

Mid-Tertiary elapid snakes (Squamata, Colubroidea) from Riversleigh, northern Australia: early steps in a continent-wide adaptive radiation

Serpents élapidés (Squamata, Colubroidea) du Tertiaire moyen de Riversleigh, Nord de l'Australie : étapes précoces d'une radiation adaptive répandue sur un continent entier

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Abstract

Vertebral and cranial remains of elapid snakes have been collected from fossil assemblages at Riversleigh, north-west Queensland, Australia; most are Miocene but one may be late Oligocene and another as young as Pliocene. The oldest specimen (probably the oldest elapid yet known anywhere) is a vertebra that can be referred provisionally to the extant taxon *Laticauda* (Hydrophiinae, sensu Slowinski and Keogh, 2000), implying that the basal divergences among Australasian hydrophiine lineages had occurred by the early Miocene, in contrast to most previous estimates for the age of this geographically isolated adaptive radiation. Associated vertebrae and jaw elements from a Late Miocene deposit are described as *Incongruelaps iteratus* nov. gen. et sp., which has a unique combination of unusual derived characters otherwise found separately in several extant hydrophiine taxa that are only distantly related. Associated vertebrae from other sites, and two parietals from a possibly Pliocene deposit, suggest the presence of several other taxa distinct from extant forms, but the amount of material (and knowledge of variation in extant taxa) is currently insufficient to diagnose these forms. The Tertiary elapids of Riversleigh thus appear to be relatively diverse taxonomically, but low in abundance and, with one exception, not referable to extant taxa below the level of Hydrophiinae. This implies that the present diversity of hydrophiine elapids (31 recognized terrestrial genera, and approximately 16 marine) represents the result of substantial extinction as well as the “cone of increasing diversity” that could be inferred from phylogenetic studies on extant forms.

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Résumé

Les assemblages fossiles de Riversleigh au Nord-Ouest du Queensland, Australie, contiennent des fragments de vertèbres et crânes de serpents élapidés ; la plupart sont miocènes, mais un pourrait être oligocène tandis qu'un autre pourrait être aussi récent que pliocène. Le plus ancien spécimen (probablement, le plus ancien élapidé du monde connu jusqu'ici) est une vertèbre qui peut être attribuée provisoirement au taxon existant *Laticauda* (Hydrophiinae, sensu Slowinski et Keogh, 2000), ce qui implique que les principales divergences entre les lignées d'hydrophiinés australasiens avaient déjà eu lieu au Miocène inférieur, au contraire de la plupart des estimations proposées pour l'âge de cette radiation adaptative géographiquement isolée. Les fragments de vertèbres et mâchoires trouvés ensemble dans un gisement du Miocène supérieur sont décrits comme appartenant à *Incongruelaps iteratus* nov. gen., nov. sp., caractérisé par une combinaison unique de caractères autrement trouvés séparément dans plusieurs taxons actuels d'hydrophiiné qui ne sont pas étroitement apparentés. Les vertèbres associées

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d'autres sites et deux pariétaux d'un gisement possiblement pliocène suggèrent la présence de plusieurs autres taxons distincts des formes connues, mais la quantité de matériel (et la connaissance de la variabilité au sein des taxons modernes) n'est actuellement pas suffisante pour identifier ces formes. Les élapidés tertiaires de Riversleigh apparaissent donc relativement variés quant à leur taxonomie, mais peu abondants. À une exception près, ils ne peuvent être attribués à des taxons actuels au-dessous du niveau des Hydrophiinae. Ceci implique que l'actuelle diversité des élapidés hydrophiinés (31 genres terrestres et environ 16 marins reconnus) résulte d'une extinction substantielle ainsi que d'un « cône de diversité croissante » qui pourrait être reconnu par l'étude phylogénétique des formes actuelles.

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1. Introduction

Elapidae (venomous snakes with fixed fangs at the front of the upper jaw) is one of a number of highly successful and widely distributed lineages within the large group of “advanced” snakes (Caenophidia), and the only one to have radiated widely in the Australian region. Other caenophidian lineages that occur in Australia and New Guinea include *Acrochordus* (Acrochordidae) and six homalopsine, one natricine, and three colubrine genera (Colubridae s.l.). These genera all probably represent quite recent (Plio-Pleistocene) range expansions of the Southeast Asian fauna, and all but *Myron* and *Heurnia* (Homalopsinae) are widespread outside Australasia. In each case, dispersal across water, either by swimming or rafting, may have been facilitated by aquatic and/or arboreal habits (McDowell, 1987; Cadle, 1987; Shine, 1991; Greer, 1997).

In contrast, there are over 100 terrestrial elapid species (here placed in 31 genera) endemic to the region (Australia, New Guinea, the Solomon Islands and Fiji), and this is also the centre of diversity (and probable origin) of two lineages of living sea snakes, one comprising the genus *Laticauda* (“sea kraits”) and the other the 16 or so genera of “true sea snakes” (Hoffstetter, 1939; McDowell, 1967, 1987). The Australasian elapids and their marine derivatives apparently represent a single monophyletic group, termed the Hydrophiinae (sensu Slowinski and Keogh, 2000, see Diagnosis below). Such an isolated radiation is of great interest to evolutionary biologists, and there have been numerous attempts to unravel relationships among extant members of the lineage (e.g., Wallach, 1985; Lee, 1997; Greer, 1997; Keogh et al., 1998, 2000; Rasmussen, 2002; Scanlon and Lee, in press), as well as comparative studies of their ecology (Shine, 1991; Greer, 1997, and references therein). It would be a great advantage in such studies to know more about the actual time scale of the radiation, and the morphology and biology of its early members; such information can be provided directly by the fossil record.

One of the most detailed discussions of the geographic origin and radiations of elapids remains Hoffstetter (1939: 52 ff.). Hoffstetter (1939) noted the absence of terrestrial elapids from New Zealand and Madagascar, their presence in the Neotropics, and the broad geographic and temporal distribution of the genus *Naja*. He also undertook an assessment

of the “level of evolution” of various extant forms based on skull structure, and particularly features of the palatine bone. Based on these considerations, Hoffstetter proposed that elapids originated in eastern Asia (possibly but not necessarily the Indo-Malayan region), dispersing at an early stage to Melanesia (and thence mainland Australia), with later dispersals from the eastern Asian source to Africa, and via the Bering route to the Americas. He concurred with M.A. Smith (1926) that “laticaudines” (then considered to include *Aipysurus* and *Emydocephalus* as well as *Laticauda*) and “hydrophiids” (all other sea snakes) were independently derived from terrestrial elapids, but differed from Smith in proposing that both marine groups were related to Australian rather than Indo-Malayan forms. Storr (1964), like Hoffstetter, regarded elapids as “one of the oldest elements in the Australian herpetofauna”, with the high level of endemism (e.g., in southwestern Australia, and in New Guinea) indicating they are now in decline.

Subsequent acceptance of continental drift and phylogenetic methods resulted in more precise estimates of the timing and nature of the Australasian elapid radiation. Until the early Paleocene (~64 MYA) Australia had land connections with South America via Antarctica, and thus was effectively still part of Gondwana (Audley-Charles, 1987; Woodburne and Case, 1996). There followed a period of isolation as the Australian plate drifted north from the Antarctic (preceded by various micro-plates or terranes, of uncertain biogeographic significance); the isolation ended as the tectonic collision with Southeast Asia produced the Sunda and Melanesian island arcs, thus forming a filter-bridge allowing dispersal of terrestrial animals from the north (Hall, 2001). The hiatus defines a dichotomy between an older Gondwanan biota, and more modern groups of northern origin. Elapids are widely recognized to be part of the latter fauna. Cogger and Heatwole (1981) suggested that elapids and some other reptilian lineages were groups of “intermediate” age: early arrivals from the north, which evolved in relative isolation here for some 30–35 million years with “little or no modification by later migrations of the same families until well into the Quaternary”. While Cogger and Heatwole (1981) did not adopt Storr’s (1964) suggestion that the group was in decline, Schwaner et al. (1985) noted that “a generalization seems to have developed that the Australian herpeto-

fauna (including elapid snakes) underwent an adaptive radiation over the past 30–35 million years and now is being overtaken by further reptilian invasions from the north”. Schwaner et al. contrast this interpretation with Stanley’s (1979) view of the Neogene as the “Age of Snakes” and suggestion that elapids, like most other snake lineages, are a dynamic, speciating group. Their molecular clock studies using transferrin immunological distances suggested a more recent timing for the radiation, around 12 to 15 MYA. Molnar (1991) implied an even more recent date, stating that Australia’s complete isolation from reptilian migration lasted from the Eocene to the Pliocene.

Direct evidence for the time of first entry to the Australasian region is hard to obtain, but various indirect sources can contribute to an estimate. There is evidence from biogeographical patterns in extant forms (Hoffstetter, 1939; Storr, 1964), molecular clocks (Schwaner et al., 1985), and the patchy fossil record (see below), but continental drift and global sea level changes must also be considered. Hutchinson and Donnellan (1993) note that the geological history of the Asian-Australasian “gap” remains poorly understood, and “geology is not likely to provide rigid constraints on biogeographic hypotheses”. Nevertheless, we must suppose that the gradual northward drift of Australasia makes dispersal from the north progressively more likely, but superimposed on this trend are several intervals of reduced sea level, exposing greater land areas and narrowing water gaps. Sea levels were low through most of the late Oligocene due to global “ice-house” conditions beginning before 30 MYA (Frakes et al., 1987), corresponding well with the timescale suggested by Cogger and Heatwole (1981) for the mid-Tertiary dispersals.

Whereas Smith and Plane (1985) inferred from the mid-Miocene presence of pythonine booids in Australia that they must have been a Gondwanan element of the fauna (see also Kluge, 1993; Scanlon, 2001), there has been no published support for a Gondwanan origin of Australasian elapids. Keogh (1998), Keogh et al. (1998) regarded the monophyly of Australasian elapids (plus sea snakes), and Asian affinities of American coral snakes, as evidence against a Gondwanan origin. However, the sister-group relationship between Australasian and Afro-Asian elapids (Slowinski and Keogh, 2000) is symmetric, and thus equally consistent with origin in either geographic location. Evidence for their ultimate centre of origin comes from a comprehensive phylogenetic analysis of colubroid snakes (Lawson and Slowinski, unpublished) indicating that the nearest relatives of elapids are all African colubroids, which strongly supports African origins; but again, this would be consistent with dispersal into Australasia through either Asia or Antarctica. On the other hand, the evidence for extensive (probably two-way) interchange of elapid lineages between Africa and Asia (Slowinski and Keogh, 2000), and demonstration that New World coral snakes are nested within an Asian lineage (Slowinski et al., 2001), remove any motivation to prefer a Gondwanan model. The traditional scenario, of dispersal into Australasia from the north, better accounts for these patterns and is thus

adopted as a working hypothesis, and the Gondwanan model will not be discussed further here (but see Scanlon and Lee, in press).

The fossil history of Elapidae currently extends to the early Miocene in Europe (middle Orléanian, MN 4; Rage and Augé, 1993; Szyndlar and Schleich, 1993; this biozone corresponds to 16.0 – ~17.0 MYA according to Daams et al., 1999), and to the middle Miocene in Africa (mid/late Astarcian, MN7; Szyndlar and Rage, 1990) and North America (late Barstovian, Holman, 2000). However, these early fossils appear to belong to distinctive modern lineages – *Naja* in Europe and Africa, and forms referred to *Micrurus* in both North America and Europe (Rage, 1987; Szyndlar and Rage, 1990; Szyndlar and Schleich, 1993) – so that the initial radiation of elapids must have been somewhat earlier. Until now, the fossil history of elapids in Australia has been extremely limited, very recent, and of little practical relevance to questions of the age and pattern of the radiation. Pleistocene elapid fossils have been described from Victoria Cave at Naracoorte, South Australia (referred to the extant genera *Pseudonaja*, *Pseudechis* and *Notechis*; Smith, 1975, 1976; Reed and Bourne, 2000) and reported from the fluvialite Wyandotte Formation, North Queensland (not identified beyond “probably elapid”; McNamara, 1990). Further elapid remains are known from Pleistocene deposits in Queensland (Darling Downs, Floraville, and Riversleigh), New South Wales (Wellington Caves), Victoria (Bacchus Marsh), and cave sites in the southwest of Western Australia (Scanlon, 1995 and unpublished data). While not yet described, most of this material represents large species similar to *Pseudechis* or *Pseudonaja* (unpublished observations). Early to middle Pliocene elapid remains are known from several sites including Bluff Downs (Allingham Formation, North Queensland; Archer and Wade, 1976; Scanlon and Mackness, 2002; not acrochordid, as suggested by Smith and Plane, 1985), Chinchilla (eastern Queensland; H. Godthelp and J. Scanlon, unpublished) and Corra-Lynn Cave, Yorke Peninsula (South Australia; Pledge, 1992) but also remain undescribed. A fragmentary elapid vertebra has also been collected from the middle Miocene Bullock Creek Local Fauna, Northern Territory (Scanlon, 1992, 1996).

Discoveries at the Riversleigh World Heritage Fossil Property, northwestern Queensland, extend the record of elapids in Australia back to the early Miocene and possibly late Oligocene. In the vicinity of the Gregory River at Riversleigh Station (19°01’S, 138°40’E) during the mid-Tertiary, the region underwent several cycles of uplift, erosion, and redeposition, resulting in a complex series of freshwater lacustrine, alluvial, tufa and karst deposits (Archer et al., 1989, 1991, 1997; Megirian, 1992; Creaser, 1997). The mid-Tertiary sequence (late Oligocene to late Miocene) is sometimes referred to collectively as the “Carl Creek Limestone” (Megirian, 1992), but others use this term in a more restricted sense (see Archer et al., 1997) noting the plethora of very different sediment types (most of which are distinguished palaeontologically and chronologically but unnamed) rang-

ing from lacustrine to fluvial, karstic and fissure deposits. These are often separated by significant temporal gaps, angular unconformities, non-lithological continuity with intruded mid- and sometimes late Tertiary cave deposits and fissure fills containing mid- and late Tertiary fossil assemblages. Fossils occur abundantly at many localities within this system, representing a large number of vertebrate taxa (with occasional invertebrate and plant remains) spanning at least the last 24 million years. Associated remains from contiguous, apparently contemporaneous deposits (most often, single sites) have been named as “local faunas” (LFs). Most of these are grouped informally into “Systems” A, B, and C (Archer et al., 1989, 1997) or, roughly equivalent to them, the Verdon Creek, Godthelp Hill, and Gag Plateau Sequences (Creaser, 1997). System A sites share mammalian species with central Australian deposits dated magnetostratigraphically to Late Oligocene (~24–25 MYA, Woodburne et al., 1993); System C contains a sequence of assemblages that probably span the Middle Miocene (~16.3 to 10.4 MYA); and System B is intermediate in age, probably Early Miocene (Archer et al., 1997). Pliocene and Pleistocene cave and fissure fill deposits in the area will not be discussed here because they are not known to include diagnostic elapid material.

Elapids are known from one deposit in the Godthelp Hill Sequence (System B), and a number of others from the younger (System C) Gag Plateau Sequence. The initial attribution of elapid remains to the Upper Site LF (Godthelp Hill, System B; Archer et al., 1989, 1991) was an error due to one of us (JS), but elapids are now known from stratigraphically lower (RSO Site, Godthelp Hill) as well as higher deposits in the Riversleigh sequences. This material is described below, with discussion of the diagnostic characters of vertebrae and jaw elements, the systematic status of the fossils, and their implications for the age and pattern of the Australasian elapid radiation.

2. Materials and methods

All of the fossil material described here from Tertiary freshwater limestone deposits of the Riversleigh World Heritage Property around the Gregory River, north-west Queensland, has been collected and prepared by a team at the University of New South Wales led by M. Archer, and including H. Godthelp, S.J. Hand, postgraduate students, and volunteers. All Riversleigh material has been or will be housed in the Queensland Museum palaeontological collection (QM F). The fossils described here are prepared using acetic acid (see Archer et al., 1991), measured with either vernier or electronic calipers, and drawn using a binocular microscope and camera lucida.

For this work, one or more skulls of nearly all extant terrestrial hydrophiine genera have been examined by the senior author (material listed in Appendix). Complete or partial articulated vertebral columns of many of the species have also been examined. The description and comparison of

vertebrae, however, has not yet reached a stage allowing most fossil forms to be referred to or rigorously distinguished from extant taxa. In the absence of previous analyses of Australian elapids based on osteology, comparisons are based on overall similarity, and hypotheses of homology and polarity are provisional.

Published literature descriptions were also consulted, although the comparative osteological description of extant Australian elapid snakes has never been systematically pursued. The anatomy of *Acanthophis antarcticus* was described by McKay (1889), skulls of some forms were figured by Boulenger (1896), and Hoffstetter (1939) commented on some cranial and vertebral features. Bogert (1943), Bogert and Matalas (1945), and Williams and Parker (1964) figured some cranial elements of a few Melanesian taxa; Worrell (1956, 1963) figured the skulls of a number of Australian taxa and proposed diagnoses of some species based on cranial characters; and McDowell (1967, 1969, 1970) figured and described the skulls, and gave brief descriptions of trunk vertebrae, for a number of Melanesian and northern Australian forms. Smith (1975) described and figured the vertebrae of four extant genera, and was able to identify some Pleistocene fossils to a generic level. Scanlon and Shine (1988) figured the skulls of several species of *Simoselaps*, with comments on their dentition and comparisons with some other forms. Camilleri and Shine (1990) reported on sexual dimorphism in the skull of *Pseudechis porphyriacus*. Shea et al. (1993), Greer (1997) and Scanlon and Lee (in press) also figure skulls of a number of taxa.

