic.—Rieppel and Zaher (2000: 494) state that snakes lack a crista alaris on the prootic (“an anterior extension of the cupola anterior to the otic capsule, made up of membrane bone... set off from the trigeminal notch at the anterior margin of the prootic by the

supratrigeminal process"; Rieppel and Zaher 2000: 492), and imply this may be a synapomorphy with amphisbaenians and *Dibamus*. Reference to the supratrigeminal process is unhelpful in this context, as it is absent in most if not all varanoids, including mosasaurs, and has never been reported in snakes. As shown here, *Wonambi* has a long anterior extension of the prootic above and beyond the trigeminal notch, its anterior tip slightly expanded and laterally overlapping the descending flange of the parietal, and resembling the alar process of *Platecarpus* in most details apart from its greater proportional length and more horizontal orientation. The prootic in *Dinilyisia* is similar in these respects to *Wonambi*, though known in less detail due to the articulated condition of the described material (Estes et al. 1970; Caldwell and Albino 2002). Both *Pachyrhachis* and *Haasiophis* also appear to have similar, anteriorly pointed prootics overlapping the parietal; in *Pachyrhachis*, these were identified in dorsal view by Haas (1979: 60, and his figs. 4 and 6; see also Lee and Caldwell 1998). In *Haasiophis*, the prootic is clearly visible dorsally on the left side in the published photograph (Tchernov et al. 2000: fig. 1) but not so interpreted by its authors (see also Rieppel et al. 2003), who labeled as "prootics" what I regard as the madtsoiid-like, prominent lateral processes of the pterygoids (Lee and Scanlon 2002). In recent snakes the prootic lacks a pointed process but its anterodorsal margin still usually overlaps the parietal quite extensively (Scanlon 1996; Rieppel and Zaher 2000: 494), so that the "absence" of the crista alaris in scolecophidian and alethinophidian snakes can be seen as a matter of degree.

Based on phylogenetic relationships inferred by Lee and Scanlon (2002), the long and pointed, but shallow, alar process shared by *Wonambi*, *Dinilyisia*, and apparently also *Pachyrhachis* and *Haasiophis*, is parsimoniously considered an evolutionary intermediate between the varanoid and modern snake conditions. Lee and Scanlon (2002, character 131) distinguished two states based on anterior extent of the alar process; all modern snakes were assigned the apomorphic (reduced) state. However, one might recognize a distinct character based on the dorsal extent of the process, and then the anteriorly shallow prootic of the fossil snakes would be coded as apomorphic, while modern snakes would be assigned the same state as lizards (optimizing as a reversal). To elucidate the actual evolutionary pathway, it is important to also consider the relationship of the trigeminal notch to the otic capsule (as implied by Rieppel and Zaher's 2000 definition of the crista alaris), i.e., how far the anterior semicircular canal extends into the alar process beyond the rear of the notch. This criterion has not been applied in our analyses to date because information on the three-dimensional internal structure of the bone is available for few taxa, including no fossil snakes (not shown in X-rays of *Haasiophis*, Rieppel et al. 2003). The expansion of the otic capsule (particularly the semicircular canals) relative to other cranial structures has been interpreted as a consequence of miniaturisation of the head in an ancestral snake (Rieppel 1984a); it apparently characterizes modern snakes (Scolecoptidia and Alethino-

ptidia), but there is no evidence for it in the basal lineages known only from fossils. It seems highly unlikely, from the proportions of the prootic in *Wonambi*, that the semicircular canal extended more than slightly beyond the rear of the trigeminal foramen.

The "closed sutural contact" between the prootic and parietal in mosasaurs (terms of Lee 1997, 1998; Lee and Caldwell 1998; Rieppel and Zaher 2000) is also contrasted with a clasping or syndesmotoc contact in snakes (terms of Rieppel and Zaher 2000). However, this may be only a difference in terminology, for no comparison has been presented to show that the manner of contact in the two groups is actually different. Comparing illustrated material of mosasaurs (e.g., Russell 1967: *Clidastes*, fig. 13; *Tylosaurus*, fig. 15) with *Wonambi*, there is no obvious difference in the nature of this contact. If the extent of interdigitation is sometimes, or even generally greater in mosasaurs, this by no means implies lack of comparability, being parsimoniously considered an autapomorphy of mosasaurs (Rieppel and Zaher 2000) and possibly a straightforward consequence of large size.

