

Montityphonoides: the Miocene snake *Morelia riversleighensis* (Smith & Plane, 1985) and the geographical origin of pythons

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Two alternative hypotheses for the biogeographic origin of pythonine snakes, 'Laurasian' and 'Gondwanan', make different predictions for the early fossil record of the group in Australia and elsewhere. Most python fossils from the Oligo-Miocene of Riversleigh (Queensland) represent a single species, *Morelia riversleighensis* (Smith & Plane, 1985) new combination. *Morelia antiqua* Smith & Plane, 1985 (Miocene of Bullock Creek, Northern Territory) is indistinguishable from *M. riversleighensis* and is treated as synonymous. Phylogenetic analysis of cranial characters (adding the fossil taxon to a data matrix slightly modified from that of Kluge 1993a) indicates close relationships to extant species of *Morelia*, but also differences, so *M. riversleighensis* is regarded as a valid species. No other pythonine lineages have been identified in the same deposits, but a younger (possibly Pliocene) deposit at Riversleigh includes a distinct taxon resembling species of *Liasis* or *Python*. Kluge's (1993a) hypothesis of phylogeny remains the most parsimonious interpretation of character evidence, and implies that pythons evolved in Australasia (as part of Gondwana). The fossil record does not yet conclusively exclude either of the competing biogeographic hypotheses. However, the non-appearance in the Miocene of six lineages supposedly more basal than *Morelia*, together with much older possible records of pythonines in Europe, is more consistent with alternative phylogenetic hypotheses implying a northern, Tertiary origin for Australian pythons.

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PYTHONS (Booidea, Pythoninae) occur widely in tropical and subtropical parts of the Old World, but 18 of the 24 species are found in Australia and/or New Guinea (McDowell 1975, Cogger 1992, Kluge 1993a). Thus, a central question for the history of the group (Fig. 1) is whether pythonines (1) originated within Australia from ancestors which were part of a Gondwanan fauna shared with the other southern continents, and then expanded into Asia and beyond (Smith & Plane 1985, Kluge 1993a), or (2) evolved on the Laurasian (and/or African) land mass, entered the Australian region from the north, and underwent further radiation here (McDowell 1975, Cadle 1987, Underwood & Stimson 1990). The answer to this question remains uncertain.

The boa-like snakes have often been considered among the most ancient and primitive (e.g. Boulenger 1893, Hoffstetter 1961); and it is with such plesiomorphic assemblages that the effects of successive research cycles on

classification tend to be most marked (cf. Kluge 1991). Such cycles, involving reassessments of polarity and homology of characters and ingroup-outgroup assumptions, can lead to major changes in phylogenetic hypotheses and the associated classifications. The history of classification in this assemblage has involved the delineation of groups of related species within it, and the splitting off of other groups considered to have affinities elsewhere. McDowell (1975) proposed removing *Loxocemus*, *Xenopeltis*, the bolyeriids (*Bolyeria* and *Casarea*) and tropidophiids (*Tropidophis*, *Trachyboa*, *Ungaliophis* and *Exiliboa*) from the group formerly known as Boidae (*sensu* Boulenger 1893, Romer 1956, Frazzetta 1959, 1975; cf. Underwood 1976), and introduced Booidea as a superfamily with its present content (i.e. erycines, boines and pythonines). All of these changes are further supported by recent analyses (Kluge 1989, 1991, 1993b, 1993a, Cundall *et al.* 1993). The extinct madtsoiids, originally classified among boids

(Simpson 1933, Hoffstetter 1961), were also removed by McDowell (1987) and represent a more basal lineage of snakes (Scanlon 1996, Rage 1998, Scanlon & Lee 2000).

Here I will use the subfamily names Pythoninae, Boinae and Erycinae for the three groups within Booidea, leaving the family level unspecified since relationships among the three lineages remain disputed (Kluge 1991, Cundall *et al.* 1993). The affinities of the Calabar 'ground python' (*Calabaria reinhardtii*) have been problematic, as it has been regarded as a distinct subfamily of Boidae (Underwood 1976), derived within the genus *Python* (McDowell 1975), or the sister group to the New World erycines *Charina* and *Lichanura* (and referred to *Charina* by Kluge 1993b). Apart from some doubt concerning this taxon (due to the likelihood of morphological convergence among fossorial snakes), the monophyly of each group seems assured and their boundaries are likely to remain stable. Here, the informal term 'pythons' refers to members of Pythoninae only. Each subfamily is distributed broadly, and they appear to have been distinct since the Cretaceous. In the Australasian region, there are extant representatives of both Pythoninae (absent only from the extreme south) and Boinae (only north of Torres Strait, i.e. absent from mainland Australia), but none of Erycinae. Fossil pythons are known in Australia from Oligo-Miocene to Quaternary times (see below), but no fossils of boines are yet known from this region.

Classification of Pythons

Opinions have differed on whether or not the Australasian pythonine genera form a monophyletic group, and on the nearly equivalent question of their biogeographic origin. McDowell (1975) listed characters suggesting that Australasian species are most closely related to the South-East Asian *Python reticulatus* (and *P. timoriensis*), and less closely to the African and other Asian species of *Python* (including the type species, *P. molurus*). Since McDowell retained an apparently paraphyletic concept of *Python*, and even transferred some Australasian species to this genus, interpretation of his classification as a phylogenetic hypothesis has sometimes led to confusion.

Schwaner & Dessauer (1981) used immunodiffusion of transferrins and albumins in a comparison of Papuan pythons with some other booids, but used only one non-Australasian python (*P. regius* of Africa). While they demonstrated lower genetic distances between

species of *Liasis* and Papuan species of *Python* (*sensu* McDowell 1975, but referred to *Morelia* by Cogger *et al.* 1983), their results have no particular implications for the 'Python reticulatus Group' of McDowell (*contra* Smith & Plane 1985), because neither *P. reticulatus* nor *P. timoriensis* was tested. A phylogenetic hypothesis Schwaner & Dessauer did test was not proposed until somewhat later (Kluge 1993a, see below).

A later phylogenetic analysis and classification of pythons (Underwood & Stimson 1990; cladistic in a Hennigian sense, but using only limited outgroup comparisons and a 'clique' approach rather than maximum parsimony) supports the monophyly of the Australasian forms, but also the monophyly of African and Asian *Python*. Their preferred phylogenetic hypothesis for *Python* species implies that the group originated in south-east Asia, and invaded Africa twice; small size was suggested to be primitive, and the 'giant' species *P. reticulatus*, *P. sebae* and *P. molurus* were considered closely related. Underwood & Stimson's conclusions are consistent with Schwaner & Dessauer's (1981) immunodiffusion results mentioned above, which implied a closer relationship between species of *Liasis* and *Morelia* than of either with *Python regius*.

However, another recent revision of python phylogeny (Kluge 1993a; based on a larger character set polarized by extensive outgroup comparison, and applying successive character-weighting as proposed by Farris 1969) arrives at rather different conclusions: *Aspidites* is the sister group to all other pythons; the species formerly included in *Liasis* and/or *Bothrochilus* form a 'comb' of successive sister taxa to (*Morelia* + *Python*); and the species of *Python* represent a highly derived monophyletic group. Thus, according to Kluge the Australian and New Guinea species are a paraphyletic assemblage, with the implication that pythons probably evolved in Australia and spread out from here to Asia and Africa. These results contrast strongly with the conclusions of McDowell (1975) and Underwood & Stimson (1990), and also conflict with the genetic distance results of Schwaner & Dessauer (1981).

The extant pythons were for a considerable time included in five or six genera: *Aspidites*, *Chondropython*, *Liasis* (and/or *Bothrochilus*), *Morelia* and *Python* (Stimson 1969, McDowell 1975, Cogger *et al.* 1983). Confusion concerning the correct application of Gray's (1842) generic name *Liasis* was resolved by declaring its type species to be *L. mackloti*, a species first referred to the genus in 1844 by Duméril & Bibron (Stimson

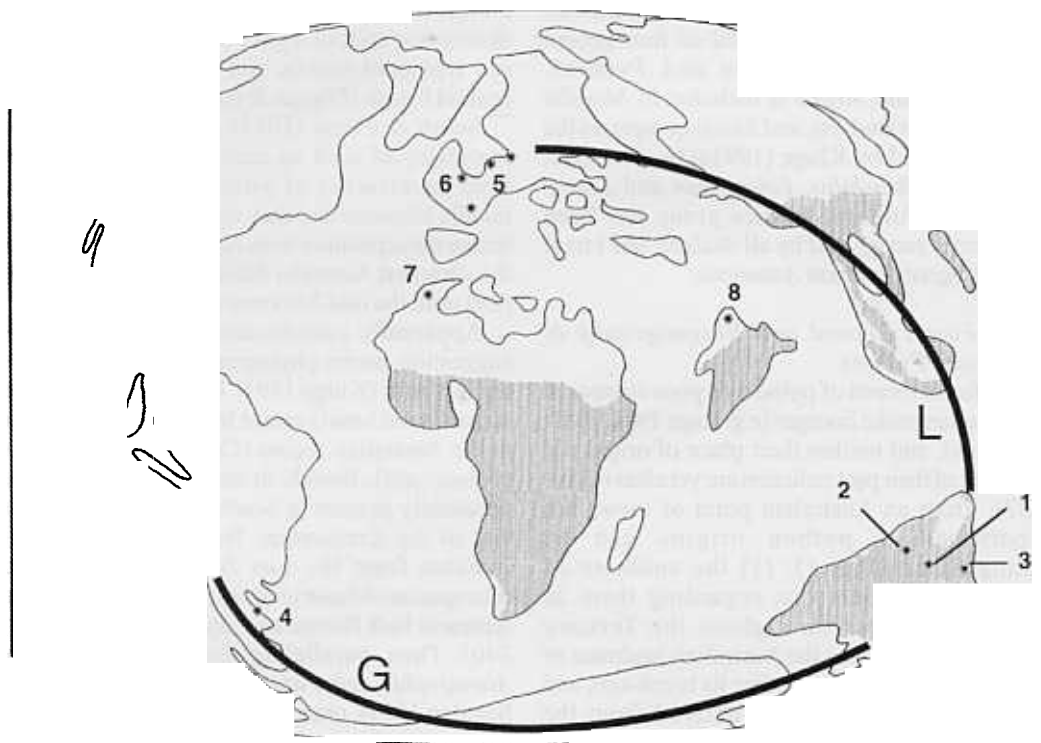


Fig. 1. Continental reconstruction for early Eocene (Ypresian), after Smith *et al.* (1994), indicating approximate location of booid fossil sites mentioned in the main text: 1, Riversleigh, Queensland; 2, Bullock Creek, Northern Territory; 3, Bluff Downs, Queensland; 4, Los Alamitos, Rio Negro, Argentina; 5, Messel and Geiseltal, Germany; 6, Prémontré and Saint-Maximin, France; 7, Beni Mellal, Morocco; 8 Mochiwala, Pakistan (actually north of continental boundary). Continental positions for the Eocene are used because the earliest fossils attributed (uncertainly) to Pythoninae date from this time. Shading shows Recent distribution of pythonines on land areas exposed in the Eocene. Heavy curves show possible routes of vertebrate dispersal to and from Australia: G, southern or Gondwanan; L, northern or Laurasian.

& McDowell 1986). Attempts to avoid paraphyletic taxa have led to various further changes being proposed, either in the direction of 'lumping' (Storr *et al.* 1986, Underwood & Stimson 1990) or 'splitting' (Wells & Wellington 1984, 1985; Kluge 1993a). Underwood & Stimson (1990) synonymise *Chondropython* and *Liasis* with *Morelia*, leaving only three genera (*Python*, *Aspidites* and *Morelia*), a change already adopted by Storr *et al.* (1986) based on then-unpublished results. Kluge (1993a) recognised eight genera, seven of them in the Australian region.

As already mentioned, Kluge's (1993a) analysis indicates a monophyletic 'crown group' including the species of *Morelia* and *Python*, and also a number of species which, in his preferred hypothesis, form a 'comb' of successive sister groups to this clade. However, the relationships in the middle part of the phylogeny are subject to extensive character conflict. For example, in an analysis of skeletal data alone, representing 72 of

his 121 characters, the shortest cladogram is obtained when *Liasis* (*sensu lato*, equivalent to *Bothrochilus* of Cogger *et al.* 1983) forms the monophyletic sister group to *Morelia* and *Python* (Kluge 1993a: fig. 23). *Liasis* in this broad sense is thus diagnosable by synapomorphies (some of them unique and 'unreversed'; see Scanlon & Mackness in press), whether or not it is actually monophyletic.

In view of this conflict among studies and characters, it seems that the phylogeny and classification of pythons have not been finalised. Indeed, Kluge (1993a) could not honestly have done otherwise than construct a 'monophyletic taxonomy' based on the most parsimonious cladogram resulting from his chosen (and defended) methods. Nevertheless, rather than adopting a classification including four monotypic genera and cutting across the boundaries of previously recognised 'species groups', I prefer to take a 'conservative' approach by retaining

Liasis in the broad (and palaeontologically useable) sense, and thus a total of four genera (*Aspidites*, *Liasis*, *Morelia* and *Python*). '*Chondropython*' *viridis* is included in *Morelia* (as in all recent studies), and *Liasis* comprises the species referred by Kluge (1993a) to *Antaresia*, *Apodora*, *Bothrochilus*, *Leiopython* and *Liasis*. The *Liasis childreni* species group has been consistently recognised by all studies, and I treat it as a subgeneric taxon *Antaresia*.

World Fossil Record and Biogeography of Booids and Pythons

The fossil record of pythons is poor compared to some other snake lineages (e.g. Rage 1984, 1987; see below), and neither their place of origin nor the extent of their past radiation are yet clear (Cadle 1987). From an Australian point of view, two hypotheses of python origins can be distinguished (Fig. 1): (1) the southern or Gondwanan hypothesis, regarding them as having been here throughout the Tertiary (implying an origin on the Australian landmass or elsewhere in Gondwana before its break-up), and Afro-Asian lineages to be derived from the Australasian radiation; and (2) the northern or Laurasian hypothesis, proposing that pythons originated elsewhere (Asia, or possibly Africa or Europe), and that they arrived from the north and radiated in Australasia in the later Tertiary.

This is only a meaningful dichotomy if we reject ideas of rapid global dispersal for this group, or origins so far back in time as to erase all patterns. Taking this rejection as read, the fossil record is certainly relevant to the question: the discovery of pythonine fossils in South American, Antarctic, or sufficiently old Australian deposits would mark the end of controversy, by falsifying the central prediction of the Laurasian hypothesis and supporting a Gondwanan connection (cf. Ball 1975). Equally, old enough pythonines in the northern continents must surely mean the end for the Gondwanan hypothesis (there might be room for argument, within reasonable limits, about how old is 'old enough').

Cogger & Heatwole (1981) regarded pythonines as one of several lineages of reptiles which entered the Australian region from Asia in the mid-Tertiary, suggesting that pythons had radiated here in isolation for 30–35 million years before migrations were once again made possible by climatic fluctuations in the Quaternary. This model implies the Australasian pythons to be monophyletic, as proposed by Underwood (1976, Underwood & Stimson 1990); it is also parsimonious in providing

a uniform explanation for similar patterns of distribution and phylogeny in (for example) elapid and typhlopoid snakes, and varanid, scincid and agamid lizards (Cogger & Heatwole 1981).

Smith & Plane (1985) do not consider the possibility of such an early dispersal, and infer from the presence of pythons in the Australian middle Miocene that they must have been present before the separation from Antarctica. This reflects the view that Australia did not make contact with Asia until the mid-Miocene (e.g. Main 1987).