Institutional abbreviations for Recent comparative material: AMS, Australian Museum, Sydney; ANWC, Australian National Wildlife Collection, Canberra; JS, collection of the first author; MV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum of Arts and Sciences, Darwin; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth.

3. Systematics

Higher-level taxa of snakes listed below are those accepted by Rieppel (1988), and with regard to extant lineages are consistent with most recent phylogenetic analyses (e.g., Cundall et al., 1993; Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon, 2002). Within Colubroidea we adopt the phylogenetic hypothesis of Lawson and Slowinski (ms), and within Elapidae most features of those of Slowinski and Keogh (2000) and Keogh et al. (1998, 2000). Generic classification of Hydrophiinae follows Greer (1997) as amended by Keogh et al. (2000), except that *Glyphodon* is recognized as distinct from *Furina* (Scanlon, in press). Categorical ranks are not used here for taxa above the level of the genus.

SQUAMATA Oppel, 1811

SERPENTES Linnaeus, 1758

ALETHINOPHIDIA Nopcsa, 1923

MACROSTOMATA Müller, 1830

CAENOPHIDIA Hoffstetter, 1939

COLUBROIDEA Oppel, 1811

ELAPIDAE Boie, 1827

Diagnosis: Most skeletal characters of elapids fall within the much wider range of variation seen in Colubridae sensu lato (Auffenberg, 1963; Rage, 1984; Holman, 2000). The proteroglyph (front-fanged) maxilla is the most distinctive element: well separated from premaxilla due to reduction of the anterior process, and with the two most anterior teeth enlarged, set more or less side by side, and modified as tubular fangs; a suture along the anterior face of each fang connects the two apertures of the lumen. Similarly enclosed canals, or open grooves, are sometimes present in posterior maxillary, and rarely in anterior dentary or palatal teeth. A maxillary diastema is typically present between the fangs and smaller posterior teeth: absence of teeth behind the fangs, or continuation of the tooth row without a diastema, have originated more than once within Elapidae as derived conditions (polarity inferred from phylogenetic analyses; Keogh et al., 1998; Slowinski and Keogh, 2000; Slowinski et al., 2001). The skull is otherwise similar to that of Colubridae s.l.: snout complex usually articulated to the braincase through a condylar articulation between the septomaxillae and the frontals; supratemporal usually projecting caudally beyond the reduced paroccipital process; maxilla with two medial processes, without ascending process, in mobile rocking and/or sliding contact with prefrontal, and prefrontal usually with hinge joint against frontal; optic foramen usually between the frontal, parietal and parabasisphenoid; coronoid absent. However, the quadrate is usually less elongate and closer to vertical than in many colubroid lineages.

Vertebrae with paracotylar, “parazygantral”, and prezygapophyseal foramina often present in addition to subcentral and lateral foramina. Proportions of vertebrae variable, but usually not so lightly built or elongate as in many Colubridae s.l. Neural arch usually depressed, without epizygapophyseal spines. Neural spine with horizontal dorsal edge, relatively low, rarely as high as long; anterior edge overhanging or straight, posterior edge overhanging except in a few (mostly burrowing) forms. Subcentral ridges well developed. Condyle on a short to moderate neck, moderately oblique. Cotyle rounded to oval, subcotylar tubercles present or absent. Hypapophyses well developed throughout the vertebral column, straight or weakly sigmoid in lateral view, strongly laterally compressed; in posterior trunk, often coming to a point posteriorly below the condyle. Zygosphenes thin dorso-ventrally, convex or horizontal in anterior view; concave, arcuate, straight or convex from above.

Remarks: Elapid vertebrae are most similar to those of some natricine and homalopsine “colubrids” (Rage, 1984), and identification of postcranial material is therefore subject to uncertainty while comparisons with these groups are incomplete. The only non-elapids with a “proteroglyph” maxilla are the two species of *Homoroselaps* (Atractaspididae;

McDowell, 1968; Slowinski and Keogh, 2000; Lawson and Slowinski, ms).

Recent phylogenetic analyses of colubroids (Cadle, 1988; Heise et al., 1995; Kraus and Brown, 1998; Zaher, 1999; Gravlund, 2001; Lawson and Slowinski, ms) indicate that Elapidae is deeply nested within the diverse assemblage traditionally termed the “family” Colubridae. Lawson and Slowinski (ms) recognize Elapidae as one of 12 “families” within Colubroidea, and as most closely related to African lineages referred to Atractaspididae and Lamprophiidae (the latter of uncertain monophyly, but similar in proposed content to Boodontinae of earlier systems). Elapids (including sea snakes) have variously been assigned to several families and/or subfamilies, but evidence for monophyly of most of the proposed groups has been weak or absent until recently. Slowinski and Keogh (2000) provide evidence for reciprocal monophyly of two groups corresponding to the African, Asian and American terrestrial elapids (which they include in Elapinae) and the Australasian terrestrial and marine taxa (Hydrophiinae).

HYDROPHIINAE Fitzinger, 1843

Remarks on diagnosis and definition: Hydrophiinae (sensu McDowell, 1987, i.e., Australasian terrestrial elapids and “true” sea snakes) is diagnosed by the absence of maxillary and choanal processes of the palatine, and clasping articulation of the palatine and pterygoid, but these elements are presently unknown in Australian fossils. The vertebrae, parietals, and maxilla described below are referred to this group on the basis of their overall similarity to corresponding elements of extant species; in particular, the maxilla has at least five solid teeth posterior to the fangs, which exceeds the maximum reported in non-hydrophiine elapids. All Recent terrestrial elapids of Australia and New Guinea are included in Hydrophiinae, along with either one or both of the two extant clades of sea snakes. Slowinski and Keogh (2000) argue for inclusion of *Laticauda* in Hydrophiinae (*contra* McDowell, 1987) based on DNA sequence evidence, although such inclusion weakens the morphological diagnosis: *Laticauda* retains a well-developed lateral process of the palatine that is perforated for the palatine nerve, and thus seems likely to be basal to core hydrophiines, which share a derived trait of a reduced and imperforate (or absent) process (McDowell, 1970). The relatively rigid, clasping palatopterygoid articulation in *Laticauda* and other hydrophiines also differs from the squamous overlap or simple hinge joint in other elapids. However, wider comparison suggests the condition in hydrophiines (“palatine draggers”, McDowell, 1970) may be plesiomorphic for elapids, and the state in elapines (“palatine erectors”) a synapomorphy.

The literal sense of “Hydrophiinae” seems apt for the slightly more inclusive group, as one basal lineage (*Laticauda*) as well as some of the most derived forms (true sea snakes, or Hydrophiini) are marine; thus, it might be appropriate to define Hydrophiinae ostensibly using a node-based phylogenetic definition (Cantino and de Queiroz, 2000) as

“the least inclusive clade containing *Laticauda laticaudata* and *Hydrophis fasciatus*”. An apomorphy-based definition is less feasible given that the support for this group is currently mostly molecular. Uncertainty regarding the contents of Hydrophiinae (thus defined) relates to *Parapistocalamus hederi*, the only terrestrial Australasian taxon excluded from Hydrophiinae by McDowell (1970, 1987). No genetic data are available for this species (hence, not classified by Slowinski and Keogh, 2000) and its skeletal morphology remains poorly known, but it is provisionally included here based on morphological similarities with *Laticauda*, and palatine characters similar to other Melanesian hydrophiines (Williams and Parker, 1964; McDowell, 1969, 1970).

Elapidae incertae sedis (*Laticauda* sp.?)

Material: A single vertebra (QM F42690, Fig. 1) of a juvenile elapid is known from RSO Site, one of the lowest lying and presumed to be among the oldest of the Godthelp Hill Sequence of deposits (“System B”, Archer et al., 1989). The deposit is considered to be either latest Oligocene or (more likely) early Miocene in age (cf. Archer et al., 1997; Table 1).

Description: A short, broad, middle or posterior trunk vertebra with large, subcircular zygapophyseal facets, prominent, blunt, downcurved prezygapophyseal processes, broad zygosphenes, distal parts of the low neural spine and hypapophysis both somewhat expanded laterally and weakly divided by longitudinal grooves on their distal surfaces. The vertebra is complete except for slight damage to the right parapophyseal process, postzygapophyseal facets, and lower rim of the cotyle, but encrusted with dendrites, which obscure some details. Centrum forming an approximately equilateral triangle between paradiapophyses and condyle, defined laterally by prominent subcentral ridges. Subcentral, lateral, paracotylar and “parazygantral” foramina present but small.

Neural spine low, with overhanging anterior edge at rear of zygosphenes, and vertical posterior edge; dorsal surface of spine expanded, with slight median concavity. Neural arch moderately vaulted, margins in posterior view only slightly convex; in dorsal view, rounded posterior margins smoothly continuous with lateral margins of postzygapophyses, and forming a broad but angular median notch above zygantrum. Neural canal arched, approximately as wide as high, with internal lateral ridges below centre. The neural canal is much larger than the small round cotyle and condyle, indicating this is a juvenile vertebra.

Zygapophyseal facets horizontal, above base of neural canal (level with internal lateral ridges). Facets large, broadly oval or subcircular, with long axis at about 45° from sagittal plane; blunt, somewhat flattened prezygapophyseal processes less than half-length of facets, directed laterally and slightly anteriorly and ventrally. No foramina visible on the anterior face of the processes, possibly present but obscured by dendritic growth. Interzygapophyseal ridge smooth, weakly defined in middle of its length. Zygosphenes wide, with arched, rounded median lobe (anterior edge arcuate in

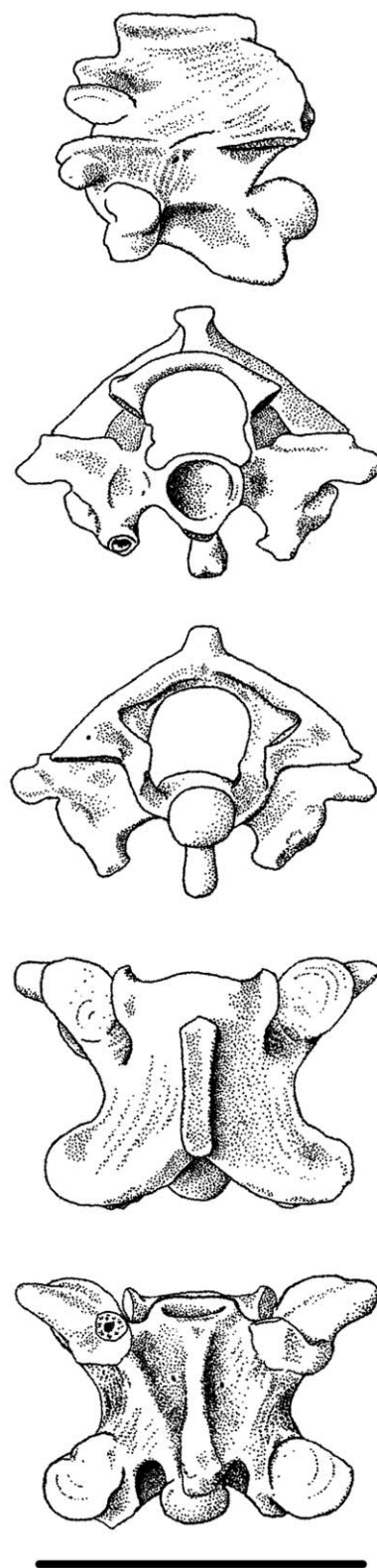


Fig. 1. Trunk vertebra of a juvenile elapid snake (QM F42690) from RSO Site, Riversleigh (Late Oligocene or Early Miocene) in (top to bottom) lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 2 mm.

Fig. 1. Vertèbre du tronc d'un élapidé juvénile provenant du site « RSO » de Riversleigh (Oligocène supérieur ou Miocène inférieur) en vues (de haut en bas) latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 2 mm.

Table 1

Riversleigh Tertiary deposits known to include elapid remains, showing range of possible ages and other snake families present (Scanlon, 1996; see Archer et al., 1989, 1997 for explanation of “site”, “local fauna” (LF), and ‘system’ names). “E.” = Early, “M.” = Middle (or Medial), “L.” = Late. Note that earlier listing of an elapid in the Upper Site LF (Archer et al., 1989) was in error

Les gisements du Tertiaire de Riversleigh connus pour contenir des restes d’élapidés, montrent l’étendue des âges possibles ainsi que d’autres familles d’ophidiens présents (Scanlon, 1996 ; voir Archer et al., 1989, 1997 pour la description des termes « site », « faune locale » (LF) et « systèmes »). « E » = inférieur, « M » = moyen, « L » = supérieur. Notez que l’attribution d’un élapidé à Upper Site LF (Archer et al., 1989) résultait d’une erreur

Site or LF name	Âge	Pythonine	Typhlopoid	Madtsioid	Elapid
Two Trees LF	M. Mio. – E. Plio.	+	–	–	+
Encore Site LF	early L. Mio.	+	+	+	+
Tertiary System C					
Main Site	M. Mio.	+	–	–	+
Henk’s Hollow	M. Mio.	+	+	+	+
Group Site	M. Mio.	–	–	–	+
Bob’s Boulder	M. Mio.	–	+	–	+
Gotham City	M. Mio.	+	+	+	+
Tertiary System B					
RSO Site	L. Oligo.– E. Mio.	+	+	+	+

dorsal view), and prominent lateral lobes with anterior angle but rounded laterally. In anterior and posterior view, zygosphenes and zygantrum roof with slight concavities separating lateral from convex median lobes. Oval zygosphenal facets face more ventrally than laterally, at about 50° from vertical, defining planes that intersect at floor of neural canal. Zygantral facets project slightly from neural arch, just visible in dorsal view.

Paradiapophyses extend strongly below cotyle, bearing parapophyseal processes that extend anteromedially. Subcentral ridges and grooves are strongly defined, the ridges approximately straight in ventral view, extending from diapophyses to the narrow condylar neck. The grooves (subcentral paramedian lymphatic fossae, sensu LaDuke, 1991) indicate the vertebra is probably a posterior precaudal. Haemal keel narrow in the middle of the vertebra, widening to about half width of cotyle anteriorly (due to damage at this point, it is not clear whether it formed distinct subcotylar tubercles) and forming a moderately prominent hypapophysis posteriorly (about as deep as the condyle). The ventral margin is sigmoid in lateral view, rounded posteriorly (covered by dendrites so may be slightly angular, but certainly not acute) and the posterior edge nearly vertical, immediately joining the condyle without an intervening notch. Hypapophysis thickened ventrally, with indications of a medioventral groove posteriorly.

Remarks: This specimen is strikingly similar to posterior trunk vertebrae of *Laticauda colubrina* (Fig. 2). With the exception of the anteriorly notched zygosphenes in *L. colubrina*, and possibly the subcotylar tubercles and prezygapophyseal foramina, which may or may not have been present in the fossil, the differences in size and proportions could be attributed to ontogenetic change alone. Distinctive features of both include the neural spine with an expanded and concave distal surface, and distal bifurcation of the hypapophysis; the relatively short, broad form of the vertebra; large, oval zygapophyseal facets; and prominent, blunt, depressed and anteroventrally inclined prezygapophyseal processes. Given the great age of the fossil, and its inland location (thus

probable terrestrial or at least freshwater habits), it is most unlikely to be conspecific with any extant *Laticauda*. However, *L. laticaudata* (the only other *Laticauda* species yet compared) differs from both *L. colubrina* and the fossil in having more elongate vertebrae (at the same region of the trunk), more pointed prezygapophyseal processes, narrower zygapophyseal facets, and lacking any distal expansion or bifurcation of the neural spine or hypapophysis. In these respects *L. laticaudata* resembles most other elapids examined, implying that the fossil is nested within *Laticauda*, not basal to it.

Oldest Australian elapid and the immunological “clock”

Although the stratigraphy and biochronology of the Riversleigh deposits are still poorly understood, the elapid vertebra from RSO Site is either latest Oligocene or early Miocene in age (i.e., near the Chattian/Aquitainian boundary, 24 to 23 MYA) and thus much older than any of the other specimens reported here. Indeed, this appears to be the oldest elapid yet known in the world, as the record of *Naja* and *Micrurus* in Europe extends only to mammal biozone MN4, or approximately 16.0–17.0 MYA (see above, Introduction). The presence of a probable hydrophiine elapid in northern Australia at such a time has a bearing on the age of this radiation, and of its divergence from African and Asian elapids, as proposed by Schwaner et al. (1985).