The lateral wing of the parietal in *Wonambi* and *Dinilyisia* is much more extensive than in extant snakes (though matched in length by a less prominent crest in some anilioids and booids: e.g., *Cylindrophis ruffus*, personal observation; *Eunectes murinus* [Linnaeus, 1758], Bellairs and Kamal 1981: fig. 67), so that this can be seen as an apomorphy shared by the two fossil snakes (Lee and Scanlon 2002, character 67). When coded in this manner and mapped on the cladogram (*ibidem*: fig. 11A), it is equally parsimonious to regard it as a synapomorphy reversed in an ancestor of modern snakes, or a convergence. However, alternative interpretations of this feature are possible, since the conditions in other basal snakes (*Pachyrhachis* and *Haasiophis*) are currently unclear due to their manner of preservation. Rather than a novel feature in early snakes, the large crest might instead be plesiomorphic at this level, and represent the edge of the lizard parietal roof. The condition in *Wonambi* and *Dinilyisia*, with the crest expanding and horizontally dividing the lateral surface for muscle attachment, would then be transitional between lizards (in which jaw adductors attach to either the ventrolateral or the dorsolateral surface of a lateral crest, dorsolateral to the descensus if present) and modern snakes with a reduced crest but relatively much larger muscle attachment surfaces (possibly a correlate of reduction in head width, as with other features related to fossoriality or miniaturization).

The relation of the parietal to the supraoccipital.—The supraoccipital of *Wonambi* has not been found but its morphology is highly constrained by known contact surfaces with prootic, parietal, and exoccipital, as noted above. Like many other snakes, *Wonambi* had an overlap of the posterior margin of the parietal over the supraoccipital, which occupied the middle third of the parietal as preserved. The boundary is sinuous but somewhat asymmetrical in dorsal view (SAM P27777), and the contact was about as deep as wide,

even disregarding the high sagittal crest (which clearly would have extended onto the supraoccipital). A median ridge on the posteroventral face of the parietal separates paired concavities, and is further divided by a groove containing several small foramina. Comparison with disarticulated material of booids (e.g., *Liasis olivacea*) as well as lizards (e.g., *Varanus* spp.) suggests that it is the median groove that corresponds to the parietal fossa receiving the small processus ascendens of the supraoccipital, while the lateral concavities received the larger marginal processes. These features of the squamate supraoccipital are clearly identifiable in booids, and their presence in *Wonambi* is indicated by the complementary features of the parietal. The parietal-supraoccipital contact is most similar to that of anilioids such as *Cylindrophis* and *Anilius*, rather than booids and many other macrostomatans where the parietal has a strong posterior overlap, but the median tongue-in-groove articulation of lizards can be identified in booids as well as *Wonambi*, and may be retained in most modern snakes.

It has been inferred above that, as in most lizards and many alethinophidians, the posterolateral parts of the parietal (supratemporal processes or suspensorial rami) were in contact with the supratemporals; however, there is no physical necessity that this contact coincided with a direct overlap of both elements on the dorsal surface of the prootic (as in *Dinilyisia* and *Cylindrophis*) or prootic and supraoccipital (as in some other alethinophidians). In fact the ridges defining the supratemporal facet on the paroccipital process seem consistent with the parietal and supratemporal having formed an arch separated from the dorsal surface of the prootic and supraoccipital by a small space, a vestige of the post-temporal fenestra (as occurs in some lizards, e.g., *Cherminotus*, Borsuk-Białynicka 1984). The possibility of such a state (albeit not considered likely in *Wonambi*) leads me to question Rieppel and Zaher's assertion (2000: 495) that "Character coding... should account for the presence or absence of posttemporal fossae, rather than for the degree of contact between parietal and supraoccipital"; presence or absence of such a vestigial fenestra (which remains an open question for *Wonambi*) would actually be quite independent of the degree of contact between parietal and supraoccipital (already known).

The relation of the supratemporal to the paroccipital process.—Again, Rieppel and Zaher (2000: 496) state that the arrangement by which the supratemporal attaches to the paroccipital process in *Varanus* and mosasaurs is structurally very different from that in snakes. In this case, again, *Wonambi* appears to show close structural similarity to the varanoids, more indeed than to most snakes. However, although it has a strongly bounded and internally divided facet for the supratemporal, it is more snake-like than *Dinilyisia*, which clearly displays an interdigitating suture between the supratemporal and prootic (Estes et al. 1970); such a suture is regarded by Rieppel and Zaher (2000) as an autapomorphy of mosasaurs.

The basicranium and palatobasal articulation.—As in most other snakes the dorsum sellae of *Wonambi* (and *Yurlunggur*; Scanlon 2003) is low and not overhanging, and there are no retractor pits or median crest within the hypophysial pit. The canal for nerve VI 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 more or less parallel into the orbital region of the skull. These differences from typical lizards such as *Varanus*, and also (in most cases) from mosasaurs, can be coded as several discrete characters (e.g., Lee and Scanlon 2002, characters 116, 126, 128–129), but this region remains poorly known in some other important fossils (*Pachyrhachis*, *Haasiophis*, and for some characters *Dinilyisia*).

