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AUSTRALIA'S OLDEST KNOWN SNAKES: *PATAGONIOPHIS*, *ALAMITOPHIS*, AND CF. *MADTSOIA* (SQUAMATA: MADTSOIIDAE) FROM THE EOCENE OF QUEENSLAND

JOHN D. SCANLON

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Small madtsoiid snakes referred to *Patagoniophis* and *Alamitophis* are represented by specimens of all major regions of the vertebral column from the Tingamarra Local Fauna (Early Eocene; Murgon, Queensland, Australia), and are diagnosed as distinct from members of the same genera from the Late Cretaceous (Campanian - ?Maastrichtian) of Patagonia, Argentina. The Tingamarra deposit has also produced ribs and dentary bones of two distinct morphotypes, which are provisionally assigned to the same two taxa. A single rib fragment represents a larger form comparable to South American *Madtsoia* spp., although not positively identifiable as a madtsoiid. It is inferred that two (and probably three) madtsoiid lineages had Antarctic-spanning distributions during the Late Cretaceous and/or Paleocene, with implications for their biology and that of their Neogene and Quaternary descendants. ❒ *Ophidia, Madtsoiidae, Patagoniophis australiensis sp. nov., Alamitophis tingamarra sp. nov., vertebrae, mandible, historical biogeography.*

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The oldest snakes known from Australia occur in the Tingamarra Local Fauna, recovered from the Early Eocene (Ypresian, Godthelp et al., 1992; Scanlon, 1993) Boat Mountain deposit, near Murgon in SE Queensland (26°S, 152°E). The fauna also includes earliest known remains of marsupial and placental mammals (including bats) from Australia, birds (including the world's oldest passerines), trionychid turtles, mekosuchine crocodiles, frogs, lungfish, and teleosts (Godthelp et al., 1992, 1999; Tyler & Godthelp, 1993; Archer et al., 1993; Willis et al. 1993; Boles et al. 1994; Hand et al., 1994; Salisbury & Willis, 1996; Boles 1995, 1997, 1999; White, 2001). Scanlon (1993) reported isolated but well-preserved vertebrae represent two snake taxa, small members of the extinct family Madtsoiidae similar to (respectively) *Patagoniophis parvus* and *Alamitophis argentinus*, from the Late Cretaceous of Patagonia, Argentina (Albino, 1986).

Differences from the Patagonian type material previously appeared consistent with intracolumnar and individual variation within each taxon, so that recognition of new species was not justified at the time. Another species of *Alamitophis* has subsequently been described from Patagonia (*A. elongatus* Albino, 1994), additional diagnostic material has been identified from Tingamarra (Scanlon, 1996, and this work), and other species of small madtsoiids have been described from younger Australian deposits (*Nanowana* spp., Scanlon, 1997). A full taxonomic treatment of the Tingamarra snake material is therefore now warranted.

MATERIALS AND METHODS

All fossil specimens described here are from the MP1 horizon in the sequence of lacustrine clays exposed at Tingamarra, Boat Mountain, near Murgon, south-east Queensland (possibly a member of the Oakdale Sandstone Formation, see Salisbury & Willis, 1996), and were collected by Henk Godthelp, Michael Archer, volunteers, and students from the School of Biological Sciences, University of New South Wales, Sydney, in the mid-1980's to early 1990's. The age of 54.6 Ma was obtained by K/Ar on authigenic illites (Godthelp et al., 1992), and this early Eocene date is corroborated by the stage of evolution of the fauna (Hand et al., 1994; Boles, 1999; Godthelp et al., 1999: 293; contra the opinion of Woodburne & Case, 1996, based on a single doubtfully interpreted mammal tooth).

Small specimens, including all snake material, were obtained by wet-sieving, initial reduction of clay sediments being carried out in the field and the remainder by Syp Praesouthsouk and Anna Gillespie in the Vertebrate Palaeontology Laboratory, School of Biological Sciences, University of New South Wales. Specimens were drawn using a binocular microscope and camera lucida, and measured using a Wild MM235 digital length-measuring set. Scanning electron micrographs were made at Westfield Hospital, Sydney, with the assistance of Coral Gilkeson (Westmead Dental Clinic) and Jeanette Muirhead (UNSW School of Biological Sciences). Specimens with QMF prefix are deposited in the Queensland Museum, Brisbane.

All Murgon snake remains are disarticulated and no association among elements can be demonstrated, so identification of some elements is indirect, based on relative frequency and size of morphotypes; such specimens are listed as 'referred' rather than type material. All vertebrae from the Murgon deposit complete enough for comparison are consistent with adult rather than juvenile snakes, and all are either trunk vertebrae (with paradiapophyses for rib articulation; posterior to the axis, anterior to the cloacal series) or caudals (postcloacal vertebrae bearing fixed, unforked pleurapophyses). Descriptive terminology and criteria for inferring ontogenetic stage and intracolumnar position of snake vertebrae are discussed in numerous works including Simpson (1933), Auffenberg (1963), Hoffstetter & Gasc (1969), Rage (1984), Szyndlar (1984), and LaDuke (1991); serial variation has also been studied by the author in associated partial skeletons of Australian madtsoiids (Scanlon, 1992, 1996, 1997; Scanlon & Lee, 2000; and unpublished data) as well as other extant and fossil squamates (Scanlon, 2001; Scanlon & Mackness, 2002; Lee & Scanlon, 2002; Scanlon et al., 2003). In the absence of a shoulder girdle, the posterior limit of the neck of snakes is indefinite and its extent therefore contentious, but this does not justify restriction of the term 'cervical' to just the atlas and axis, or the atlas alone (LaDuke, 1991: 5; Caldwell, 2000: 731-2; see also Cohn & Tickle, 1999: Fig. 1; Polly et al., 2001). Tooth or alveolar positions are referred to using cardinal or ordinal numerals, counting from the anterior (mesial) end of the tooth row on the element concerned. Categorical ranks are not used for taxa above that of genus.

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1811

OPHIDIA Brongniart, 1800

Family MADTSOIIDAE Hoffstetter, 1961

DIAGNOSIS (modified from Rage, 1998). 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.

REMARKS. Whereas Serpentes Linnaeus, 1758 comprises Scolecophidia and Alethinophidia and includes all extant snakes, Scanlon & Lee (2000; see also Lee & Scanlon, 2002; Scanlon, 2003) presented evidence that Madtsoiidae lies outside this clade but within the more broadly defined Ophidia (sensu Lee, 1998). Taxa included in Madtsoiidae, all extinct, are listed by Rage (1998) and Rage & Werner (1999). While few of the included taxa are known from cranial remains, monophyly of this group is here accepted provisionally on the basis of vertebral characters (Scanlon, 1992; Rage, 1998), although paraphyly with respect to modern snakes cannot be ruled out (Scanlon, 2003).

Presence of haemal keels throughout the middle and posterior trunk is shared with most snakes, but derived relative to other squamates; absence of posterior hypapophyses is plesiomorphic (cf. Underwood, 1967; Hoffstetter, 1968).

Laterally paired projections of the haemal keel are variable in form and not represented in all described madtsoiids, but not reported in any other snakes and hence a distinctive apomorphy of some or all of this group (Scanlon, 1992; Albino, 1996); the term 'paired hypapophyses' (Simpson, 1933) is taken simply to mean 'paired inferior processes' of the haemal keel and does not imply (serial) homology with 'true' median hypapophyses, since both kinds of structures occur together on some vertebrae.

Presence of parazygantral foramina is usually considered autapomorphic for Madtsoiidae, but they are also present in *Simoliophis* (Hoffstetter, 1955: fig. 22), some palaeophiid-like aquatic lineages such as *Tuscahomaophis* (Holman & Case, 1992), and some Colubroidea (e.g. hydrophiine elapids; Scanlon et al., 2003). Some vertebrae referred to *Madtsoia* sp. (e.g. Albino, 1986) and most vertebrae of large Australian madtsoiids (*Wonambi naracoortensis* Smith, 1976, and *Yurlunggur* spp.; Scanlon, 1992, 1996) have the parazygantral foramina divided into two or three on each side, rather than the single foramen usual or constant in non-Australian and small Australian taxa, but (contrary to Rieppel et al., 2002) there is no longer any reason to doubt the structures are homologous across the group (as did Rage, 1984, 1987; but not Rage, 1998).

Lack of prezygapophyseal processes is considered plesiomorphic, as they are absent in limbed terrestrial squamates, marine varanoids, and a number of early fossil snakes (*Simoliophis*, *Pachyrhachis*, *Eupodophis*, *Haasiophis*, *Lapparentophis*, *Pouitella*, and unnamed forms of similar grades; Hoffstetter, 1959; Rage, 1988; Cuny et al., 1990; Lee & Caldwell, 1998; Rage & Escuillié, 2000, 2002; Rieppel et al., 2003), while slightly developed in *Dinilysia* (Hecht, 1982; Rage & Albino, 1989) and generally present in Scolecophidia and Alethinophidia (secondarily absent in some Boinae; Underwood, 1976).

Occurrence of paracotylar foramina is variable among varanoid lizards (e.g. present in some *Varanus* and *Megalania*, pers. obs.) and within *Dinilysia* (Rage & Albino, 1989) and Alethinophidia (Hoffstetter & Gasc, 1969; Underwood, 1976), as well as among early fossil snake lineages, so polarity is uncertain.

Unlike most vertebrae of modern snakes, in madtsoiids the surfaces for rib articulation (paradiapophyses, or synapophyses) are borne on more or less distinctly projecting transverse processes. Having the diapophyses extending as far as or further laterally than the zygapophyses in middle and posterior trunk vertebrae is more plesiomorphic (more similar to limbed varanoids and the early fossil snakes mentioned above) than Scolecophidia and Alethinophidia (McDowell, 1987); however, the relative width of these processes varies considerably among madtsoiids, and the extreme seen in South American *Madtsoia* spp. (Simpson, 1933; Rage, 1998) is probably apomorphic.