Morphological, and most of the biochemical and genetic evidence, indicates that *Laticauda* is a basal lineage of the Australasian radiation, possibly the immediate sister group of all other extant lineages (McDowell, 1970; Schwaner et al., 1985; Keogh, 1998; Keogh et al., 1998). Transferrin immunologic distances (TIDs) of *Laticauda* species from Australian terrestrial elapids are similar to those between some of the Australian genera (Schwaner et al., 1985), which implies that the split between *Laticauda* and the other hydrophiines did not greatly pre-date the basal divergences within the other Hydrophiinae. Schwaner et al. (1985) estimated divergence times from TIDs by assuming that transferrin evolves at about 1.6 amino acid substitutions per million

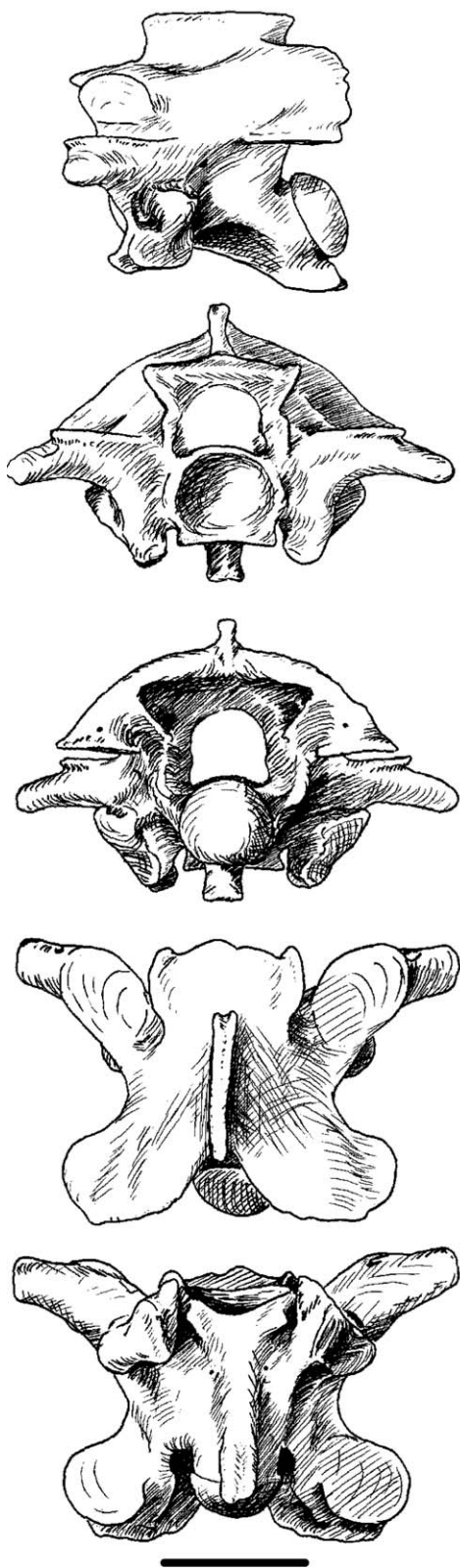


Fig. 2. Posterior trunk vertebra (number 164) of Recent *Laticauda colubrina* (SAM R26960), in (top to bottom) lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 2 mm.

Fig. 2. Vertèbre de la région postérieure du tronc chez le Récent *Laticauda colubrina* (SAM R26960), en vues (de haut en bas) latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 2 mm.

years, so that time of divergence (MYA) is approximately 0.3 times TID between two taxa. This implied a date of 12 MYA for the divergence between *Laticauda* and other Hydrophiinae (and thus for the origin of the latter clade). Dates of two deeper cladistic events were also estimated: Australasian and marine elapids (Hydrophiinae in the sense used here) vs. African and Asian taxa (Elapinae) at about 20 MYA, and elapids vs. “colubrids” (*Aparallactus* and *Dendrelaphis*) at about 35 MYA.

The RSO Site elapid (here considered to have lived 23–24 MYA) is thus somewhat older than the molecular-clock estimate for the initial divergence of elapines and hydrophiines, and the fossil record can be reconciled with the molecular dates only if the fossil lies outside both extant clades. This appears unlikely on biogeographic grounds, as well as in terms of the highly distinctive morphology shared with an extant species of *Laticauda*. On the other hand, if the provisional identification of affinities with *Laticauda* is correct, the fossil would lie within Hydrophiinae and the rate of transferrin evolution would be roughly half of that assumed by Schwaner et al. (1985). Resolution of this apparent inconsistency must wait for additional data relating to several areas of uncertainty: precise phylogenetic position and age of the fossil, and actual rates of molecular evolution in colubroid lineages.

***Incongruelaps iteratus* nov. gen. et sp.**

Figs. 3–5

Holotype: QM F42691 (Fig. 3(C)), a mid-trunk vertebra.

Type Locality: Encore Site, Riversleigh World Heritage Fossil Property.

Age: Late Miocene, approximately 10 MYA, based on biocorrelation of included fauna (Archer et al., 1997; Myers et al., 2001).

Etymology: Generic name from *incongruus* (Lat., “incongruous”, “disharmonious”) in reference to characters suggesting disparate, inconsistent affinities within Hydrophiinae; and *Elaps*, obsolete name on which names of Elapidae and many extant genera are based (McDowell, 1968); gender is masculine. Species epithet *iteratus* (Lat., “repeated”) in reference to the name of the type locality, and the multiple elements represented.

Diagnosis: Small elapid snake with relatively elongate vertebrae, subcentral ridges not prominent and nearly parallel posteriorly, subcentral grooves weakly defined or absent, and relatively small condyle and cotyle; narrow oval prezygapophyseal facets, prominent prezygapophyseal processes extending anterior to the facets; small, rounded postzygapophyseal facets; narrow zygosphenes with lateral and median lobes defined in dorsal view by discrete shallow emarginations (not broad concavities), median lobe with nearly straight transverse edge or divided by median notch; posterior margins of neural arch sinuous in dorsal view, producing a narrow and acute median emargination. Maxilla with fang weakly curved, its surface ornamented with fine longitudinal ridges; palatine process with short and blunt

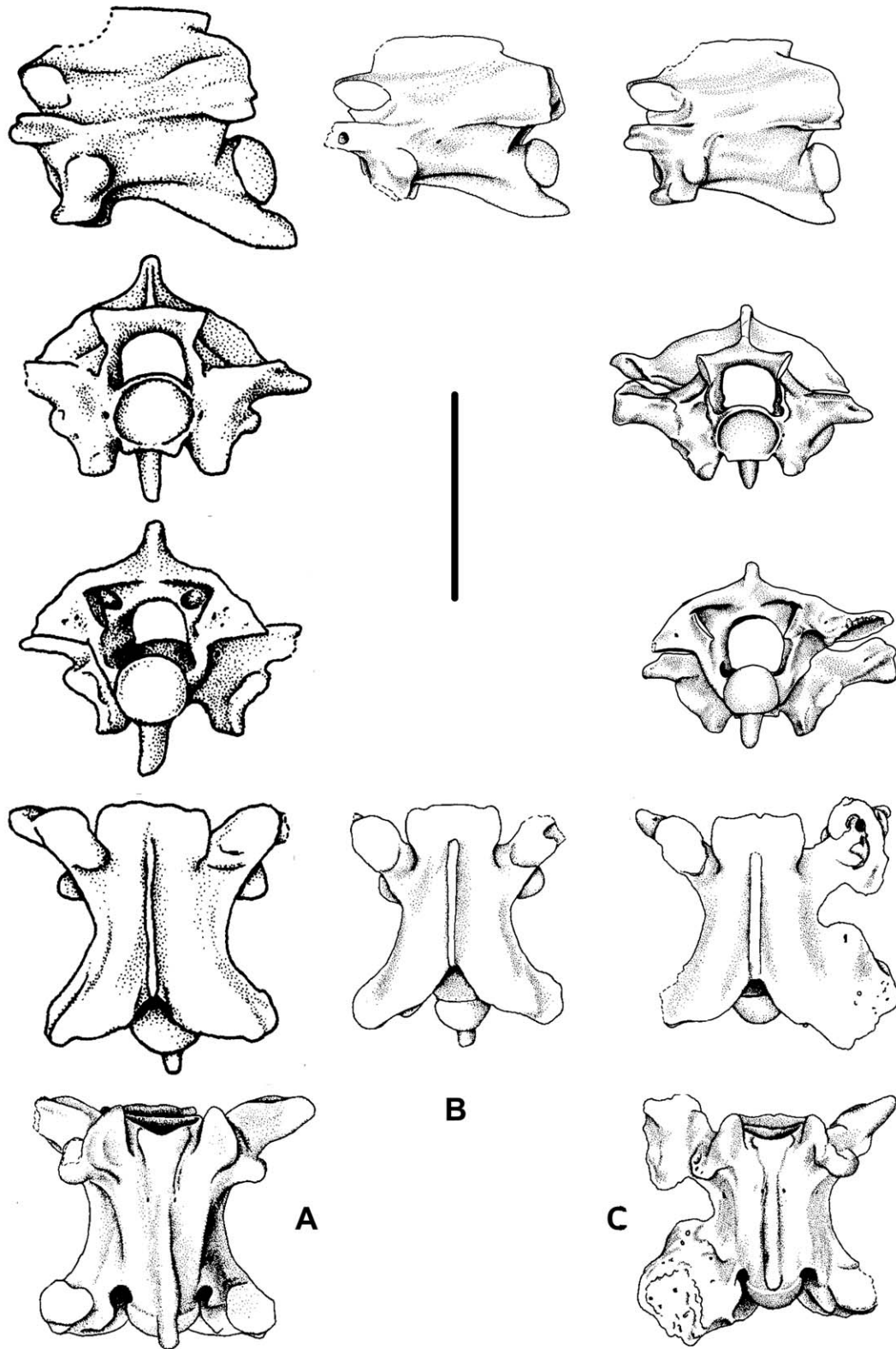


Fig. 3. Trunk vertebrae of *Incongruelaps iteratus* n. gen., n. sp. from Encore Site, Riversleigh (early Late Miocene). **A**, referred anterior trunk vertebra (one of 4 registered as QM F23272); **B**, referred posterior trunk vertebra (one of 13 registered as QM F23264); **C**, holotype posterior trunk vertebra (QM F42691). Top to bottom: lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 5 mm.

Fig. 3. Vertèbres du tronc chez *Incongruelaps iteratus* n. gen., n. sp., provenant du site « Encore » de Riversleigh (début du Miocène supérieur). **A**, vertèbre référée de la région antérieure (une des 4 enregistrées QM F23272) ; **B**, vertèbres référée de la région postérieure (une des 13 enregistrées QM F23264) ; **C**, vertèbre de la région postérieure (holotype QM F42691). De haut en bas, vues latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 5 mm.

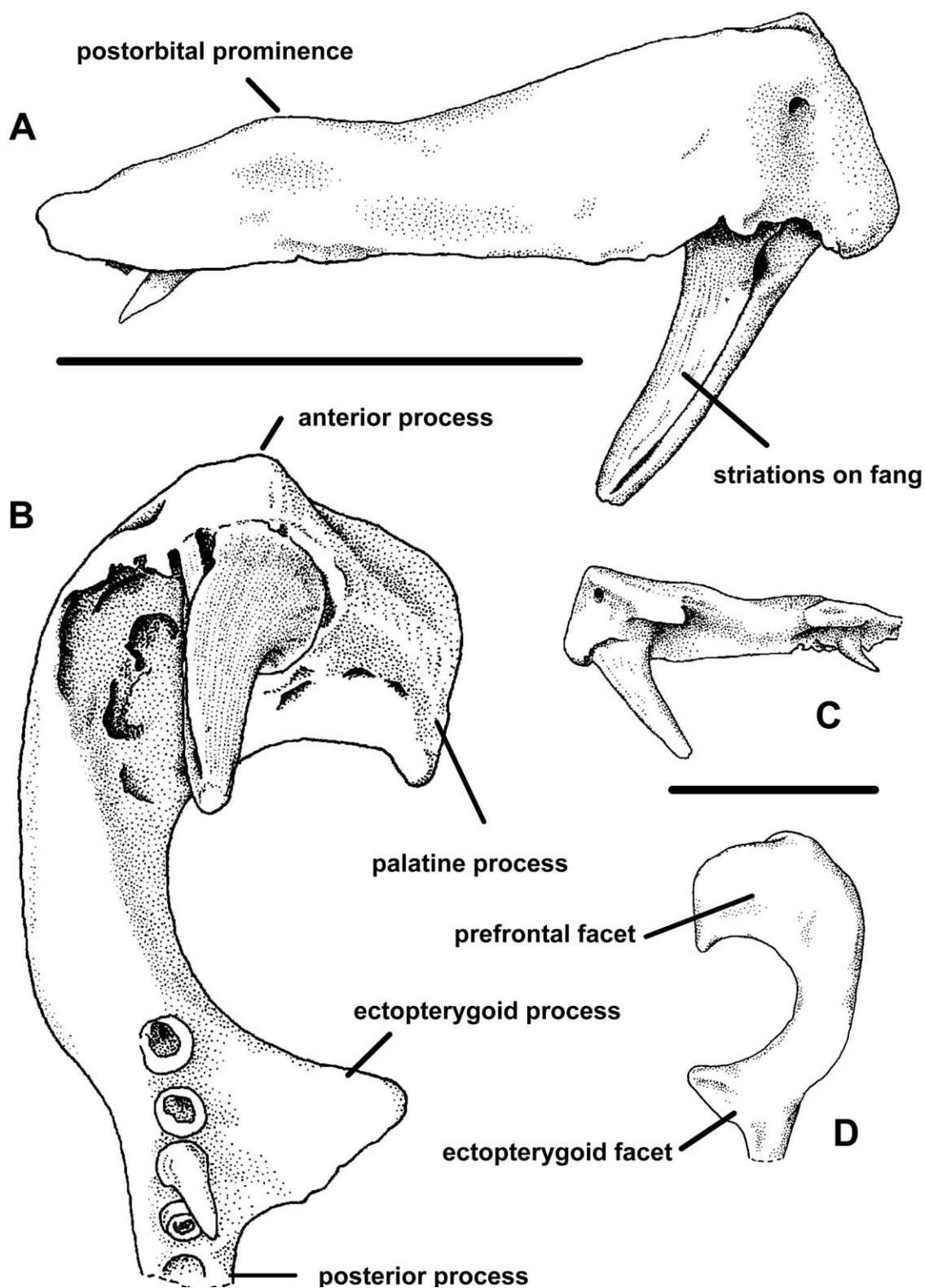


Fig. 4. Right maxilla referred to *Incongruelaps iteratus* n. gen., n. sp. (QM F23085), from Encore Site, Riversleigh (early Late Miocene), in (A–D) lateral, ventral, medial, and dorsal views. Scale bars = 3 mm (separate for A and B, C and D respectively).

Fig. 4. Maxillaire droit attribué à *Incongruelaps iteratus* n. gen., n. sp. (QM F23085), provenant du site « Encore » de Riversleigh (début du Miocène supérieur), en vues (A–D) latérale, ventrale, médiale et dorsale. Échelle = 3 mm (différentes pour A, B et C, D respectivement).

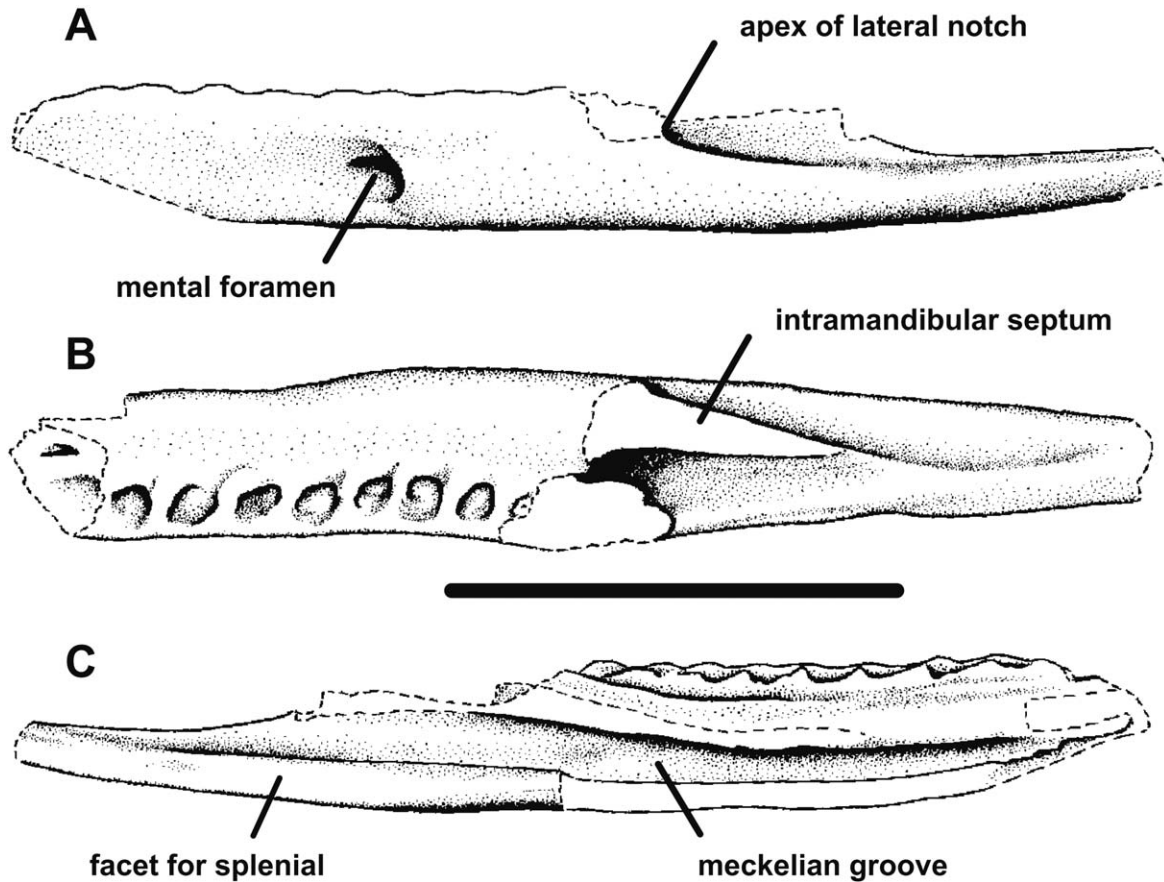


Fig. 5. Left dentary fragment referred to *Incongruelaps iteratus* n. gen., n. sp. (QM F23473), from Encore Site, Riversleigh (early Late Miocene), in (A–C) lateral, dorsal, and medial views. Scale bar = 3 mm.

Fig. 5. Fragment de la dentaire gauche attribué à *Incongruelaps iteratus* n. gen., n. sp. (QM F23473), provenant du site « Encore » de Riversleigh (début du Miocène supérieur), en vues (A–C) latérale, dorsale et médiane. Échelle = 3 mm.

posterior extension medially; ectopterygoid process a blunt, medially directed triangle; five or more small, solid posterior teeth following a diastema longer than the fang, the second solid tooth level with the apex of the ectopterygoid process; fourth and subsequent solid teeth on a narrow posterior process defined by concavities on both sides. Dentary with relatively small, uniform, closely spaced teeth in middle of element, with four alveoli between mental foramen and anterior apex of lateral notch for surangular.