The basiptyergoid processes of *Wonambi* are well developed but, as in mosasaurs rather than *Varanus* or typical lizards, they project ventrolaterally rather than anterolaterally, their distal facets are barely wider than the pedicels, and elongated longitudinally rather than strongly oblique and converging anteriorly (in some of these respects, *Dinilyisia* seems more lizard-like than madtsoiids or even mosasaurs; Estes et al. 1970: fig. 2). The base of the basiptyergoid process is "pierced by the Vidian canal. The posterior opening of the Vidian canal lies halfway between the posterior base of the basiptyergoid process and the basisphenoid-basioccipital suture, below the crista prootica" (Rieppel and Zaher 2000: 498–499, referring to *Varanus* and mosasaurs); exactly the same is true of *Wonambi* (this work), and also *Dinilyisia*, apart from its autapomorphic lack of a prootic crest (Estes et al. 1970: fig. 5). In both *Wonambi* and *Yurlunggur* (and *Dinilyisia*), as in mosasaurs, "the anterior openings of the Vidian canal open into a shallow groove on the lateral aspect of the para-basisphenoid" (Rieppel and Zaher 2000: 499). In these snakes, as far as can be inferred without direct observation of soft tissues, the basicranial relations of the palatine nerve and artery (assumed to emerge from the lower anterior opening) are not distinguishable from those of mosasaurs.

As discussed elsewhere (Scanlon 2003), the condition in *Yurlunggur* in which the abducens canal opens extracranially just dorsal to the anterior Vidian canal opening appears to be shared with *Wonambi* and *Dinilyisia*, and is interpreted as a transitional state between that of typical lizards and the common state in alethinophidian snakes where both openings are intracranial, enclosed laterally by contact of the parietal with the "sphenoid wing". The upper anterior opening in *Dinilyisia* was previously suggested to be for the cid-nerve (Rieppel 1979; McDowell 1987), but this region of the skull of *D. patagonica* is similar to that of the madtsoiid *Yurlunggur* sp. in both the external openings and, as far as revealed by Estes et al.'s (1970: fig. 5B) excavation within the bone, the course and relationships of the internal canals.

The possible presence of an epiptyergoid in *Wonambi* requires some further comment, especially as it may help to explain how both the Vidian and abducens canal openings attained the "intracranial" positions typical of alethinophi-

dians. Just at the medial end of the slot between parietal, prootic and sphenoid is the apex of the clinoid (or alar) process, which in lizards attaches to the pila antotica (Rieppel and Zaher 2000: 498), so that the topographic relationships of the inferred epipterygoid with parietal descensus, alar crest of prootic, and clinoid process all appear to be matched in *Wonambi*. The lateral extent of this putative element is unknown, but it may have overlapped the dorsolateral face of the basipterygoid process (note the smooth, triangular facet-like surface immediately dorsal to the pterygoid facet, Fig. 10A) and lower anterior process of the prootic, and may even have contributed to the pterygoid articulation as does the epipterygoid in lizards (a dorsal depression on the pterygoid adjacent to the facet, comparable to the collumellar fossa of lizards, is reported above). It might even have had a posterior extension partially enclosing or effectively dividing the trigeminal foramen, like the laterosphenoid in alethinophidians, but there is currently no evidence to support this.

Estes et al. (1970) report a “pebble-like” element lying on the dorsal surface of the pterygoid in the type skull of *Dinilysia* (right side only), which they suggested might be a dislodged part of the prootic; here I consider the possibility that it may instead be an epipterygoid. In *Dinilysia* (like *Wonambi* and alethinophidians), there is a posterior extension of the descending process of the parietal, overlapped dorsally by the alar process of the prootic; the pebble-like element is narrowly separated from both of these processes, so the position of its dorsal end can be considered topographically equivalent to that of the lizard epipterygoid (which often overlaps the tip of the alar crest, close to its parietal contact). The condition of the epipterygoid suggested here in *Dinilysia* is strikingly similar to that of the supposed jugal (Estes et al. 1970), being reduced to a small lenticular bone lying on the jaw element (maxilla, pterygoid) and replaced dorsally by a ventral extension of the skull roof (postorbital, parietal).

In lizards, both V_2 and V_3 (maxillary and mandibular branches of the trigeminal nerve) pass laterally posterior to the epipterygoid (Rieppel 1989), while in alethinophidians they are separated by the laterosphenoid bridge fused to the prootic, V_2 passing anteromedial to it. The laterosphenoid is developmentally mixed and variable in modern snakes, forming from a separate endochondral centre of ossification or in continuity with the prootic, and sometimes entirely from dermal bone (Haluska and Alberch 1983). The epipterygoid and laterosphenoid can be considered homologous if a historical series of intermediates is hypothesized (Rieppel 1989) in which V_2 came to pass medial to the epipterygoid, presumably dorsally (requiring a separation from the parietal). Such an intermediate condition might be represented in *Dinilysia*, where the putative epipterygoid is directly lateral to the trigeminal foramen but separated from the parietal; V_2 could have passed anterodorsal to it even if there was a persistent (antero-posteriorly oriented) connection between epipterygoid and parietal. The putative transition need not appear perfectly gradual in terms of adult

morphology, as it would involve alteration of relatively early stages of development.