A median anterior indentation of the zygosphene is present in most madtsoiids and presumed to be plesiomorphic (shared with the early fossil snake taxa listed above, and approaching the deeply notched condition of the zygosphene where present in lizards), but replaced by a straight margin or median prominence (as in most Scolecophidia and Alethinophidia) in some small madtsoiids (Scanlon, 1993, 1997; Albino 1994, 1996; Rage, 1996), and hence this character is omitted from the diagnosis. Presence of true chevrons on caudal vertebrae has been observed directly only in *Wonambi naracoortensis* (Scanlon & Lee, 2000), so this plesiomorphic feature is also omitted from the diagnosis although varanid-like pedicels for articulation of (probable) chevrons are known in several other madtsoiid taxa (e.g. *Alamitophis*, see below). All modern snakes (Serpentes) have caudal haemal arches modified or absent, not forming chevrons or articulated to the centrum (Hoffstetter & Gasc, 1969; Lee & Scanlon, 2002: characters 204-206).

Patagoniophis Albino, 1986

TYPE SPECIES. *Patagoniophis parvus* Albino, 1986.

DIAGNOSIS (modified from Albino, 1986, 1987; Scanlon, 1993). Very small madtsoiids (vertebrae usually less than 5mm wide), centrum relatively long and narrow. Neural spine low, long and thin, neural arch low, zygosphene shallow. Haemal keel in middle and posterior trunk defined laterally by distinct but shallow grooves.

The smallest known madtsoiids, somewhat smaller than species of *Alamitophis*, *Nanowana*, and *Herensugea*, and much smaller than the remaining taxa. Further distinguished from all except *Herensugea caristiorum* by the low neural spine, and lack of several probable apomorphies of the latter species: in *Patagoniophis* the zygapophyses are inclined above horizontal, zygosphene concave anteriorly, subcentral grooves shallow, neural arch smooth dorsally or with only faint bulges flanking the neural spine.

Patagoniophis australiensis sp. nov.

(Figs 1-3, 4A-B, 5)

Patagoniophis sp. cf. *P. parvus* Albino, 1986: Scanlon, 1993: p. 4-5, Figs 1, 3A

DIAGNOSIS. Distinguished from *P. parvus* by the subcentral ridges being strongly concave behind the transverse processes in ventral view, becoming approximately parallel on the posterior part of the vertebra, rather than straight or weakly curved throughout; more depressed neural arch; broader, less strongly arched zygosphene; and smaller size.

MATERIAL. HOLOTYPE: QMF19710 (Fig. 1E), a mid-trunk vertebra from MP1 horizon, Main Quarry, Tingamarra, Boat Mountain, near Murgon, south-east Queensland. PARATYPES: Anterior trunk vertebrae: QMF19023 (Figs 1C, 2A),QMF19711-16, QMF23892; middle trunk vertebrae: QMF19717 (Figs 1D, 2B), QMF19718-20, QMF24395, QMF24468, QMF24471, QMF24749; posterior trunk vertebrae: QMF19027 (Fig.

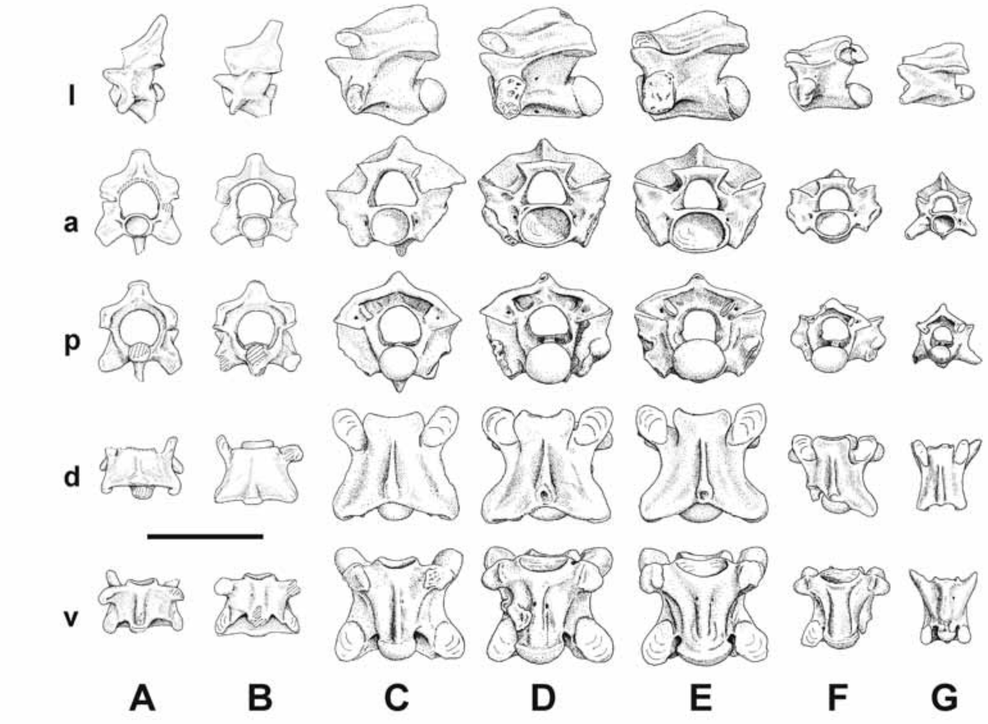

FIG. 1. Type and referred vertebrae of *Patagoniophis australiensis* sp. nov. from the Tingamarra Local Fauna, Murgon, Queensland. A (QMF22806), B (QMF20240), likely 3rd and 4th cervical vertebrae; C (QMF19023), anterior trunk; D (QMF19717), middle trunk; E (QMF19710), middle to posterior trunk, holotype; F (F19027), posterior trunk; G (QMF19024), mid-caudal. l, lateral; a, anterior; p, posterior; d, dorsal; v, ventral views. Scale bar = 3 mm. Photographically reduced copies of C-G were previously published in Scanlon (1993: fig. 1).

1F), QMF19030, QMF19721-26 (Fig. 3), QMF24391, QMF24393-94, QMF24576, QMF24754; caudal vertebrae: QMF19024 (Fig. 1G), QMF19727-28, QMF24252, QMF24575a. REFERRED MATERIAL: Based on relative abundance and size, the following specimens are referred provisionally to the same species: anteriormost trunk ('cervical') vertebrae F19716, F20240 (Fig. 1B), F22806 (Fig. 1A); ribs F19032 (Fig. 4A), F20824, F23285, F23894, F24464 (Fig. 4B), F24465, F24466, F24575b, F24750; dentary F29617 (Fig. 5). It is likely that the available fossils (type and referred) are derived from the remains of several adult individuals. Most of the specimens are fragmentary, and there are numerous additional pieces probably of the same form, but too incomplete to distinguish taxonomically at this stage.

AGE. Tingamarra Local Fauna, Early Eocene, 54.6 +/- 0.05 MYBP (Godthelp et al., 1992).

ETYMOLOGY. Neo-Latin, 'from Australia'.

DESCRIPTION OF HOLOTYPE. A mid-trunk vertebra, intact except that the articular surfaces of the paradiapophyses are slightly worn, the lateral margin of the left postzygapophysis is chipped, and the dorsoposterior extremity of the neural spine (possibly a separate ossification) is missing. The centrum and transverse processes are relatively massive, the neural arch broad (slightly wider than long across the zygapophyses) but shallow, and the neural spine very low (contributing barely 10 percent of the total height of the vertebra).

Prezygapophyseal facets are trapezoidal (lozenge-shaped), postzygapophyseal facets obovate, both with long axes at about 30-40° from the sagittal plane; the zygapophyses are moderately steeply inclined (approximately 25° from horizontal) and elevated, defining planes that pass above the internal lateral ridges of the neural canal, and intersect above the floor of the canal. Interzygapophyseal ridges are well developed, and smoothly concave laterally. The