Referred material: Right maxilla (QM F23085), left dentary fragment (F23473), 30 fragmentary to complete vertebrae (QM F23264 [13 specimens], F23265 [4], F23270 [3], F23272 [4], F23273 [2], F42692 [4]), incomplete ribs, including 4 rib heads (F23267); all found in close proximity and consistent in size with a single adult individual.

Description of the holotype: A relatively slender and elongate trunk vertebra, nearly undamaged but with the right pre- and postzygapophyses affected by irregular exostotic growth due to localized trauma or infection (other material indicates this does not affect the diagnostic value of other parts of the vertebra, see below). Centrum considerably longer than wide, wider than the condyle, and defined below by subcentral ridges, which are parallel for most of their length and not prominent (subcentral depressions weak).

Condyle and cotyle relatively small (equal in size to neural canal), subcircular, with ventral margin straight (in cotyle, straight section joins weakly defined subcotylar tubercles); precondylar constriction weak. Neural spine low, overhanging posteriorly. Neural arch elongate, moderately vaulted, with sinuous or weakly scalloped posterior margins separated by a deep but narrow median emargination of zygantral roof, exposing condyle and part of neural canal floor in dorsal view; interzygapophyseal ridge weakly defined, neural arch narrowest anterior to middle of its length. Zygapophyseal facets oval and fairly small, their long axes oriented slightly closer to sagittal than transverse direction; facets horizontal, slightly dorsal to plane of internal lateral ridges of neural canal; prezygapophyseal processes prominent, moderately pointed in dorsal view (but more so in horizontal view, i.e. somewhat flattened), with slight anterior curve, directed anterolaterally at near 45° from sagittal plane. Zygosphenes relatively narrow but broader than neural canal, lateral facets oval and elongated anteroposteriorly (long axis about 30° from horizontal in lateral view), facing more laterally than ventrally (about 30° from vertical in anterior view, defining planes that intersect near centre of cotyle); zygosphenes roof shallow, horizontal, with anterior edge relatively straight, a distinct but shallow median notch dividing the otherwise

slightly convex median lobe. Small, paired subcentral, lateral, paracotylar, parazygantral, and prezygapophyseal foramina.

Paradiapophyses deeper than cotyle, extending well below centrum, facing as much ventrally as laterally; well developed but blunt parapophyseal processes, directed anteriorly, and not constricting the space between parapophyses and subcotylar tubercles. Haemal keel narrows behind subcotylar tubercles, narrowest anterior to subcentral foramina, which are located about one-third distance from cotyle to condyle rim; posterior part of haemal keel produced as narrow hypapophysis, slightly sigmoid in lateral view, less than depth of condyle, with bluntly angular tip posterior to centre of condyle and separated from condyle lower margin by a broad notch. Except for the notches immediately below the cotyle, there is no development of subcentral grooves so the subcentral ridges are only weakly defined.

Maxilla: QM F23085 (Fig. 4), a right maxilla, undamaged except for the posterior process, which is broken through the fifth alveolus posterior to the diastema. One fang ankylosed and nearly complete, four posterior teeth ankylosed but only one complete.

The bone is relatively short and broad, with only a short and blunt anterior process immediately adjacent to the first fang. Foramina occur near the dorsal ends of both vertically elongate hollows defining this process. The anterior medial (palatine) process extends medial and only slightly posterior to the fang, with a short pointed extension at its posteromedial corner; the articular surface for the prefrontal extends for the full width of the maxilla across this process. The fang is relatively short, about 1.5 times the greatest depth of the bone, only slightly curved but directed posteriorly nearly as much as ventrally. The tip is damaged, and so the fang was originally slightly longer than figured. Venom canal of fang anterolateral in position, forming a visible suture connecting the basal and terminal openings of the lumen; the fang bears closely spaced longitudinal striations over its whole surface except adjacent to the venom canal. Second (unoccupied) fang position slightly posterior to first; diastema between second fang and first solid tooth approximately equal to fang length. The first four solid teeth are ankylosed, but only the third is preserved. The solid posterior teeth are about one third the diameter of the fang, and the single complete tooth is also approximately one third of the fang length. It is a relatively robust tooth with a slight sigmoid curve, ungrooved, with lateral and lingual ridges producing a blade-like tip. The bone is broken posteriorly through the unoccupied alveolus of the fifth solid tooth; the original length of the tooth row is uncertain, and several more teeth may or may not have been present on the narrow posterior process. The ectopterygoid process (posterior medial process) approximates an equilateral triangle, its base extending from the first to fourth solid tooth; the anterior edge is slightly concave and smoothly continuous with the medial edge anterior to it, while the posterior edge is separated from the medial edge of the narrow posterior process by a slight angular convexity

between the third and fourth solid teeth. The lateral edge of the maxilla is smoothly convex, becoming concave posteriorly at an angular inflexion level with the first solid tooth; this inflexion corresponds to a suborbital expansion of the dorso-lateral edge, defined in lateral view by anterior and posterior concavities.

Dentary: QM F23473 (Fig. 5) is a partial left dentary, missing the anterior tip, upper posterior process, tip of lower posterior process, and somewhat broken along medial edges. Seven complete alveoli are present along the lateral edge of the dorsal face, with part of another posteriorly; the alveoli decrease slightly in size from anterior to posterior, and none of them show signs of ankylosed teeth. In lateral view the alveolar margin is nearly straight, and in dorsal view the tooth row is slightly concave laterally. The dorsal surface of the dentary is about three times as wide as the alveoli, and slightly concave transversely. The alveoli are slightly elongate, their maximum diameters oriented anterolateral to posteromedial. A large mental foramen opens anteriorly on the lateral surface below the fifth preserved alveolus; its vertical diameter is nearly half the total depth of the bone, and a concavity extends from it forward to the anterior tip of the fragment. The ventral margin of the bone has a slight dorsal curvature posteriorly, below the lateral fossa for the surangular. The posterior dorsal process is broken off through the intramandibular septum as well as the tooth row, forming two almost separated areas of damage; the lower part of the septum continues as a ridge on the dorsal surface of the ventral process, extending almost to its posterior end (as preserved). The septum separates the mandibular canal (which leads into the mental foramen) laterally from the meckelian groove medially. In medial view, the meckelian groove narrows anteriorly; the ridge defining it dorsally is broken except for a portion from the first to third alveolus. The ventromedial ridge below the meckelian groove bears a sharply defined facet for the splenial posteriorly, changing to a rounded edge just behind the middle of the fragment; the anterior half of this ridge is broken away.

Additional vertebrae and ribs: About 30 elapid vertebrae are known from this deposit (mostly fragmentary), and also some incomplete ribs. As in the holotype, the other vertebrae are relatively elongate, with a low neural spine, and prominent, dorso-ventrally flattened prezygapophyseal processes. In most specimens the anterior edge of the zygosphenes is “four-lobed”, with a median notch more or less as in the holotype (Fig. 3(A)); in others the edge has a straight median portion separated by slight notches from the two lateral lobes (Fig. 3(B)). Variation in vertebral size, proportions, and form of the hypapophysis appears consistent with typical intracolumnar variation in the anterior to posterior trunk of a single skeleton. The other near-complete specimens (e.g., Fig. 3(A, B)) collectively demonstrate that the pathology of the type vertebra is limited to the obvious irregularity of part of the right side, so that in other respects it serves as a typical (and very well preserved) specimen.

Remarks: The numerous, morphologically distinctive elapid vertebrae from Encore Site appear to be consistent with a single individual, and this interpretation allows the maxilla and dentary to be referred provisionally to the same skeleton, and thus to provide information on the same taxon. However, only one vertebra is designated as a type, since the possibility (however remote) of misassociation cannot be refuted by the evidence now available.

Very similar (but possibly less elongate) vertebrae are known from Main Site, and a smaller but otherwise similar form from Gotham City Site (Table 1; see below). Unlike these specimens, all other Riversleigh elapids (like most extant species examined) have relatively broader vertebrae, and either a single rounded median lobe on the zygosphene or (in larger forms only) a broad median concavity. Vertebral elongation comparable to the Encore form has been seen among extant elapids only in the whipsnakes *Demansia*, and suggests a slender, “racer-like” body form (cf. also *Coluber*, *Masticophis* etc. among other colubroids; Holman, 2000). In *Glyphodon tristis*, the zygosphene has a straight-edged median section separated by notches from the lateral lobes, as in some of the Encore specimens. However, the *Glyphodon* vertebrae are primitive with respect to the fossil in being less elongate, and share several possible synapomorphies with *Furina* (e.g., *F. barnardi*, SAM R27022): forward-curving prezygapophyseal processes, scalloped posterior border of the neural arch, and notched or forked anterior end of neural spine. *Furina* spp. have a trilobed zygosphene as in most other genera, and the straight zygosphene edge in the fossil and *Glyphodon* is here considered convergent. Comparisons of elapid vertebral form capable of isolating phylogenetically informative characters from intracolumnar, ontogenetic, and ecomorphological variation remain far from complete, but the vertebrae from Encore Site are sufficiently distinctive to justify the recognition of a new taxon.

The cranial material is not as strikingly distinctive, but the maxilla in particular provides a number of features that can be compared with a broad sample of taxa. The elapid maxilla may be divided for convenience into a series of regions from anterior to posterior: toothless anterior process, prefrontal region (with fangs, dorsal facet for prefrontal sloping down posteriorly, and medial palatine process), suborbital region (relatively horizontal in lateral view, with or without teeth posterior to diastema), and ectopterygoid region (with medial process, teeth usually present, and dorsal edge sloping down posteriorly). The following characters can be evaluated based on maxillary morphology preserved in the fossil (see Table 2); in most cases the primitive state (usually, State 0) within hydrophiines can be identified by comparison with other elapids (Elapines, represented by specimens of *Naja*, *Ophiophagus*, *Bungarus* and *Micrurus*). The characters scored here are, by themselves, clearly insufficient for a meaningful phylogenetic analysis of Hydrophiinae; they will contribute to such analyses in future, but the table is given here as a concise summary of comparative observations discussed below. Variation within genera (indicated as polymor-

phism in Table 2) in most cases represents variation between species, but intraspecific variation also occurs and they are here treated as equivalent.

- The anterior process in the fossil is short and blunt in ventral view, as in most of the terrestrial and marine elapids examined (State 0). A minority of taxa have a more prominent or acute process (State 1). Only *Furina* and *Simoselaps* have been found to exhibit both conditions.
- The anterior process is positioned ventrally, so that in lateral view the anterior edge is oblique (sloping posterodorsally) relative to the long axis of the bone, as in most extant elapid genera (State 0). In a minority of taxa the anterior process is in a more dorsal position producing a bulbous, vertical or overhanging anterior edge (1). Both conditions have been observed in *Salomonelaps*, *Pseudechis*, *Oxyuranus*, *Glyphodon*, *Demansia*, and *Drysdalia*; both are also present in the outgroup (e.g., variable within *Ophiophagus*).
- The alveolus of the first tooth (fang) is centred slightly anterior to the second alveolus, as in most elapid taxa (State 1). This is intermediate to two other states recognized here: *Parapistocalamus*, *Toxicocalamus*, *Furina*, *Simoselaps*, *Paroplocephalus*, *Ephalophis*, *Emydocephalus*, and *Hydrophis* have less longitudinal overlap, hence the fangs are more obliquely aligned (0), while in *Pelamis* they are quite transverse (2). States 0 and 1 are known in *Naja*, *Vermicella*, *Hydrelaps*, and *Aipysurus*, 1 and 2 in *Salomonelaps* and *Suta*, and all states (or 0 and 2 only) in *Micrurus*, *Glyphodon*, *Elapognathus*, and *Denisonia*. This character forms a morphocline 0-1-2.
- The fang is weakly but uniformly curved; such slight curvature is seen in *Micropechis*, *Aspidomorphus*, *Rhinoplocephalus*, *Cryptophis*, *Parasuta*, and *Emydocephalus* (State 2). In other forms where the curvature is as uniform, it is greater throughout (*Bungarus*, *Laticauda*, *Pseudonaja*, *Oxyuranus*, *Neelaps*, *Cacophis*, *Acanthophis*, *Denisonia*, *Notechis*, *Tropidechis*, *Aipysurus*; State 1). The plesiomorphic condition (State 0) is to have the fangs straight distally, with stronger curvature localized near the base, which characterizes most of the remaining taxa. States 0 and 1 both occur in *Pseudechis*, *Furina*, *Elapognathus*, *Echiopsis*, and *Hydrophis*, 1 and 2 in *Glyphodon* and *Simoselaps*, and all three conditions in *Suta*. This character forms a morphocline 0-1-2.
- The fang is quite short, its total length less than twice the maximum depth of the maxilla, as in the majority of elapids (State 1). Fang length is equal to or more than twice depth of maxilla in some *Naja*, some *Salomonelaps*, *Ogmodon*, *Micropechis*, *Pseudechis*, *Oxyuranus*, *Elapognathus coronatus*, *Echiopsis*, *Acanthophis*, *Denisonia*, *Paroplocephalus*, *Cryptophis boschmai*, some *Suta*, and some *Hydrophis* (State 0). The shortest fangs of any species examined (by this or other criteria considered) occur in *Cryptophis nigrostriatus*.

Table 2

Taxon x character-state matrix for characters of the maxilla (1–13), dentary (14), and parietal (15–16) defined in the text. Basic taxa are the genera of Hydrophiinae (excluding some marine forms) listed in Material Examined; several elapine taxa are also included as an outgroup. Variation within or between species of basic taxa treated as polymorphism: abbreviations “a” = (0 and 1), “b” = (1 and 2), “c” = (0 and 2, or 0, 1 and 2)

Matrice de taxon x caractère pour les caractères du maxillaire, dentaire et pariétal, qui sont définis dans le texte. Les taxons de base sont les genres d'Hydrophiinae (mise à part quelques formes marines) listés dans l'Appendice. Plusieurs taxons d'élapins sont aussi inclus comme un extra-groupe. Les variations intraspécifiques ou interspécifiques sont considérées comme polymorphisme : abréviations « a » = (0 & 1), « b » = (1 & 2), « c » = (0 & 2, ou 0, 1 & 2)

	5	1 0	1 5	
<i>Bungarus</i>	11111	00101	01000	0
<i>Micrurus</i>	00c01	0000a	0–00a	1
<i>Naja</i>	00b0a	00abb	00010	0
<i>Ophiophagus</i>	0a101	00101	02000	0
<i>Acanthophis</i>	01110	00b21	0b000	1
<i>Aspidomorphus</i>	10121	00200	1baa1	0
<i>Austrelaps</i>	01101	00210	12000	0
<i>Cacophis</i>	10111	10111	ab1a1	a
<i>Cryptophis</i>	0012a	00b1a	aa1a0	a
<i>Demansia</i>	0a101	00ba2	12aa1	0
<i>Denisonia</i>	10c10	00110	a20a0	0
<i>Drysdalia</i>	1a101	00000	0a001	0
<i>Echiopsis</i>	011a0	00b10	010a0	0
<i>Elapognathus</i>	01caa	00200	a1aa0	0
<i>Furina</i>	a00a1	00bac	abaa0	a
<i>Glyphodon</i>	1acb1	0021a	12aa0	1
<i>Hemiaspis</i>	01101	00b10	120a0	0
<i>Hoplocephalus</i>	00101	0012a	020a0	0
<i>Laticauda</i>	00111	00011	0201a	0
<i>Loveridgelaps</i>	00101	00b1b	02a00	0
<i>Micropechis</i>	00120	00211	01000	1
<i>Neelaps</i>	00111	00a12	00001	0
<i>Notechis</i>	00111	00210	a20a0	0
<i>Ogmodon</i>	00100	01112	12001	1
<i>Oxyuranus</i>	0a110	00020	a2010	1
<i>Parapistocal.</i>	10001?–110	0–001	0	
<i>Parasuta</i>	0012a	002a0	0a10a	a
<i>Paroploceph.</i>	00000	00221	01010	0
<i>Pseudechis</i>	0a1a0	00210	a1000	0
<i>Pseudonaja</i>	01111	00010	12010	0
<i>Rhinoploceph.</i>	00121	00110	00101	1
<i>Salomonelaps</i>	0ab0a	001b1	ac000	0
<i>Simoselaps</i>	a00b1	00c1b	aaa01	a
<i>Suta</i>	00bca	00ba1	acaaa	1
<i>Toxicocalamus</i>	10001	01212	a2001	0
<i>Tropidechis</i>	00111	00200	a2010	1
<i>Vermicella</i>	10a01	002a0	00a0a	1
<i>Aipysurus</i>	00a11	00cab	1200a	0
<i>Ephalophis</i>	00001	000a1	12111	0
<i>Emydocephalus</i>	10021	0–002	0-0-a	1
<i>Hydrelaps</i>	00a01	0000b	a1101	0
<i>Hydrophis</i>	100aa	00cab	a2a01	0
<i>Pelamis</i>	10201	00011	12100	0
Encore sp.	00121	10111	1111?	?
Two Trees sp. 1	?????	?????	?????	0
Two Trees sp. 2	?????	?????	?????	1

- The fine longitudinal striations seen on the surface of the fang have only been observed in *Cacophis*, where they occur in some but not all specimens examined (State 1), but they are more numerous in the fossil; all other elapids examined have smooth fangs (State 0).