Based on the surface texture of the bone, the articular surfaces of the basipterygoid processes in the madtsoiids may well have been cartilaginous, and thus may have had a lizard-like synovial joint with the pterygoid (developmentally related to the epipterygoid, see Irish 1989). On the other hand, these snakes lack the “parasphenoid wing” (McDowell 1975) that enters laterally between the parietal and prootic in alethinophidians. This position in the braincase wall would be occupied (in *Wonambi* but not *Dinilysia*) by the supposed epipterygoid, which may thus contribute to the “parasphenoid wing” (as suggested by McDowell 1967) rather than, or as well as, the “laterosphenoid”.

In squamate lineages where the parietal is expanded ventrally to contribute to a lateral braincase wall, a vertical, rod-like epipterygoid, connecting the basipterygoid articulation to the tip of the descending process of the parietal, necessarily shortens (e.g., *Anniella*, Anguillidae; *Anelytropsis*, Dibamidae), leading to disappearance as the gap closes (e.g., *Dibamus*; McDowell and Bogert 1954; Rieppel 1984b; Greer 1985). On the other hand, we might suppose that in ancestral snakes the epipterygoid retained appreciable length by “reclining” along the margins of the sphenoid and parietal instead of remaining vertical, and did not disappear (at least in the alethinophidian lineage) but “broke up” and fused to the surrounding bones. Then no structure in extant snakes would be strictly homologous, one-to-one, with the epipterygoid of lizards (Bellairs and Kamal 1981: 185–191). Rather, the “parasphenoid wing” would correspond to the dorsal part of the basipterygoid process and, fused to it, the anteroventral part of the epipterygoid, while the “laterosphenoid” would derive from the dorsal and posterior part of the epipterygoid fusing to the prootic. Whether or not traces of such a morphocline are retained in the ontogeny of extant snakes (de Beer 1937; McDowell 1967; Irish 1989), adult stages preserved as fossils should also help to clarify the question.

Starting from the state hypothesized in *Wonambi*, with an oblique epipterygoid partly incorporated in the braincase wall, the enclosure of the primary anterior openings of the Vidian and abducens canals (characterizing basal alethinophidians) could apparently be accomplished in one step by fusion of the epipterygoid to the sphenoid, dorsal and anterior to the basipterygoid facet. The condition observed in *Wonambi* makes such a transformation appear plausible, but the homology of this part of the skull of snakes will remain debatable until even better-preserved fossils are available.

While the prominent basipterygoid processes are comparable to those of some booids (apart from the “unfinished” appearance of the surface), the opposing facets on the pterygoids are quite different. Those of booids typically form elongate, narrow “rails” allowing extensive anteroposterior sliding of the pterygoids against the braincase as part of the prey-transport system (“pterygoid walk”). The facet on the pterygoid in *Wonambi* is relatively short and distinctly bounded anteriorly and posteriorly, so it was not capable of

such long anteroposterior excursions without separating from the basiptyergoid facet, and the apparently tight contacts of maxilla with prefrontal, and palatine with vomer, also suggest little or no anteroposterior mobility of the palatamaxillary arch as a whole. Instead, the narrow cylindrical facet of the pterygoid may have been able to slide transversely across the broader, flatter basiptyergoid facet, and also allowed rotation about a longitudinal axis through their contact (erecting and lowering the lateral part of the pterygoid and, with it, the ectopterygoid and posterior end of the maxilla). The condition in *Wonambi* differs somewhat from that seen in *Nanowana godthelpi* and *Yurlunggur* (Scanlon 1996, 1997) where the pterygoid facet is equally distinct but flat rather than cylindrical, and faces more dorsally than medially; the latter state is also found in the alethinophidian *Cylindrophis* (SAM R36779).

Details of embryonic development, or even whether the basiptyergoid articulation is ligamentous or synovial, can not be determined directly in extinct groups known only as fossils; Kluge (2004) has recently noted that “The all too frequent departures from terminal addition, and the same structures developing from different embryological rudiments have rendered the empirical test of ontogeny impotent in any particular application.” Consequently it is impossible to use these supposed differences to demonstrate that structures in snakes (including madtsoiids and *Dinilysia*) are “not comparable” to basiptyergoid processes of non-ophidian squamates (including mosasaurs) as argued by Rieppel and Zaher (2000: 497; the similar argument by Kluge 1991, was concerned primarily with extant forms). Actual comparison of this region of the skull between the madtsoiids (or *Dinilysia*) and *Varanus* (or especially mosasaurs) reveals structural similarity in the relative size, shape, orientation, and surface texture of the articular facets, their pedicels, and the opposing facets on the pterygoids, as well as their relationship to the Vidian canals, dorsum sellae, hypophysial pit, and surfaces for muscle attachment (see below; also Estes et al. 1970; McDowell 1967, 1974). On the basis of this structural similarity, the palatobasal articulations of these fossil snakes are here treated as primary homologues of the basiptyergoid articulations of non-ophidian squamates, an interpretation consistent with other evidence for their basal phylogenetic position relative to other snakes (Scanlon and Lee 2000; Lee and Scanlon 2002). Primary homology between structures in fossil and extant snakes (like those between mosasaurs and extant varanids) must similarly be tested in terms of structural similarity of comparable (i.e., fossilizable) elements, and consistency with “global” phylogenetic analyses. The structural similarity of the basiptyergoid processes and opposing facets in mosasaurs and *Wonambi* on the one hand, and *Wonambi* and *Cylindrophis* on the other, tends to support a hypothesis of continuity (hence homology), in contrast with the interpretations of Kluge (1991) and Rieppel and Zaher (2000; see also Tchernov et al. 2000; Rieppel et al. 2003).