Apparently corroborating Smith & Plane's suggestion, recent phylogenetic studies of boines and pythons (Kluge 1991, 1993a) imply that the oldest (most basal) extant lineages of both occur in the Australian region (*Candoia* and *Aspidites* respectively). Booids in the current sense were apparently present in South America before the end of the Cretaceous; fragmentary vertebral remains from the Los Alamos Formation (Campanian-Maastrichtian) in Patagonia seem to represent both Boinae and Erycinae (Albino 1990: 340). Thus, paralleling the madtsoiid genera *Alamitophis* and *Patagoniophis* (Albino 1986, Scanlon 1993), one or more booid lineages could have entered Australia from South America (or vice versa) via Antarctica before final separation of the continents at about 64 Ma (Woodburne & Case 1996). (Dispersal east and west from an Antarctic origin is another possibility, here treated as equivalent.)

However, there is no proof that booids did actually 'take advantage' of the Antarctic route; no pythonines have been found in South America, and no boines or erycines in Australia. The boine *Candoia* has no known fossil record, does not occur on the Australian mainland, and its western Pacific, equatorial distribution, like that of the iguanid *Brachylophus*, has been considered a possible result of waif or 'sweepstakes' dispersal from South America (McDowell 1979, Gibbons 1985, Scanlon 1993). Alternatively, and in better accord with its phylogenetic isolation (Kluge 1993b), it may be derived from Eurasian boines, which are known in Europe from the Eocene to early Miocene (Szyndlar & Schleich 1993; see below). Australian lineages of varanid lizards and typhlopoid and elapid snakes are certainly (or for *Ramphotyphlops*, probably) of south-east Asian origin (Tyler 1979, Cadle 1987, Sprackland 1991), but these groups, like pythons, already occur in the early Miocene and possibly late Oligocene of Australia (Estes 1984, Murray & Megirian 1992, Scanlon 1992, 1996). Madtsoiids are still the only squamate lineage showing a Gondwanan

distribution, early Tertiary presence in Australia, and close taxonomic links between South America and Australia; but as noted above they are not closely related to booids (Hutchinson & Donnellan 1993, Scanlon 1993, Rage 1998, Scanlon & Lee 2000).

After their earliest appearance in South America, booids reached North America and Europe by the Maastrichtian, and attain considerable diversity in both regions by the Eocene (Rage 1984, 1987); some, if not all of these forms can be referred to the extant subfamilies Boinae and Erycinae. Thus, as boines are known in the early Tertiary of Europe, there seem to be better grounds for regarding *Candoia* as a Laurasian relict on the periphery of south-east Asia, than a Gondwanan relict on the margin of Australasia. Booids with python-like toothed premaxillae, supraorbitals, and/or perforated palatines are known from the Eocene of Germany (Messel and Geiseltal; Szyndlar & Böhme 1993, Szyndlar 1994) and France (Prémontré, Paris Basin, and Saint-Maximin, Gard Phosphorites; Augé *et al.* 1997, Duffaud & Rage 1997), and pythonines are known more definitely from the latest lower or earliest middle Miocene (MN 4/5) of France, middle Miocene of Morocco, and late Miocene of Pakistan (Hoffstetter 1964, Rage 1976, 1987, Demarcq *et al.* 1983), by which time they were also in Australia (Smith & Plane 1985, this work). Dispersal from an Australian origin to Europe by the early Miocene (presumably requiring approach of the Australian and Asian landmasses as a first step) would be more difficult than in the opposite direction, where over-water dispersal would be the final stage of a range expansion which may have begun much earlier. This argument implies that the pythons originated in Eurasia or Africa, and it would be considerably strengthened if the presence of pythonines is confirmed in the Eocene of Germany or France.

Thus, both of the conflicting hypotheses of the biogeographic origin of pythons receive some circumstantial support, but available evidence is still inconclusive. To solve the question it is important to continue investigation of the phylogenetic relationships of extant forms using all available forms of evidence. As part of this investigation, fossils may provide information not only on the actual ages and locations of evolutionary events, but also on the morphology of extinct lineages, which can be critical for correct resolution of phylogeny (Gauthier *et al.* 1988, Donoghue *et al.* 1989, Lee 1998).

Australian Fossil Record

Relatively few terrestrial vertebrate fossils are known from the Cretaceous and early Tertiary of Australia; the oldest known fauna containing snakes is from the early Eocene, and it does not include any booids (Scanlon 1993). Two Miocene fossil pythons have been described from Australia, both by Smith & Plane (1985): *Montypythonoides riversleighensis* and *Morelia antiqua*. Both were large pythons from northern Australia, and approximately middle Miocene in age. *M. riversleighensis* was based on an incomplete maxilla and associated vertebrae from Henk's Hollow Site, Riversleigh, Qld (with additional vertebrae referred from other Riversleigh sites; recent assessments of the age of these deposits suggest that the oldest are late Oligocene, see below). *M. antiqua* is based on a nearly complete dentary from Blast Site, Bullock Creek, NT. Kluge (1993a) referred both taxa to the synonymy of widespread extant species (*Morelia spilota* and *Liasis olivaceus* respectively), reflecting the absence of obvious support for specific difference, and overall similarity of corresponding elements.

Vertebrae of an even larger pythonine are known from the Pliocene of north-eastern Qld (Bluff Downs Local Fauna, ?*Morelia* sp. in Archer & Wade 1976; Spring Park Local Fauna, Mackness *et al.* 1994) and can be referred, with some doubt, to *Liasis* (*sensu stricto*); an associated dentary fragment indicates a high number of teeth, as in *L. mackloti* rather than *L. olivaceus* (Scanlon & Mackness in press). A few Pleistocene remains have been referred to this group (e.g. Lydekker 1888, Swinton 1924, Longman 1925); they have not been restudied in detail, and will not be considered further except to note that those from Wellington Caves (Lydekker 1888) represent a large elapid, not a python (nor madtsoiid, although *Wonambi* does occur in these deposits; Scanlon 1995).

The conflict among previous studies suggests that the fossil record in Australia will have implications for the phylogenetic status and biogeographic origin of Pythoninae, and it may also provide information about the tempo and modes of evolution in the group. This paper reports associated jaw elements and vertebrae from several deposits at Riversleigh, which allow sets of osteological characters of single individuals to be considered jointly in discussing their status and affinities. Comparisons are made with type material of both of the taxa named by Smith & Plane (1985), as well as with extant forms. The emphasis of the description here is on jaw

elements, because variation among pythonine taxa in vertebral morphology is relatively slight (e.g. Kluge 1993a used no characters from the vertebrae).

Among the questions which could be answered by the mid-Tertiary fossil record are: were pythons more or less diverse in Australia than they are today? What phylogenetic positions do the fossils show with respect to the living taxa of the same region, and other parts of the world? Are they primitive species, potential ancestors of part or all of the living fauna?

SYSTEMATIC PALAEONTOLOGY

Most of the fossil material 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. Unless stated otherwise, all Riversleigh material has been or will be deposited at the Queensland Museum (QMF). Pythonine material from Bullock Creek, Northern Territory, has been collected and prepared by M. Plane (formerly Bureau of Mineral Resources, Canberra), T. H. Rich (Museum of Victoria) and P. Murray, D. Megirian and K. Roth (Northern Territory Museum of Arts and Sciences), and are held in the corresponding collections (CPC, NMVP, NTMP respectively).

Fossils are prepared using acetic acid (see Archer *et al.* 1994), measured with either vernier or electronic calipers, and drawn using a binocular microscope and camera lucida. Alveoli on toothed elements are referred to by numerals, counted from anterior to posterior.

While regarding binomina as indispensable for communication, I choose not to apply categorical ranks to taxa above the genus.

SQUAMATA Oppel, 1811
 PYTHONOMORPHA Cope, 1869
 SERPENTES Linnaeus, 1758
 ALETHINOPHIDIA Nopcsa, 1923
 MACROSTOMATA Müller, 1831
 BOOIDEA Gray, 1825
 PYTHONINAE Fitzinger, 1826

Morelia Gray, 1842

Diagnosis. Characters diagnostic of *Morelia* or more inclusive clades of Pythoninae (according to Kluge 1993a), and which can be evaluated in the material described below, are: two teeth on each ramus of premaxilla; anterior palatine teeth

longer (or at least, thicker and more erect) than posterior ones; posterior margin of palatine choanal process deeply concave; anterior margin of premaxilla concave; ventral openings of premaxillary channels posterior to alveoli; lateral bulge present on maxilla.

Morelia riversleighensis (Smith & Plane, 1985) comb. nov. (Figs 2-10)

1985 *Montypythonoides riversleighensis*; Smith & Plane, p. 191.

1985 *Morelia antiquus*; Smith & Plane, p. 192.

1992 *Morelia antiqua*; Scanlon, p. 49.

1993 *Morelia spilota* (LaCépède, 1804), partim; Kluge, p. 55

1993 *Liasis olivaceus* Gray, 1842, partim; Kluge, p. 55.

Stratigraphic and geographic range. Occurs in deposits of Systems A, B and C at Riversleigh, northwestern Queensland (*sensu* Archer *et al.* 1989; probable Late Oligocene to early Middle Miocene) and Camfield Beds, Northern Territory (Bullock Creek LF, late Middle Miocene).

Diagnosis. The following diagnosis gives all characters of systematic value within Pythoninae which can be evaluated for the type and referred material of *M. riversleighensis*, thus repeating the apomorphies of *Morelia* or more inclusive groups listed above, and also including probable plesiomorphies relative to other species of *Morelia*. The combination of character states is unique, but no definite autapomorphies of *M. riversleighensis* are known.

Moderately large *Morelia* with at least 15 (probably 17-18) alveoli on the maxilla, 17-18 on the dentary, 6 on the palatine, 2 on each side of the premaxilla. Anterior maxillary and dentary teeth moderately long (distinctly longer than posterior teeth), curved basally but nearly straight for most of their length; marginal teeth with prominent lateral cutting ridges for most of their length, medial cutting ridges also present distally. Anterior maxillary foramen on lateral face of maxilla small; lateral bulge present on the suborbital portion of the maxilla, projecting laterally to a moderate extent; palatine process of maxilla nearly as wide as long, adjacent to alveoli 7-9 which are relatively widely spaced, followed by a convex medial expansion of maxilla adjacent to alveoli 10-13 (the two expansions separated by a smooth concavity in smaller specimens, an angular notch in larger ones where the palatine process overlaps the other

dorsally). Anterior palatine teeth distinctly thicker and more erect, and probably longer, than posterior ones; choanal process of palatine about as wide as long, anterior and posterior margins slightly concave and directed anteromedially and dorsally from shaft of palatine; maxillary process narrow; medial pterygoid process moderate in length. Median space between premaxillary alveoli equivalent to one alveolus, anterior margin of premaxilla concave; small premaxillary channels piercing bone posteromedial to alveoli, no median anterior fenestra; medial margins of choanal processes of premaxilla project strongly ventrad; premaxilla only slightly angular laterally, without dorsolateral projections, and with lateral margins sloping posteriorly. Mental foramen on lateral face of dentary relatively small, shallow dorsoventrally, forming acute angle posteriorly. Compound mandibular bone with distinct ventrolateral crest; surangular foramen shallow; coronoid eminence of surangular relatively distinct, steep anteriorly and posteriorly; prearticular lamina relatively long, low and straight, extending to coronoid facet; relatively long and narrow horizontal lamina between prearticular and surangular laminae anterior and dorsal to mandibular fossa; coronoid and angular in longitudinal contact, meeting posteriorly at about 45°. Maximum total length estimated at 4-6 m. Hypapophyses continue relatively long in anterior trunk before reducing sharply at transition to mid-trunk region; zygapophyses angled at less than 10° above horizontal; zygosphenes with anterior median prominence (trilobate in dorsal view); neural spine 'hatchet-shaped' in lateral view, with right or acute angle anteriorly and acute angle posteriorly; usually one pair of subcentral foramina per vertebra in adults.

Type Material. *M. riversleighensis*, Holotype: incomplete right maxilla, QMF12926 (=AR 4058), Henk's Hollow Local Fauna, Riversleigh; Tertiary System C (Archer *et al.* 1989). Paratypes: seven vertebrae from Henk's Hollow (QMF12927-12933), one from D-Site (AR 3190), two from Gag Site (AR 3526, AR 3982); one isolated tooth from Henk's Hollow (AR 4133), two from Gag Site (AR 3936, AR 4015). Some of these registrations were reported incorrectly by Smith & Plane (1985).

M. antiqua, Holotype: nearly complete right dentary, CPC 25077 (not CPC 20577 as given by Smith & Plane; Davis 1994; Fig. 10). Blast Site, Camfield Beds (Bullock Creek Local Fauna), Northern Territory.

Referred Material. Riversleigh: Henk's Hollow Site (HH): fragment of large left maxilla (AR 5752) consistent in size and morphology with the *M. riversleighensis* holotype; anterior part of large left dentary (AR 8699) also likely to represent the same individual; anterior part of smaller right maxilla (AR 11576); anterior parts of two large palatines (AR 8725 and AR 9681); vertebrae (AR 5407, 5453, 5455, 5901p, 6048, 6132, 6595, 6694 (2), 6700, 6701, 6702, 6768 (8), 6769, 6770, 7130, 7613, 7617, 7619, 7747, 7748, 7758 (2), 7759 (2), 8071, 8099, 8108, 8324, 8327, 8333, 8696 (4), 8723 ('bulk'), 9039, 9049p ('bulk'), 9119, 9121, 9127, 9132, 9451, 9550, 11213, 11573 (bulk fragments)); isolated teeth (AR 6856, 7531, 7534, 8093, 8139, 8720, 9053, 9495, 14373).

Neville's Garden Site (NG): anterior part of small left dentary (QMF23130, Fig. 3).

Upper Site: partial skeleton comprising right dentary and anterior part of right compound bone (both AR 13392, Fig. 4 A-C), left maxilla (AR 13136, Fig. 4 D-G), 89 partial to complete vertebrae (AR 10842, plot of measurements Fig. 5), and fragments of ribs including 11 rib heads (AR 13134, 13135, 14123).

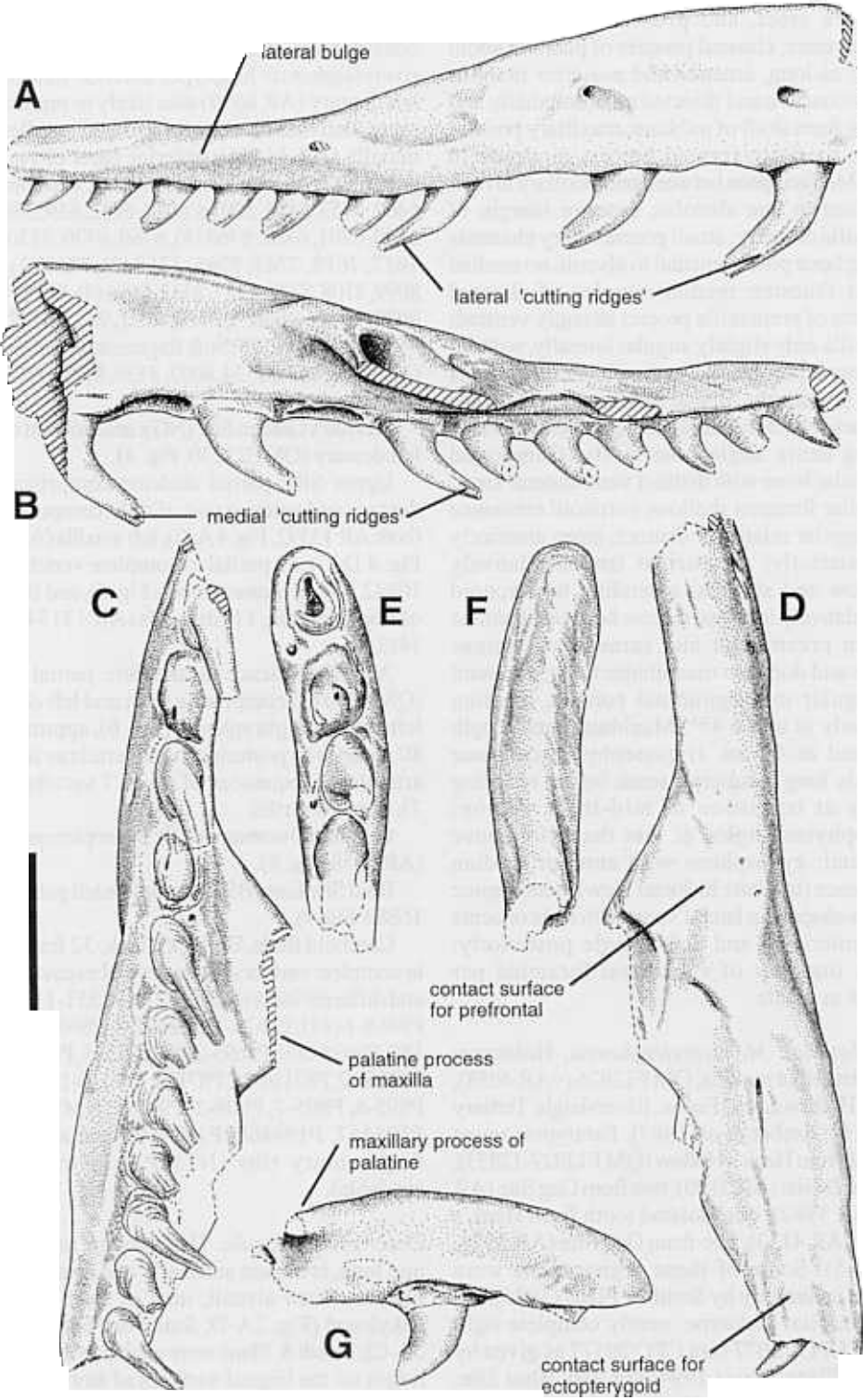
Archie's Absence (Snake) Site: partial skeleton (QMF23073) comprising right and left dentaries, left angular, right splenial (Fig. 6), approximately 80 anterior to posterior trunk vertebrae including articulated sequences of up to 7 vertebrae (Fig. 7), numerous ribs.