- A diastema is present between the fangs and posterior teeth (State 0), as in all hydrophiine genera other than *Ogmodon*, *Toxicocalamus* and the marine *Kerilia* (the latter not examined in this study) (State 1). The character is not applicable when no teeth are present behind the

fangs, but scored for the outgroup taxon *Micrurus* based on its close relative *Micruroides* (Slowinski, 1995).

- The palatine process has a short and blunt posterior extension of its medial edge in the fossil, as in most elapids (State 1). Two other states are recognized: such an extension is absent, the process simply rounded or bluntly angular, in *Micrurus*, *Laticauda*, *Pseudonaja*, *Oxyuranus*, *Drysdalia*, *Ephalophis*, *Hydrelaps*, *Emydocephalus*, *Pelamis*, and some *Naja*, *Neelaps*, *Simoselaps*, *Aipysurus* and *Hydrophis* (State 0); or considerably longer and acute in *Toxicocalamus*, *Vermicella*, *Micropechis*, *Pseudechis*, *Glyphodon*, *Aspidomorphus*, *Elapognathus*, *Austrelaps*, *Notechis*, *Tropidechis*, *Paroplocephalus*, and some specimens of *Loveridgelaps*, *Furina*, *Simoselaps*, *Demansia*, *Hemiaspis*, *Echiopsis*, *Acanthophis*, *Cryptophis*, *Parasuta*, *Aipysurus* and *Hydrophis* (State 2). In the most extreme expression of State 2, the posterior extension nearly or quite touches the ectopterygoid process so that the maxilla completely surrounds the anterior part of the infraorbital fenestra (e.g., some *Pseudechis* and *Vermicella*). There is no distinct facet on the medial face of the process in the fossil (as there is in *Naja*), indicating that the palatine probably lacked a lateral process as in most hydrophiines.
- In lateral view there is an angular dorsolateral prominence separating the suborbital margin from the ectopterygoid region, presumably for insertion of the postorbital ligament, as in the majority of hydrophiines (State 1). The same state is assigned to taxa with a weak to strongly developed prominence, but these are intermediate to two other states: the prominence is absent (maxilla smooth dorsally) in *Aspidomorphus*, *Elapognathus*, *Drysdalia*, *Tropidechis*, *Hydrelaps*, *Emydocephalus*, and some *Furina*, *Vermicella*, *Parasuta*, *Suta*, *Ephalophis*, *Aipysurus*, and *Hydrophis* (State 0), while in *Oxyuranus*, *Acanthophis*, *Paroplocephalus*, *Hoplocephalus*, and some *Naja* and *Salomonelaps*, the dorsal prominence forms a vertical step or distinct overhanging process abutting the anterior tip of the ectopterygoid (State 2). These states form a morphocline, 0-1-2.
- The medial ectopterygoid process forms an acute but blunt triangle directed medially, as in most elapines and many hydrophiine taxa (State 1). This is intermediate to two other states recognized here. The process is sharp and directed anteromedially in *Parapistocalamus*, *Pseudechis*, *Pseudonaja*, *Oxyuranus*, *Vermicella*, *Aspidomorphus*, *Hemiaspis*, *Elapognathus*, *Echiopsis*, *Drysdalia*, *Denisonia*, *Austrelaps*, *Notechis*, *Tropidechis*, *Rhinoplocephalus*, *Parasuta*, and some *Micrurus*, *Glyphodon*, *Furina*, *Hoplocephalus*, and *Cryptophis* (State 0). In *Toxicocalamus*, *Ogmodon*, *Demansia*, *Neelaps*, *Acanthophis*, and some *Naja*, *Loveridgelaps*, and *Simoselaps*, the process is not angular but bluntly convex and anteroposteriorly longer than wide (State 2).

These states form a morphocline 0-1-2, with the intermediate considered plesiomorphic.

- The number of posterior teeth (at least five) is higher than observed in any elapines (0–4, see also Bogert, 1943), but falls within the wider range in hydrophiines (0–18). Four or fewer teeth is here considered plesiomorphic (State 0), five or more derived (State 1); the latter condition characterizes *Ogmodon*, *Demansia*, *Glyphodon*, *Aspidomorphus*, *Hemiaspis*, *Austrelaps*, *Ephalophis*, *Aipysurus*, and *Pelamis*, but numerous hydrophiine taxa span both states (*Salomonelaps*, *Toxicocalamus*, *Pseudechis*, *Oxyuranus*, *Furina*, *Simoselaps*, *Cacophis*, *Elapognathus*, *Denisonia*, *Notechis*, *Tropidechis*, *Suta*, *Hydrelaps*, *Hydrophis*). If the fangs of elapids are derived from posterior teeth as in many Colubridae (Jackson and Fritts, 1995, 1996), the presence of numerous solid teeth posterior to them is derived (McDowell, 1968), and the same polarity can be inferred by the outgroup criterion if *Laticauda* and Elapinae form successive outgroups to the remaining Hydrophiinae. Multiple instances of reversal (secondary reduction in tooth number) are also inferred within Hydrophiinae.
- Only one of the posterior maxillary teeth is anterior to the apex of the medial (ectopterygoid) process, as in *Bungarus*, *Micropechis*, *Pseudechis*, *Paroplocephalus*, *Hydrelaps* (State 1); two or more teeth are anterior to the apex (extending into the suborbital region) in *Ophiophagus*, *Laticauda*, *Loveridgelaps*, *Toxicocalamus*, *Ogmodon*, *Pseudonaja*, *Oxyuranus*, *Demansia*, *Glyphodon*, *Hemiaspis*, *Denisonia*, *Austrelaps*, *Notechis*, *Hoplocephalus*, *Tropidechis*, *Ephalophis*, *Aipysurus*, *Hydrophis*, and *Pelamis* (State 2), while all teeth are posterior to the apex in *Naja*, *Vermicella*, *Neelaps*, *Aspidomorphus*, *Cryptophis*, and some *Salomonelaps*, *Simoselaps*, *Drysdalia*, *Rhinoplocephalus*, *Cryptophis*, *Parasuta*, and *Suta* (State 0). These states form a morphocline 0-1-2. States 0 and 1 both occur in *Simoselaps*, *Elapognathus*, *Echiopsis*, *Drysdalia*, *Cryptophis*, and *Parasuta*; 1 and 2 both occur in *Furina*, *Cacophis*, *Aspidomorphus*, and *Acanthophis*, while *Salomonelaps* and *Suta* show all three states.
- The teeth extend posteriorly along a narrow process defined by lateral and medial concavities. This posterior process (overlapped by the shaft of the ectopterygoid) is equally distinct in *Cacophis*, *Rhinoplocephalus*, *Cryptophis*, *Parasuta*, *Ephalophis*, *Hydrelaps*, and *Pelamis* (State 1). In the other taxa (including all elapines) the posterior process is either absent, or defined by a concavity on only one side (State 0), but both states have been recorded in *Loveridgelaps*, *Demansia*, *Glyphodon*, *Furina*, *Simoselaps*, *Vermicella*, *Aspidomorphus*, *Elapognathus*, and *Suta*.

Because of its very incomplete preservation the dentary is less informative. The only real “landmarks” preserved are the alveoli, the dorsal and ventral margins of the bone, the mental foramen, and the anterior limit of the fossa for the compound.

The foramen and fossa are separated longitudinally by four alveoli, a distance rather more than the depth of the dentary in this region. This is a longer gap than observed in any of the extant elapids examined except for *Demansia simplex*, but is approached by *Hemiaspis*, *Pseudonaja*, and some other *Demansia* which have generally slender jaws and small, closely-spaced teeth. In Table 2, character 14 is scored as: number of alveoli between mental foramen and lateral fossa less than three (0), three or more (1).

In summary (Table 2), the highest number of cranial characters matching those of the fossil (13 of 14) is found in *Cryptophis* and *Suta*, with 12 in *Cacophis*, 11 in *Furina* and *Simoselaps*, and 10 in *Demansia*, *Glyphodon* and *Salomone-laps*. *Cryptophis* and *Suta* are closely related to each other (along with *Rhinoplocephalus* and *Parasuta*) within the viviparous clade (Shine, 1985; Greer, 1997) and quite variable in maxillary morphology; the only feature of the fossil maxilla outside the range of variation in these genera is the striations on the surface of the fang (character 6). These are shared only with *Cacophis*, from which the fossil differs in having a short and blunt anterior process (1) and straighter fang (4). *Cacophis* is not closely related to the *Cryptophis*-*Suta* group, but usually considered a close relative of *Furina* and *Glyphodon* (McDowell 1967, Schwaner et al., 1985; Wallach, 1985; Keogh et al., 1998; Scanlon, in press).

At present there is no evidence of more than one individual in the associated elapid material from Encore, so the comparisons suggest a “mosaic” of similarities (some derived) with widely distinct extant genera. This mosaic evolution, or incongruent parallelism in different characters, makes precise phylogenetic placement impossible at this stage. If any one character can be preferred as most likely to be informative, the striations on the surface of the fang appear to support a relationship with *Cacophis*. The possibility that the material might be from several different individuals cannot be ruled out (given the material is disarticulated); however, this is unlikely given the scarcity of elapid fossils and the fact that the identity and size of the preserved elements are all consistent with a single individual.

The extant taxa most similar to the fossil in maxillary morphology are nocturnal, shelter and often forage under rocks, logs and leaf litter, feed almost entirely on skinks (Shine, 1991), and are widely distributed in forested regions of eastern and northern Australia, including rainforest (*Suta* spp. occupy relatively xeric habitats, which is clearly derived). A particular feature that could suggest nocturnal habits is the short suborbital region of the maxilla, indicating a relatively small eye, and this may also be plesiomorphic (as seen in *Pseudechis*, *Micropechis*, *Loveridgelaps*, *Salomone-laps*). Their similarities with each other and with the fossil may thus be due to symplesiomorphy and/or convergence in trophic biology, and no definite phylogenetic conclusion can be reached on this evidence; however, they give a hint as to the habits of the Miocene snake. Its non-specialized morphology and comparisons with extant taxa suggests a terrestrial habit (possibly “sheltering”, but not fossorial), probably

primarily scincivorous (widespread in Hydrophiinae including basal terrestrial forms, hence probably plesiomorphic).

In contrast to the affinities and habits suggested by the maxilla, the relatively small and closely spaced alveoli of the dentary, and its nearly straight and parallel dorsal and ventral margins, are quite unlike conditions in nocturnal scincivores like *Cryptophis*, *Cacophis*, *Furina* and *Glyphodon*, which have relatively thick teeth and a bowed dentary. In these respects (not yet scored as discrete characters), the fossil instead resembles *Hemiaspis signata*, *Pseudechis porphyriacus* and some species of *Pseudonaja* and *Demansia*, mainly diurnal forms with more generalized diets. As the elongate vertebrae suggest a relatively slender body form, associated in extant terrestrial snakes with diurnal activity and pursuit of fast-moving prey (e.g., *Demansia*, *Masticophis*), the plesiomorphic features of the maxilla should probably be discounted as indicators of the habits of this snake.

Hydrophiinae sp. cf. *Incongruelaps iteratus*

Material and description: QM F42693 (Fig. 6), from Main Site (Gag Plateau, Riversleigh), middle Miocene. Four elapid vertebrae are known from this site, all somewhat damaged but presenting features that allow comparison with material from other sites. Several unusual features shared with the material from Encore Site suggest identification or close affinity with *I. iteratus*: the zygosphenes are notched in the midline, the subcentral ridges relatively weak and parallel posteriorly, and the larger trunk vertebrae are relatively elongate. The zygapophyses slope slightly upwards, which reflects a more anterior position in the trunk than the type described above (cf. variation in sample from Group Site, below).

Hydrophiinae gen. indet. spp. 1 and 2

Figs. 7–9

Material: Two Trees Site: QM F23071, F42694 (parietals), F42695 (11 vertebrae), F42696 (4), F42697 (9), F42698 (6 ribs). It seems a remarkable coincidence that the only elapid braincase elements known from the Australian fossil record are two parietals from a single site, but representing distinct taxa. The age of the site is uncertain, at most late Middle Miocene and possibly as young as Pliocene (see Remarks below).

Description:

- Parietal form 1 (sp. 1). QM F23071 (Fig. 7) is the larger of the two parietal specimens, maximum length 6.9 mm. Broken to left of midline, but right side complete except for slight erosion of the ventral margin. Dorsal border with frontals nearly directly transverse where preserved on left side, oblique on right, separated by a bluntly triangular median prominence. Just behind the frontal border there are a number of fine, slightly sinuous longitudinal grooves on the dorsal surface. Broad triangular anterolateral (supraorbital) and lateral (postorbital) processes form prominent shelves above and behind the orbit (preserved on the right only); the middle part of the

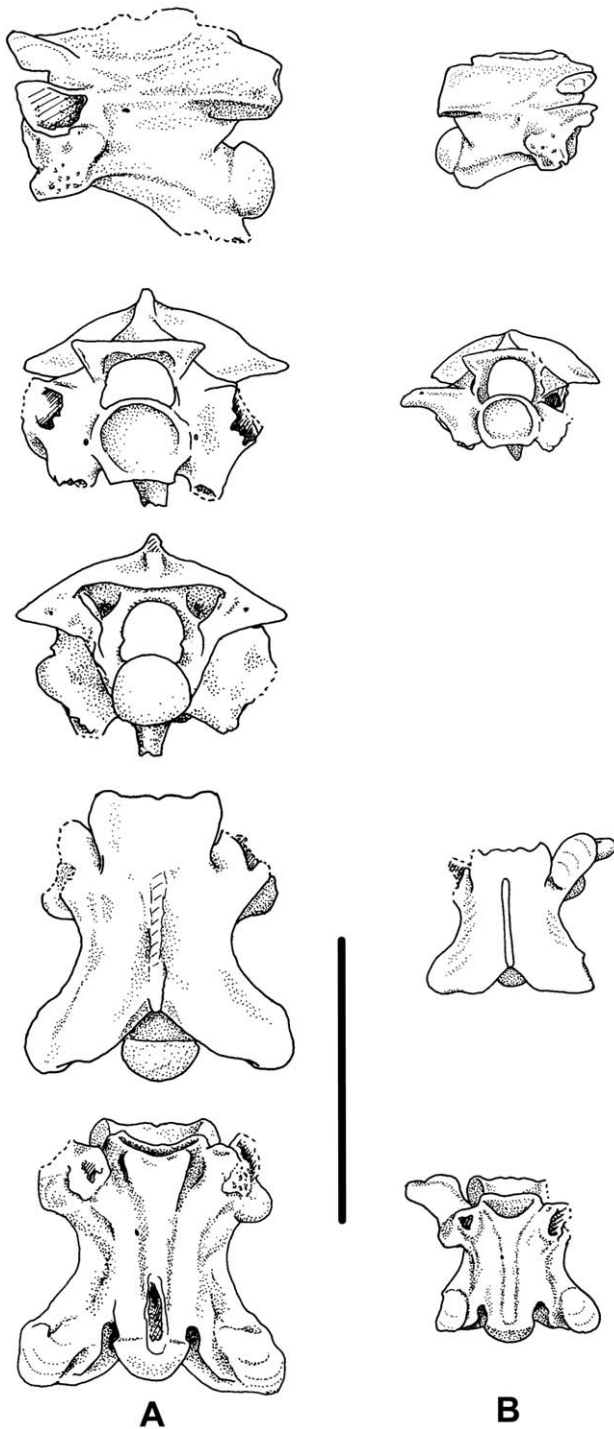


Fig. 6. Hydrophiinae sp. cf. *Incongruelaps iteratus* (QM F42693), vertebrae from Main Site, Riversleigh (Tertiary System C, middle Miocene). **A**, middle trunk; **B**, posterior trunk vertebra. Top to bottom, lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 5 mm.

Fig. 6. Hydrophiinae sp. cf. *Incongruelaps iteratus* (QM F42693), vertèbres provenant du site « Main », de Riversleigh (System C du Tertiaire, Miocène moyen). **A**, vertèbre du tronc moyen ; **B**, vertèbre de la région postérieure du tronc. De haut en bas, vues latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 5 mm.

supraorbital shelf is slightly elevated, and overlaps the anterior portion slightly at a fold-like notch on the margin. A shallow groove for attachment of the postorbital bone extends along the margin of both processes, on the ventral side of the supraorbital shelf and the dorsal side of the postorbital process, thus forming a distinct notch or cusp between the two processes where the groove crosses the orbital margin.

On the dorsolateral surface, a low crest (crista parietalis) marks the boundary of adductor muscle attachment, extending from the orbital margin of the supraorbital process at an approximately right angle to the edge of the bone; crest more weakly defined in the middle third of its length (partly obscured by low, irregular transverse wrinkles of the bone surface), but well defined in the posterior third where it converges toward its opposite member. The two crests remain separated by a shallow median concavity (0.5 mm wide posteriorly), so there is no true sagittal crest. There is no pair of parietal foramina, but they are represented by a small, transversely elongate depression posterior to the centre of the dorsal surface (occurrence of these foramina is variable in extant taxa; Scanlon, in press). The braincase posterior to the postorbital shelf is smoothly bulbous laterally, but the posterior part of the dorsal surface is broadly concave lateral to the crista parietalis. Posterolateral and posterior margin on the right side consists of four nearly straight segments, defining an angular concavity for the prootic, and implying a broadly W-shaped contact (with median concavity) with the supraoccipital. The recessed contact surface for the anterodorsal part of the prootic is partly exposed laterally, but for much less than half the depth of the parietal (this may have been reduced by breakage).

Anterior to the postorbital process, the lateral surface is the smoothly concave posterior and medial wall of the orbit. The anterior margin is formed by (in dorsal to ventral order) the supraorbital process, a concave margin for contact with the frontal descensus, the more strongly concave margin of the optic fenestra (approximately semicircular, and extending less than a third of the total depth of the bone), and the suboptic process. The latter was damaged before being illustrated, but complete when first examined, forming a blunt cone directed anteriorly (as in the other parietal specimen, see below).