The posteriorly undercut lateral projection above the posterior Vidian canal opening, well-developed in *Wonambi*

(“prootic flange” in Rieppel et al. 2002), is also often present in alethinophidians, but absent in *Dinilysia*. This is labelled as part of the “laterosphenoid” by Bellairs and Kamal (1981: fig. 67), but *Wonambi* shows that it may occur independently of the laterosphenoid bridge (also confirmed in *Yurlunggur*, personal observations). This projection is structurally similar to the anteroventral part of the crista prootica of lizards, and here regarded as plesiomorphic rather than a new feature of alethinophidian snakes; its absence in *Dinilysia* is thus interpreted as a loss, paralleled in various modern snake lineages (e.g., within elapids, Scanlon and Lee 2004).

The basioccipital.—The basioccipital of *Wonambi* is comparable in overall shape and most details with those of generalized lizards such as *Ctenosaura* (Iguanidae; Oelrich 1956), including presence of a distinct transverse channel within the dorsolateral sutural surface (representing the floor of the recessus scalae tympani opening laterally at the occipital recess) and deep ventrolateral depressions for muscle attachment on either side of a sagittal keel. This element shows considerable variation among extant and fossil varanoids and mosasaurs (e.g., McDowell and Bogert 1954; Russell 1967; Borsuk-Białynicka 1984; Norell and Gao 1997), none of which seem to approach the *Wonambi* condition more closely than *Ctenosaura* does. There are well-developed sphenoccipital tubercles (basal tubera) at the anterolateral margins of the basioccipital, which also involve the posterolateral corners of the sphenoid, the posteroventral corners of the prootics, the ventrolateral part of the crista interfenestralis (opisthotic) and anterolateral part of the crista tuberalis (exoccipital). The tubercles are located halfway between the occipital condyle and the basiptyergoid processes, as in *Varanus*. As in mosasaurs and other snakes (but not *Varanus*) they show no signs of being capped by epiphyses. The shape and relative position of the basioccipital-basisphenoid suture can clearly vary within certain limits without affecting any of these surrounding structures or their functions. There does not appear to be any evidence that the sphenoccipital tubercle forms a functional articulation with the quadrate process of the pterygoid in any squamate (*contra* Tchernov et al. 2000; supplementary information, character 64).

Apart from the largest and most conservative features, identification of vascular and nervous foramina of madtsoiids must be somewhat speculative due to the lack of direct evidence of soft tissues, or extant close relatives. I therefore comment only briefly on a possible connection between foramina in the rear wall of the hypophysial pit (between the carotid foramina from the Vidian canals), and on the dorsal midline of the basioccipital in madtsoiids. In the mosasaur *Platecarpus*, there is a bilobate median tunnel through the basisphenoid and basioccipital, with a large dorsal opening on the latter, interpreted by Russell (1967: figs. 10, 11) as for the basilar artery (see also Rieppel and Zaher 2000). In most amniotes the basilar artery, formed by anastomosis of caudal rami of the cerebral carotids (Rieppel 1979: 417), is intracranial and leaves no trace on the skeleton, but Rieppel

(1979: fig. 5) shows what seems to be a Y-shaped groove for this vessel on and posterior to the dorsum sellae in *Xenopeltis*. Presumably, formation of a closed tunnel as in *Platecarpus* (and apparently *Dolichosaurus*, Caldwell 2000: fig. 7) could proceed by progressive deepening and eventual dorsal closure of such a groove. An extracranial course of the basilar artery through the basisphenoid and basioccipital in madtsoiids, as in *Platecarpus* except for the much smaller relative size of the vessel, could account for the foramina and sinus in the dorsum sellae (present in *Yurlunggur*, Scanlon 2003; possibly present but obscured by infilling matrix in *Wonambi*) and median dorsal foramen on the basioccipital (observed in *Wonambi*).

Cranial nerves VII and VIII.—The presence of a single external foramen for the facial nerve is a condition commonly present in *Varanus*, mosasaurs, and some extant snakes (Rieppel and Zaher 2000: 502–503). Because the number of foramina varies within each of these taxa, the possibility that a second, ventral opening existed in *Wonambi* (obscured by matrix?) seems quite unimportant. The other distinction mentioned by these authors, whether the geniculate ganglion is intra- or extracranial, amounts (in terms of observable, i.e., bony structures) to whether there is a single or separate foramina for nerves VII and VIII on the internal wall of the skull. As described above, in SAM P30178A the internal opening is single, and the canal for nerve VII opens to the outside from a pocket in the prootic connected with the vestibular recess, rather than direct from the intracranial space. Again, this is variable within most of the groups considered and hence of little or no systematic significance.