Gag Site (Dwornamor LF): incomplete premaxilla (AR 5658, Fig. 8).

Boid Site East (BSE): complete left palatine (AR 16880, Fig. 9).

Camfield Beds, Bullock Creek: 32 fragmentary to complete vertebrae from several excavation sites and different individuals (NTMP8551-11, P869-2, P8668-1 (x4), P8675-12, P8692-4, P8695-1, P8695-180, P8695-209, P8695-248, P8712-5, P8792-5 (x2), P87105-2, P87110-21, P87114, P87115-12, P895 (x2), P895-6, P895-7, P908-3, P908-5; NMV P198466, P198467, P198468, P198469), and a number of fragmentary ribs (NTMP registrations not available).

Description. Maxilla. The holotype maxilla, 42.9 mm long, is broken anteriorly and posteriorly, but retains eleven alveoli, nine of them with teeth ankylosed (Fig. 2A-D; Smith & Plane 1985: fig. 2A-C). Smith & Plane were unable to detect cutting ridges on the lingual surfaces of any of the teeth, but they are present on several of the more complete ones (it should be remembered that while labial cutting ridges extend for most of the length



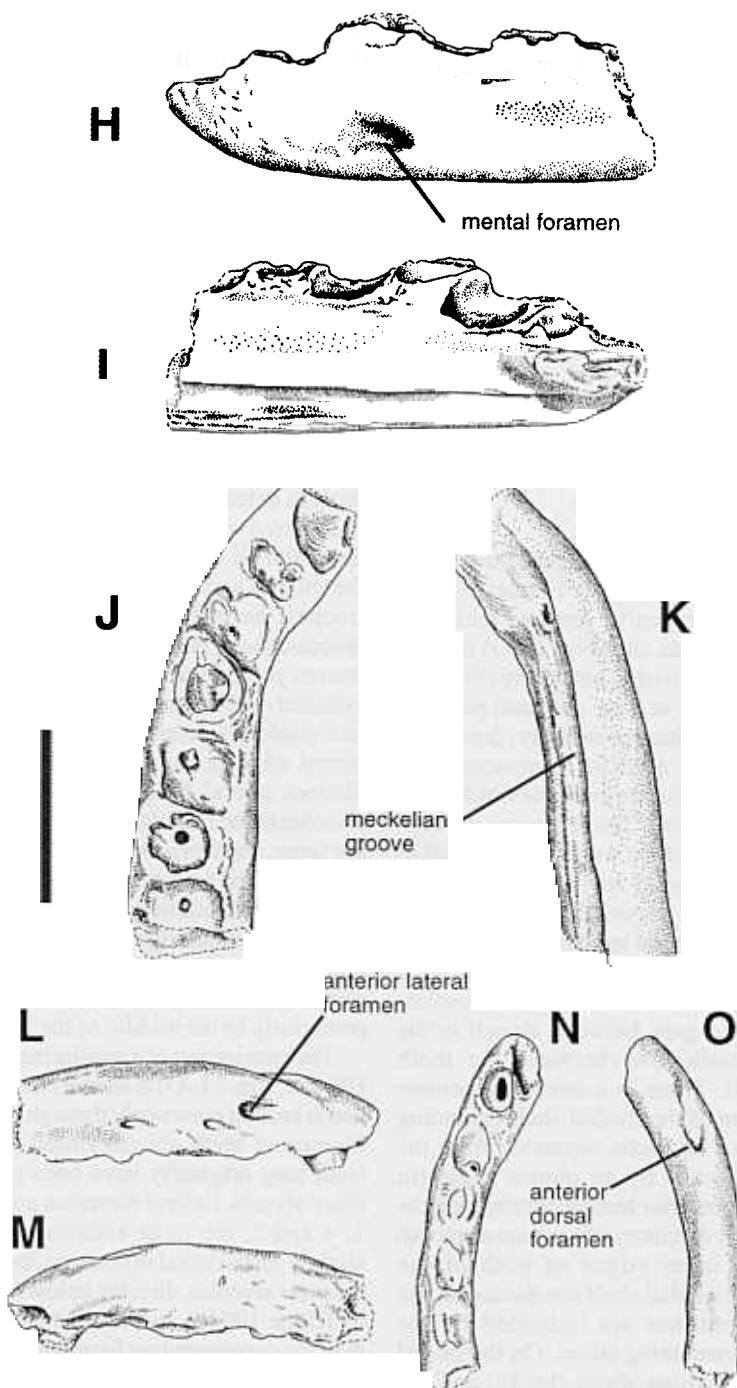


Fig. 2 (opposite and above). *Morelia riversleighensis* (Smith & Plane, 1985); type and referred material from HH Site, Riversleigh. A-D, holotype right maxilla (QM F12926) in lateral, medial, ventral, and dorsal views; E-G, right palatine (AR 9681) in ventral, dorsal, and lateral views; H-K, anterior portion of left dentary (AR 8699); A-K are consistent with a single individual; C-F show approximate natural relationships of palatal elements. L-O, anterior right maxillary fragment of a smaller individual (AR 11576) in lateral, medial, ventral, and dorsal views. Scale bar = 10 mm.

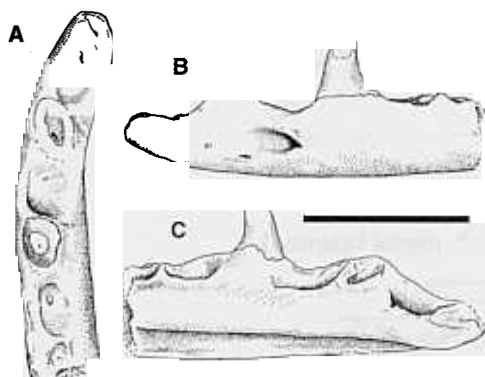


Fig. 3. Anterior dentary fragment of a small python, probably juvenile *Morelia riversleighensis* (QM F23130, Neville's Garden Site) in (A-C) dorsal, lateral, and medial views. Scale bar = 5 mm.

of python teeth, ridges on the lingual side extend only a short distance from the tip; Frazzetta 1966). Comparison with the smaller anterior maxillary fragment from the same site (Fig. 2L-O) implies that three alveoli are missing anteriorly (Smith & Plane estimated two); at least one, and possibly as many as four are lacking posteriorly (depending which extant form is used for comparison; no comparable fossil maxillae are available which retain the rear of the tooth row). Those present are here counted as 4 to 14, and the total is considered to have been in the range 15 to 18. The tooth row has a slight sigmoid curve, the posterior part tending laterally while the teeth become directed more medially than posteriorly. The palatine process extends from the 7th to the 9th alveolus: there are increased gaps between alveoli in the centre of the tooth row (between the teeth counted as 6-10). There is a smoothly convex posterior swelling of the medial shelf extending from the 10th to 13th tooth, separated from the main palatine process by an obtuse angle (in ventral view, the posterior lamina overlapping the anterior for a short distance) rather than a smooth concavity. The inner edges of both of the expansions of the medial shelf are damaged, but their probable outlines are indicated by the curvature of the remaining edges. On the lateral face, there are foramina above the 4th and 6th alveoli. No trace of the anterior dorsal foramen is visible (it occurs above the 3rd alveolus in other *Morelia* maxillae examined). Posterior to the two large foramina above the palatine process is a longitudinal dorsal channel containing two small foramina.

The maxilla of the Upper Site partial skeleton

(AR 13136, Fig. 4D-G) is 27.0 mm long and represents a smaller (probably younger) snake than the holotype; it is broken anteriorly and posteriorly, and has lost most of the palatine process and the posterior part of the dorsal surface, but retains eleven alveoli and a number of other features comparable to the holotype. The anterodorsal foramen (presumed to be above the 3rd alveolus as in other *Morelia*, *Python* and *Liasis* material examined) is just behind the anterior break, indicating that two alveoli are missing anteriorly; assuming approximately equal length of maxilla and dentary (usual in extant pythons), probably three or four alveoli (or possibly more) are lacking posteriorly. Counting those present as 3 to 13, alveoli 4, 7, 8, 10, 12 and 13 had ankylosed teeth, but only fragments of them remain. The palatine process extends from the 7th to the 9th alveolus (numbered as above); the gaps between these three alveoli are distinctly longer than between the others, and the gradient in diameter is also steepest here. Posterior to the main palatine process, there is a smooth concavity defining a convex posterior medial shelf. The tooth row has a distinct double curve, bending medially anteriorly and slightly laterally posteriorly; although the lateral edge is damaged posteriorly, there is a distinct lateral bulge extending from the 8th alveolus to the rear of the fragment. Laterally, there are large, anteriorly open foramina above alveoli 3, 4 and 6, and a pustule-like swelling just above 7 (presumably pathological). On the dorsal surface near the broken edge of the palatine process, a large foramen opens medially and is connected to another (unroofed due to breakage) which opens posteriorly in the middle of the bone.

The anterior part of a smaller maxilla (AR 11576, HH Site; Fig. 2 L-O) is almost complete anteriorly, and is broken posteriorly through the 7th alveolus. Stumps of teeth are ankylosed in 2 and 4, but teeth may originally have been present in some other alveoli. Lateral foramina are present above 3, 4 and 5, the most anterior being larger and slightly more dorsal in position, but much smaller than the alveolus directly below it (Character 14 of Kluge 1993a) and thus considerably smaller than the corresponding foramen in extant *Morelia spilota*. The anterodorsal foramen is above 3, and the groove extending forward from it reaches to above 2. At the posterior end of the fragment, the anterior edge of the palatine process can be seen as a dorsomedial ridge.

Premaxilla. The single specimen (AR 5658, Gag Site; Fig. 8) has been broken in several places, so that its original shape cannot be determined

completely, but a number of comparisons can be made with extant pythons. There are two alveoli on each side of the midline (teeth are ankylosed in the lateral pair), and the medial alveoli are separated by a gap equivalent to one alveolus in width. In dorsal view, the anterior margin is concave (the lateral alveoli are slightly anterior to the medial pair), and the maxillary processes are convex but somewhat angular; their posterior edges are concave but more longitudinal than transverse (both these features are as in *Liasis olivaceus*, *Morelia spilota* and *M. amethistina*, and differ from *Python molurus*, *Antaresia childreni* and both species of *Aspidites*). The maxillary processes are concave dorsally, as in other pythons. Premaxilla channels (Kluge 1991) are relatively small (as in *Morelia*, not large as in *Liasis olivaceus* and *L. mackloti*), located within concavities adjacent to the narrow nasal process, and open ventrally anterior to the vomerine processes and posterior to the alveoli. The nasal process forms a sharp crest dorsally, but is thicker ventrally, the crest defined by slight lateral concavities, not distinct grooves as in some species (e.g. *L. olivaceus*). The crest is broken along the dorsal edge, so that the small ascending process, if present, is not preserved (an ascending process was regarded by Kluge 1991 as present only in boines, but occurs among pythons at least in *Liasis* and *Morelia* spp.). The basal portions of teeth preserved are at a shallow angle to the ventral edge of the nasal process, suggesting an original steep orientation of the process (as in e.g. *Morelia spilota*) rather than a near horizontal position (as in e.g. *Liasis olivaceus*). The vomerine processes are broken, but the remaining portions are much more prominent ventrally than in most other pythons examined, retaining a strongly concave anterior edge in lateral view. This incomplete specimen is referred provisionally to *M. riversleighensis* because of its large size, and presence in the same site as paratype material of this large python. The possibility that it represented a madtsoiid snake was initially considered (a large dentary referred to *Yurlunggur* sp. is known from this site; AR 6021, Archer *et al.* 1994: 71), but toothed premaxillae have not been found in any known members of that group, pythonine vertebrae are more numerous in this site than those of large madtsoiids, and the derived similarities to some species of *Morelia* seem conclusive.

Palatine. A complete left palatine with 6 alveoli (AR 16880, Boid Site East (BSE); Fig. 9); the anterior shaft with an overgrowth of bone medially

suggesting it may have been broken and healed during life. Teeth are ankylosed but broken in alveoli 3, 4 and 6, the remaining portions showing strong posterior curvature; alveolar size decreases uniformly from 2 to 6, width more strongly than length. This strong gradient is sufficient evidence to score the specimen as having 'long' rather than 'short' anterior teeth (Kluge 1993a, character 51). The choanal process is very similar to those in *Morelia spilota*, with nearly parallel anterior and posterior edges directed anteriorly, medially and dorsally. Its posterior edge is sharply distinguished from the medial pterygoid process by a strong concavity (Kluge 1993a, character 53). Absence of contact with the vomer is inferred on the basis of the relatively small size of the process (Kluge 1993a, character 52). The palatine (or sphenopalatine) foramen is completely enclosed by a bridge of bone connecting the dorsolateral part of the shaft to the maxillary process, as in most pythons, the only consistent exception being *Morelia amethistina* (Frazzetta 1959, Kluge 1993a). A groove extends posterolaterally from the foramen, probably indicating the line of fusion between the maxillary and lateral pterygoid processes. The maxillary process thus defined is relatively narrow (anteroposteriorly) and thick (dorsoventrally) (Kluge 1993a, character 55). The medial pterygoid process is as long as the posterior two palatine alveoli. Kluge (1993a) defines his character 56 in terms of a comparison to anterior pterygoid tooth bases, but anterior pterygoid teeth are only slightly smaller than those of the posterior palatine in most pythons, so the process can be scored as 'of modest length' rather than 'long'.

Two badly worn fragments of palatines from HH Site include alveoli 1 to 5 (AR 9681) and 1 to 4 (AR 8725); both apparently come from the right side and the former is somewhat larger, but both are too large to come from the same individual as the maxilla AR 11576 (this implies the presence of at least three individual pythons in the deposit). The more complete specimen retains part of the choanal process, beginning level with the 5th alveolus; this is consistent with *Morelia spilota* (and most other pythons) which typically have six palatine teeth, but not *M. amethistina* which usually has four, or some other taxa with eight or more.