- Parietal form 2 (sp. 2). QM F42694 (Fig. 8) is the left side of a parietal, maximum length 6.3 mm. Broken along an irregular line from just medial to left supraorbital process, to a posterior extremity inferred to be very close to the midline (thus, maximum length measurement closely approximates the true value). The supraorbital process is well developed but relatively narrower than in the other specimen, and lacks a notch on its anterolateral margin, but is equally well distinguished by a notch and overhang from the postorbital process.

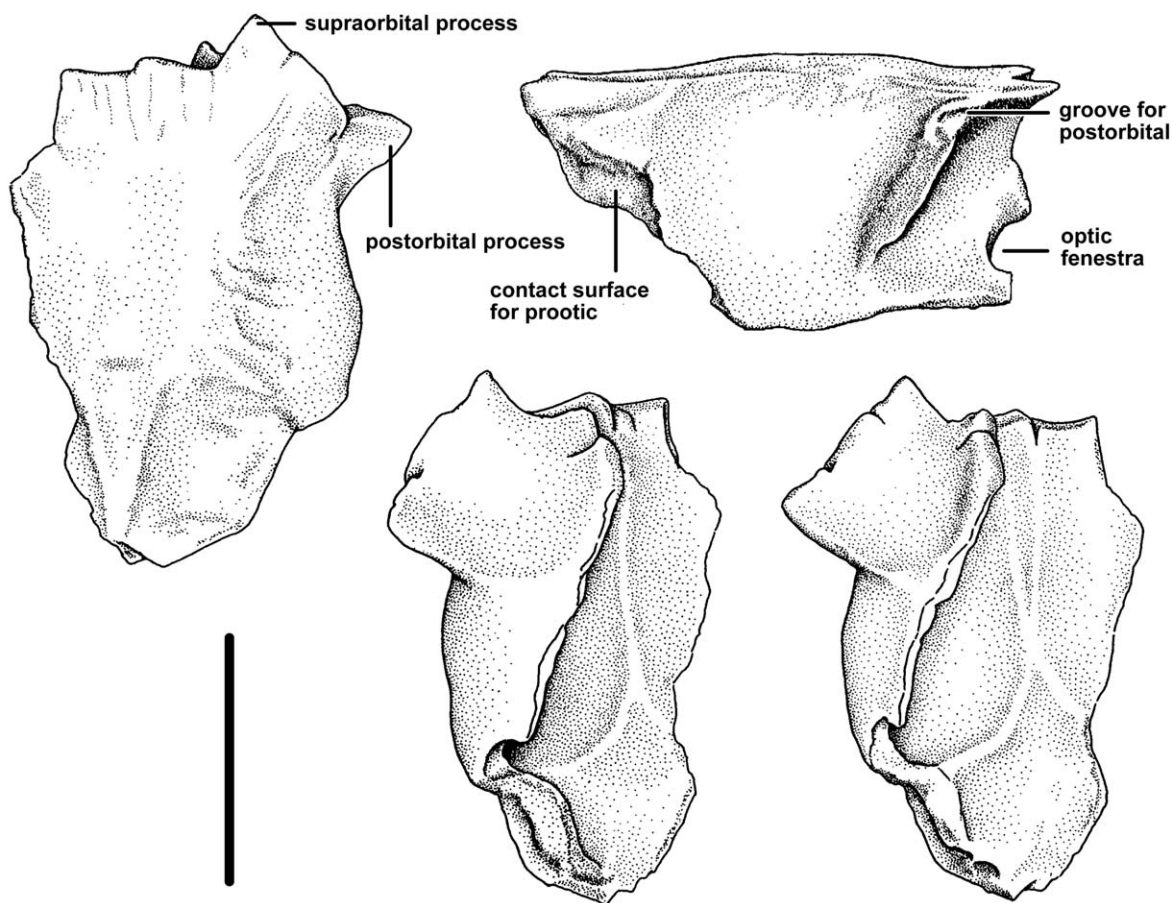


Fig. 7. Parietal of *Hydrophiinae* gen. indet. sp. 1 (QM F23071) from Two Trees Site, Riversleigh (middle to late Miocene, or early Pliocene) in dorsal, lateral, and two ventral views. Scale bar = 3 mm.

Fig. 7. Pariétal d'un *Hydrophiinae* gen. indéterminé, sp. 1 (QM F23071) provenant du site « Two Trees » de Riversleigh (Miocène moyen au supérieur, ou Pliocène inférieur), en vues dorsale, latérale et deux vues ventrale. Échelle = 3 mm.

The latter appears similar in lateral view and the groove for attachment of the postorbital is similarly developed, but the postorbital process is much less prominent laterally in its middle and ventral part, so that it forms a narrow, elongate, roughly rectangular projection in dorsal view rather than a broad triangle.

The preserved parts of the adductor crest are more weakly developed than in the first specimen. The posterior part of the crest, and any parietal foramina, pits or sculpture near the midline, are not preserved. As in the first specimen the parietal is smoothly bulbous laterally, and concave dorsally in its posterior part, but the margins of contact with the prootic and supraoccipital are weakly undulating rather than angular; there is no evidence of a median posterior concavity. The recessed contact surface for the prootic is very large, its lateral exposure extending most of the depth of the parietal.

The parietal contribution to the posterior and medial wall of the orbit is similar in extent in both specimens, but the anterior border is distinctly different. While the supraorbital and suboptic processes are similar, the concave margin of the optic fenestra is shallow, more weakly defined, and extends much further dorsally; the

frontal border is thus shorter, and also nearly vertical rather than sloping anteroventrally in its ventral part; rather than a deep anterior prominence of the middle part of the parietal border there is only a slight crest, which was apparently overlapped laterally by the frontal descensus.

- **Vertebrae and ribs.** This site contains trunk vertebrae from individuals of considerably different sizes (ranging in centrum length from 1 to 4 mm), and it is not clear whether they can be differentiated taxonomically, or which of them can be associated with the different-sized parietal specimens. All are similar in most respects, with most of the observed variation attributable to ontogenetic and intracolumnar effects. The following description concentrates on the best-preserved material (Fig. 9), which appears consistent with a single adult skeleton; some comments on other specimens are included parenthetically.

Neural arch broad and depressed, with dorsolateral margins convex or straight in posterior view, straight or slightly concave in dorsal view on either side of a narrow median posterior emargination. Interzygapophyseal ridge strongly developed and smoothly concave later-

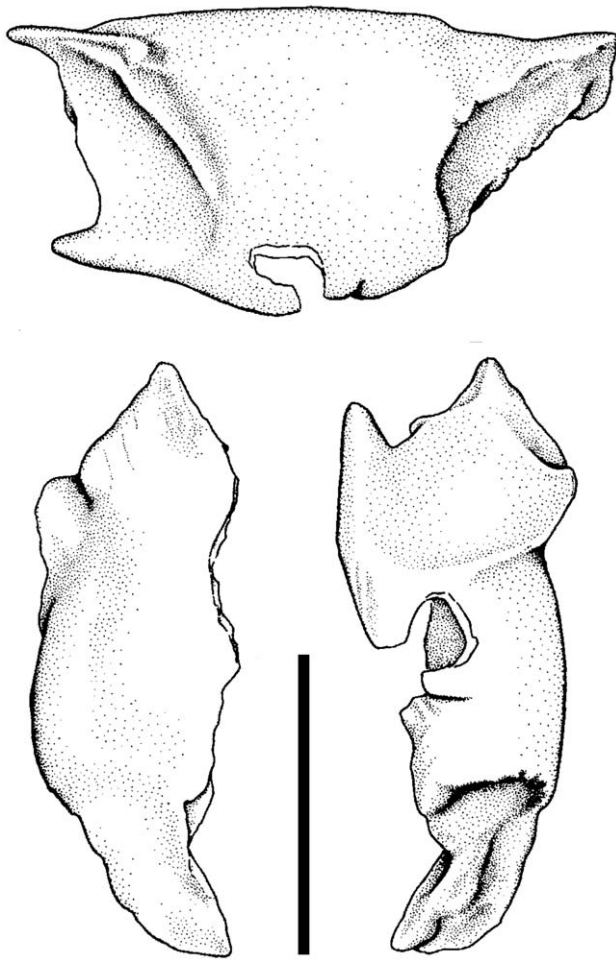


Fig. 8. Parietal of *Hydrophiinae* gen. indet. sp. 2 (QM F42694) from Two Trees Site, Riversleigh (middle to late Miocene, or early Pliocene) in dorsal, lateral, and ventral views. Scale bar = 3 mm.

Fig. 8. Pariétal d'un *Hydrophiinae* gen. indéterminé, sp. 2 (QM F42694) provenant du site « Two Trees » de Riversleigh (Miocène moyen au supérieur, ou Pliocène inférieur), en vues dorsale, latérale et ventrale. Échelle = 3 mm.

ally, narrowest at the middle of the vertebra. Moderately high neural spine beginning level with rear edge of zygosphenal facets; dorsal edge of spine not straight but slightly convex and sloping down posteriorly, overhanging posteriorly but usually not anteriorly. Prezygapophyseal facets oval to subtriangular, long axis about 45° from sagittal plane; postzygapophyseal facets less regular and variable in outline but mostly broader. Prezygapophyseal processes short, acute in dorsal view but blunt in anterior view, not extending anterior to prezygapophyseal facets, and with a large anterior foramen. Zygosphenon with weakly convex median lobe separated by smooth concavities from more prominent lateral lobes. Roof of zygosphenon horizontal in adult trunk vertebrae, arched in adult 'cervical' vertebrae and in all juvenile vertebrae. Zygosphenal facets oval, long axis approximately 30° from horizontal in lateral view; usually

slightly convex laterally, but approximating planes that would intersect at or slightly below the floor of the neural canal.

Relatively deep centrum defined below by prominent subcentral ridges that taper almost uniformly to the base of a well-developed condylar "neck"; condyle and cotyle larger than neural canal (except in cervical and juvenile vertebrae), nearly hemispherical, and only slightly oblique. Paradiapophyses large, extending ventrally well beyond cotyle; diapophysis and parapophysis equally large in lateral view, and parapophyseal processes well developed, extending anteroventrally. Subcotylar processes prominent and pointed, directed ventrolaterally and defining an anterior expansion of the haemal keel that is almost as wide as the cotyle. Haemal keel reduces gradually in width, not constricted at level of subcentral foramina. Hypapophysis with sigmoid anteroventral edge, rounded or bluntly acute distally, projecting posteriorly beyond condyle in anterior and mid-trunk vertebrae.

Adult and juvenile vertebrae differ in the form of the haemal keel and hypapophysis. In adults the keel is sharply defined by subcentral grooves. The anterior triangular expansion bears prominent, ventrolaterally pointed subcotylar processes as described above; the hypapophysis has a sigmoid lower edge and is relatively blunt posteriorly. The juvenile vertebrae also have distinct subcentral grooves, but the haemal keel is less sharply defined in ventral view, and subcotylar processes less prominent. The hypapophysis is less deep, its lower edge being straight rather than sigmoid, with a relatively sharp point below the condyle.

Remarks: The Two Trees deposit is only doubtfully attributed to the Middle Miocene System C sequence on the basis of topographic position, and may be somewhat younger, possibly even Pliocene. Archer et al. (1997) note that "Correlation of Two Trees Site, despite its high position on the Gag Plateau, is very uncertain. ... Like other localized, "crown" deposits on the tops and flanks of the Tertiary plateaus, it may be considerably younger in age than the sediment on which it rests". The extant genus *Bettongia* (Marsupialia, Potoroidae) is represented by a plesiomorphic species from the site (*B. moyesi* FLANNERY and ARCHER, 1987) (Flannery and Archer, 1987), but is not yet known from other Riversleigh deposits. This site has also produced a palatine bone of a large pythonine snake distinct from *Morelia riversleighensis* (a long-lived species recognized from Systems A, B, C and the mid-Miocene Bullock Creek LF; Scanlon, 2001), and which may instead be referable to the Pliocene *Liasis dubudingala* SCANLON and MACKNESS, 2002.

A number of features of the parietals represent more or less discrete states of characters that can be scored for living taxa. Most of these will be discussed elsewhere (Scanlon, in prep.), but Table 2 includes two characters (15–16) relating to the postorbital process. Many elapids, including most

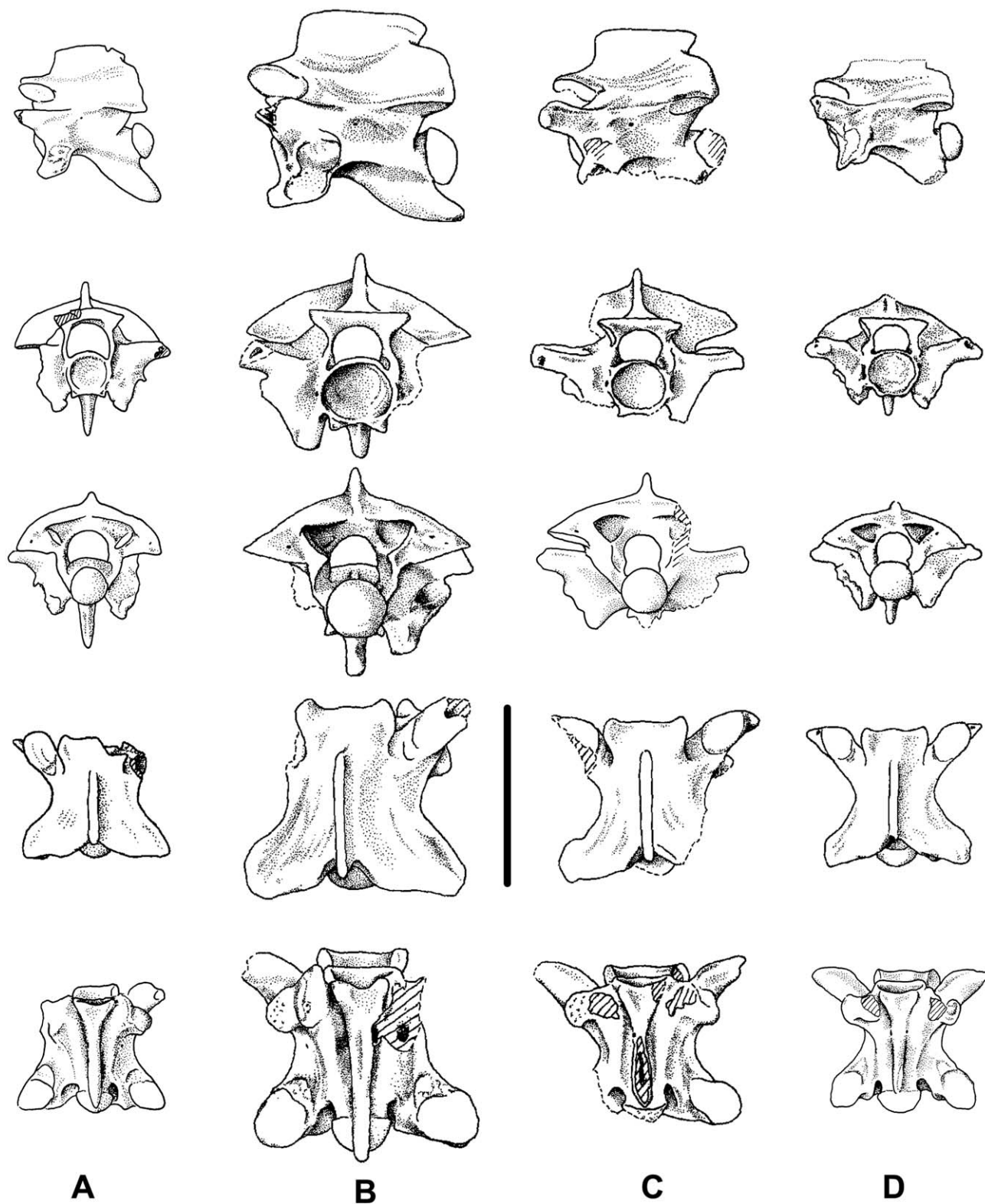


Fig. 9. Hydrophiinae indet. four well-preserved vertebrae (QM F42695) from Two Trees Site, Riversleigh (middle to late Miocene, or early Pliocene). Left to right, vertebrae from the anterior, middle, and two from the posterior trunk region, possibly of a single skeleton (although at least two individual elapid snakes are represented by parietals in the deposit). Top to bottom, lateral, anterior, posterior, dorsal, and ventral views (lateral view of B reversed). Scale bar = 5 mm.

Fig. 9. Hydrophiinae indéterminé, quatre vertèbres bien préservées (QM F42695) provenant du site « Two Trees », de Riversleigh (Miocène moyen au supérieur, ou Pliocène inférieur). De gauche à droite, vertèbre de la région antérieure, médiane, et deux de la région postérieure du tronc, probablement d'un même squelette (bien que, basé sur les fragments du pariétal, il y aurait au moins deux individus dans ces gisements). De haut en bas, vues latérale, antérieure, postérieure, dorsale et ventrale (vue latérale B inversée). Échelle = 5 mm.

elapines as well as *Salomonelaps* and other Melanesian taxa, have the postorbital processes quite prominent and acute, but anteroposteriorly short, as in the fossil parietal form 1. In the corresponding derived states, the process is much less prominent (15), and/or elongated posteriorly (16); these vary quite independently, but the second parietal possesses both apomorphies. Despite these and some other differences, both parietals resemble in proportions and most details such extant taxa as *Bungarus*, *Laticauda*, *Salomonelaps*, *Loveridge-laps*, *Pseudechis*, *Pseudonaja* and *Hemiaspis*, but differ more significantly from most other elapids examined. These extant genera do not form a monophyletic group, but represent relatively basal lineages (Schwaner et al., 1985; Wallach, 1985; Slowinski and Keogh, 2000); most of the character states expressed on the fossil parietals are therefore likely to be primitive for Hydrophiinae as a whole. The fossils can therefore be neither referred to extant genera, nor readily diagnosed as distinct. On the other hand, the differences between the two parietal specimens are consistent with a level of differentiation often subjectively attributed to separate genera.