The fenestra vestibuli (fenestra ovalis).—Much has been written about the ear region in squamates (e.g., Rieppel 1979a, b, 1985; Rieppel and Zaher 2000), but it is sometimes unclear precisely what is meant by the synonymous terms “fenestra vestibuli” or “fenestra ovalis” (= “foramen ovale”, Oelrich 1956; “fenestra ovale”, used by Rieppel and Zaher 2000, is incorrect). These terms are correctly used only for the opening occupied by the stapedial footplate, not for the lateral opening in the crista circumfenestralis through which the stapedial shaft emerges, because the lateral enclosure of the juxtastapedial recess is a “new” and variable feature of snakes.

The crista prootica is reduced in *Wonambi* (and in alethinophidians), relative to *Varanus* and mosasaurs, in being broadly interrupted in the vicinity of the facialis (VII) foramen, but otherwise topographically similar. The lateral head vein is not observable in fossils but there is no reason to suppose its relationship to the crista prootica differed in any other way from that in lizards (the same parsimonious assumption made by Russell 1967, and Rieppel and Zaher 2000, in the case of mosasaurs).

The crista interfenestralis is particularly apparent, being exposed in lateral view and forming part of the dorsal margin and distal face of the sphenoccipital tubercle. The crests surrounding the fenestra together constitute the “crista circumfenestralis” (here considered a purely descriptive term

that should not imply detailed homology). In the case of *Wonambi*, the crista circumfenestralis is composed of part of the posterolateral edge of the prootic as well as the horizontal dorsal part of the crista prootica, part of the ventrolateral margin of the paroccipital process, lateral part of the crista interfenestralis, anterior part of the crista tuberalis, and (posteriorly, and least prominently) the buttress-like vertical ridge connecting the crista tuberalis to the paroccipital process. Rieppel and Zaher (2000: 504) consider the bony flanges projecting around the ear in *Varanus* and mosasaurs as topologically dissimilar to those of “basal snakes” because in scolecophidians and anilioids the crista interfenestralis is either not distinct (fused laterally to the crista tuberalis) or enclosed within the juxtastapedial recess. The condition in *Wonambi* (more basal than scolecophidians or anilioids; Scanlon and Lee 2000) shows detailed similarity to that of varanoids and also some alethinophidians, as discussed in the following paragraphs.

The embryonic fissura metotica is divided in squamates into a posterior (and usually dorsal) foramen jugulare and an anterior recessus scalae tympani (Rieppel 1979, 1985). This has been considered to be accomplished by different developmental mechanisms in extant lizards and snakes, but Rieppel (1988) considers that this need not affect decisions about homology of the resulting structures (see also Kluge 2004 as quoted above); this indeed seems a necessary assumption in palaeontology, and here the terms used for lizards are applied to snakes when topological relationships are the same. The lower lateral opening is the occipital recess of lizards, but in snakes it is reduced or subdivided in several different ways, in association with variation in the position of crests surrounding the ear, size and orientation of the stapedial footplate, and the ventral and lateral extent of the opisthotic and exoccipital.

Like lizards (and scolecophidians), *Dinilysia* has a single lower opening, here considered the occipital recess (= fenestra rotunda, Estes et al. 1970; apertura lateralis recessus scalae tympani, Rieppel 1979). However, *Dinilysia* is unusual in that the process of the exoccipital that forms the posterior wall of this aperture in lizards and other snakes (crista tuberalis) is reduced, accommodating the very large stapedial footplate (Estes et al. 1970; Rieppel 1979). The narrow process of the opisthotic separating the fenestra ovalis and occipital recess is the crista interfenestralis, the ventrolateral end of which forms part of the sphenoccipital tubercle in both *Dinilysia* and *Wonambi*.

Some alethinophidian snakes have the occipital recess further subdivided into the fenestra pseudorotunda, just posterolateral to the fenestra ovalis, and the apertura lateralis (*sensu stricto*) anteroventral to it, partly bordered by the basioccipital. The exoccipital and opisthotic may be fused laterally between the two openings (anilioids; Rieppel 1979), but in booids a distinct line of contact may be visible laterally where the crista interfenestralis forms part of the crista circumfenestralis (Rieppel 1979: fig. 9), whether a separate apertura lateralis is present (*Lichanura*) or absent (*Loxocemus*, *Trachyboa*). In other cases the lower part of the opisthotic is distinct, but hid-

den from lateral view by contact of the exoccipital and prootic, so that there is a single occipital recess enclosed within the juxtastapedial recess (*Xenopeltis*, Rieppel 1979; *Liasis olivacea*, personal observations). Rieppel (1988), Tchernov et al. (2000; supplementary material, character 75) and Rieppel et al. (2002: 820) adopt a more restrictive (but never explicit) definition such that the term “fenestra pseudorotunda” is applicable only in anilioids and supposedly represents a synapomorphy of *Anilius* and *Cylindrophis*. As it seems to be the more lateral opening (or the separating bony contact) that disappears within Alethinophidia, the medial one (which I interpret as the structural equivalent of the fenestra pseudorotunda of anilioids) is apparently retained in all snakes. There may be shared derived features in this region of *Cylindrophis* and *Anilius*, but they have not yet been adequately described, and Tchernov et al.’s character was consequently rejected by Lee and Scanlon (2002: 381).