Mandibles. The best preserved dentary referred to this species is the holotype of *M. antiqua* (Fig. 10; Smith & Plane 1985: fig. 2H-J), which is similar to those from sites at Riversleigh in most respects, including overall shape, number,

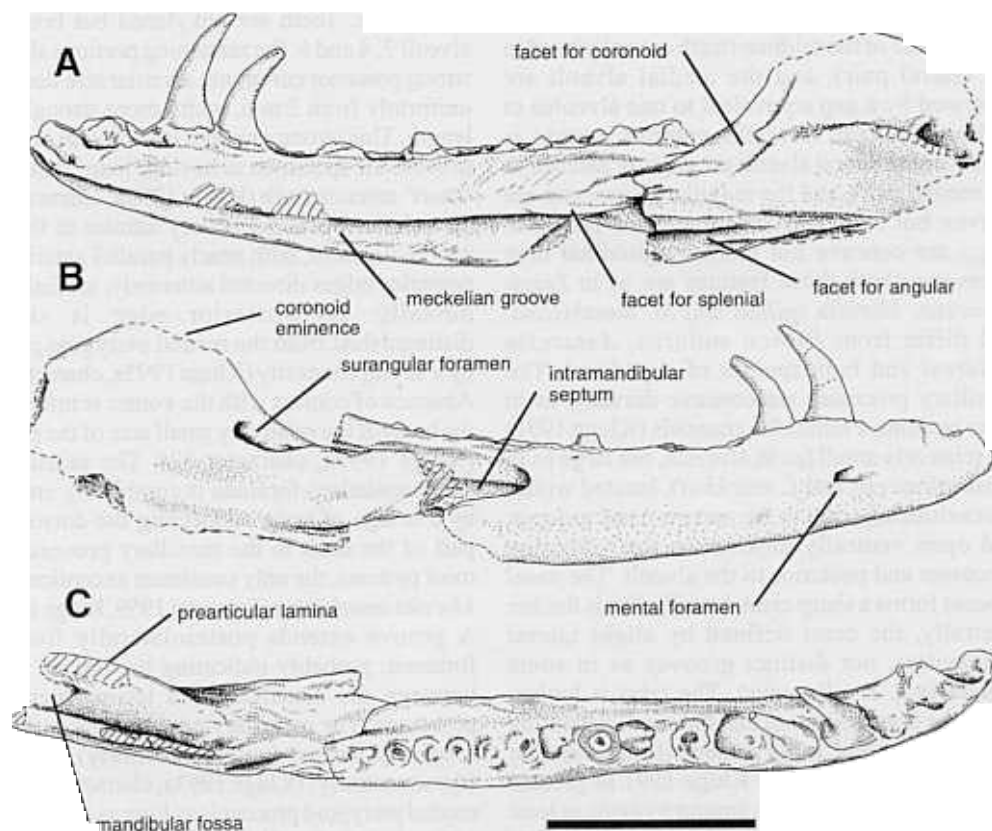


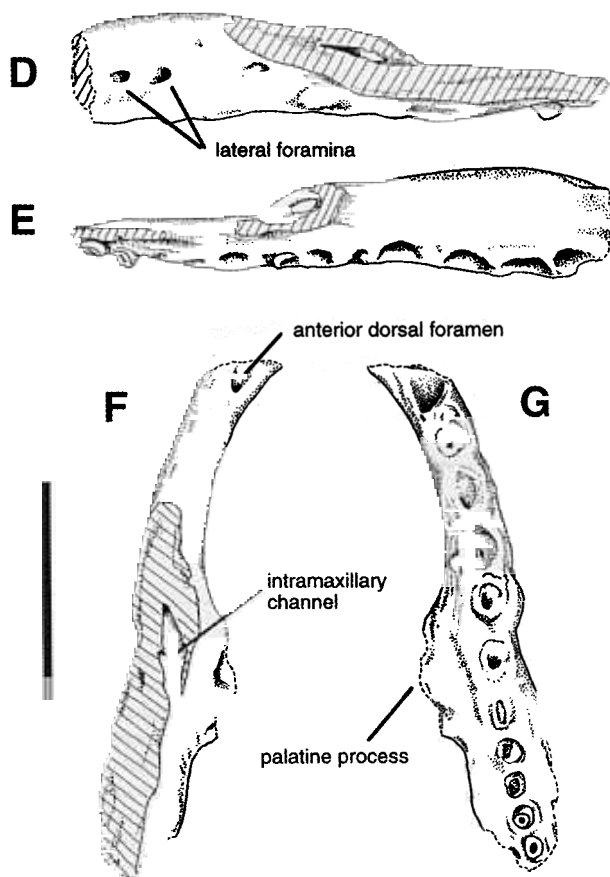
Fig. 4 (above and opposite). *Morelia riversleighensis* (Smith and Plane, 1985); parts attributed to a single skeleton from Upper Site, Riversleigh. A-C, right dentary and compound mandibular elements (AR 13392) in medial, lateral, and dorsal, views (shown as if articulated). D-G, left maxilla (AR 13136) in lateral, medial, dorsal, and ventral views. Scale bar = 10 mm.

form and relative length of the teeth, and the acute posterior notch of the mental foramen.

The anterior part of a left dentary (AR 8699, HH Site; Fig. 2 H-K) is consistent in size with the *M. riversleighensis* holotype; approximately 23 mm long, lacking part of the 1st alveolus and broken posteriorly through the 7th. Traces of ankylosed teeth are present in alveoli 2, 4 and 6. The meckelian groove is open to the anterior tip, and contains a foramen facing ventrally below the second alveolus. The ventral edge of the dentary is only slightly convex apart from the strong upward curve below the 2nd alveolus. The most anterior three alveoli are deflected medially and slightly ventrally from the others. Depth at the 4th alveolus (position of mental foramen) is 7.0 mm, the posterior margin of the foramen forming an acute notch (see below).

The partial skeleton from Upper Site is particularly valuable in that it gives us an

associated maxilla (AR13136 described above), dentary, and compound mandibular element (AR13392). The dentary is 34.3 mm in length, but lacks the posterior tip of the upper posterior process and most of the lower process. The distance from the anterior tip to the lateral notch is 23.8 mm. There are 17 alveoli; possibly one more was originally present more posteriorly, but probably no more (based on comparison with extant forms and other fossils). At least traces of ankylosed teeth are present in alveoli 4, 5, 7, 9, 11, 12, 13, 14, 15 and 17, but only the 4th and 5th teeth are mostly complete: the preserved parts of these teeth are 7.0 and 5.7 mm in length, and the 4th is somewhat more erect than the 5th. A weak anterolateral ridge is present on the distal part of each tooth. The anterior part of the tooth row is nearly straight in lateral view, the posterior part (from the 10th alveolus) elevated at about 10°. In dorsal view the alveoli lie in a straight line apart



from 1-4 which curve medially. The meckelian groove is open to the anterior tip, its diameter increasing smoothly posteriorly, while its upper edge is smoothly curved and approximately parallel to the tooth row from the 4th tooth back. There is a foramen facing ventrally within the groove below the 2nd alveolus. The ventral edge of the dentary is smooth and slightly convex for its whole length, with slightly greater curvature producing a bulge (in lateral view) below the middle of the 2nd alveolus. Depth at the 4th tooth (position of mental foramen) 5.7 mm; the single mental foramen opens anteriorly, and its posterior margin forms an acute notch in lateral view. The posterior lateral fossa extends to below the anterior edge of the 11th alveolus; the upper process bears a weak lateral ridge close to its dorsal edge. The dorsomedial face between the tooth row and meckelian groove is smoothly convex (in transverse section) for most of its length, but posteriorly from the 11th alveolus forms a dorsomedial ridge defining slightly concave dorsal and medial surfaces. The medial face (facet for the dorsal part of the splenial and anterior part of the

coronoid) is notched posteriorly, producing a blunt posteroventral prominence, and the dorsal lamina ends abruptly at the level of the 16th alveolus so that the last two (or possibly three) alveoli are on a narrow posterolateral process. Because of the damage to the ventromedial margin posteriorly, the facet for the ventral part of the splenial is mostly lost, but an inflexion of the edge just anterior to the midpoint of the dentary indicates the position of the anterior tip of the splenial spine.

The anterior part of the right compound bone is broken at most of its margins, but preserves most of the anterior process, the anterior parts of the surangular and prearticular laminae with the surangular foramen, most of the coronoid process, anterior margin of the mandibular fossa, and most of the facets for angular and coronoid. The lateral face is mostly smoothly convex, apart from the moderately large surangular foramen and a ventral longitudinal trough; the ventrolateral crest (below this trough) for adductor muscle insertion is mostly broken away. Anteriorly, the trough forms the articulating surface for the lower posterior

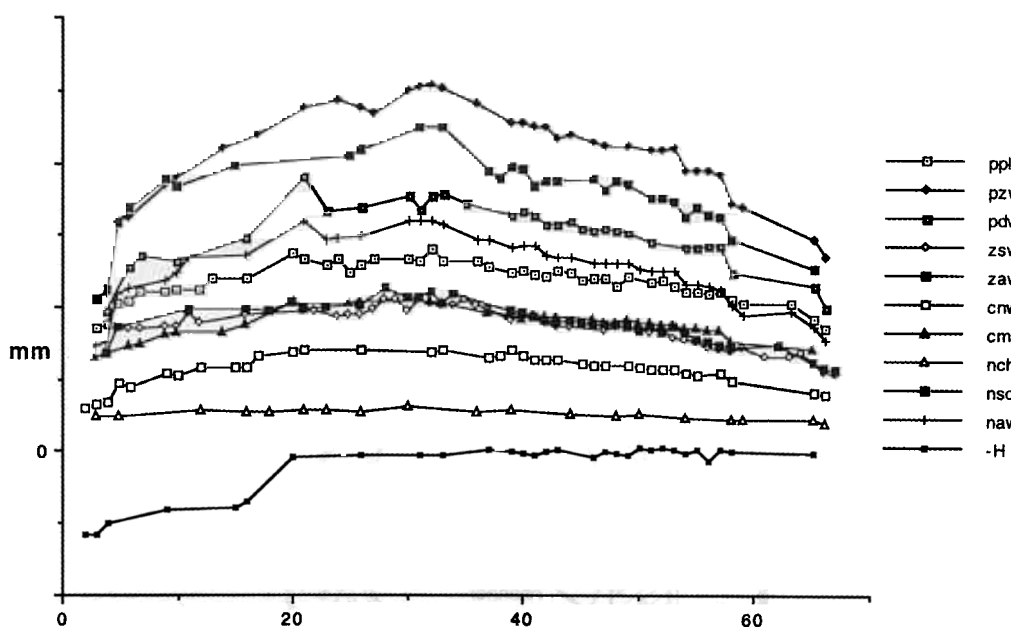
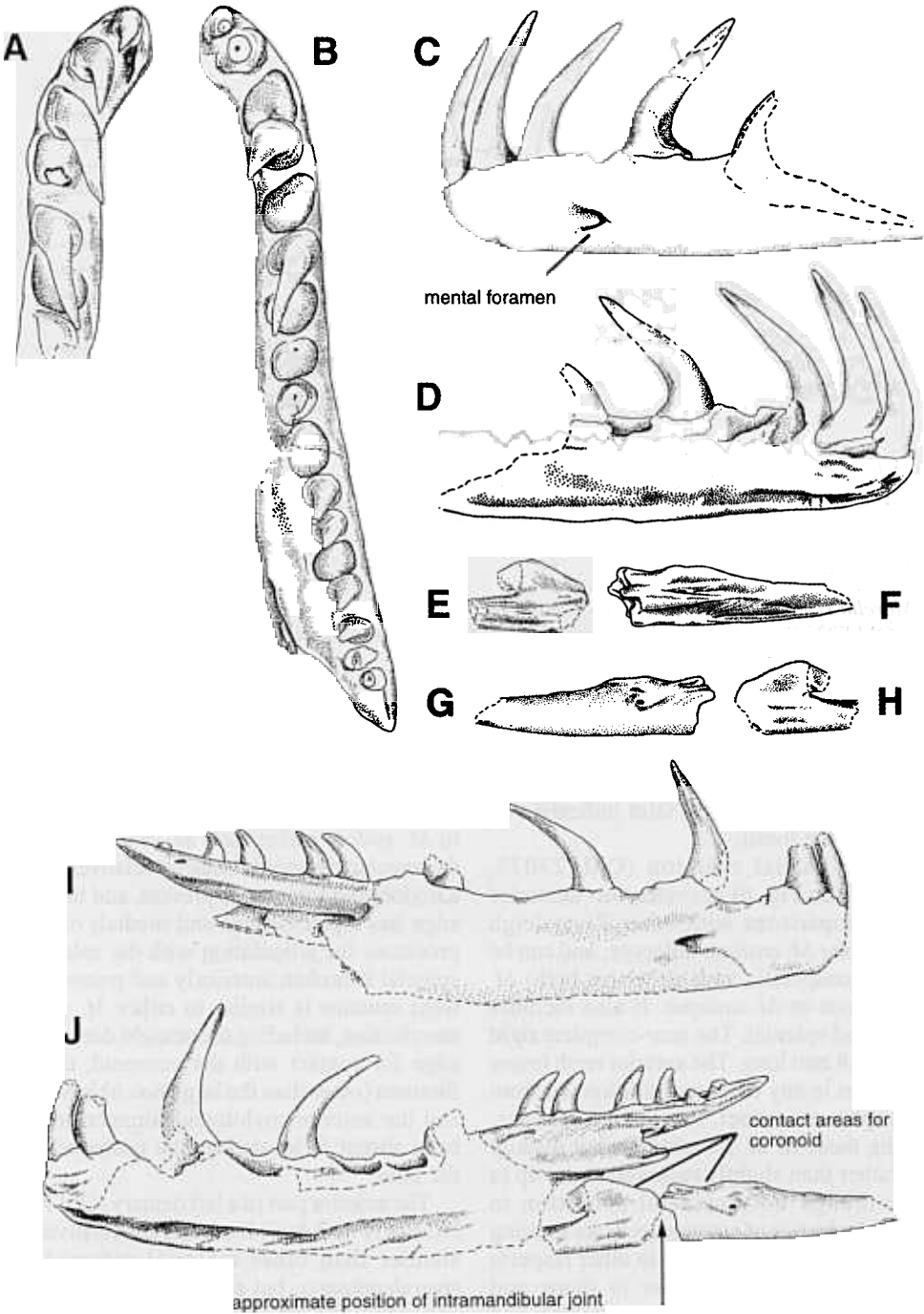


Fig. 5. *Morelia riversleighensis* (Smith and Plane, 1985); plot of measurements (mm) of vertebrae (AR 10842) from single skeleton from Upper Site, Riversleigh, in approximate antero-posterior order. Abbreviations: ppl = maximum length across facets of prezygapophyses to postzygapophyses, pzw = maximum width across prezygapophyseal processes, pdw = maximum width across paradiapophyses, zsw = width of zygosphenes, zaw = internal width of zygantrum, cnw = width of condyle, cml = length of centrum from rim of cotyle to rim of condyle, nch = internal height of neural canal, nsc = distance from anterodorsal tip of neural spine to ventral rim of condyle, piw = width between ventral edges of parapophyses, pdfl = maximum length of paradiapophyseal facet, zh = height of zygosphenes, -H = nsc-nsh. Many measurements are minima, affected by damage to the specimens.

process of the dentary, and here it is sharply defined dorsally by the ventral edge of the anterior process of the surangular. This anterior process is formed by vertical (lateral) and horizontal (medial) laminae; it is incomplete anteriorly but makes a good fit with the dentary. The surangular foramen, opening anteriorly, is dorsolateral and just posterior to the anterior process. The anterior edge of the coronoid process (formed by the surangular lamina) is concave and not very steep, but the upper part is broken off so it is not clear whether it was angular or rounded dorsally; the part of the dorsoposterior edge preserved is nearly straight, but steeper than in most pythons examined. The dorsomedial edge of the anterior process, and anteromedial edge of the coronoid process, form the facet for the coronoid bone, the posterior and ventral margin of which is clearly defined. The prearticular lamina

is low and its dorsal edge, as far as preserved, is nearly horizontal; it forms a distinct crest as far forward as the coronoid facet. There is a distinct notch in the posterior edge of the coronoid facet just above the prearticular crest. The floor of the trough between the surangular and prearticular crests ends shortly before the posterior end of the fragment, forming the anterior edge of the mandibular fossa. The ventromedial face of the fragment is the facet for the angular, which has a horizontal line of contact with the coronoid facet anteriorly and tapers towards the worn ventral edge posteriorly; the facet is marked by a series of longitudinal grooves and ridges. The irregular anterior edge of this vertical medial lamina extends to about the mid-point of the anterior process, and there is a distinct sharp notch (visible dorsally) between the vertical and horizontal laminae at this point. This notch is a remnant of

Fig. 6 (opposite). *Morelia riversleighensis* (Smith and Plane, 1985); parts attributed to a single skeleton (QM F23073) from Archie's Absence (Snake) Site, Riversleigh. A, C, D left dentary; B, I, J right dentary; E, H splenial (right side, image reversed); F, G left angular. A, B dorsal; C, E, F, I lateral; D, G, H, J medial views. J includes right splenial and a reversed image of the left angular to show approximate position of intramandibular joint and surfaces contacting the coronoid. Scale bar = 10 mm.