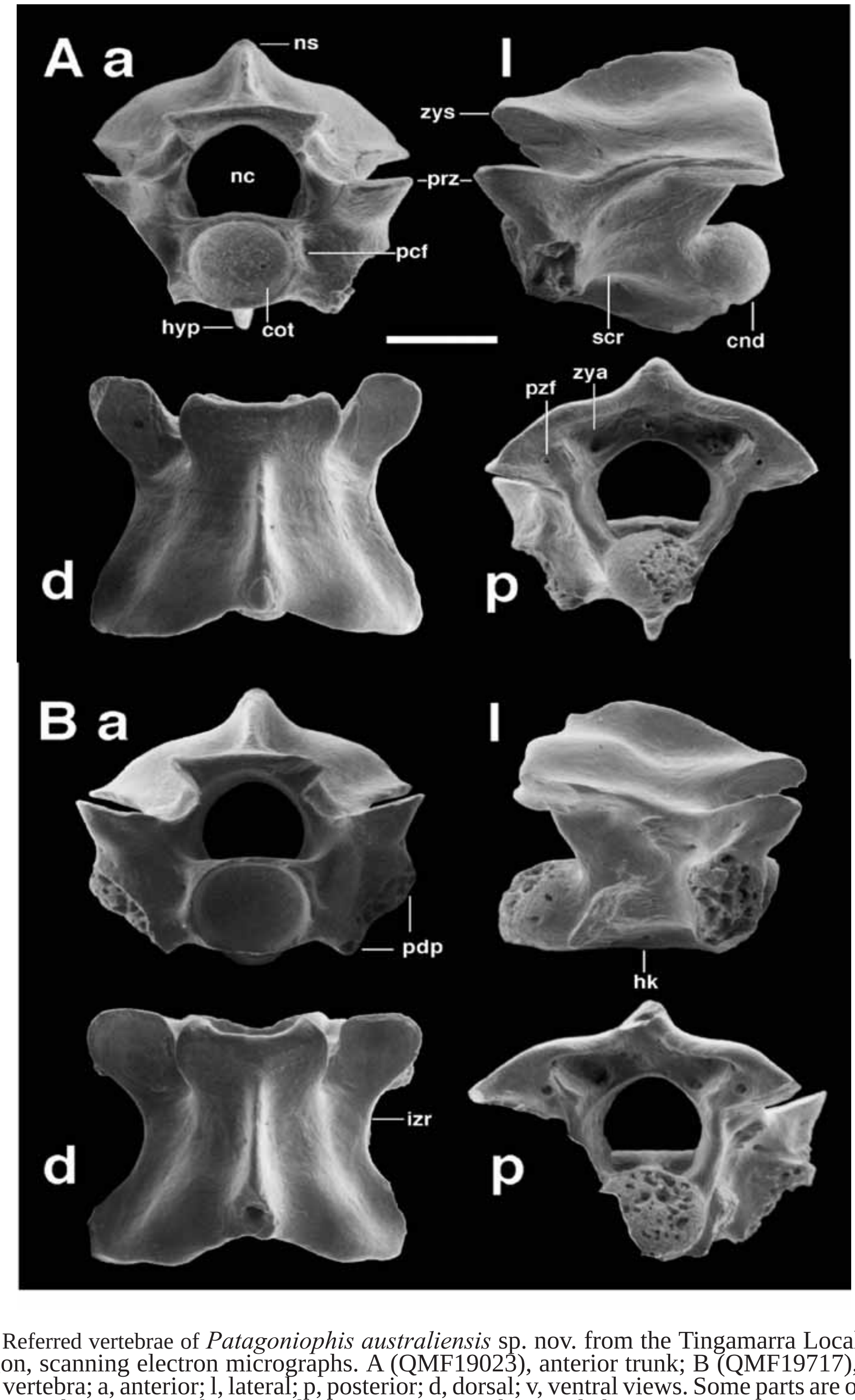

FIG. 2. Referred vertebrae of *Patagoniophis australiensis* sp. nov. from the Tingamarra Local Fauna, Murgon, scanning electron micrographs. A (QMF19023), anterior trunk; B (QMF19717), middle trunk vertebra; a, anterior; l, lateral; p, posterior; d, dorsal; v, ventral views. Some parts are obscured by mount; the same vertebrae are shown in Fig. 1C and D. Scale bar = 1mm.

condyle and cotyle are large, wider than high, and only weakly inclined, so that a considerable part of the condylar surface is visible from below. Neural canal arched in anterior view (appearing more square from behind), about as high as wide, and rather smaller than cotyle.

Zygosphene not overhanging preygapophyseal facets but wider than cotyle, and much wider than deep, with lateral facets more than 30° from vertical. The zygosphene is very weakly arched in anterior view, its shallow anterior face weakly demarcated from the interior of the neural canal, and concave for its full width in dorsal view. The zygantral roof is thin medially where it is interrupted (not overhung) by the posterior edge of the neural spine, and becomes slightly thicker laterally; in dorsal view the posterior margin of the neural arch forms a broad concavity, not demarcated laterally from the convex postzygapophyseal margins; the condyle is broadly exposed in dorsal view, but none of the neural canal floor. The parazygantral area on the rear of the neural arch is a narrow trapezoid bounded on its three longer sides by the postzygapophyseal and zygantral facets and neural arch roof, the ventromedial border short.

The neural spine commences anteriorly as a low, blunt ridge near the posterior limit of the zygosphene, and rises uniformly for about three-quarters of its length (just under 30° from horizontal); the posterior quarter slopes down posteriorly, and in dorsal view forms an oval expansion with a central cavity exposed by slight damage.

Subcentral ridges, distinct on the lateral side but not demarcated from the main ventral surface of the centrum, extend from the parapophyses to the base of the condylar ‘neck’, which is defined by a moderate constriction. The ridges are strongly concave laterally, narrowing fairly steeply just behind the transverse processes but nearly parallel on the posterior part of the centrum. The haemal keel is defined by slight depressions or (on the middle and posterior part of the centrum) shallow step-like grooves; the depressions diverge anteriorly, not reaching the rim of the cotyle but passing around it to the paracotylar depressions. Posteriorly the keel is weakly trilobed, with a faint outer pair of grooves defining a broad posterior expansion (equivalent of the ‘paired hypapophyses’, Simpson, 1933) onto which the low median keel extends. In lateral view the centrum is concave ventrally, and the posterior part of the keel projects very weakly below the level of the condyle.

The transverse processes are worn distally, but still extend nearly as far laterally as the zygapophyses, and are visible from above. The articular surfaces for the ribs are subrectangular and vertically aligned in lateral view, not distinctly subdivided into dia- and parapophysis, with only a weak concavity in the posterior margin; they are less than twice as wide as deep, and slightly deeper than the cotyle, extending beyond it dorsally but not ventrally. The diapophyseal surface is partly preserved on the right, extending broadly onto the posterior aspect of the process. The cranial and caudal margins of the articular surfaces are posterior to those of the zygosphenal facet, and much of the cotylar rim is visible laterally.

Paired subcentral, paracotylar, and parazygantral foramina present, all about the same size; lateral foramina smaller.

Measurements (mm). length from prezygapophysis to postzygapophysis (ppl) 2.94, width across prezygapophyses (pzw) 3.21, width across paradiapophyses (pdw; slightly worn) 3.09, width across postzygapophyses (ptw) 3.13, minimum width of neural arch (naw) 2.04, width of zygosphene (zsw) 1.45, width of zygantrum (zaw) 1.61, width of condyle (cnw) 1.34, height of condyle (cnh; maximum oblique measurement) 1.03, width of cotyle (ctw) 1.36, height of cotyle (cth) 1.12, centrum midline length (cml; cotyle to condyle rim on ventral surface) 2.07, height of neural canal (nch) 0.76, width of neural canal (ncw) 0.81, maximum distance across neural spine and condyle (nsc) 2.79, maximum distance across neural spine and haemal keel (nsh) 2.82, thickness of zygosphene (zyh) 0.30, depth from zygosphene to cotyle (zct) 2.19, length of paradiapophyseal articular facet (pdpl; worn) 1.22, anteroposterior width of paradiapophyseal articular facet (pdpw) 0.75, width between ventral (inner) margins of paradiapophyseal articular facets (piw) 1.82.

Other vertebrae and serial variation. Several vertebrae are known from the region immediately posterior to the axis (Fig. 1A, B), here considered cervicals. The figured specimens may be the third and fourth vertebra of a single individual, as they have regional features comparable to the third cervical vertebra of *Yurlunggur camfieldensis* Scanlon, 1992 (‘No. 1’, fig. 1A in that work), and an anterior cervical referred to *Yurlunggur* sp. from Riversleigh

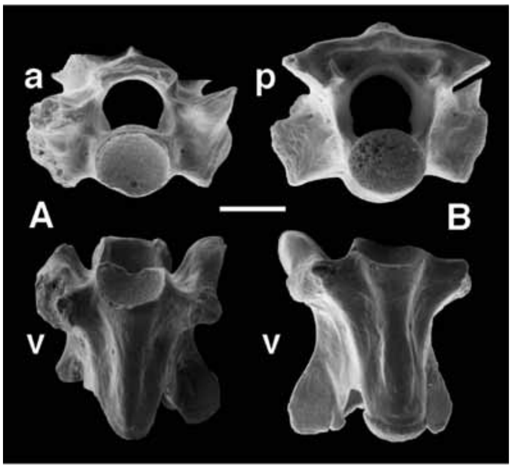

FIG. 3. Referred posterior trunk vertebrae of *Patagoniophis australiensis* sp. nov. from the Tingamarra Local Fauna, Murgon, scanning electron micrographs. Specimens shown in A and B come from the series QMF19721-19726 with the same data, but individual registrations are uncertain. a, anterior; p, posterior; v, ventral views. Scale bar = 1mm.

(QMF23036; Scanlon, 1996). QMF19716 (not figured, consisting of the centrum with both paradiapophyses, but lacking the condyle, hypapophysis and most of the neural arch) has relatively larger cotyle and larger but less ventrally prominent paradiapophyses, so comes from a slightly more posterior position than the other two.

The zygapophyseal articular surfaces are almost horizontal in QMF22806 and QMF20240, well above the floor of the neural canal; in QMF19716 the remaining prezygapophyseal facet is steeper, but would still intersect the midline above the neural canal floor. The facets are narrowly subtriangular, with long axes almost parallel to the midline; the interzygapophyseal ridges are laterally concave but weakly defined. The transverse processes project posteriorly in QMF22806 but laterally in QMF20240; the articular facets, weakly subdivided into diapophysis and parapophysis, are inclined at about 45° in lateral view, face ventrally as much as laterally, and are broadly exposed posteriorly. The cotyle is slightly wider than high. The neural canal is approximately the same absolute size in all three vertebrae, much larger than the cotyle and approximately circular except that distinct internal lateral ridges define small ventrolateral lobes. The centrum in ventral view is wider than long; subcentral ridges are barely defined. The haemal keel begins just behind the cotylar rim, immediately forming a steep but ventrally concave anterior edge of the hypapopysis. The depth of the hypapophysis is considerably more than that of the condyle, but incomplete in all these specimens; the remaining section of the posterior edge is almost vertical in both more complete specimens, and the broken distal surface shows dense bone pierced by small channels (anteroposteriorly double in QMF19716). The zygosphene (preserved only in QMF20240) is formed by a slight thickening of the anterior edge of the neural canal roof, with facets barely defined; it is strongly arched, with the anterior margin straight in dorsal view. The neural arch and spine are similar in both more complete specimens, with concavities above and below the level of the zygosphene, the lateral ones being rather small. The posterior edge lacks a distinct median emargination in dorsal view, and its lateral portions are vertical or slightly overhung, forming dorsolateral processes which are rounded in QMF22806 but more angular in the larger QMF20240. The neural spine begins just posterior to the zygosphene as a narrow ridge, concave above; it is thin anteriorly, becoming broad posteriorly, with an antero-posteriorly short, triangular dorsal expansion that faces slightly posteriorly. The zygantral facets are hardly defined. Small subcentral, lateral, paracotylar, parazygantral and zygantral foramina are present at least unilaterally (some obscured by matrix remaining in hollows).