The condition in *Wonambi* seems a good candidate as a primitive state for Alethinophidia. There are distinct medial and lateral openings, with a line of contact but no fusion of the opisthotic and exoccipital lateral to the fenestra pseudorotunda, so that both a crista interfenestralis and crista tuberalis can be distinguished as in lizards. Both crests extend laterally to contribute to the spheno-occipital tubercle as in lizards, but not dorsally to enclose the juxtastapedial recess as in most other snakes. Thus, contrary to Rieppel and Zaher (2000: 504), the bony flanges projecting around the vestibular fenestra in *Varanus* and mosasaurs are topographically equivalent to those in this snake. The withdrawal of the crista interfenestralis into the juxtastapedial recess, or its fusion with the exoccipital lateral to the fenestra pseudorotunda, are further derived conditions seen in some alethinophidians (e.g., Rieppel 1979) and should be informative in future phylogenetic analyses.

The fissura metotica.—Most of the substantive statements made by Rieppel and Zaher (2000) under this heading, concerning structures and relationships in *Varanus* and/or mosasaurs, apply equally to *Wonambi* (see above). On the other hand, the same structures can easily be identified in booids and other snakes (e.g., figures in Rieppel 1979; Rieppel and Zaher 2001). I therefore find no basis in adult skulls for Rieppel and Zaher’s (2000: 506) interpretation that “in snakes, the otico-occipital complex is of a fundamentally different structure”. Possibly their statement referred to the apparently distinct manner in which the metotic fissure is subdivided during embryonic development, either by apposition of the otic capsule to the basal plate and occipital arch, as in “lizards”, or by a ventrally extending strut of cartilage that connects the posteroventral corner of the otic capsule with the basal plate without fusing with the occipital arch, as in snakes (Kamal 1971; Rieppel 1988; Rieppel and Zaher 2001: 253). However, this difference in cartilage formation (or at least, differently described cartilage formation) has no necessary effects in the adult bony skull and cannot be used in arguments concerning extinct taxa such as mosasaurs and madtsoiids.

Conclusions

The skull of the extinct giant snake *Wonambi naracoortensis* is more than 50% known, based on material from four South Australian deposits of Pliocene and Pleistocene age. Description of new material, and new data on specimens previously described in a semi-prepared condition, provide a more complete picture of cranial morphology in this taxon.

Rieppel et al.’s (2002) “test” of the phylogenetic relationships of *Wonambi* is rejected because of numerous misinterpretations of its morphology (attributable to the limited representation and partly prepared state of the material they examined), neglect of all comparative data on other Madtsoiidae, and distortion of their data matrix by a priori hypotheses of relationships (e.g., in coding the laterosphenoid bridge as “present” in *Wonambi*, although it is unambiguously absent in the only known prootic).

While no new phylogenetic hypothesis or taxonomic arrangement is proposed in this paper, many of its results have already been incorporated in published analyses (Scanlon and Lee 2000; Lee and Scanlon 2002). *Wonambi naracoortensis* is only one lately extinct, terminal branch of a morphologically diverse lineage with a fossil history as long as all modern snakes combined, and as such should not be given undue emphasis at the expense of other members of the group. Work in progress on other Australian material (including *Nanowana* spp., *Wonambi barriei*, and recently discovered partial skeletons of *Yurlunggur*) will soon allow phylogenetic analyses to include multiple madtsoiid species, testing the current “generic” concepts as well as monophyly of the “family”, and casting a stronger light on the phylogenetic pattern, character evolution, and biogeography of early snakes.

Since the first description of vertebral remains now referred to Madtsoiidae, they have usually been considered to be boa-like, if not actually boid snakes. But based on details of the skull now known, it is clear that *Wonambi* and other madtsoiids are most similar, among living snakes, not to booids but to the most basal alethinophidians (anilioids), and in particular to those least modified for a fossorial way of life, especially *Cylindrophis*. As shown previously, features of the braincase imply a phylogenetic position outside Alethinophidia—indeed, outside the dichotomy of Alethinophidia and Scolecophidia, which comprise all living snake lineages (Scanlon 1996; Scanlon and Lee 2000; Lee and Scanlon 2002; Scanlon 2003). Structure of palatal and mandibular elements implies that, despite the relatively elongate jaws leading some to assume madtsoiids belonged to the clade Macrostromata, kinesis was similar or more limited than that in anilioids, and probably did not involve the “pterygoid walk” for intra-oral prey transport (Cundall 1995). Moreover, unlike all scolecophidians and basal alethinophidians, and perhaps also unlike *Dinilysia*, there seems to be no evidence that the ancestors of madtsoiids were ever specialized for fossorial habits (Scanlon and Lee 2000). Phylogenetic analyses indicate that Madtsoiidae is one of the most basal lineages of terrestrial

(non-aquatic) snakes, and their morphology may help to illuminate the implied transition from aquatic to terrestrial habits.