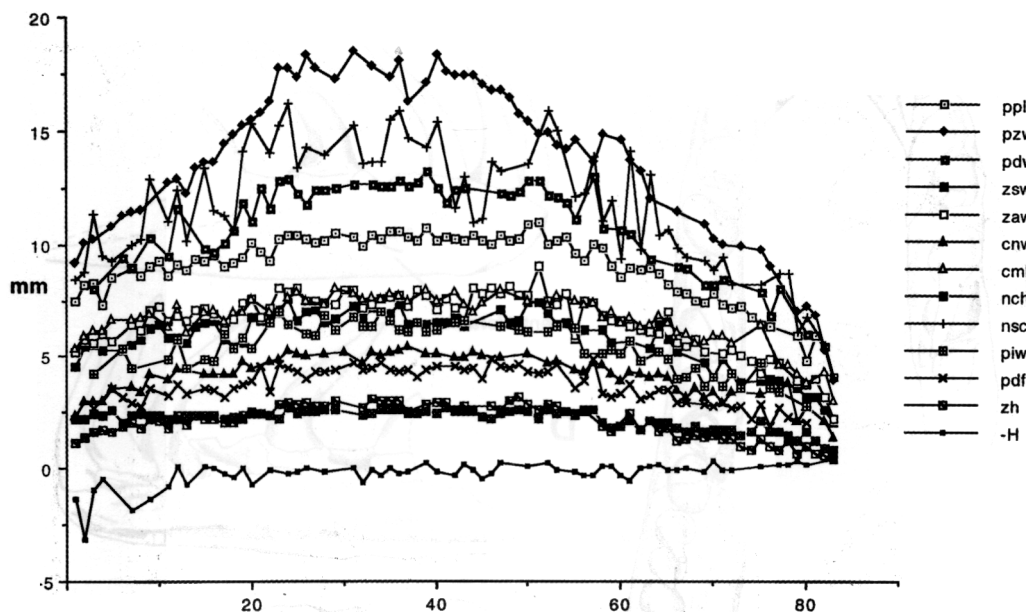


Fig. 7. *Morelia riversleighensis* (Smith & Plane, 1985); plot of measurements (mm) of vertebrae from single skeleton (QM F23073) from Archie's Absence (Snake) Site, Riversleigh, in approximate antero-posterior order. Abbreviations as in Fig. 5.

the suture between surangular and prearticular; in some comparative specimens (e.g. some *Morelia amethistina*) it continues as a distinct narrow groove beyond the coronoid and into the mandibular fossa, but only a faint indication of this is seen in the fossil.

The other partial skeleton (QMF23073, AA(Snake) Site; Fig. 6) provides two dentaries allowing comparisons with other Riversleigh material and the *M. antiqua* holotype, and can be considered conspecific with either (or both) *M. riversleighensis* or *M. antiqua*. It also includes an angular and splenial. The near-complete right dentary is 47.8 mm long. The anterior teeth (more complete than in any other pythons known from Riversleigh) are erect, long and slender, resembling those of *M. amethistina* but distally straight rather than slightly recurved at the tip (a common though not universal condition in *amethistina*); the tips of anterior teeth are missing in the *M. antiqua* holotype, but in other respects the teeth are extremely similar in shape and orientation. Posterior teeth are shorter and strongly curved posteromedially, and although the middle part of the tooth row does not preserve tooth tips in either it is clear that there was a marked 'notch' in the tooth row in both, due to both tooth length and orientation. The left angular and part of the right splenial were found only centimetres away, but not in articulation with the

dentaries. The angular is slightly damaged posteriorly; the dorsal edge is concave dorsoposteriorly, thickened anteriorly for contact with the coronoid (similar to the outline of the coronoid facet on AR 13392 from Upper Site, and to *M. spilota* rather than *M. amethistina* where the angular-coronoid contact is relatively shorter); a mylohyoid foramen is present, and the anterior edge has a pair (lateral and medial) of peg-like processes for articulation with the splenial. The splenial is broken anteriorly and posteriorly, but what remains is similar to either *M. spilota* or *amethistina*, including the straight dorsoposterior edge for contact with the coronoid; no medial foramen (other than the large notch) is preserved, and the anterior mylohyoid foramen may have been absent or located on the posterior edge of the bone.

The anterior part of a left dentary (QM F23130, NG Site; Fig. 3 A-C) is smaller and relatively more slender than other material referred to *M. riversleighensis*, but probably consistent with a younger individual of the same taxon. As in other dentaries referred to this species, the mental foramen forms an acute notch posteriorly.

Vertebral column. Vertebrae from Upper Site (AR 10842; plot of measurements Fig. 5), like the jaw elements, are rather poorly preserved, chalky and worn, so that surface features are often obscured and prominences (zygapophyses,

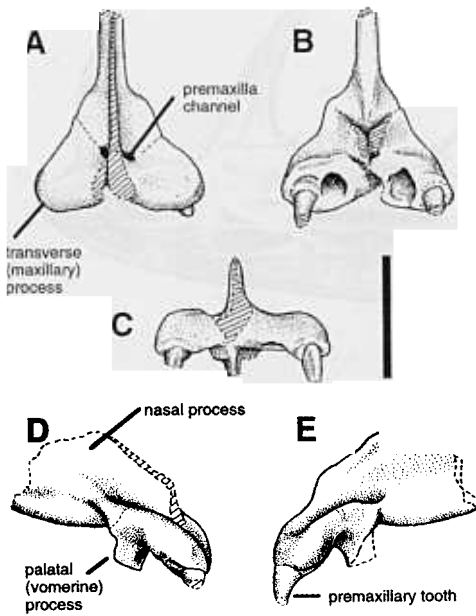


Fig. 8. Premaxilla referred to *Morelia riversleighensis* (AR 5658, Gag Site) in (A-E) dorsal, ventral (anterior to bottom of page), anterior, and right and left lateral views. Scale bar = 5 mm.

hypapophyses and neural spines) are rarely intact. The triangular centrum is somewhat longer than wide in ventral view, with well defined subcentral ridges from the parapophyses to the condyle, slightly convex laterally between anterior and posterior constrictions. The haemal keel, blunt in section for most of its length, extends from just behind the cotylar rim (from which it is sometimes separated by a shallow transverse groove) to just before the condyle, defined laterally by deep depressions which barely extend to the cotyle, producing ventrolateral emarginations of the cotylar rim. The keel is concave ventrally, in its posterior part it projects slightly below the condyle, has a sharp ventral edge and forms an acute point in ventral and lateral views. Condyle and cotyle slightly wider than deep, moderately oblique in lateral view; cotyle wider than neural canal, and about as wide as the zygosphen. Zygapophyseal facets inclined slightly (less than 10°) above horizontal, defining planes which intersect at or just below the floor of the neural canal. Prezygapophyseal facets subtriangular, with nearly straight anterior edge angled slightly anterior to the transverse plane and long axis at about 60° from the sagittal plane. Postzygapophyseal facets similarly shaped, but with more

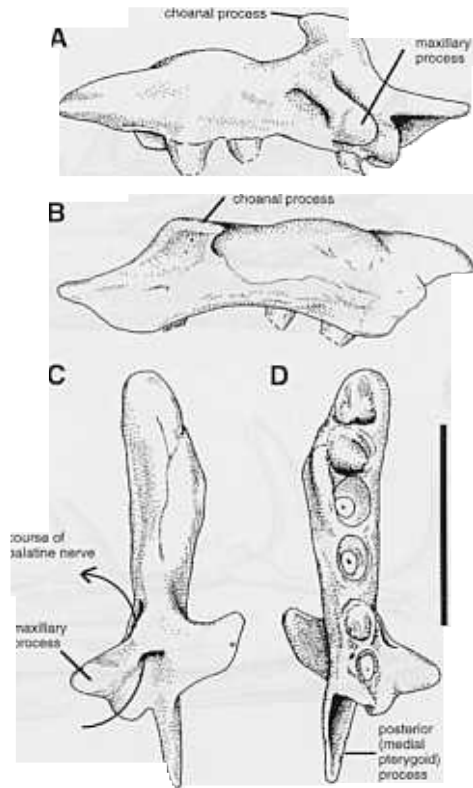


Fig. 9. Left palatine referred to *Morelia riversleighensis* (AR 16880, Boid Site East) in (A-D) lateral, medial, dorsal, and ventral views. Scale bar = 10 mm.

transverse posterior edge. Interzygapophyseal ridge strongly developed, concave laterally and separated by quite sharp angular inflexions from the zygapophyses. Acute but short prezygapophyseal processes project anterolaterally beyond the facets, forming the continuation of a ventral crest on the prezygapophysis separating anterior and posterior surfaces for muscle attachment. Zygosphen about as deep as neural canal, and wider than deep; its dorsal edge in anterior view is concave on either side of a rounded central lobe which is slightly lower than the lateral facets. Zygosphenal facets oval, mostly somewhat higher than long, with long axis directed anterodorsally in lateral view; in anterior view, facets inclined at about 45° from vertical, defining planes which intersect near the floor of the neural canal (above it anteriorly, at or below in posterior vertebrae). In dorsal view, the anterior edge of the zygosphen is concave between rounded lateral lobes and a strongly defined median prominence; the latter is higher than wide, occupying the

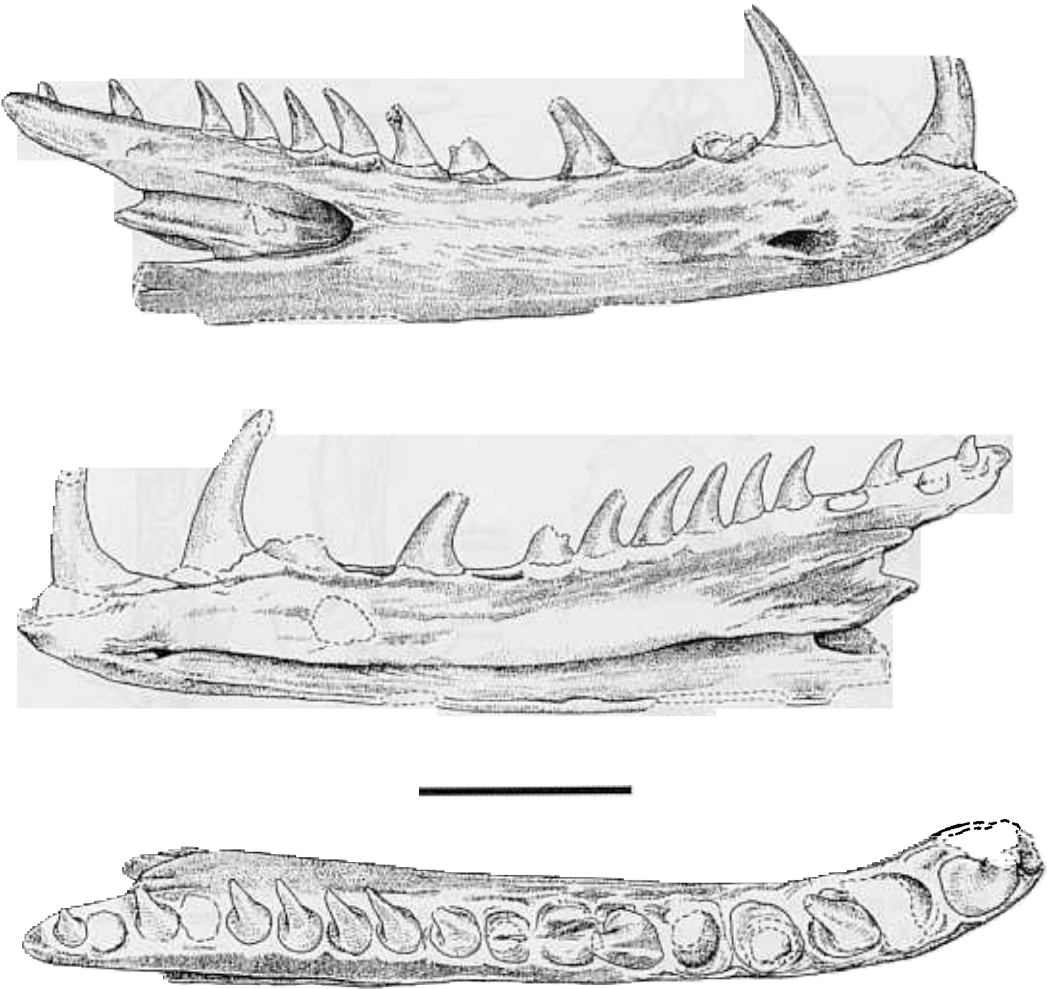


Fig. 10. Holotype right dentary of *Morelia antiqua* Smith & Plane, 1985 (CPC 25077, Camfield Beds, NT) in (A-C) lateral, medial, and dorsal views. This taxon is here treated as synonymous with *Morelia riversleighensis*. Scale bar = 10 mm.

ventral half of the anterior face of the zygosphene, and immediately below it is a transverse ridge marking the roof of the neural canal. The posterior edge of the neural arch is divided into lateral and dorsal concavities by convex prominences dorsolateral to the zygantrum. The roof of the zygantrum increases in depth medially where the neural arch sweeps smoothly into the broad base of the neural spine. The posterior edge of the zygantral roof in dorsal view forms a V-shaped notch interrupted by the neural spine; the zygantral facets are barely visible from above. The neural spine is 'hatchet-shaped', commencing at the posterior edge of the zygosphene, rising vertically or overhanging slightly anteriorly. The posterior edge overhangs more strongly, forming an acute

angle with the dorsal edge when intact. The crests of the posterior neural arch extend obliquely up the lateral faces of the spine, forming a cusp in lateral view. The paradiapophyses do not extend beyond the lower edge of the cotyle except in the most anterior vertebrae; they are positioned below or slightly posterior to the prezygapophyses, but are generally not visible from above. Paracotylar foramina are not present in the depressions on either side of the cotyle, but tiny parazygantral foramina or pits do occur, mostly unilaterally, on a minority of vertebrae. Lateral and subcentral foramina are regularly present, the latter (one pair only) usually located symmetrically in the deepest part of the subcentral depressions.

Typical features of anterior vertebrae, apart

from bearing prominent hypapophyses instead of low keels, include relatively smaller and rounder condyle and cotyle, higher neural canal, parapophyses extending below the cotyle, and subcentral ridges more strongly concave, so centrum relatively narrower posteriorly than at midbody. Subcentral depressions are poorly defined in the anterior region. The haemal keel begins at the cotylar rim, but the hypapophysis projects only below the posterior third of the centrum; in lateral profile, its anterior edge is sigmoid and posterior edge slightly convex (intact in only one vertebra). The neural spine is anteroposteriorly short in the most anterior region, but does not appear to be distinctly higher or lower than in the anterior trunk generally. In the posterior trunk region, the centrum is relatively longer, the neural spine lower, and subcentral depressions extend anteriorly to separate the parapophyses sharply from the cotylar rim. Just before the cloacal region the haemal keel becomes more prominent and swollen posteriorly, then reduces to a low but distinct keel again (in the smallest vertebra to bear free ribs) before reappearing as paired haemapophyses in the caudal region. Caudal vertebrae appear to have had very low neural spines. Pleurapophyses of caudal vertebrae project ventrolaterally and anteriorly, and are somewhat flattened dorsoventrally.