Until both intracolumnar and ontogenetic variation are more fully known, the taxonomic identification of these cervical vertebrae is uncertain, but several factors make it more probable that they belong to *Patagoniophis* rather than *Alamitophis*. One is the relative frequency of trunk vertebrae of the two taxa; vertebrae of *Patagoniophis* are several times more abundant than those of the other form. As both of the more complete cervicals are similar enough to belong to the same taxon, it is thus more likely to be the more abundant of the two (the slightly larger fragment seems likely to be of the same taxon as the others, but is too incomplete to identify). Moreover, the characters used to distinguish trunk vertebrae can also be applied here: the zygantral roof become thicker (not thinner) laterally; the postzygapophyses are not distinguished by an angular concavity from the interzygapophyseal ridge; the diapophyses do not extend anteriorly beyond the cotylar rim; the zygosphene lacks a median anterior prominence; the neural spine widens sharply posteriorly; the subcentral depressions do not extend forward to the cotylar rim. These morphological features are consistent with those of *Patagoniophis*, being the lack of (mostly autapomorphic) characters of *Alamitophis*. However, some or all of these could be expected to be reduced in the extreme anterior region of *Alamitophis*, so that a definite identification cannot be made until vertebrae from this region are known from both taxa.

The neural spine is both relatively and absolutely higher in these specimens than in more posterior vertebrae of *Patagoniophis*. However, it is common in snakes for vertebrae in the most anterior trunk to have a relatively high neural spine (e.g. pythonines, erycines, many colubroids; Hoffstetter & Rage, 1972; Rage, 1972; LaDuke, 1991; *Wonambi naracoortensis*, Barrie, 1990), although in some madtsoiids the opposite is the case (*Yurlunggur camfieldensis* Scanlon, 1992).

Some other aspects of intracolumnar variation were reported previously (Scanlon, 1993). The virtues of basing taxonomic comparisons on ‘posterior trunk’ vertebrae are that they are the most numerous in the skeleton, hence the most likely to be represented in a small sample of isolated bones (Simpson, 1933), and also that the form of the haemal keel in this region (e.g. presence of hypapophyses) provides useful taxonomic information in extant groups, as has long been recognised. The vertebra selected as the holotype is from the region transitional between anterior trunk sensu lato (with single narrow haemal keels and/or hypapophyses) and posterior trunk (in this taxon, with broader, flatter keels defined laterally by distinct grooves). Such a transitional region with more or less trilobed haemal keels is now represented in a number of madtsoiid taxa (including *Wonambi* spp., *Yurlunggur* spp., and *Nanowana godthelpi*; Scanlon, 1992, 1996, 1997; Scanlon & Lee, 2000); this should be useful for comparisons between these taxa, as the transition occurs close to the position of maximum vertebral size and identifies a relatively precise region (cf. LaDuke, 1991: 6), in contrast to ‘posterior trunk’ which encompasses wide variation in size and shape within a single skeleton.

Ribs. As described previously (Scanlon, 1993), two distinct kinds of rib heads are represented by multiple specimens (Fig. 4A-D). No ribs have been identified from any small South American madtsoiids (A. Albino, pers. comm.), so the best we can do is state that the more abundant rib type (e.g. QMF19032, Fig. 4A) is likely to represent the same taxon as the more abundant vertebrae, i.e. *Patagoniophis australiensis* sp. nov.

The proximal articulating surface in this form is roughly similar in shape to those of *Wonambi naracoortensis* and *Yurlunggur* spp., but it differs in several details. The rib head is elongate dorsoventrally in proximal view, about three times as high as wide, including the dorsomedial process here called the ‘tuber costae’ (without implying homology with structures in taxa other than snakes). The medial edge is slightly sinuous (concave dorsally and convex ventrally), formed by a ridge bounding the articulating surface and prolonged dorsally onto the tuber costae. The lateral edge forms two subequal rounded lobes corresponding to the concave diapophyseal and saddle-shaped parapophyseal surfaces. The tuber costae forms about one third of the total height and is trapezoidal in shape, slightly more than half the width of the rib head at its base, with straight lateral and medial margins tapering to a squarish tip, still more than a third of the total width. The overall outline thus resembles an inverted Greek letter β with a thick stem.

The rib shaft is oval in cross-section distally, joining the head smoothly so that ridges and hollows in the proximal part of the shaft correspond to convexities and concavities in the margin of the articulating surface. A foramen is present on the lateral face of the shaft, on the ridge corresponding to the broadest part of the diapophyseal facet.

The rounded, subequal lateral lobes recall the ‘waisted’ 8-shape typical of alethinophidian taxa examined, which is approached more closely in *Madtsoia camposi* Rage, 1998 and in one Murgon specimen described below. The length of the tuber costae (as measured from either the concavity of the lateral edge, or the slightly more dorsal boundary of the concave articular surface) seems to be unique among known madtsoiids. However, its orientation (only slightly deflected medially from the long axis of the articulating surface) is similar to that in *Wonambi* and *Yurlunggur* (Scanlon, 1996), differing from *Madtsoia bai* Simpson, 1933 and *M. camposi*, as well as most alethinophidians, where it is distinctly angled. As in other madtsoiids (Simpson, 1933; Scanlon, 1996; Rage, 1998), the tuber costae is relatively broader and less sharply defined from the articular surface than in any

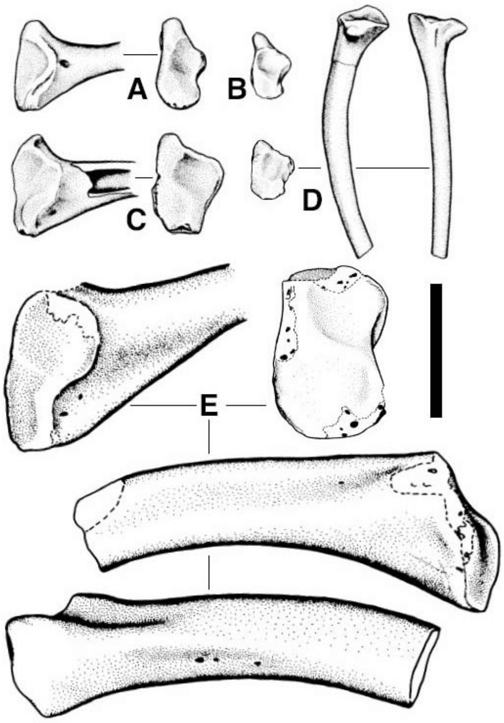

FIG. 4. Rib-heads of snakes from the Tingamarra Local Fauna (ribs from left side of body except A and E, which are reversed for ease of comparison). A (QMF19032) and B (QMF24464) referred to *Patagoniophis australiensis* sp. nov.; C (QMF19033) and D (QMF23898) referred to *Alamitophis tingamarra* sp. nov.; E (QM F52167), ?Madtsoiidae indet., cf. *Madtsoia* sp. Shown in anterolateral (A,C,E), proximal (A-E), dorsal (D, centre), lateral (D, far right), dorsoposterior and ventral (E, lower two figures) views. Scale bar = 3 mm. Specimens in A and C previously figured in Scanlon (1993: fig. 3), redrawn.

modern snakes compared (Alethinophidia and Scolecophidia).

Dentary. The two dentaries known from the deposit (Figs 5, 8) are similar to each other in most comparable respects, but have several differences that suggest they represent distinct taxa. Both resemble *Nanowana godthelpi* Scanlon, 1997 in the absence of ankylosed teeth from most alveoli, enlargement pattern of alveoli, relative size and shape of mental foramina, and presence of a distinct smooth 'bulb' on the anteromedial tip. Absence of teeth in these specimens is attributable to post-mortem wear, in contrast to *N. godthelpi* where they are also absent in unworn specimens, implying the presence of fibrous attachment (probably 'hinges', i.e. arthrodont dentition) rather than ankylosis (Scanlon, 1997). Differences between the Murgon specimens include size, position of first alveolus relative to anterior tip, degree of disparity in alveolar diameter, and detailed form of the crests defining the meckelian groove. As available vertebral material indicates that *Patagoniophis* is generally somewhat smaller than *Alamitophis*, the jaw fragments are provisionally referred to the two taxa on the basis of relative size (see Discussion).

QMF29617 (Fig. 5) is the anterior portion of a left dentary, broken posteriorly through the 11th alveolus; total length 5.71 mm, length from anterior tip to rear of 6th alveolus 3.13, maximum depth (at 6th) 1.52, max. alveolar width 0.51, lateral edge to dorsal margin of meckelian groove 1.03. There do not appear to be traces of ankylosed teeth in any except the 11th alveolus, which retains the stump of a tooth. Alveolar diameter varies little along the preserved part of the jaw (but the 6th is apparently the largest), and the row is only slightly (but sinuously) curved; the anteromedial extremity is prominent (similar to the 'bulb' in some Riversleigh taxa, but more dorsoventrally flattened), with nearly enough space for an additional alveolus anterior to the first. In lateral view, the dorsal edge can be viewed as horizontal (i.e. the alveolar margins lie approximately within a plane). There are three mental foramina, level with alveoli 3-4, 5-6, and 8; the third is smaller than the other two. The meckelian groove is open ventromedially, constricted anteriorly by incurved crests, but widens posterior to the fifth alveolus. Its dorsal edge is continuous anteriorly with the ventral edge of the bulb, and strongly overhung (hence sharply defined in medial view) for its full length, but somewhat concave and 'bevelled' at the level of the 8th alveolus (ventral view). The ventromedial edge (forming a lower 'lip' for the groove, thinnest from the third to fifth alveolus) is damaged posterior to the 7th alveolus, but intact more anteriorly; it differs from other madtsoiids in being steeply inclined, projecting ventrally rather than medially, so that the meckelian groove is open in ventral view. This resembles the common and apparently primitive condition in lizards (cf. Lee, 1998, character 115), so could be considered a reversal.