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Appendix 1

Material examined

***Wonambi naracoortensis* Smith, 1976.**—Victoria Fossil Cave, Naracoorte, South Australia (VF). Single vertebra per registration unless stated otherwise: SAM P16168 (holotype); SAM P16129t, P16144k, P16166, P16167, P16170a, P16170b (paratypes); SAM P25554 (3 vertebrae, 2 of them fused), P27486, P32505, P28869 (1 vertebra and 1 rib head), P25555, P25581, P25681 (2 vertebrae), P25582, P28375, P25579 (3 vertebrae), P27735, P25672, P25674, P28070, P27763, P25673, P27575; FU1589, FU1463, FU1572. Rib fragments: SAM P28868 (2), P27487 (1), P27488 (1). Cranial elements: SAM P16170c (anterior fragment of right dentary), SAM P16172 (partial right maxilla), SAM P27777 (parietal), FU1762 (posterior fragment of left maxilla).

Henschke's Quarry Fossil Cave, Naracoorte, South Australia (HQ). SAM P30178A (= HJD2: 84Wi, partial skeleton including numerous vertebrae and ribs, upper and lower jaw elements, ectopterygoid, parabasisphenoid, basioccipital, left prootic, both exoccipitals, and two unconnected pieces of parietal), SAM P30178B (= HJD1: 83Wi, smaller partial skeleton including numerous vertebrae, ribs, a complete right maxilla, and fragment of pterygoid); additional axial elements not referred to one or other skeleton are assigned to P30178, without suffix.

Corra-Lynn Cave, Curramulka, South Australia (CL). Single vertebra per registration unless stated otherwise: SAM P26528 (2 good verts, 6 fragmentary, 3 rib heads), P26534, P26535 (vertebra figured by Pledge 1992), P29879–88, P29890, P29896 (rib), P29910, P29911, P29912 (rib), P29952, P29953, P31785 (suborbital portion of left maxilla), P31786, P31801 (anterior portion of right pterygoid), unreg. (approx 20 fragmentary verts, 1 rib).

Curramulka Quarry, South Australia (CQ: fissure fill RF95, collected by J.A. McNamara 5/5/97; date probably Pleistocene based on associated *Thylacoleo* cf. *carnifex* and a suite of *Sthenurus* spp., no taxa suggesting admixture of Curramulka Fauna Pliocene or Late Pleistocene–Holocene elements; James McNamara, personal communication 2002). SAM P40158, anterior portion of right maxilla and numerous badly worn vertebral fragments.

Wellington Caves, New South Wales. Vertebrae: AMS F72999, F92050; 2 additional vertebrae collected by the author in 1995.

***Wonambi barriei* Scanlon in Scanlon and Lee, 2000** (cranial material only).—Riversleigh, Queensland (Early Miocene). Partial left maxilla QM F40193 (WW Site). Other material all from CS Site: right and left pterygoid fragments F23047, F23048; right and left palatines F40190, F40191 (attribution to *Wonambi* uncertain); articular and prearticular region of left compound bone F23077, F23078; anterior part of right dentary (with 7 alveoli and 2 mental foramina) AR 12467. [A partial right maxilla listed by Scanlon and Lee 2000, F39932 from CS, appears too large to be consistent with the same taxon.]

***Nanowana godthelpi* Scanlon, 1997 and *N. schrenki* Scanlon, 1997.**—See material listed in original description).

***Yurlunggur* (unnamed spp.)**.—Riversleigh, Queensland (Late Oligocene–Middle Miocene). Maxillary fragments QM F23046, F23049, F23050, F39330 (CS); palatines AR 11054 (WW), AR 10684 (CS), AR 12192 (Upper); pterygoids QM F51378 (WH), F51379 (CS); ectopterygoid F19740 (WW); sphenoid F23041 (MM); braincase F45111 (Hiatus A); partial dentaries F36441 (RV), AR 10589, AR 10779, AR 12467, QM F23057 (CS), F23064, F51380 (Upper), F51381 (Gag), F23074 (BB); articular region of compound F23066 (BSE). Additional material of associated partial skeletons from Hiatus A and CS sites under preparation at UNSW and Riversleigh Fossil Centre: QM F numbers not yet assigned.

Other squamate taxa mentioned

***Dinilysia patagonica* Woodward, 1901.**—Cast of holotype skull examined at Université Pierre et Marie Curie, Paris, courtesy of J.-C. Rage.

***Cylindrophis ruffus* (Laurenti, 1768).**—SAM R 36779, skull.

Pythonidae.—Material listed by Scanlon (2001), and fossils prepared and under study at Riversleigh Fossil Centre.

***Varanus varius* (White, 1790).**—Several partial to complete skeletons (AR 5378 and uncatalogued).

***Varanus acanthurus* Boulenger, 1885.**—Two complete skeletons (AR).