Fig. 5 shows measurements of 83 partial to complete trunk vertebrae, all referred to the same skeleton and arranged in interpreted antero-posterior order; most of the vertical scatter results from damage to processes (especially neural spine and hypapophysis). Five or six additional vertebrae are more poorly preserved and not measured (the doubt as to number results from non-overlapping anterodorsal and posteroventral portions of what could be a single vertebra; the broken surfaces are worn, precluding reattachment or measurement across the break).

The 67 vertebrae from the 'AA Snake' QMF23073 (Fig. 7; ~30% of the precloacal column, based on *M. spilota*) includes nine single and articulated sequences of two (x11), three (x1), four (x2), five (x1), six (x2) and seven (x1) vertebrae. In most if not all cases, this partial disarticulation occurred prior to deposition; short pieces predominate anteriorly, longer ones posteriorly. No cloacal or caudal vertebrae were found. The vertebrae are similar in morphology and intracolumnar variation to those from Henk's Hollow and Upper sites, but intermediate in size (consistent with size relations of the jaw elements).

Hypapophysis depth within the anterior (precloacal) trunk remains nearly constant for a considerable length before a sharp reduction (near the heart), rather than decreasing steadily. This is similar to extant species of *Morelia* and *Python*, not *Aspidites* and *Liasis* (s.l., including studied species of *Antaresia*, *Liasis*, and *Apodora*).

Remarks. The Upper Site deposit contains remains of a highly diverse vertebrate fauna (Archer *et al.* 1989, 1994), but apparently only one individual python. The presence of upper and lower jaw elements consistent with each other in size, morphology and state of preservation, in association with a good sample of vertebrae showing the same consistency, makes this the most complete fossil python yet described from Australia. The jaw elements show clear affinities with extant Australian pythons of the genus *Morelia*, and this individual provides a 'key' allowing the holotypes and associated material of *Montpythonoides riversleighensis* and *Morelia antiqua* to be compared to a single specimen of comparable age and locality. It is unfortunate that, unlike much of the other material described here, most of the bones from Upper Site have suffered considerable erosion prior to fossilisation.

The only notable differences between the Upper Site and Henk's Hollow (holotype) maxillae is the shape of the palatine process, which is defined posteriorly by a smooth concavity rather than an angular cusp in AR 13136. This can be attributed to ontogenetic change; larger specimens of python species are characterised by more prominent bony crests than smaller individuals (Kluge 1993a), and thus further growth of the palatine process and posteromedial shelf of the bone from the condition in AR 13136 would plausibly lead to the more angular condition in QM F12926. There might have been a difference of about one alveolus in the relative position of the palatine process and the associated widely spaced alveoli. Such variation could be expected within a species; for comparison, in *M. spilota* the total number of maxillary teeth ranges from 15 to 21 (Kluge 1993a, table 1; presumably a geographically heterogeneous sample).

Nor does the holotype of *Morelia antiqua* differ significantly from the Upper Site dentary other than ontogenetically. It is thus possible to refer the Upper Site pythonine provisionally to the synonymy of both *M. riversleighensis* and *M. antiqua*, and thus to synonymise both species described by Smith & Plane (1985). The action of Smith & Plane in describing two separate taxa

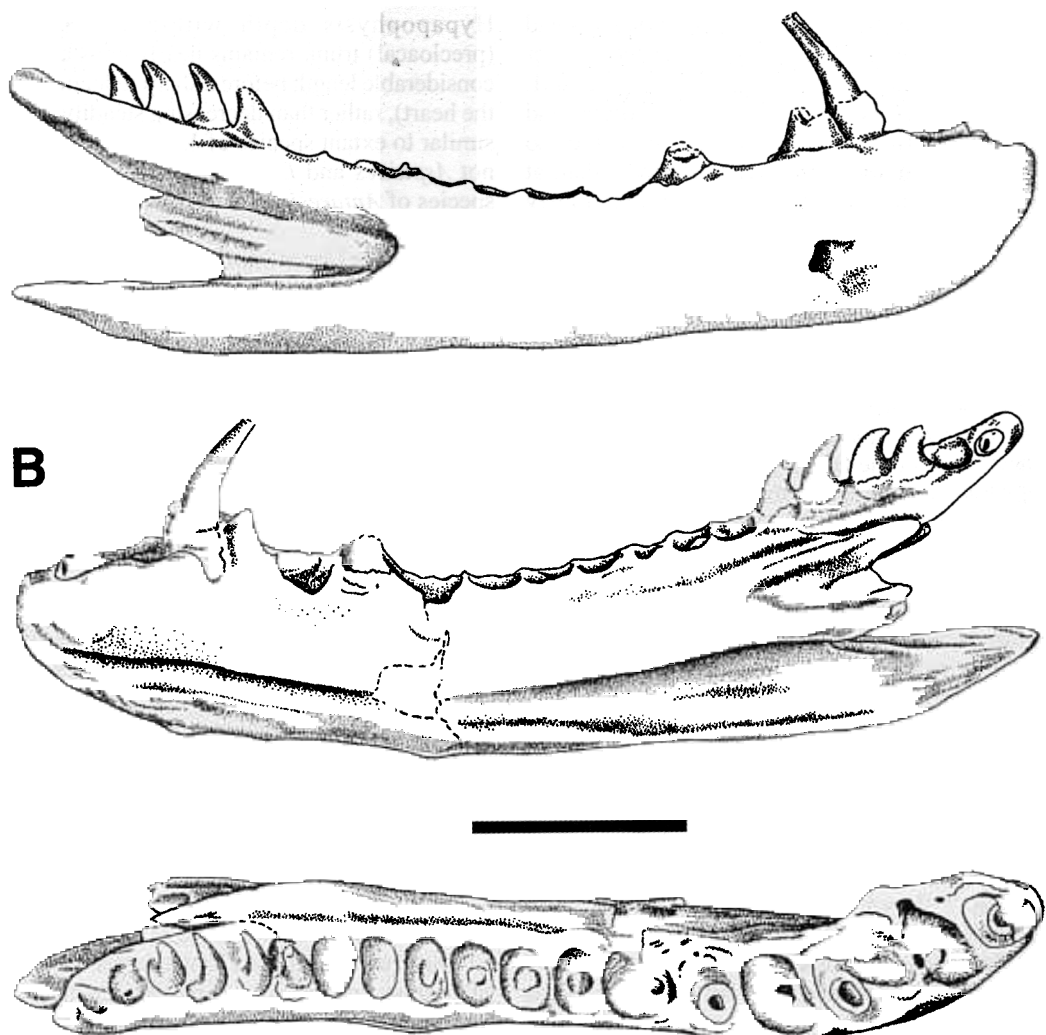


Fig. 11. Pythoninae indet. (*M. riversleighensis*, other *Morelia* or *Python* sp.) (QM F23033), WH Site, Riversleigh. Right dentary in (A-C) lateral, medial, and dorsal views. Scale bar = 10 mm.

based on non-overlapping material, while not difficult to understand in view of the temporal and geographic separation of the deposits, appears to be unjustified in this case. The material of this presumed species is now sufficient to allow more meaningful comparisons with extant snakes than was possible for either alone. The Archie's Absence pythonine can also be referred to this taxon, and provides additional jaw elements (splenial, angular) and articulated vertebral sequences which add to our knowledge of its morphology.

There is now no justification for maintaining *Montityphonoides* as a genus separate from *Morelia*. In fact the characters on which the distinction of *Montityphonoides* Smith & Plane was based are in one case erroneous ('absence'

of lingual cutting ridges of the teeth, this work, Fig. 2B), in the other equivalent to the derived condition in all *Morelia*, and thus diagnostic of that genus (lateral bulge of maxilla, Kluge 1993a). The separate question of the specific status of *M. riversleighensis* has been touched on by Kluge (*ibid.*), who considered that described material of this taxon does not exhibit autapomorphies with respect to *M. amethystina* or *M. spilota*, and tentatively referred it to the synonymy of *spilota* on the basis of syntopy.

No unique or unambiguous autapomorphies of *M. riversleighensis* have been found in the more extensive sample of cranial material described above, but the question of its status and relationships are examined below by including it in a phylogenetic analysis of all pythonine species.

If *M. riversleighensis* were to group unambiguously with a single modern species, one would be justified in synonymizing it with that species.

Taxonomically Indeterminate Material

***Morelia* or *Python* sp. indet. (possible *M. riversleighensis*)**

A large complete dentary (QM F23033) and one vertebra (AR 10411) from White Hunter Site (WH), Riversleigh. The complete right dentary (Fig. 11) is generally similar to those of *M. riversleighensis* but considerably more robust, with the mental foramen nearly square rather than forming an acute posterior notch, and posterior alveoli transversely expanded. 19 alveoli; 1, 3, 4, 6, 14, 15, 16 and 17 with ankylosed teeth, tooth 3 incomplete, 14 lacking tip, 15-17 complete, other teeth broken near base. The specimen is relatively deep and robust: length to upper posterior tip 47.7 mm, depth at 4th tooth (and mental foramen) 9.3 mm. Dorsolateral edge convex anteriorly in lateral view (to 7th alveolus), slightly concave posteriorly. Ventral margin of dentary strongly convex anteriorly, slightly concave below 7th tooth and nearly straight posteriorly. The posterior lateral fossa extends to below the anterior edge of the 11th alveolus. Upper posterior process above lateral fossa slightly shallower than ventral process, deepest below 15th-16th teeth; its lateral surface is smooth. The lower posterior process is pointed, extending slightly further posteriorly than the upper branch. The mental foramen is deeper than long, its ventral edge weakly defined and thus facing anteroventrally; the posterior edge of the foramen is somewhat angular but not forming an acute angle. In dorsal view the tooth row forms a double curve, 1-4 deflected medially and 14-19 curving laterally. Most of the third tooth is present, originally about as deep as the bone below it; it is curved posteriorly in its ventral part but straight distally as far as preserved. The posterior teeth are much shorter, curved strongly medially and slightly posteriorly. There is a marked reduction in anteroposterior alveolar diameter from the 7th to 8th. All of the preserved tooth crowns have cutting ridges on the distal third, anterolateral on the third tooth but posterolateral on the 14th to 17th. The 3rd tooth lacks any sign of a medial ridge (it may have been limited to near the tip, which is not preserved); the 14th to 17th have anteromedial ridges, the anterior face of each tooth between the two ridges flattened and apparently with thickened enamel. In medial view the 1st to 7th alveoli form a dorsally convex curve; from 8

to 19 the jaw is slightly concave dorsally. The meckelian groove is open to the anterior tip, uniform in diameter for its anterior half but widening posteriorly; its upper edge is approximately parallel to the tooth row but diverges slightly ventrally from the maximum depth of the groove below the 13th to 14th alveoli. The dorsomedial face between the tooth row and meckelian groove bears a shallow longitudinal trough for most of its length, defining an 'alveolar ridge' above. The medial face above the groove (bearing a well-defined facet for the dorsal part of the splenial and anterior part of the coronoid) is notched posteriorly, producing a posteroventral prominence (slightly damaged), and the dorsal lamina ends abruptly between the 17th and 18th alveolus so that the last two alveoli are on a narrow posterolateral process. An inflexion of the medioventral edge just anterior to the midpoint of the dentary (below the 7th alveolus) indicates the position of the anterior tip of the splenial.

The robust anterior portion and pointed posterior ventral process are most similar to some extant species of *Morelia* and *Python*, but unlike other genera where the dentary is shallower or tapered anteriorly, and the posterior process is rounded. It differs from available material of *Morelia spilota* in the lower posterior process extending slightly further posteriorly than the upper, tooth-bearing process, and from dentaries referred to *M. riversleighensis* in being much more robust, especially anteriorly, and the mental foramen being deeper and lacking an acute posterior notch. The depth of the jaw, especially anteriorly, resembles a specimen of *P. reticulatus* figured by Kluge (1993a, fig. 14c, UMMVP82), but not other available *Python* material (including a *P. reticulatus* of comparable size to the fossil, where the dentaries are shallow and tapered); a syntype dentary of *Palaeopython cadurcensis* illustrated by Rage (1984: fig. 12B; MNHN 16317) shows similar proportions. The features which appear to distinguish this specimen from *M. riversleighensis* may be only consequences of large size and irregular growth due to trauma. The number of alveoli is higher than observed in *Aspidites melanocephalus*, *Apodora papuana*, *Morelia carinata*, *M. oenpelliensis*, *M. viridis* and *Python sebae*, and lower than species of *Antaresia* and *Leiopython*, or *P. timoriensis*. What remains of the dentition indicates that the anterior teeth were considerably longer than the posterior teeth, unlike the species of *Aspidites*. The size of the dentary and associated vertebrae imply a large size, probably more than 3 metres total length.

The WH dentary can be scored for the following characters: 64(1), 65(1), 66(0?) (not scorable directly for slight/marked change in dentary tooth height due to the absence of most teeth, but the marked reduction in alveolar diameter from the seventh to eighth tooth position probably reflects a change in overall tooth size; Kluge records the derived state only for *Leiopython albertisii*, *Bothrochilus boa*, *Antaresia* species, *Morelia spilota*, *M. viridis* and *Python timoriensis*, but appears to recognise an intermediate state for *Liasis olivaceus* in his discussion of *Morelia antiqua*; Kluge 1993a: 55), 121(1 or 2). This combination of states is the same as *Morelia spilota* and *M. riversleighensis*, but other differences have been noted from these species. Given the large size of the specimen and the fact that it apparently suffered a fracture earlier in life, its unusually robust form may be explained by a combination of allometry and pathological remodelling, so that it would be inappropriate to recognise a new taxon based on this material. WH is stratigraphically isolated but, on topographic and faunal grounds, regarded as approximately intermediate between Systems A and B (Archer *et al.* 1989), i.e. within the range of type material of *M. riversleighensis*. Other vertebrae from this site, including articulated series, appear to be too small to belong to the same individual, and have not yet been studied in detail.

?*Morelia* indet. cf. *M. spilota*

An anterior maxillary fragment (QM F24726, Cleft of Ages Site (COA 2A), Fig. 12) is broken anteriorly as well as posteriorly, retaining four alveoli thought to be 3 - 6; teeth ankylosed but broken in 4 and 6. The fragment is curved in dorsal view, widening anteriorly, and a deep trough containing the anterior dorsal foramen extends obliquely anterolaterally above 3-4. The tooth bases are large, elongated parallel to the posterior part of the shaft. A small lateral foramen is present between 5 and 6, and a much larger one above 4, equal in size to the base of the tooth (Kluge 1993a, character 14(1)). This character distinguishes the specimen from *M. riversleighensis* (material from HH and Upper Sites) and *M. oenpelliensis*, but the large foramen occurs in all other species of *Morelia* and *Python*. There is thus insufficient information to refer the specimen to any species or group of species, but a general similarity to *M. spilota* suggests it may represent the (*spilota*, *carinata*, *viridis*) clade. The deposit is thought to be younger than other sites at Riversleigh which contain *M. riversleighensis*.