QMF29617 probably had at least 15 alveoli (and possibly 17 or more), because the anterior edge of the lateral fossa is not visible, and is followed by 4 to 6 or more teeth in other madtsoiids where the dentary is known. It differs from species of *Nanowana* and *Yurlunggur* (but resembles *Wonambi* and *Madtsoia*) in the meckelian groove being sharply defined dorsally for its full length, without a smooth or 'soft' middle portion apparent in medial view.

Alamitophis Albino, 1986

TYPE SPECIES. *Alamitophis argentinus* Albino, 1986

REFERRED SPECIES. *Alamitophis elongatus* Albino, 1994

DIAGNOSIS (modified from Albino, 1986, 1987, 1994; Scanlon, 1993): small madtsoiids (vertebrae up to about 8mm wide), centrum relatively narrow. Haemal keel extends to cotylar rim anteriorly; in posterior trunk vertebrae, keel thick and delimited laterally by deep depressions. Zygapophyses weakly to strongly inclined from horizontal. Neural arch moderately elevated; neural spine moderately high, back-sloping, transversely thin (but not sharp-edged) anteriorly and thicker posteriorly. Zygosphene dorsoventrally thin, and not or only slightly wider than cotyle; zygantral roof thinning laterally in mid- and posterior trunk. Paradiapophyses of trunk vertebrae project anteriorly beyond rim of cotyle.

The relatively high neural arch and spine, narrow zygosphene, and form of the haemal keel distinguish *Alamitophis* from the other small madtsoiids (*Patagoniophis*, *Herensugea*, *Nanowana*); among larger forms, most have similar or higher neural arches or spines, but only *Wonambi* has such relatively narrow zygosphenes, and its haemal keels are also different (weakly defined laterally by shallow depressions). The distinct lateral thinning of the zygantral roof and relatively anterior position of the paradiapophyses appear to be unique to this genus.

Alamitophis tingamarra sp. nov.
(Figs 4C-D, 6-8)

Alamitophis sp. cf. *A. argentinus* Albino, 1986 (Scanlon, 1993: p. 5-6, figs 2, 3B)

DIAGNOSIS. Distinguished from *A. argentinus* (and species of most other madtsoiid genera) by smooth median prominence on the anterior border of the zygosphene (synapomorphy with *A. elongatus*); from *A. elongatus* by the less elongate centrum (lack of a probable autapomorphy of the latter species); and from both species by smaller size, and more weakly defined subcentral ridges (probable autapomorphies). The zygapophyses are only slightly angled above the horizontal (less than 10° in material examined), similar to most described *Alamitophis* material but differing from the holotype of *A. elongatus*, which has strongly inclined zygapophyses (Albino, 1994).

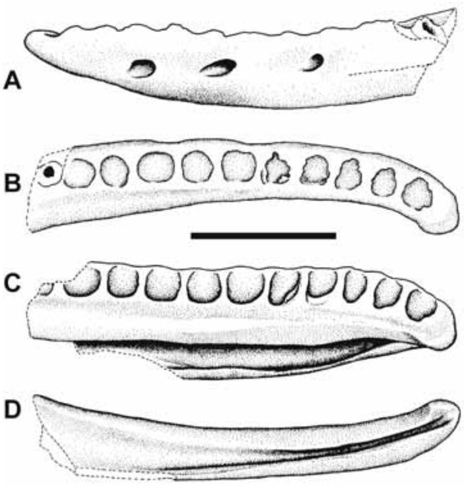

FIG. 5. Anterior portion of left dentary (QMF29617) from the Tingamarra Local Fauna, referred to *Patagoniophis australiensis* sp. nov. A, lateral, B, dorsal, C, dorsomedial, and D, ventral views. Scale bar = 2mm.

MATERIAL. HOLOTYPE: QMF19729 (Figs 6C, 7), a mid- to posterior trunk vertebra from MP1 horizon, Main Quarry, Tingamarra, Boat Mountain, near Murgon, south-east Queensland. PARATYPES: Anterior trunk vertebrae: QMF19735 (Fig. 6A); middle trunk vertebrae: QMF19029, QMF19730, QMF19731, QMF19734 (Fig. 6B); posterior trunk vertebra QMF20233; caudal vertebrae: QMF19732 (Fig. 6D), QMF19733. REFERRED MATERIAL: Ribs: QMF19026, QMF19033 (Fig. 4C, D), QMF20920, QMF23898; dentary: QMF23893 (Fig. 8).

AGE. Tingamarra Local Fauna, Early Eocene, 54.6 +/- 0.05 MYBP (Godthelp et al., 1992).

ETYMOLOGY. Referring to the Local Fauna and the property from which it was collected.

DESCRIPTION OF HOLOTYPE. A vertebra from the anterior part of the posterior trunk region, well preserved except that the articular surfaces of the paradiapophyses are worn, and the margin of the left postzygapophysis and right prezygapophysis are chipped. The centrum is massive, the transverse processes relatively small and in a low position, the neural arch broad (wider than long across the zygapophyses), vaulted, with a moderately high neural spine (contributing nearly 20 percent of the total height of the vertebra).

Prezygapophyseal facet (complete on left side) trapezoidal, postzygapophyseal facets obovate, both with long axes at about 30-40 from the sagittal plane; the zygapophyses are weakly inclined (less than 10 from horizontal) but moderately elevated, defining planes that pass through the weak internal lateral ridges of the neural canal, and intersect above the floor of the canal. Interzygapophyseal ridges are well developed, with slight angularities where they meet the zygapophyses. The condyle and cotyle are large, wider than high, and moderately inclined, so that a considerable part of the condylar surface is visible from below. Neural canal subtriangular in anterior view (appearing more square from behind), slightly wider than high, and rather smaller than cotyle.

Zygosphene not overhanging prezygapophyseal facets, slightly narrower than cotyle, width about twice depth of facets,which slope at about 30 from vertical. The roof of the zygosphene is horizontal in anterior view, the anterior face about half as deep in the midline as at the lateral facets, weakly demarcated from the interior of the neural canal; in dorsal view the anterior margin is trilobate, the rounded median projection slightly more prominent than the lateral lobes, and somewhat asymmetric. The zygantral roof is thickest medially where it is interrupted and overhung by the posterior edge of the neural spine, and becomes noticeably thinner laterally; in dorsal view the posterior margin of the neural arch forms a broad, rounded concavity for the width of the zygantrum, somewhat distinct from the (posteriorly sinuous) postzygapophyseal margins; the condyle is broadly exposed in dorsal view, about as far as its anterodorsal margin. The ventromedial margins of the parazygantral surfaces are about as long as the zygantral facets, and form fairly distinct, ventrally concave ridges.

The neural spine commences anteriorly as a blunt ridge near the anterior edge of the zygosphene, and rises for about three-quarters of its length (sigmoid with two angular inflections, and steepest in the middle part at aboout 45); the posterior quarter slopes down posteriorly, and in dorsal view forms a teardrop- or bottle-shaped expansion with a smooth, transversely convex surface.

Subcentral ridges, only indistinctly defined from the lateral and ventral surfaces of the centrum, extend from the parapophyses to the base of the condylar ‘neck’, which is defined by a moderate constriction. The ridges are weakly sinuous or arcuate, tapering almost uniformly but slightly convex laterally in the central part. The haemal keel is defined by deep depressions that diverge anteriorly, not reaching the rim of the cotyle but passing around it to the paracotylar depressions. Posteriorly the keel is very faintly trilobed, with a faint inner pair of grooves defining short, posteriorly divergent lateral branches from the median ridge. In lateral view the centrum is concave ventrally, and the posterior part of the keel projects slightly below the level of the condyle.

The small transverse processes are worn distally, and hidden in dorsal view by the prezygapophyses. The articular surfaces for the ribs face more ventrally than laterally, are subrectangular in lateral view, less than twice as wide as deep, and considerably less deep than the cotyle, level with it ventrally but extending barely above the level of its centre. The diapophyses extend posteriorly beyond the zygosphenal facets, while the parapophyses (weakly delimited by concavities in anterior and posterior margins) project anteriorly beyond the zygosphene. The diapophyseal articular surface is partly preserved on the left, extending broadly onto the posterior aspect of the process.

Paired subcentral, lateral, paracotylar, and parazygantral foramina present, the parazygantrals largest.

Measurements (mm; abbreviations defined above). ppl 2.86, pzw 3.38, pdw (worn) 2.98, ptw 3.31, naw 2.82, zsw 1.43, zaw 1.67, cnw 1.30, cnh 1.17, ctw 1.48, cth 1.26,cml 2.19, nch 0.78, ncw 0.97, nsc 3.42, nsh 3.32, zyh 0.27, zct 2.40, pdpl (worn) 1.00, pdpw 0.78, piw 1.64.

Other vertebrae and serial variation. The number of well-preserved vertebrae available is small, but anterior, middle and posterior trunk, and anterior caudal regions are represented.