In extant forms, the depth of the optic foramen is approximately proportional to the size of the eye itself. In QM F23071 the small foramen indicates a small-eyed nocturnal species, while F42694 has a large foramen and thus relatively large eyes, suggesting it was probably diurnal (the only large-eyed but predominantly nocturnal elapids are *Tropidechis* and *Hoplocephalus*, which form a monophyletic group derived from a *Notechis*-like diurnal ancestor, probably within the last 5 MY; Schwaner et al., 1985; Keogh et al., 1998, 2000).

The vertebrae from this site, like the parietals, represent relatively generalized and plesiomorphic hydrophiines, but can not currently be diagnosed to any extant or new taxon.

HYDROPHIINAE indet.

Other vertebral material without associated cranial elements probably represents several additional taxa. The sites listed below all belong to the Gag Plateau sequence (Tertiary System C) and are considered to be middle Miocene in age (Archer et al., 1987, 1997).

- Group Site. QM F42699 (12 vertebrae). This site contains the largest number of well-preserved elapid vertebrae yet known from Riversleigh. Fig. 10 shows one anterior and one middle trunk vertebra, four from the posterior trunk, and two caudals of similar size but rather different proportions (one anterior, one posterior). Many if not all of the differences within the sample may be attributed to serial variation, and possibly only a single individual is represented.

The neural arch is broad (in most but not all vertebrae) but moderately vaulted, with posterior margins smoothly convex in posterior view, and also dorsally where they form a broad median emargination. Neural spine low to moderate, sloping down and usually overhanging posteriorly, but quite variable. Prezygapophy-

seal facets oval, with long diameter close to 45° from sagittal plane; postzygapophyseal facets smaller and more angular, roughly trapezoidal. Prezygapophyseal processes short and relatively deep, not extending beyond the facets anteriorly, with anterior foramina level with the outer edge of the facets. Zygosphenes broad, trilobate with rounded median lobe in dorsal view; horizontal in most vertebrae, with rather shallow and steeply overhanging facets defining planes meeting at or just below floor of neural canal. The grooves defining the haemal keel laterally are not as sharply incised as in the Two Trees material, and the subcotylar processes are present but rounded rather than pointed (consistent with correlated variation between states of the subcentral grooves and subcotylar processes, as suggested by LaDuke, 1991). The largest trunk vertebra has a deep hypapophysis, rounded distally in lateral view, with a smoothly sigmoid anterior edge and obtusely angular posterior edge below the condyle; more posterior vertebrae have the process less deep and becoming more acute in lateral view. In one vertebra (Fig. 10(A)) the hypapophysis is nearly as deep but more oblique, and appears peculiar because of damage to its posterior margin; the arched zygosphenes, ventrally prominent paradipophyses, and several small prominences on the rear of the neural arch, indicate an anterior (“cervical”) position. The broad anterior caudal, and much narrower posterior caudal, suggests that (if they represent the same taxon) the distal part of the tail may have been somewhat laterally compressed, but not approaching the condition in true sea snakes.

Vertebrae similar in size, proportions and hypapophysis shape to the largest specimen occur at about the 20th vertebra in adult *Cacophis squamulosus*. Similar proportions but larger size occur in the same region of *Pseudonaja* spp. and probably other genera (this region has not been examined in most taxa).

- Gotham City Site. QM F42700 (5 vertebrae); two large vertebrae (incomplete), and three small (two of latter articulated; Fig. 11), probably not consistent with one individual. The small posterior trunk vertebrae are similar to those from Group Site, but the most complete of the large anterior vertebrae has some unusual features: the neural arch is strongly elevated posteriorly, its posterior margin rather straight in dorsal view with a narrow median emargination; the neural spine is high and overhanging anteriorly; and subcentral ridges weakly defined.
- Henk’s Hollow Site. QM F42701 (5 vertebrae). Mid-trunk vertebrae from this site are fragmentary, but there are good anterior trunk, and caudal, vertebrae (Fig. 12). These have the narrow posterior emargination of the neural arch also seen in material from Gotham and Two Trees, but the samples do not allow adequate comparisons at the same intracolumnar position.

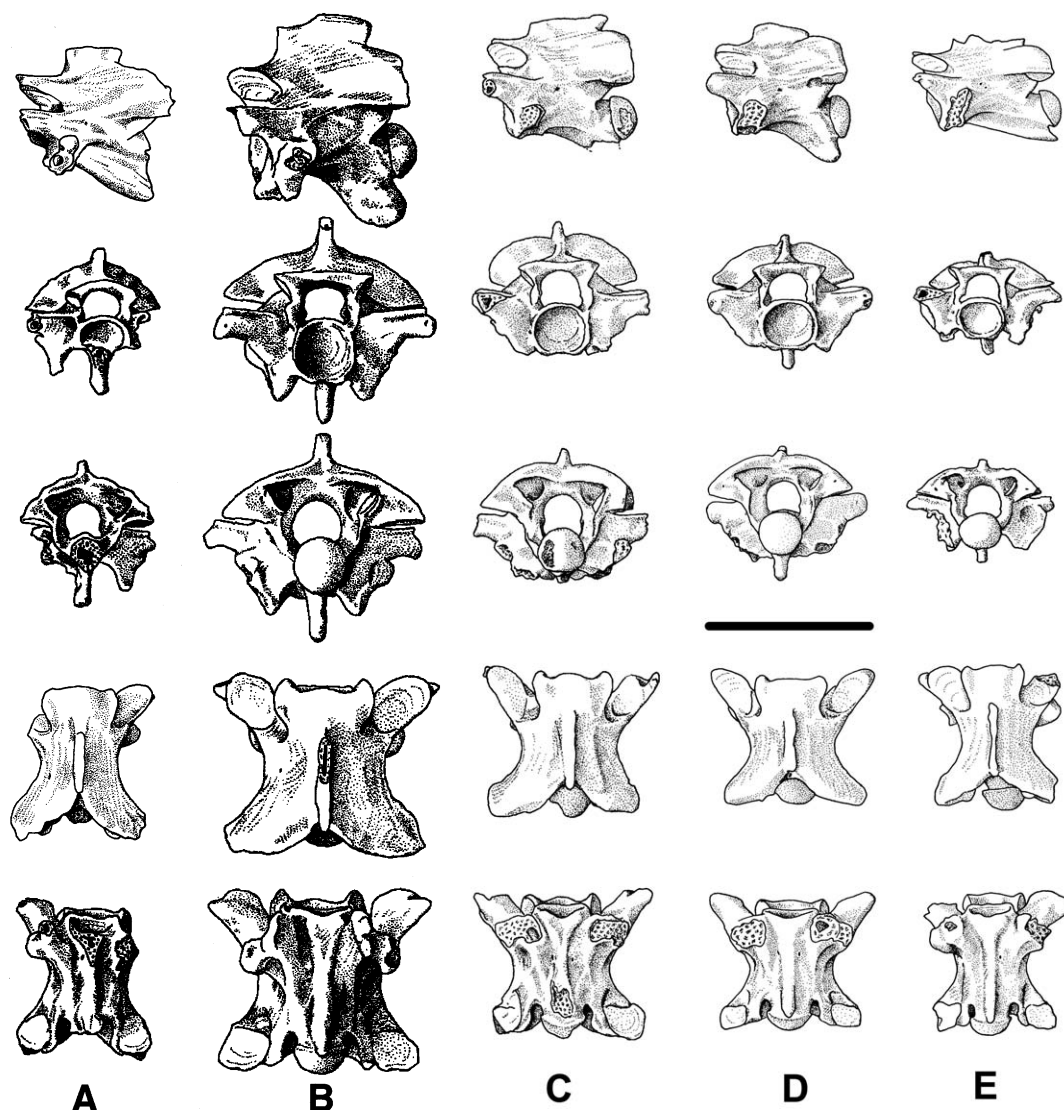


Fig. 10. Hydrophiinae indet. eight well-preserved vertebrae (QM F42699) from Group Site, Riversleigh (Tertiary System C, middle Miocene). Left to right, vertebrae from the anterior (A), middle (B), and four from the posterior trunk region (C–F), one anterior caudal (G) and one mid-caudal (H). Top to bottom, lateral, anterior, posterior, dorsal, and ventral views (lateral views of A and F reversed). Scale bar = 5 mm.

Fig. 10. Hydrophiinae indéterminé, huit vertèbres bien préservées (QM F42699) provenant du site « Group » de Riversleigh (Système C du Tertiaire, Miocène moyen). De gauche à droite, vertèbre de la région antérieure (A), moyenne (B), quatre vertèbres de la région postérieure du tronc (C–F), une de la région caudale antérieure (G) et une caudale moyenne (H). De haut en bas, vues latérale, antérieure, postérieure, dorsale et ventrale (vues latérales A et F inversées). Échelle = 5 mm.

A well-preserved anterior trunk (“cervical”) vertebra (Fig. 12(A)) is complete on the right but lacks the zygapophyses and diapophysis on the left. The centrum is slightly longer than wide, and neural canal somewhat larger than cotyle. Condyle and cotyle round, slightly oblique. Subcentral, lateral and paracotylar foramina present. Neural spine low and short, with backwardly inclined anterior edge well posterior to zygosphenes, and weakly defined posterior limit. Neural arch with weakly undulating, dorsally convex posterior edges and a relatively small notch above zygantrum. Neural canal arched, about as wide as high, with internal lateral ridges below centre. Zygapophyseal facets inclined above horizontal, level with internal lateral ridges, defining planes

that intersect at base of neural canal. Facets narrow (prezygapophyseal facet subtriangular, postzygapophyseal oval), with long axis at about 30° from sagittal plane. Small prezygapophyseal process directed anterolaterally, sharp in dorsal but bluntly angular in anterior view, with small foramen. Interzygapophyseal ridge smooth, weakly defined in middle of its length. Zygosphenes wide, with arched, rounded median lobe and prominent lateral lobes with anterior angle but rounded laterally. Narrowly oval zygosphenal facets have their long axes inclined steeply anterodorsally, and face ventrolaterally, at about 45° from vertical, defining planes that intersect at base of neural canal. Paradiapophyses extend strongly below cotyle, parapophyseal processes

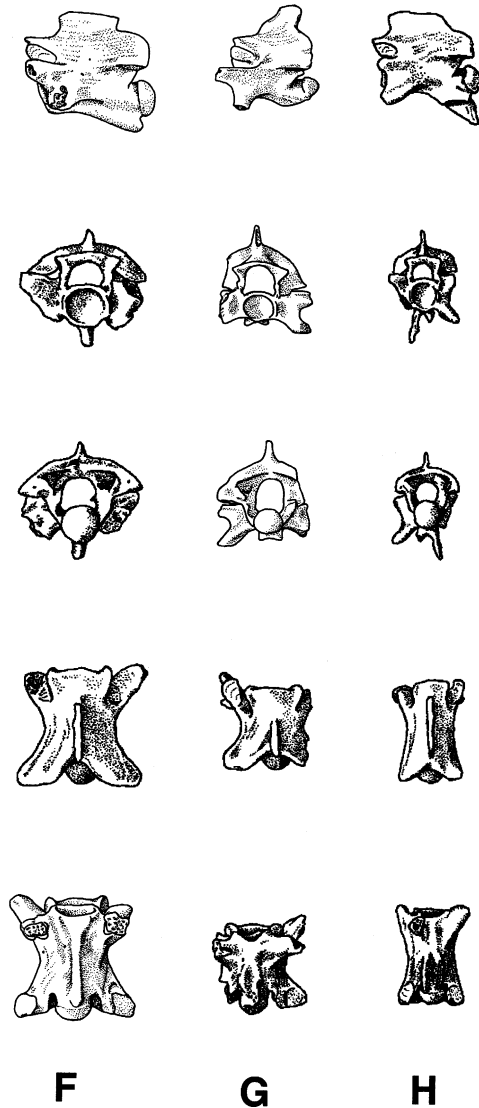


Fig. 10 (suite).

acute and directed anteroventrally. Subcentral ridges and grooves are only weakly defined. Low, blunt subcotylar tubercles; hypapophysis becomes prominent only just before mid-length of the centrum, extending strongly ventrally and somewhat posteriorly, with parallel anterior and posterior edges and a bluntly angular tip. A caudal vertebra (Fig. 12(B)) lacks parts of the zygosphenes, both prezygapophyses and pleurapophyses. The centrum is much longer than wide, and neural canal slightly smaller than cotyle. Subcentral, lateral and paracotylar foramina present. Neural arch shallowly arched and with a broad, blunt notch above zyganchrum; a distinct hollow between dorsal edge of neural arch and zyganchrum roof. Neural spine short but about as high as long, with backwardly inclined anterior edge well posterior to zygosphenes, and a steep posterior edge. Neural canal arched, about as wide as high, with internal lateral ridges below centre. Zygapophyseal facets horizontal, level with base of neural canal. Facets small, subtrian-

gular, with long axis at about 45° from sagittal plane. Prezygapophyseal processes not preserved. Interzygapophyseal ridge smooth, weakly defined in middle of its length. Zygosphenes wide, similar to cervical in anterior view but with damaged facets and anterior edge. Subcotylar tubercles absent; haemapophysis prominent below posterior half of the centrum, elongate antero-posteriorly and fairly strongly forked.

- Bob's Boulder Site. QM F23075 (Fig. 13). Two fragmentary vertebrae, comparable to the smaller adult vertebrae from Two Trees Site. The relatively elongate form, and weak, posteriorly parallel subcentral ridges, are resemblances to *Incongruelaps* gen. nov. However, the subcotylar tubercles are unusually close to the midline and the lateral margins of the anterior part of the haemal keel are convex (ventral view), producing a 'wine-glass' shape not seen in any other specimens. This difference is likely to reflect at least specific difference from the other fossils.

4. General discussion

As elapids are relatively rare elements of most of the local faunas where they do occur, it is likely that, except where there is evidence to the contrary, each deposit contains the remains of only a single individual and hence, a single taxon (cf. Scanlon, 1992). The only site where the presence of two taxa is strongly indicated is Two Trees (based on parietals), but the samples from Group and Gotham City seem likely to combine skeletons of different sizes, if not distinct taxa. Association of cranial elements with vertebral material is relevant for two sites: Two Trees (where vertebrae can not be assigned with any probability to one or the other skeleton represented by parietals) and Encore (where all vertebrae are consistent with a single skeleton, allowing the two jaw elements to be referred to the same individual).

Phylogenetic analysis of extant forms can provide evidence for the existence and various attributes of inferred common ancestors, but such ancestral forms are likely to represent only a minority of the actual elapid fauna that has existed in Australasia over the last 25 million years. For instance, the melange of derived traits observed in *Incongruelaps* – which occur in distantly related extant forms – could not have been predicted from optimisation of characters in a phylogeny based only on extant taxa. The fossil elapids known from Riversleigh represent at least four distinct taxa, but their relationships to each other and to extant genera are unresolved; the more informative cranial elements (parietals, maxilla) indicate relatively plesiomorphic and generalized members of the Hydrophiinae. All are relatively small, with none approaching the body sizes characteristic of widespread extant taxa such as *Pseudechis* and *Pseudonaja*. This may accurately reflect an early elapid fauna of limited diversity and small body sizes. On the other hand, the continental fauna might well have already diversified, but with generalized plesiomorphic forms being most abundant at River-

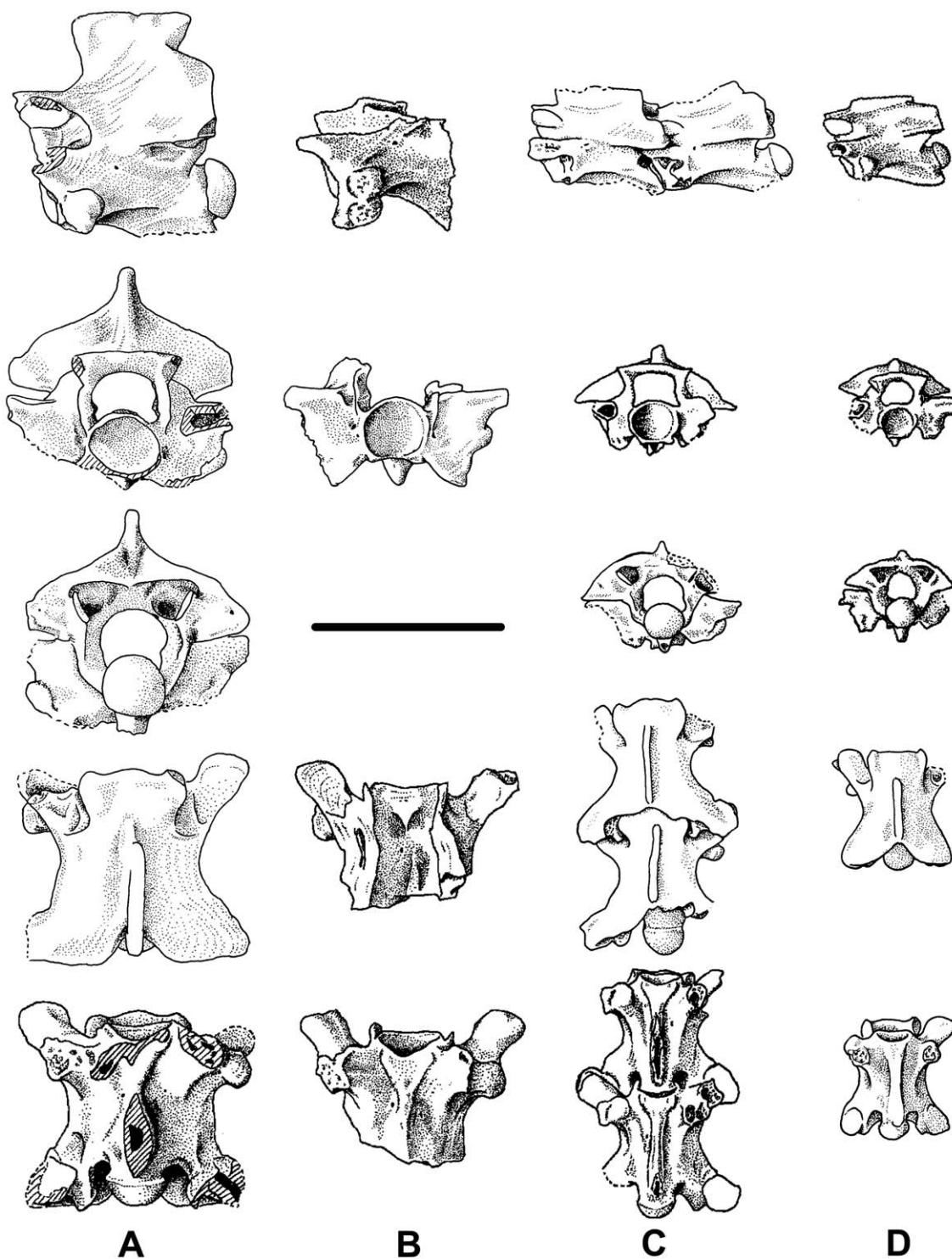


Fig. 11. Hydrophiinae indet. (QM F42700), vertebrae from Gotham City Site, Riversleigh (Tertiary System C, middle Miocene). **A** and **B**, vertebrae from the middle trunk region; **C** and **D**, from the posterior trunk of a smaller snake, possibly a distinct taxon. Top to bottom, lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 5 mm.