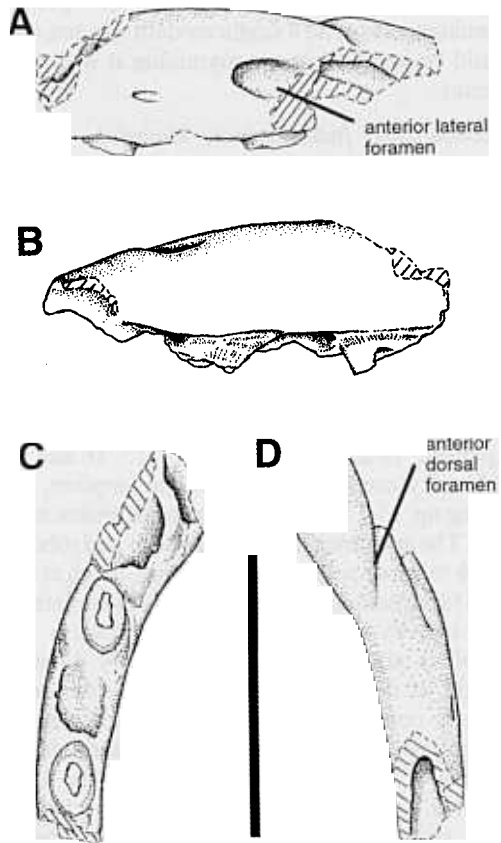


Fig. 12. ?*Morelia* indet., cf. *Morelia spilota* (QM F24726), Cleft of Ages (COA2A) Site, Riversleigh. Anterior fragment of right maxilla. A-D, lateral, medial, ventral, and dorsal views. Scale bar = 10 mm.

Pythoninae indet. cf. *Morelia* sp.

The posterior part of a small (presumably juvenile) right compound bone (AR 12700, Fig. 13) is known from Gotham City Site, along with vertebrae (AR 8045, 8777, 12173p) and ribs (AR 6793, 8558). The compound fragment is 8.3 mm in length, broken transversely through the mandibular fossa. The surangular lamina is convex dorsally, and laterally in section, and concave on its medial face. The prearticular lamina is just over half the depth of the surangular where they join posteriorly close to the articular facet, and its upper edge is horizontal as far as it is preserved. The laminae converge to form the floor of the mandibular canal, which is distinct from the ventral edge of the bone, a longitudinal channel or sinus extending below it and exposed by breakage. The ventral edge where preserved is concave, most

strongly just below the articular facet, and a ventrolateral ridge is present. The saddle-shaped facet is limited anteriorly by a prominent transverse ridge, and is lower posteriorly; it extends ventrally on both sides, furthest on the medial face. The lateral and medial edges of the facet are notched; the concavity faces anteroventrally laterally, posteroventrally medially. An oval pit is present just below the lateral notch, and a relatively large foramen is present posterior to this, opening posteriorly. A small foramen is present in front of the anterior ridge of the articular facet, between and posterior to the prearticular and surangular laminae. The retroarticular process is damaged dorsally, but appears similar to that of extant pythons. Without study of ontogenetic sequences of extant taxa, and in view of the incompleteness of the specimen, only a general similarity to extant *Morelia* spp. can be noted.

Pythoninae indet., cf. *Liasis* sp. or *Python reticulatus*

The Two Trees Site (TT) is a deposit of uncertain age close to the topographically highest point of the 'Gag Plateau' sequence (System C, Archer *et al.* 1989), and may be considerably younger than neighbouring sites, possibly even Pliocene rather than Miocene. A single palatine (AR 8905, Fig. 14) is known from this site, which in the combination of size, the number of alveoli, position of choanal and lateral processes, and form of articulation with the pterygoid, differs from *M. riversleighensis* (AR 16880, BSE; Fig. 9) and extant Australian and New Guinea species, but resembles *P. reticulatus*. Other TT material: QM F23069 (1); AR 12810 (3 x vertebral fragments), 12811 (2 teeth), QM F23069 (2 ribs).

The large palatine lacks the choanal, posterior and most of the lateral processes, which are broken off near their bases; length 19.2 mm. There are eight alveoli, the first four large and the last four reducing in size; only the 7th has a tooth ankylosed. The choanal process extended from the rear of the 5th to the middle of the 8th alveolus, the palatine foramen from the rear of the 6th to rear of the 7th. In dorsal view, the anterior end is rounded (a small part of the anterior edge is broken), and the width of the shaft increases up to a maximum at the front of the 5th alveolus; the medial margin is slightly concave between this point and a bulge level with the 8th. The lateral margin is nearly straight anterior to the lateral process; the anterior edge of the latter is damaged, and it reaches its greatest width (less than natural) level with the front of the 7th alveolus. The

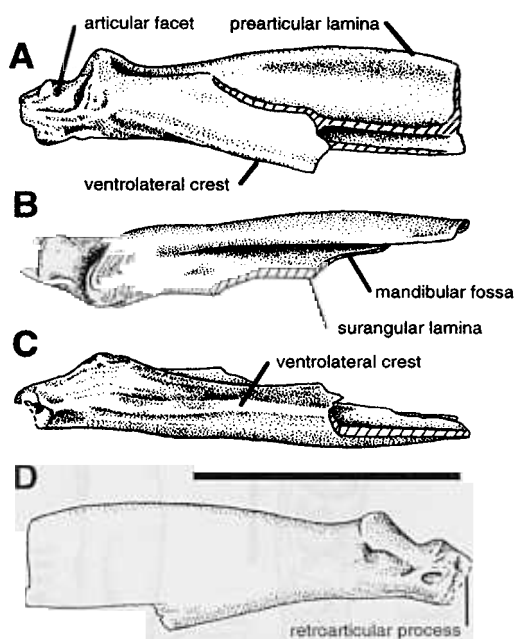


Fig. 13. Pythoninae indet. cf. *Morelia* sp. (AR 12700), Gotham City Site, Riversleigh. Right mandibular (compound) fragment of juvenile in (A-D) lateral, dorsal, ventral, and medial views. Scale bar = 5 mm.

posterior margin of the process is intact, showing a small prominence lateral to the 8th alveolus, and then narrows onto the posterior spine. In lateral view, the dorsal edge rises steeply from the anterior edge, then gradually less steep up to the front of the 5th alveolus, then rises again to form the base of the choanal process. The anterior edge of the process is on the dorsal midline of the shaft; it then angles to the medial side at about 45°, bending around the dorsal aperture of the foramen and continuing directly posteriorly; it is thickest transversely just anterior to the foramen. In lateral view, the palatine foramen is defined dorsally by the overhanging lateral process, ventrally by a ventrolateral ridge which continues anteriorly, bending first dorsally and then strongly ventrally level with the front of the 5th alveolus.

A high number of palatine teeth (character 50(2) of Kluge 1993a) characterises small species of *Liasis*, but also *P. reticulatus*; 8 are also reported as occurring in *Aspidites ramsayi* (Kluge 1993a: table 1). In character 55 (maxillary process 'broad' or 'narrow') this specimen does not appear to differ from AR 16880 (BSE, referred to *M. riversleighensis*), so state 1 can be assigned (shared with *Morelia* spp., except *amethistina* and *boeleni* where the process is absent, and *Aspidites*). None

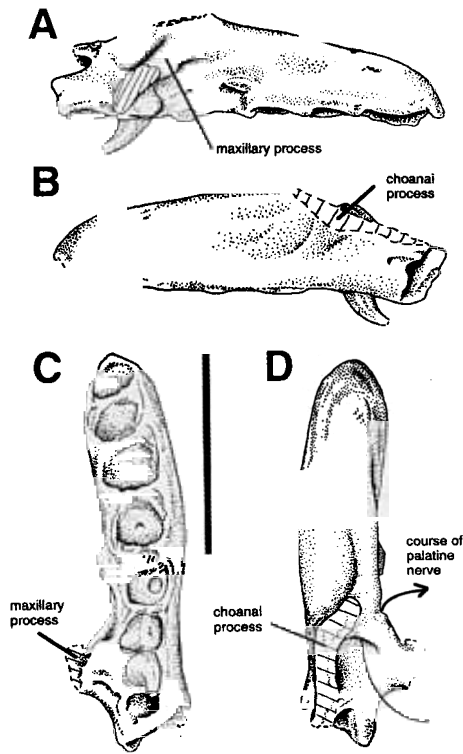


Fig. 14. Pythoninae indet., cf. *Liasis* sp. or *Python reticulatus* (AR 8905), Two Trees Site, Riversleigh. Right palatine. A-D, lateral, medial, ventral, and dorsal views. Scale bar = 10 mm.

of the other characters used by Kluge can be evaluated directly, but body size was certainly not small; state 0 can be excluded for character 121 (i.e. maximum total length approaching or exceeding 4 m).

DISCUSSION

Taphonomy and Habitat of Miocene Pythons

Relative completeness of a skeleton (in association or articulation), preservation of delicate elements, and lack of obvious wear are indicators that the animal died, and probably lived, close to the site of deposition (e.g. LaDuke 1991). At a number of Riversleigh sites, and at Bullock Creek, at least some elements of python skeletons are very well preserved, and in a few cases considerable proportions of skeletons remain in good association or articulation. HH site contains parts of several python skeletons, while AA (Snake), Upper and Boles' Bonanza sites contain single individuals. A partly articulated python

from an isolated site has also been collected for the Australian Museum (mentioned by Willis 1990), and another was found in association with medium-sized mammal skeletons (Gone Over 'Ere Site) in 1994 (pers. obs.). Although some other cases of well preserved, associated elements are known (e.g. type material of *Yurlunggur camfieldensis*, Scanlon 1992; *Nanowana godthelpi*, Scanlon 1997), no other snake taxa at Riversleigh show such a tendency to be preserved as isolated or relatively complete skeletons; they mostly occur in large mixed assemblages, or as isolated elements (Scanlon 1996). This suggests that Miocene pythons differed in habitat or behaviour from other sympatric snakes, particularly from the similar-sized madtsoiids *Wonambi* and *Yurlunggur*. Another apparent difference from madtsoiids at Riversleigh is that pythons predominate in deposits with many chiropteran remains and interpreted as cave fills (e.g. Microsite, Gotham City, and the Pliocene Rackham's Roost; Scanlon 1995, 1996). This is consistent with the habits of extant pythons which commonly inhabit caves and similar dark, enclosed spaces (e.g. hollow trees, termite mounds), and have thermoreceptive labial pits allowing efficient ambush predation on bats, geckoes and other vertebrates found in such locations (ectotherms, when active in a thermally heterogeneous environment, may be as readily detectable by this means as endothermic prey; Ehmann 1993).

AA (Snake) Site is close to but distinct from Archie's Absence Site; the latter contains a vertebra of a larger python, also comparable to paratype material of *M. riversleighensis*. The 'AA Snake' (QMF23073) material apparently represents a single individual which was only partially disarticulated at the time of burial. When found, some bones including the dentaries were exposed at the surface, so that much of the skeleton has presumably been destroyed by weathering. It is possible that other parts of the skeleton were missed in the field: it initially appeared that the skeleton was fully articulated (M. Archer pers. comm.), and thus should be contained in a contiguous series of blocks, but this was not actually the case. Acid preparation of the specimen was carried out by the author, allowing the following observations. The matrix is highly heterogeneous, varying from crystalline or sandy (almost pure white, and rapidly affected by acid) to clayey (yellow, and relatively acid-resistant) in an irregular, non-stratified manner, and including clasts in the form of pieces of many-layered evaporite crusts (up to 60 mm or more thick).

Some of these clasts had bones, including some of the python material, embedded in their (?upper) layers. This is interpreted to imply that the crust on a pool or slow-moving stream formed the substratum on which the carcass decayed and became partially disarticulated, over a length of time sufficient for some elements to become cemented into the crust, which probably required fluctuations in water level. Other parts of the python skeleton were apparently uncemented before final burial, and became embedded in other parts of the matrix, including parts of high clay content. Fragmentary and mostly worn bones and isolated teeth of numerous other vertebrates were also found in the deposit, likewise some cemented into the crusts and others 'free' in massive sediment; most were represented by no more than one identifiable element, and none have yet been identified to species (frogs, fish, turtles, skinks, bats, bandicoots, a thylacinid similar to *Nimbacinus dicksoni*, and a balungamayine kangaroo; pers. obs. and H. Godthelp, pers. comm.). The dentaries lay almost parallel to each other, in approximately their natural relative position; this would be unlikely unless they had been connected by soft tissue at the time of burial, and if the skull were still articulated with the lower jaws it would have originally been just above the surface of the rock as found. The degree of articulation of the python skeleton implies that burial occurred not very long after its death; long enough, however, for some of its bones to be cemented into exposed parts of the crust. The remaining association of the skeleton shows that deposition was due to an extremely local event, probably limited to one small pool (cf. Archer *et al.* 1994, Duncan *et al.* 1998).

Phylogenetic Analysis and the Status of M. riversleighensis

From the type locality (HH Site), we have incomplete maxillae, palatines, and dentaries from which the following can be evaluated (using the character and state labels of Kluge 1993a): 12(0 or 1); 13(0); 14(0); 15(1); 16(1); 17(1); 50(1). This combination of states is the same as in *M. oenpelliensis*, while *M. spilota* and *M. boeleni* differ only in having a large anterior maxillary foramen (14(1)). In addition to 14(1), *M. amethistina* has a reduced number of palatine teeth (50(0)), while *P. anchietae* lacks the lateral bulge of the maxilla (15(0)). All other extant pythonine species differ in three or more of these characters.

The Upper Site skeleton (maxilla, dentary, and compound) allows determination of the

following: 14(0), 15(1), 16(1), and 17(1), as in HH, plus 64(1), 65(1), 66(1), 71(0) and 72(0). The dentary characters 64–66 show the same states as in *L. boa* (though the dentary is quite differently shaped in that species due to its strongly developed proterodonty; Kluge 1993a: fig. 14) and *M. spilota*; 71(0) occurs in all except *Python* spp., and 72(0) in all except *M. carinata* and *M. viridis*.

No more of Kluge's characters can be scored by including the AA(Snake) Site and Bullock Creek material, which agree with the HH and Upper specimens in morphology. However, several features of the jaw elements from these sites, after comparison with extant species, can be coded as new characters and added to Kluge's matrix.

The specimens from Gag and BSE do not show sufficient overlap with the other sites to establish specific identity, but they allow a number of additional characters to be scored. The Gag premaxilla gives the following: 1(2); 2(1); 3(0); 4(1); 5(0); 6(0). This combination of character states is reported in *Morelia amethistina*, *M. spilota*, *Python anchietae* (polymorphic 0/1 for character 3), *P. curtus*, *P. molurus*, and *P. sebae* (Kluge 1993a, table 31). The concave anterior edge (character 2(1)) also occurs in *Liasis olivaceus* and *L. mackloti* (though these species were scored with 2(0) by Kluge), but these species both possess large premaxilla channels located between (not posterior to) the alveoli (5(1)).

BSE (palatine): 50(1); 51(1); 52(2); 53(2); 54(0); 55(1); 56(1). On the basis of these characters the palatine is most similar to *Morelia spilota* and *M. viridis*, which differ in having an elongate medial pterygoid process (56(2)), and it is here referred provisionally to *M. riversleighensis*.

The following characters can be added to the data set of Kluge (1993a):

122. *Mental foramen. Rounded posteriorly* (0), *or acute* (1). Most pythons have the posterior margin of the mental foramen rounded (e.g. Kluge 1993a, fig 14), but it is acute in lateral view in most specimens of *Morelia amethistina* (one larger specimen, AMR4908 with a mandibular length of 91.5 mm, tip to lateral notch 60, depth 9.5, does have rounded foramina), subadult (but not adult) *M. spilota*, and one adult specimen of *Liasis olivaceus* (AMR132963, mandible length 60 mm; tip to lateral notch 24, depth 5.0 mm). Basing character states on the modal condition in adults (as in Kluge 1991, 1993a), the 'acute' state is assigned to *amethistina* and *riversleighensis* only. As State 1 does not seem to occur in outgroups, State 0 is assumed to be plesiomorphic for pythons.

123. *Vomerine process of premaxilla*. Anteroventral edge not projecting ventrally (0), or projecting to form a near-right angle with the ventral edge in lateral view (1). Variation in the lateral profile of the vomerine processes has not been mentioned by other investigators (e.g. Kluge 1993a). Ventrally prominent processes, with a vertical anterior edge before turning posteriorly, have been observed among extant pythons only in *M. amethistina* and *M. oenpelliensis*; the processes have a rounded anterior swelling in *Liasis olivaceus*, but are flat in all other species examined (pers. obs.; not yet scored in *M. boeleni*, *M. carinata*, or some *Python* spp.). No such feature is known in outgroups, and its restricted distribution within pythons indicates unambiguously that State 1 is apomorphic.