The most anterior vertebra complete enough to identify as *Alamitophis* (QM F19735, Fig. 6A) has similar regional features to F19023 (*Patagoniophis*, Fig. 1C). The neural canal is wider than the cotyle, the zygosphene is arched, and the hypapophysis is prominent and narrow. The paradiapophyses do not project anteriorly to the extent seen in other vertebrae of this species.

Middle trunk features are seen in F19734 (Fig. 6B), the largest well-preserved vertebra known from the site. The zygosphene roof is slightly concave dorsally, the facets distinctly concave laterally. The haemal keel is narrow and extends slightly below the centrum for most of its length, but does not form a vertical anterior edge below the cotyle as in the *A. argentinus* holotype (Albino, 1986).

Holotype QMF19729 described above, previously reported as a middle trunk vertebra (Scanlon, 1993: fig. 2), is now considered 'posterior trunk' (or transitional) based on the anterior expansion of the haemal keel to almost the full width of the cotyle, in contrast to the anteriorly narrow keel seen in the largest mid-trunk vertebra. It also has the posterior part of the keel very weakly trifid, with faint lateral ridges not indicated in the drawings but shown in scanning electron micrographs (Fig. 7). As noted above for the holotype of *Patagoniophis australiensis* sp. nov., the development of lateral ridges on the median keel represents the transition between the single keel of the anterior trunk, and the posteriorly expanded, bifid keel characteristic of the posterior trunk in most madtsoiids (called 'paired hypapophyses' by Simpson, 1933, based on their prominent development in *Madtsoia bai*). No vertebrae of this taxon with broad or obviously bifid keel are known, but the sample of posterior trunk vertebrae remains small, and absence of more distinct paired hypapophyses can not be stated conclusively at this time.

Ribs. The less common type of rib (Fig. 4C, D) is provisonally referred to *Alamitophis* on the basis of relative abundance. The rib head is less than twice as high as wide in proximal view, the medial edge is convex rather than sinuous, the diapophyseal surface is much broader and more angular laterally than that for the parapophysis, and the tuber costae relatively small (less than a quarter of the total height, and about a third of the width). A foramen is present on the lateral face of the shaft, but more ventral in position, in the concavity below the diapophyseal ridge.

Dentary. QMF23893 (Fig. 8) is the anterior portion of a right dentary, broken posteriorly through the 8th alveolus and along parts of the ventral edge; total length 7.12mm. There is no sign of ankylosed teeth, but alveolar diameter varies considerably with an alternating pattern (1<2<7<3<5<4<6), due to variation of diameter with stage of tooth development and replacement as well as tooth size. The ventral edge is slightly concave anteriorly, and although worn from below the 4th to 6th alveoli it appears to have extended medially as a widened shelf in this region, as the portion preserved below the 6th-7th is concave; possibly this concavity marks the anterior limit of the lower process of the splenial. Two mental foramina below the 4th and 6th-7th alveoli have sharply defined oval margins except anteriorly. The anterior foramen is distinctly higher and deeper than the other; a third may or may not have been present beyond the broken posterior edge. The lateral face is smooth, with a rounded dorsolateral ridge just below the alveolar margin, and a shallow longitudinal concavity below the foramina. The medial ridge defining the upper edge of the meckelian groove is strongly overhung for most of its length, but gently so in the area of the 5th alveolus. This ridge swells ventrally and medially at its anterior end, forming a distinct median bulb medial to the groove level with the first and second alveoli. The groove is open anteriorly, forming an anterior notch in the first alveolus, not an enclosed foramen. No definite evidence of the splenial facet or lateral posterior fossa is preserved.

QM F23893 differs from known material of *N. godthelpi* in the second mental foramen being posterior to the 6th alveolus, and third (if present) posterior to the 7th; the absence of a groove on the dorsomedial face diverging from the meckelian groove, extending parallel to the tooth row from below the bulb; and the meckelian groove opening anteriorly into the first alveolus by a notch. The 'break' in the upper edge of the groove occurs below the 5th (cf. 8th) alveolus; assuming this feature is related to the extent of the upper splenial process (i.e. that the 'bevelled' section of the ridge corresponds to the foramen between dentary and splenial for the lingual branch of the inferior alveolar nerve), this may imply the dentary was considerably shorter and thus relatively more robust than in *Nanowana* or other known Australian madtsoiids, or that the splenial was relatively larger.

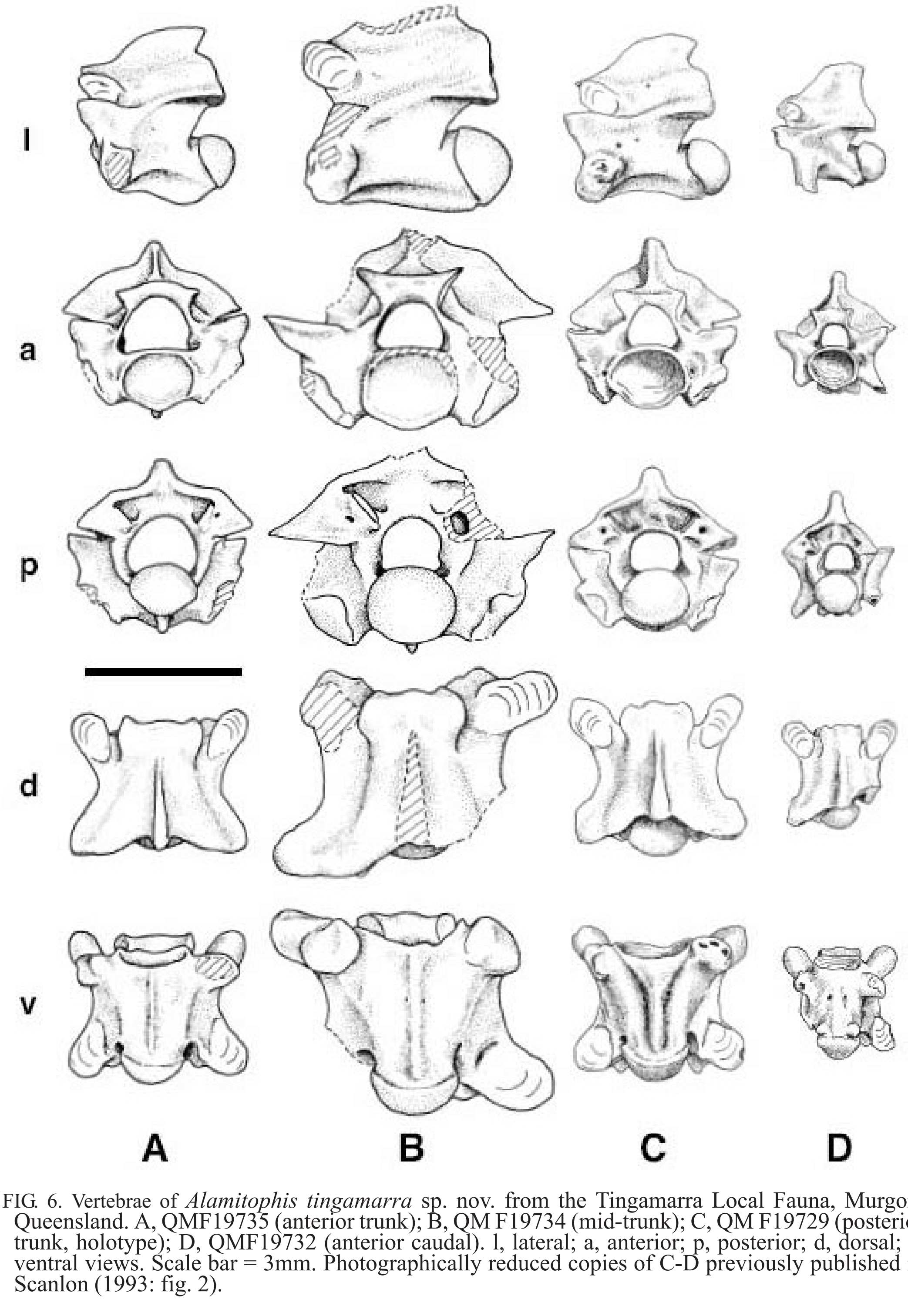

FIG. 6. Vertebrae of *Alamitophis tingamarra* sp. nov. from the Tingamarra Local Fauna, Murgon, Queensland. A, QMF19735 (anterior trunk); B, QM F19734 (mid-trunk); C, QM F19729 (posterior trunk, holotype); D, QMF19732 (anterior caudal). l, lateral; a, anterior; p, posterior; d, dorsal; v, ventral views. Scale bar = 3mm. Photographically reduced copies of C-D previously published in Scanlon (1993: fig. 2).

Family ?MADTSOIIDAE indet.

cf. **Madtsoia** sp.

Fig. 4E

MATERIAL. QMF52167, a single rib fragment from the right side of the trunk from MP1 horizon, Main Quarry, Tingamarra, Boat Mountain, near Murgon, southeast Qld. Tingamarra Local Fauna, Early Eocene, 54.6 +/- 0.05 MYBP (Godthelp et al., 1992).

DESCRIPTION. The specimen comprises the rib head and proximal portion of the shaft, but lacks the tuber costae. The proximal articulating surface has a sinuous medial edge and subequal, rounded lateral lobes as in the rib form referred to *Patagoniophis*, but is much larger (approximately 3.9 x 2.6 mm as preserved) than the paradiapophyses of any vertebrae yet known from the site. In addition to a pair of foramina in the ventrolateral hollow adjacent to the parapophyseal facet, there is a small foramen in the dorsal 'groove' (elongate hollow corresponding to the concavity of the proximal margin between the diapophyseal facet and tuber costae), and several more in a slight hollow on the ventrolateral surface. Foramina in a dorsal groove have not been seen in ribs of other Australian madtsoiids, but occur in *Madtsoia bai* (Simpson, 1933). In shape of the articular head it is much more similar to *M. camposi* (Rage, 1998), where no such foramina have been described; however, the '8'-shaped articular surface is also typical of alethinophidians.