Fig. 11. Hydrophiinae indéterminé (QM F42700), vertèbres provenant du site « Gotham City » de Riversleigh (Système C du Tertiaire, Miocène moyen). **A** et **B**, vertèbres de la région moyenne du tronc ; **C** et **D**, vertèbres de la région postérieure du tronc chez un serpent plus petit, probablement d'un taxon différent. De haut en bas, vues latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 5 mm.

sleigh due to the mesic closed forest ("rainforest") habitat there (Archer et al., 1991, 1997), which is presumably the ancestral habitat for hydrophiines. This habitat (and its fauna) could have remained relatively stable for long periods

while climatic deterioration, fragmentation of forests, and specialisation of derived hydrophiine lineages took place elsewhere on the continent. The python *Morelia riversleighensis* shows no appreciable change from the late Oligocene

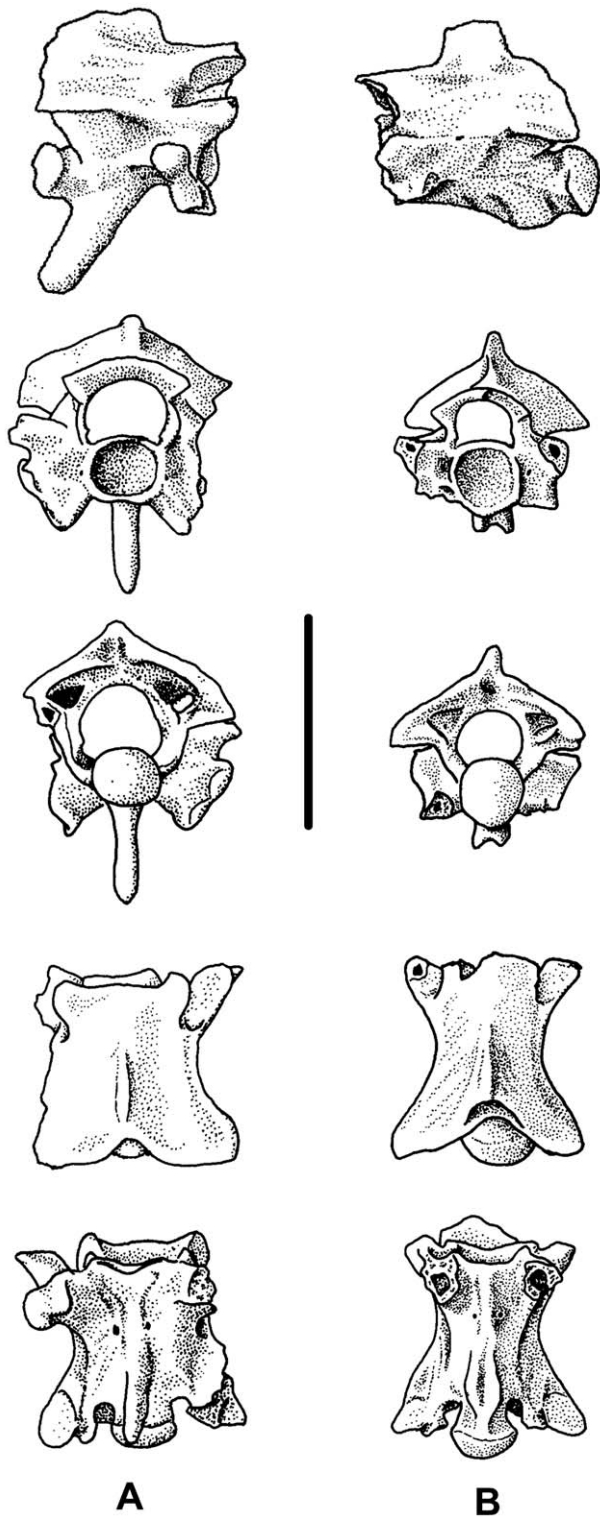


Fig. 12. Hydrophiinae indet. vertebrae from Henk's Hollow Site, Riversleigh (Tertiary System C, middle Miocene), QM F42701. **A**, anterior trunk or "cervical"; **B**, mid-caudal vertebra. Top to bottom, lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 3 mm.

Fig. 12. Hydrophiinae indéterminé, vertèbres provenant du site « Henk's Hollow » de Riversleigh (Système C du Tertiaire, Miocène moyen), QM F42701. **A**, vertèbre de la région antérieure du tronc ou « cervicale » ; **B**, vertèbre caudale moyenne. De haut en bas, vues latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 3 mm.

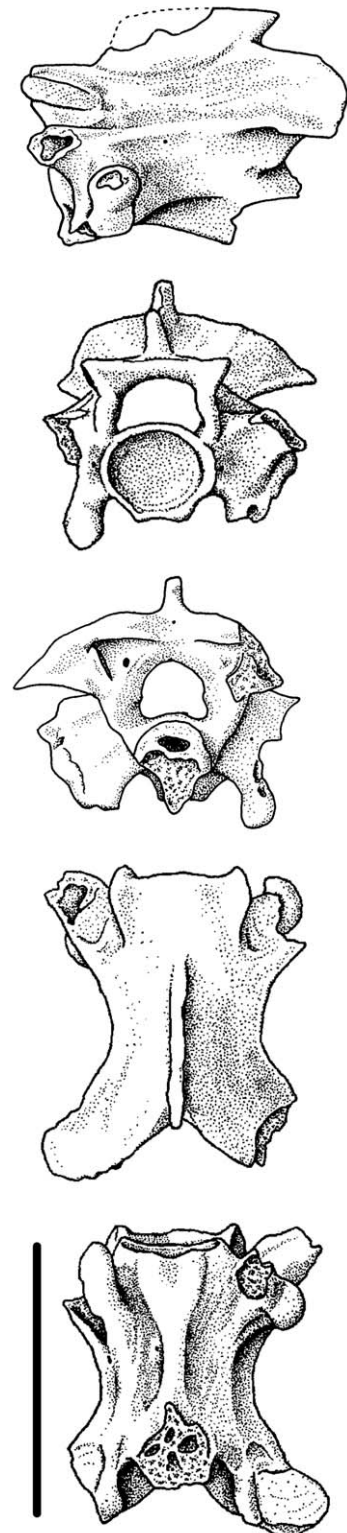


Fig. 13. Hydrophiinae indet. posterior trunk vertebra (QM F23075) from Bob's Boulder Site, Riversleigh (Tertiary System C, middle to late Miocene). Top to bottom: lateral, anterior, posterior, dorsal, and ventral views. Scale bar = 5 mm.

Fig. 13. Hydrophiinae indéterminé, vertèbres de la région postérieure du tronc (QM F23075) provenant du site « Bob's Boulder » de Riversleigh (Système C du Tertiaire, Miocène moyen au supérieur). De haut en bas : vues latérale, antérieure, postérieure, dorsale et ventrale. Échelle = 5 mm.

of Riversleigh through to the mid-Miocene Bullock Creek LF (Scanlon, 2001), whereas Szyndlar (1991b) points out that some snake species in Europe persisted nearly unchanged for 6–10 million years during the Miocene, and suggested that similar longevity could be expected in extant tropical snake faunas.

While elapids are present in the Riversleigh deposits, they do not dominate the snake fauna in terms of either abundance or species diversity. The most abundant and diverse snakes are a group of primitive “boa-like” forms, the madtsoiids, which exhibited a wide range of sizes and trophic morphologies, from small scincivores to large macrocarnivores (Scanlon, 1996, 1997; Scanlon and Lee, 2000). Also present are pythonine booids (fairly abundant but not diverse; Scanlon, 2001) and scolecophidians (fairly abundant but taxonomically indeterminate, though presumably typhlopids; Scanlon, 1996), while colubrids and acrochordids are not known at all. In contrast, elapids currently dominate the Australasian snake fauna both numerically and in terms of diversity, while madtsoiids are now totally extinct.

In the relatively well-known fossil record of colubroid snakes in Europe and North America, the Miocene represents a time of transition from faunas dominated by lineages now extinct, with the appearance and diversification of many of the extant genera and species groups (Rage, 1987; Rage and Augé, 1993; Szyndlar, 1991a, b; Szyndlar and Schleich, 1993; Holman, 2000). Such a pattern is not yet seen in the Australian record, which remained dominated by archaic lineages such as madtsoiids throughout the Miocene, with colubroids (elapids) being relatively rare. This might be an artefact of taphonomic or collecting bias against smaller elapid fossils, but it is also possible that the faunal turnover occurred much later in Australia. Rather than extant colubroids replacing more archaic colubroid lineages, which were present during the Oligocene, as in the northern continents, it is believed that colubroids were entirely lacking in Australia prior to the arrival (by over-water dispersal) of the ancestor of the hydrophiine radiation, close to the Oligocene-Miocene boundary. The adaptive radiation and consequent faunal turnover may have been considerably later and more rapid as a consequence, so that a ‘modern’ snake fauna might not have been established until the Pliocene.

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Appendix. Recent skeletal material examined

- Elapinae
Bungarus fasciatus SAM R52038. *Micrurus frontalis* AMS R131994. *Naja naja* SAM R2328, JS unnumbered. *Ophiophagus hannah* AMS R125418.
- Hydrophiinae
Acanthophis antarcticus AMS R-13-219, SAM R546, R1520, R26963, MV D3294, QM J46318, JS16, JS132; *A. pyrrhus* SAM R1580. *Aipysurus fuscus* AMS R40487; *A. laevis* AMS unnumbered; *A. eydouxii* AMS R95099, R33249. *Aspidomorphus muelleri* AMS R16614, R19013; *A. lineaticollis* AMS R125021. *Austrelaps ramsayi* SAM R33504, MV D4823, JS4; *A. superbus* SAM R265B, R2767, R3699b, R3701, R12782, R13371, R13997, MV unnumbered; *A. labialis* SAM R14104, R14617a, R13070, R14000b, R15903, R11684, R4093A, R3096A, R2664. *Cacophis squamulosus* AMS unnumbered (×4), QM J47976, J47659, J47983, JS3, JS14, SAM R2263a; *C. harriettae* QM J4443, J20278, J26544, J46288, J47658, J47982, J50600, SAM R26989, MV D8446; *C. churchilli* QM J53282, JS63; *C. krefftii* AMS unnumbered, QM J46583, SAM R26974. *Cryptophis nigrescens* AMS R-13-22, SAM R26972, MV D8329, JS30; *C. boschmai* MV D4728, JS81, JS unnumbered; *C. nigrostriatus* JS98; *C. pallidiceps* AM R30101, SAM R26880. *Demansia psammophis* AMS R-13-672, QM J7134, J46291, J26907, J47978, MV D2886, SAM R26985, R26995; *D. simplex* NTM R18625; *D. vestigiata* AMS R-13-667, SAM R27084. *Denisonia devisii* AMS unnumbered, MV D4764, D8920, JS96; *D. maculata* AMS R69972, QM J22170, MV unnumbered. *Drysdalia coronoides* SAM R39933, JS9; *D. rhodogaster* AMS R103568, JS54, JS160; *D. mastersi* SAM R27021, R6648b, R33496. *Echiopsis curta* AMS 6635, SAM R14318a, R27102, R4290, WAM R45351. *Elapognathus minor* SAM R26981, WAM R135047; *E. coronatus* AMS R74160, SAM R22964, R27127. *Emydocephalus annu-*

latus AMS R42025, WAM R28469. *Ephalophis greyae* WAMR83669. *Furina diadema* AMS R98165, SAM R6703, JS32; *F. barnardi* QM J48682, SAM R27022; *F. ornata* WAM R15088. *Glyphodon tristis* SAM R13998, MV unnumbered; *G. dunmalli* QM J23178. *Hemiaspis signata* AMS R-13-843, R142824, MV R11258, QM J23906, SAM R2264b, JS105; *H. damelii* AMS unnumbered, SAM R3142, MV22.I.1953, MV unnumbered, JS142. *Hoplocephalus bungaroides* SAM R12099; *H. bitorquatus* SAM R26992, JS64; *H. stephensi* AMS R-13-398, SAM R26965, QM J24413, J47657. *Hydrelaps darwiniensis* AMS R82577, AMS unnumbered, SAM R2270A, WAM R83668. *Hydrophis ornatus ocellatus* AMS R95004; *H. (or Disteira) kingii* AMS R95086. *Laticauda colubrina* AMS R30441, SAM R26960; *L. laticaudata* SAM R26976. *Loveridgelaps elapoides* AMS R42186. *Micropechis ikaheka* AMS R69985, QM J6970. *Neelaps calonotus* SAM R6659b, R27184, WAM R592, R5816; *N. bimaculatus* SAM R27216, WAM R20604, R40978. *Notechis ater* SAM R18832, R22574, R26169, MV D8684, R9135, W2632, ANWC REPS 12, JS58; *N. scutatus* SAM R2327, R14085, R26959, R26147, R27016, MV D4408, W2646, MV unnumbered, QM J5951. *Ogmodon vitanus* AMS R2540, R2542. *Oxyuranus microlepidotus* MV D47361, SAM R4285, R14851b, R26977, R26987; *O. scutellatus* AMS R20592, SAM R27017, R27018. *Parasuta dwyeri* JS61; *P. flagellum* SAM R26984, MV R11049, MV 15.XI.1952, MV unnumbered; *P. gouldii* AMS R98199, SAM R27126; *P. monachus* SAM R27183; *P. nigriceps* MV R11108, MV 60338; *P. spectabilis* AMS R-13-567, SAM R6351, R6626(a, c), R6628(a, b), R26353. *Paroplocephalus atriceps* WAM R29770. *Pelamis platurus* AMR107999. *Pseudechis porphyriacus* AMS R-13-652, R60412, MV W2631, W2630, D8015, MV unnumbered (×2), QM J24544, JS13, JS51; *P. australis* AMS R7073, R93040, QM J8336, J29006, WAM R31352, MV R12697, W1363, D4904, W3158a–c, JS175; *P. guttatus* SAM R26958, QM J26903, J26904, JS178; *P. colletti* AMS unnumbered, QM J47098. *Pseudonaja textilis* SAM R6757, R6765, R44184, MV D8345, D4864, R837, R12873, W2623, MV unnumbered, QM J26669; *P. nuchalis* AMS unnumbered (×2), MV W2633, D8961, D8808, R12822, D8641, D8687, D8534, W3160a–b, D9765, D9770; *P. affinis* MV D8254, D4876; *P. inframacula* MV D8685; *P. modesta* MV D3584, D5377, R782, R12818. *Rhinoplocephalus bicolor* AMS R130623, SAM R2259A, R6625. *Salomonelaps par* AMS R91262, R127228. *Simoselaps bertholdi* SAM R27210, WAM R20578, R28174; *S. littoralis* AMS R101772, WAM R86866, R86867; *S. anomalus* WAM R13815; *S. warro* AMS R14395, R19017, R46024; *S. fasciolatus* SAM R21188, WAM R5936, R8389; *S. australis* AMS R98167, JS170; *S. semifasciatus* AMS R130641, AMS unnumbered, SAM R27212, WAM R22882, R59218; *S.*

approximans AMS R71624, SAM R27186, WAM R73478; *S. roperi* (and cf.) AMS R70025, R30337, QM J59348, WAM R20349, R13823; *S. incinctus* AMS R64014. *Suta suta* AMS R142825, AMS unnumbered, SAM R2247, R2691, MV R11339, MV D4433, JS62; *S. ordensis* AMS unnumbered; *S. fasciata* SAM R27211; *S. punctata* AMS R49088, SAM R27091, R27118, MV D7748, JS144. *Toxicocalamus loriae* AMS R14785. *Tropidechis carinatus* AMS unnumbered, QM J7492, SAM R26970. *Vermicella annulata* AMS R21345, AMS unnumbered, QM J47441, J47986, JS42; *V. intermedia* AMS R12882.

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