The tuber costae is broken off too short to determine whether it was robust (typical of madtsoiids, also seen in *Dinilysia*) or slender in proximal view (characterising most if not all alethinophidian and scolecophidian ribs; Rage, 1998; pers. obs.), or its orientation relative to the axis of the articular surface (variable within Madtsoiidae).

In view of its relatively large size (discussed below), distinctive shape, and extra foramina on the shaft, this specimen is inconsistent with the two other rib forms and cannot be referred to either of the taxa named above. It cannot conclusively be excluded from Alethinophidia, but as far as preserved it is most similar to ribs of *Madtsoia* spp., although still considerably smaller than any reported form of that genus.

DISCUSSION

Vertebral morphology and systematics. Because the additional material allows variation along the vertebral column to be reconstructed more fully than when initially reported, the Murgon madtsoiid taxa can now be adequately compared to isolated vertebrae from other localities (cf. Rage, 1974: 274). Consequently, both forms are now diagnosable as distinct from the South American members of their genera, and also from other taxa of small madtsoiids described in recent years (*Herensugea* Rage, 1996; *Nanowana* Scanlon, 1997).

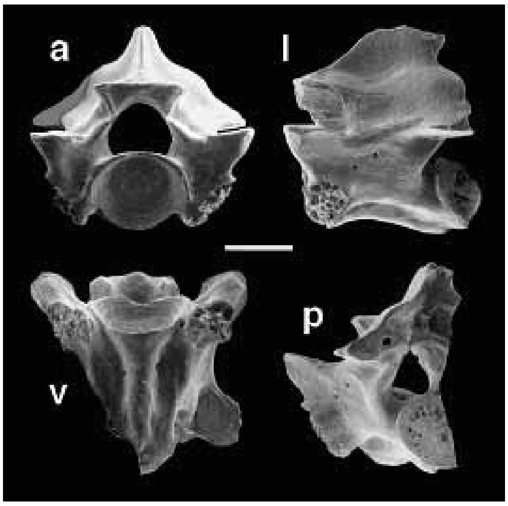

FIG. 7. Holotype posterior trunk vertebra (QM F19729) of *Alamitophis tingamarra* sp. nov., scanning electron micrographs; a, anterior; l, lateral; v, ventral; p, posterior views. Some parts are obscured by mount (outline partly restored in a); the same vertebra is shown in Fig. 6C. Scale bar = 1mm.

The specimens of *P. parvus* figured in ventral view (Albino, 1987) have the haemal keel extending with near-parallel and sharply defined lateral borders to near the cotylar rim; in the Murgon material representing all regions of the column in *P. australiensis* sp. nov., the keel becomes less sharply defined anteriorly and fails to reach the cotyle (polarity unclear, both states occur in other madtsoiids). Also, the subcentral ridges are more strongly concave in the material described here than in *P. parvus* (possible autapomorphy of *P. australiensis*, though also similar to *Herensugea caristiorum* Rage, 1996, and *Coniophis* sp., e.g. Gardner & Cifelli, 1999); size of the adult vertebrae is somewhat smaller (making *P. australiensis* the smallest known madtsoiid, an apomorphic extreme); and the zygosphene is relatively broader (possibly attributable to size difference) but less arched. These differences indicate at least a specific level

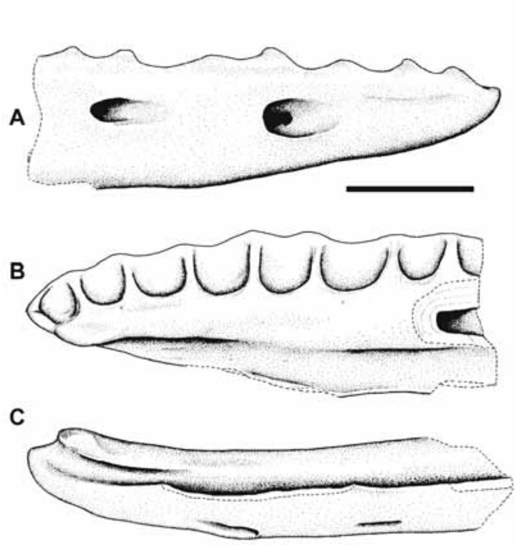

FIG. 8. Anterior portion of a right dentary (QMF23893) from the Tingamarra Local Fauna, referred to *Alamitophis tingamarra* sp. nov. A lateral, B dorsomedial, and C ventral views. Scale bar = 2mm.

of divergence. The small European form *Herensugea* (Rage, 1996) is also comparable with *P. australiensis* (in small size, depressed neural arch and very low neural spine, shallow posterior emargination of the neural arch, and the shape of the centrum, particularly the subcentral ridges in ventral view), but differs in having weakly inclined zygapophyses and (apparently) weakly trilobate zygosphenes (cf. *Alamitophis*), distinct subcentral grooves in mid-trunk vertebrae (holotype; Rage, 1996: fig. 2), and a pair of dorsal longitudinal ridges flanking the neural spine in most vertebrae (cf. some *Coniophis*, 'Aniliidae'; Gardner & Cifelli, 1999).

Alamitophis vertebrae from Murgon can now be compared with two species from the Late Cretaceous of Patagonia: *A. argentinus*, from the Los Alamitos (Cerro Cuadrado, Bajo Trapalcó and El Palomar localities, central Río Negro province; Campanian) and La Colonia Formations (La Colonia locality, north-central Chubut province; Campanian-Maastrictian), and a second form *A. elongatus* also from the Los Alamitos (Cerro Cuadrado and Bajo Trapalcó; Albino, 1994, 2000). The three forms are similar in many details, several of the features used in the generic diagnosis being quite distinctive. While the *A. argentinus* holotype is rather damaged, that species apparently lacks the median prominence on the zygosphene that is well-developed in both *A. elongatus* and the Murgon specimens, and separates these taxa from all other Madtsoiidae. This character (considered distinct from the broader, straight or weakly convex median lobe in some *Nanowana*) is a synapomorphy if Madtsoiidae is monophyletic, but polarity would be rendered uncertain if *Alamitophis* were more closely related to Scolecophidia and Alethinophidia, in which the zygosphene usually has a similar median lobe (this position was found in some unpublished analyses; Scanlon, 1996). Differences of *A. tingamarra* sp. nov. from both of the others are more weakly defined and anteriorly divergent subcentral ridges, and (if samples are representative) smaller size. The haemal keel widens anteriorly to the full width of the cotyle in posterior trunk vertebrae of *A. tingamarra*; this feature is not known in the other species, but this region may not yet be represented in the Patagonian samples.

Alamitophis represents a highly distinctive group within Madtsoiidae, and can be regarded as a clade based on the probable apomorphies mentioned above. The status of *Patagoniophis* is more problematic, as in overall morphology the vertebrae of these species resemble, or are intermediate between, both non-madtsoiid taxa (*Dinilysia*, *Coniophis* and other anilioids; e.g. Hecht, 1982; Gardner & Cifelli, 1999) and some later Australian madtsoiids (species of *Nanowana* and *Yurlunggur*; Scanlon, 1992, 1997). This probably reflects generally plesiomorphic morphology rather than synapomorphy; thus, rather than *Patagoniophis parvus* and *P. australiensis* being sister taxa, it may be seen as more likely that the latter represents the sister taxon or possible ancestor of younger Australian madtsoiids. However, as the two forms resemble each other more closely than any other madtsoiid and neither has clear synapomorphies linking it with a third taxon or clade, they are retained in a single genus until more evidence for relationships is available.

Dentary. The total length of the mandible (and thus skull) corresponding to the larger dentary specimen can be estimated roughly as three times the length of the fragment, or around 21 mm (based on proportions of the most similar known taxon, *Nanowana godthelpi* Scanlon, 1997). This is consistent with either of the two taxa known from vertebrae, whose total lengths are estimated to reach about 50cm and 80cm in *Patagoniophis* and *Alamitophis* respectively (Scanlon, 1993).

The assignment of the jaw elements to taxa on the basis of relative size is therefore uncertain and provisional.

To interpret the significance of those features in which the two dentaries differ from each other, and potentially test their assignment to the respective taxa, comparisons with other madtsoiids are required. South American species of *Madtsoia* may be useful in estimating the plesiomorphic character states of the dentary in Australian madtsoiids; further outgroup comparisons are desirable, but the analysis of Lee and Scanlon (2002) implies that the next relevant outgroups would be *Dinilysia* (where the dentary remains poorly known; Estes et al., 1970; Caldwell & Albino, 2002) and Serpentes (all modern snakes) in which morphology varies greatly among basal lineages (e.g. Lee & Scanlon, 2001). Two *Madtsoia* specimens are known; one referred by Hoffstetter (1960) to *Madtsoia* cf. *M. bai* (Riochican, Upper Paleocene of Argentina), and one of *M. camposi* (Itaboraian, Upper Paleocene of Brazil; Rage, 1998). These are relatively robust as well as large elements (particularly the Patagonian specimen) and share the following features: a well-developed but smooth 'symphyseal bulb' medial to 1-2; alveoli of relatively uniform size (apparently not reducing by the 8th); three mental foramina (below 3, 5-6, 7-8 and 2, 4, 6 respectively); the lateral fossa extending anteriorly to below the 8th alveolus; and a well-developed ventromedial shelf below the meckelian groove (widest below the 7th alveolus in both specimens). There is no visible 'smooth gap' in the dorsal margin of the meckelian groove, so the position of the inferior alveolar nerve foramen is unknown. The close similarity of the two specimens confirms Hoffstetter's (1960) referral of the isolated element to *Madtsoia*, which was questioned by Albino (1996) after discovery of large boid (sensu stricto) vertebrae in similar-aged deposits in the same area (Albino, 1993).

The position of the lateral fossa is unknown in both Murgon specimens, but was posterior to the middle of the 8th alveolus in F23893, and beyond the middle of the 11th in F29617; alveolar size is reducing by the 7th; the (putative) inferior alveolar nerve foramen, and widest point of the medioventral shelf, are below the 5th. As noted above, they differ in several respects, but these are either likely to be size-related or even ontogenetic (absolute size, and degree of disparity in alveolar diameter) or one of the alternate states cannot be equated to that in another taxon (position of first alveolus relative to anterior tip, and detailed form of the crests defining the meckelian groove) and thus cladistically informative.

Extending comparisons for the remaining features to other Australian madtsoiids (Scanlon, 1996, 1997; Lee & Scanlon 2001; and unpublished data), the following binary or multistate characters can be evaluated (see Table 1, which also includes *Cylindrophis ruffus* (Laurenti, 1768) as an exemplar of the outgroup Alethinophidia):

1. Symphyseal region with smooth 'bulb' medial to 1st alveolus (0); no bulb but longitudinal ridges and grooves present in this region (1).

2. Alveoli relatively uniform, not reducing in size by 8th (0); region of moderately enlarged alveoli and/or teeth, size reducing by 8th alveolus (1); region of greatly enlarged alveoli and/or teeth from 2nd to 4th (2). Ordered 0-1-2.

3. Dorsal margin of meckelian groove sharply defined up to at least 8th alveolus, 'smooth gap' in crest (inferior alveolar nerve foramen?) posterior to this position or possibly absent (0); 'smooth gap' present below 8th-9th alveoli (1); present below 5th alveolus (2). Unordered, because possible absence of the feature cannot be distinguished from a far posterior position in incomplete specimens.

4. Lateral fossa for surangular extends to level of the 8th alveolus (0); apex of lateral notch below 9th-12th (1); below or posterior to 13th (2). Ordered 0-1-2.

5. Ventromedial shelf of dentary well developed anteriorly, flooring meckelian groove at level of first two alveoli (0); reduced or directed more ventrally than medially, so that anterior part of meckelian groove is open ventrally (1).

6. Ventromedial shelf broadens gradually toward rear of dentary, maximum width posterior to 8th alveolus (0); maximum width around level of 7th alveolus (1); maximum at 5th alveolus (2). Ordered 0-1-2, but plesiomorphic state is hypothesised to be the intermediate state 1.

7. Single mental foramen on each dentary (0); two or three mental foramina (1). Polarity based on outgroup comparison with *Pachyrhachis*, *Haasiophis*, Scolecophidia, and Alethinophidia, assuming phylogeny of Lee and Scanlon (2002: fig. 11). A reconstruction of *Wonambi naracoortensis* with two mental foramina

Table 1. Taxon x character-state matrix (characters 1-7 defined in text; state 0 inferred to be plesiomorphic unless stated otherwise; '1/2' = either state 1 or 2). Madtsoiids *Madtsoia*, *Nanowana*, and *Wonambi* indicated by initials. Extant alethinophidian *Cylindrophis ruffus* (based on SAM R36779) included for comparison with eight madtsoiid taxa.

	1	2	3	4	5	6	7
M. bai	0	0	0	0	0	1	1
M. camposi	0	0	0	0	0	1	1
F29617 *(?P. australis)*	0	1	2	2	1	2	1
F23893 *(?A. tingamarra)*	0	1	2	1/2	1	2	1
N. godthelpi	0	1	1	1	1	0	1
N. schrenki	1	2	1	2	1	0	1
W. naracoortensis	1	0	0	2	0	0	0
Yurlunggur	1	0	0	2	0	0	1
Cylindrophis ruffus	0	0	1	1	0	1	0

(Scanlon & Lee, 2000: fig. 1) was not based on direct examination of the dentary in that taxon; further preparation by the author confirms that the foramen is actually single in the only known specimen (as originally reported by Barrie, 1990; see also Rieppel et al., 2002).

The data in Table 1 are too limited to allow a meaningful phylogenetic analysis at this stage, but provide some measures of similarity among taxa. The two *Madtsoia* species are indistinguishable in these features, *Wonambi* and *Yurlunggur* resemble each other nearly as closely, and the two *Nanowana* species are also quite similar despite their divergent dentitional specialisations (Scanlon, 1997). The two Murgon specimens resemble each other more closely than either does any other madtsoiid taxon, and although they have other differences that make it unlikely they could come from the same species, they are indistinguishable in terms of characters 1-7. The dentary morphology thus appears to provide no evidence for either of the Murgon species to be more closely related to younger Australian madtsoiids, but also cannot show they are most closely related to each other, because their shared characters could all be symplesiomorphic for Australian Madtsoiidae.

RIBS. In snakes the dimensions of the rib head correspond approximately to those of the paradiapophysis to which it articulates, and the long dimension of the paradiapophysis is approximately one third of vertebral width across the prezygapophyses (mean = 0.335, n=25 vertebrae of *Patagoniophis* and *Alamitophis* from Tingamarra; unpublished data). Using the ratio of maximum vertebral width to total vertebral column length adopted as a ‘standard’ (1:136.9 in a skeleton of *Aspidites melanocephalus*; Scanlon, 1993), the rib QMF52167 came from a snake approximately 1.6m long (3.9mm x 3 x 137 = 1603mm), or somewhat longer if it was not among the largest in the skeleton. It can be concluded from this specimen that at least one additional snake taxon (approximately twice the size of *Alamitophis tingamarra* sp. nov.) was present in Australia during the early Eocene; this was also most likely a member of Madtsoiidae, both because of morphological similarities to *Madtsoia* spp., and because no non-madtsoiid snakes are known in Australia until much later (Scanlon, 2001; Scanlon et al., 2003).

The three rib-head morphotypes from Murgon represent greater diversity in this region of the skeleton than has been documented in any recent family of snakes (Hoffstetter & Gasc, 1969), although this may be due partly to neglect of rib morphology in favour of other features. The form referred to *Alamitophis tingamarra* sp. nov. differs conspicuously in proportions from all other madtsoiids known from Australia, and is more comparable to those of *Madtsoia bai* (Simpson, 1933: fig. 5) and perhaps also *Dinilysia patagonica* Woodward, 1901 (Rage & Albino, 1989: fig. 1E). The more abundant form, referred to *Patagoniophis*, is more similar to those of *Wonambi naracoortensis*, *Yurlunggur camfieldensis*, and material from Riversleigh representing several additional taxa (Scanlon, 1996); as noted previously (Scanlon, 1993) this is consistent with *Patagoniophis australiensis* forming the sister taxon or ancestor of all post-Eocene madtsoiids. It would be equally consistent with either *Alamitophis tingamarra* or a (*Patagoniophis*, *Alamitophis*) clade forming the sister taxon (but not ancestor) of later madtsoiids, if the rib morphology attributed to *A. tingamarra* were autapomorphic for the species; however, this is considered less likely due to its greater resemblance to *Madtsoia* and *Dinilysia*.

BIOGEOGRAPHY AND ECOLOGY.

The known distribution of *Patagoniophis* and *Alamitophis* implies that their geographic ranges were connected across Antarctica at some stage between the Late Cretaceous and early Eocene (Scanlon, 1993). While long-term geographic continuity is not distinguishable from ‘dispersal’ on the currently sparse fossil evidence, it may be simplest to assume that only one-way dispersal was allowed by what may have been a transient habitat corridor, cut off from the west before connecting to the Australian landmass. Woodburne and Case (1996) reviewed geophysical and some of the palaeontological evidence bearing on the dispersal route between South America and Australia at this time, concluding that South America and the Antarctic Peninsula remained in contact until the opening of the Drake Passage about 36 Ma (late Eocene), but Australia was separated from East Antarctica by about 64 Ma (early Paleocene). Evidence for environmental conditions in Antarctica at the time mainly relates to the Antarctic Peninsula, indicating it possessed a warm- to cool-temperate climate and a plant community dominated by conifer rainforest of podocarps and araucarians, with angiosperms (including Proteaceae and *Nothofagus*) becoming more diverse through this interval (reviewed by Woodburne and Case, 1996; see also Case et al., 2000 for evidence of dinosaurian dispersal from South America to Antarctica). Climatic conditions in the rest of Antarctica, closer to the pole, were presumably less benign, and are likely to have constituted a filter barrier that limited the extent of faunal interchange (see Godthelp et al., 1999: 292). In particular, there is currently no palaeontological evidence for any other lineage of squamates either occupying Antarctica or using it as a 'bridge' between South America and Australia (Hutchinson & Donnellan, 1993; Scanlon, 2001; Scanlon et al., 2003).

Thus, it is possible that *Patagoniophis* and *Alamitophis* lived closer to the South Pole than any other contemporaneous squamates. Recent snakes of the highest latitudes are small, heliothermic, and viviparous (Shine, 1985) and extend beyond the climatic limits of lizards, so these conditions are also likely in the most southerly snakes of other times. The Australian species of both *Patagoniophis* and *Alamitophis* have smaller body sizes than their earlier Patagonian congeners, consistent with a process of 'dwarfing' affecting both lineages; if the larger rib actually belongs to an adult of a *Madtsoia* sp., it is even more dramatically dwarfed relative to South American congeners (estimated as up to 9 m long; Simpson, 1933). This inferred process of reduction in body size (along with the known temporal distribution in each area, which might be discounted due to the sparseness of the records) is more consistent with dispersal from South America to Australia, rather than the reverse. The morphological losses associated with live-bearing in amniotes are possibly irreversible (Lee & Shine, 1998), and it can therefore be suggested that descendants of any of these lineages (presumably including all later madtsoiids in Australia, such as *Wonambi* and *Yurlunggur*) were also likely to have been viviparous.

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