Further characters could be defined based on variation in vertebral form, shape of the lower posterior process and lateral notch of the dentary, the compound element of the mandible, shape of anterior teeth etc., but further comparisons are required before this can be done.

Kluge (1993a) polarised characters for pythons using the results of a preliminary analysis of extant alethinophidian snake lineages (Kluge 1991) and previous ingroup analyses of boines and erycines (Kluge 1991, 1993b). The analysis of Cundall *et al.* (1993) introduced a number of new characters and obtained a most parsimonious cladogram distinct from that of Kluge (1991). Scanlon (1996) and Scanlon & Lee (2000), using nearly all of the informative characters listed in the previous analyses, and many new osteological characters based on study of extant snakes, extinct snake lineages and lizard outgroups, obtain well-supported minimal cladograms largely similar in topology to the combined analysis of Cundall *et al.* (1993), but rooted in a different place. The results of Scanlon & Lee (2000; Fig. 15) have been used here to test the polarity of pythonine characters, based on the outgroup distributions given by Kluge (1993a). For this purpose, the most important differences from earlier analyses are in the resolution of an (erycine, (boine, pythonine)) clade, rather than an unresolved polytomy between erycines, a (boine, pythonine) clade, and the 'advanced snake' clade (Kluge 1991), or (pythonines, (boines, erycines)) as in Cundall *et al.* (1993) and Scanlon (1996). The polarity of most characters remains unchanged, but the following alterations are adopted for analyses in this paper:

2 (anterior edge of premaxilla). State 0 is assumed to be plesiomorphic, as in Kluge (1993a). However, all specimens of *Liasis olivaceus* and *L.*

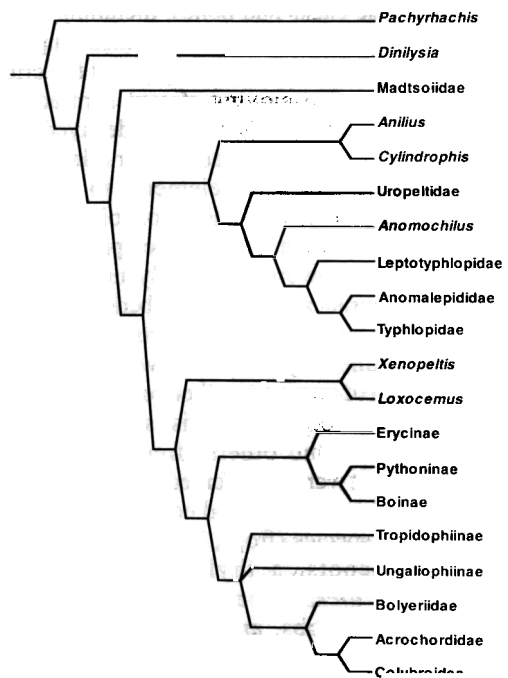


Fig. 15. Consensus cladogram of snake lineages (from Scanlon & Lee 2000) used to revise polarity of characters for phylogenetic analysis of pythons.

mackloti examined possess a concave anterior edge of the premaxilla, thus state 1 rather than state 0 as given by Kluge (1993a: table 31), and these taxa are rescored accordingly.

24 (prefrontal process of frontal). The states are given as 'The prefrontal process of the frontal projects either anteriorly or nearly laterally (0) or anterolaterally (1)'. State 0 seems to be an unnatural composite of extremes; the anterior projection is ascribed to both xenopeltid genera and *Bolyeria* only, but also describes the state in the madtsoid *Wonambi* (Scanlon in prep.). The process is reduced (and lateral) or absent in boines, lateral in ungaliophiines, anterolateral in erycines, *Trachyboa* and some *Tropidophis*. From this distribution alone (and the cladogram of Scanlon & Lee 2000) it is not possible to say whether lateral or anterolateral is more plesiomorphic. Since all pythons are scored with State 1, the character is regarded as uninformative for pythons, and excluded.

33 (postorbital-parietal contact). The primitive state also seems to be poorly defined: 'The anterior head of the dorsomedian end of the postorbital under- or overlaps (0) or abuts (1) the postorbital process of the parietal'. While state 1

exactly diagnoses the otherwise strongly supported *childreni* group (*Antaresia*), it is topographically intermediate to the two conditions which Kluge conflates as state 0, and which both occur in other pythons (though the actual distribution is not given). I therefore exclude this character.

36 (postorbital 'contact' with ectopterygoid or maxilla). The presence of state 0 (postorbital bar complete) in boines, and the erycines *Calabaria* and *Eryx*, allows it to be regarded as unequivocally primitive (originally unpolarised).

55 (width and presence of maxillary process of palatine). Boines might be disregarded as their loss of the process (state 2) is clearly autapomorphic and independent of its loss within pythonines (among boines, *Candoia carinata* and the (*Epicrates*, *Eunectes*) clade are parsimoniously interpreted as representing two secondary origins of a narrow process, with no effect at the outgroup node). Erycines other than *Eryx* have state 0, as do anilioids and bolyeriids; xenopeltids, *Eryx*, tropidophiines and ungaliophiines have state 1. Kluge considered state 1 plesiomorphic for pythons, but with the outgroup relationships assumed here, the primitive state is uncertain (or polymorphic), 0/1.

56 (length of medial pterygoid process of palatine). The distribution given by Kluge, mapped onto our outgroup cladogram, indicates that the primitive state is uncertain (or polymorphic), 0/1 (rather than unambiguously 1).

68 (lateral exposure of anterodorsal margin of coronoid). Regarded as ambiguous by Kluge, but as state 0 can be assigned to boines and erycines based on Kluge's analyses, this is considered plesiomorphic for pythons.

73 (neck width relative to head width). Kluge estimated the boine and erycine lineages as plesiomorphically having states 1 (slightly distinct) and 0 (neck as wide as head) respectively. Thus, the plesiomorphic state for pythons is 0/1 (not 0 as used by Kluge).

77 (number of postocular scales). Kluge used state 0 (1-2 postoculars) as plesiomorphic, despite obvious doubts. Boines are characterised by states 2 or 3, and erycines by 2-3 or 0, so it is parsimonious to assume state 2 or 3 is plesiomorphic for pythons (i.e. four or more postoculars).

79 (subocular scales). Since suboculars are present in most boines and erycines (exceptions in non-basal lineages noted by Kluge), presence (state 1) is unambiguously plesiomorphic for pythons (reversal of polarity).

80 (supraocular scales). State 1 (single large supraocular scale absent) characterises boines and erycines, so is plesiomorphic for pythonines (polarity ambiguous in Kluge).

81 (preocular scales). States 1-3 occur in boines, and either 0 or 1 in erycines. It is therefore most parsimonious to assume State 1 (two preoculars) is plesiomorphic for pythons.

82 (frontal scale). Absence of a distinct frontal (state 2) characterises boines and erycines, so is regarded as plesiomorphic for pythons (unpolarised in Kluge).

84 (anterior prefrontal scales). Distribution of states among boines and erycines indicates that either state 1 or 2 could be plesiomorphic for pythons (originally unpolarised).

87 (loreal). State 0 appears to characterise erycines, state 2 in boines, therefore the character cannot be polarised for pythons.

89 (preocular supralabials). If state 1 characterises boines, and state 0 erycines (except some species of *Eryx*), polarity is uncertain (0/1).

90 (subocular supralabials). Since presence of subocular scales is here regarded as plesiomorphic (character 79), the plesiomorphic state is indeterminate (N).

M. riversleighensis and the two new characters were added to the character/taxon matrix of Kluge (1993a, table 31). The following character states can be assigned to the taxon based on material referred here to *M. riversleighensis*: 1(2), 2(1), 3(0), 4(1), 5(0), 6(0), 12(0 or 1), 13(0), 14(0), 15(1), 16(1), 17(1), 50(1), 52(2), 53(2), 54(0), 55(1), 56(0 or 1), 64(1), 65(1), 66(1), 71(0), 72(0), 121(2), 122(1), 123(1). Heuristic search analyses were performed using PAUP*, with all ordered morphoclines treated as additive (so as not to discard trivially available information). The degree of support for each grouping was assessed by the support index (Bremer 1988), calculated in PAUP* using batch commands generated by TreeRot (Sorenson 1996), modified so that each search employed 100 rather than 10 random addition sequences. The bootstrapping function in PAUP (1000 bootstrap replicates, each with 10 random addition-sequence replicates; 13 parsimony-uninformative characters excluded) was also used to estimate the statistical significance of the various groupings found in each analysis. Results are shown in Fig. 16.

Many of the support index and bootstrap frequency values are quite low. Within *Morelia*, this may be an artefact of poor sampling of characters for the rare species *M. carinata* and the fossil *M. riversleighensis*. However, the low bootstrap frequencies for divisions in the 'middle'

part of the cladogram, and relatively strong conflicting signals for alternative groupings (including monophyly of *Liasis*, *sensu lato*) correspond to extensive character conflict rather than lack of data.

M. riversleighensis was most parsimoniously grouped with *oenpelliensis*, *spilota*, *carinata* and *viridis*, as the sister taxon to the well-supported (*spilota*, (*carinata*, *viridis*)) clade. However, there are also conflicts among the characters evaluated for *riversleighensis*. Kluge's character 14 (large anterior maxillary foramen) optimises as a synapomorphy of the (*Morelia*, *Python*) clade (Kluge 1993a: 54), with the small foramen in both *M. oenpelliensis* (*ibid.*, table 31) and *M. riversleighensis* appearing as two independent reversals. The newly identified characters (122, 123) also show conflict with the rest of the data. Characters parsimoniously interpreted as autapomorphies of *M. spilota* (37(0), 77(2), 81(2), 116(2)) are not represented in the material referred to *M. riversleighensis*, so their states in the fossil taxon are unknown.

Thus on present evidence, *M. riversleighensis* is not identical to any extant species, but forms the sister taxon to a radiation (the *M. spilota* group) which now occupies nearly the whole of Australia and New Guinea. I therefore recognise *Morelia riversleighensis* as a valid species, in preference to treating it as synonymous with any Recent member of the genus. Phenetically, its closest resemblance to any living species is with *M. oenpelliensis*, but there is no evidence that it shared the most distinctive apomorphy of that species (extremely elongate body and tail).

Additional taxa from Riversleigh and the rest of Australia

As noted above, the WH dentary does not justify recognition of a second large python species sympatric and contemporaneous with *M. riversleighensis*, but this possibility cannot be ruled out. Study of vertebral morphology, ontogeny and intracolumnar variation has not yet revealed taxonomically or phylogenetically informative diversity within Oligo-Miocene python material from Riversleigh. However, future work along these lines could provide evidence of additional taxa, and allow identification of vertebrae from other sites where no cranial elements are available.

The small maxilla from COA (QMF24726) cannot be identified with any extant species, but appears most similar to the (*spilota*, (*carinata*, *viridis*)) clade within *Morelia*. Since *M.*

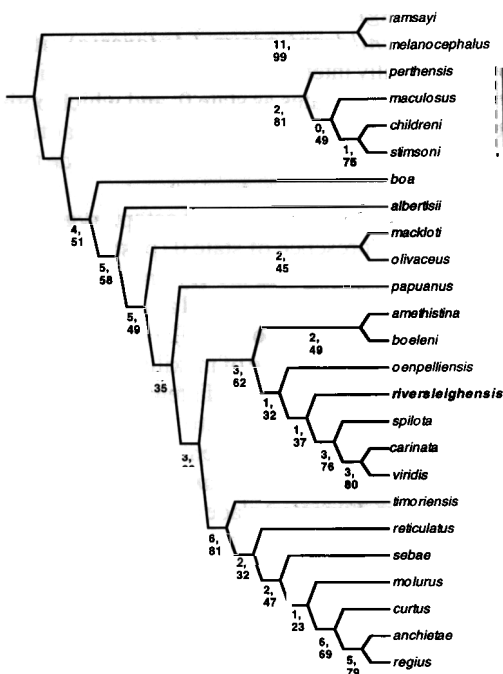


Fig. 16. One of two shortest cladograms for pythonine species obtained by heuristic search (PAUP*) from the data set of Kluge (1993a) as slightly modified here (see text), and including the fossil taxon *Morelia riversleighensis*. All characters forming ordered morphoclines are treated as additive. Numbers at nodes show support (Bremer) index and bootstrap frequency. In the other equally shortest cladogram, *maculosa* is the sister taxon to (*perthensis*, *childreni*, *stimsoni*), but this node was found in only 29% of bootstrap replicates. Solid lines beside species indicate the four genera recognised here (of which *Liasis* is shown as paraphyletic), dashed line indicates subgenus *Antaresia*.

riversleighensis is apparently the sister taxon to this clade (see above), but lacks unambiguous autapomorphies, it may be considered potentially ancestral to these extant species. The COA specimen is younger than known *M. riversleighensis* at Riversleigh, so would be consistent with this 'ancestral' interpretation and *in situ* evolution of the *spilota* group from *riversleighensis*, but several other interpretations are possible.

The bulk of pythonine material from Riversleigh and elsewhere is postcranial, and determining the number and relationships of taxa represented will require detailed study of vertebral morphology, including ontogenetic and intracolumnar variation. In comparison to madtsoiids or colubroids, pythonine (indeed, booid) vertebrae are remarkably uniform in qualitative features, but

we can hope that quantitative (morphometric) approaches may be successfully applied in future (e.g. Scanlon 1996, Baszio & Schaal 1997). The variation in hypapophysis depth along the anterior trunk is one such character found to vary in Australian pythons, apparently independent of size (this work, and Scanlon & Mackness in press). Beyond this, only a few comments can yet be made on the basis of visual comparisons and rough, preliminary measurements. Extant species of *Aspidites* and *Antaresia* are not only relatively small (<3m, <2m respectively), but have relatively depressed neural arches and low neural spines. My observations suggest that all adult python remains from the Tertiary of Riversleigh are too large, and/or their neural spines too high, to belong to either of these taxa. Most Riversleigh material, like that referred here to *M. riversleighensis*, is generally similar in proportions to *Morelia spilota*, *M. amethystina*, or *Liasis* spp. (*sensu stricto*). Thus, the evidence from isolated vertebrae has not yet been analysed exhaustively, but does not suggest a story any different from the cranial remains described here in detail.

Three pythonine vertebrae which might belong to *M. riversleighensis* are known from the Central Australian 'Leaf Locality' (Kutjumarpu Local Fauna: AR 3385, 3406, 3456), which is of similar age to the Riversleigh System B deposits.

The possibility that species of *Python* formerly occurred in Australia, suggested by the comparison of the Two Trees palatine with *P. reticulatus*, is not predicted by the biogeographic models of either Underwood & Stimson (1990) or Kluge (1993a). Although not inconsistent with them, it would require a dispersal (or original *Morelia-Python* vicariance within Australia) followed by local extinction, and is thus not parsimonious unless supported by particular evidence. Eight palatine alveoli also occur in some extant species of *Liasis*, though not the largest ones *L. olivaceus* and *L. papuanus*. The large python from the Pliocene of north-eastern Qld (Bluff Downs and Spring Park Local Faunas; Archer & Wade 1976, Mackness *et al.* 1994) can be referred provisionally to *Liasis* (*sensu stricto*) based on vertebral features, and an associated dentary fragment indicates a high number of teeth as in *L. mackloti* rather than *L. olivaceus* (Scanlon & Mackness in press). Rather than a species of *Python*, the Two Trees palatine may instead represent a giant *Liasis* similar or identical to the Bluff Downs species, but this question can probably not be resolved without the discovery of further material from one or both localities (or

more complete remains from a third site).

Rackham's Roost, a Pliocene cave deposit at Riversleigh (of similar age to Bluff Downs), contains some pythonine remains including a large form (AR 11263, an anterior caudal vertebra more than 10 mm wide across the prezyg-apophyses). However, most of the snake material represents juvenile pythons, which can not yet be identified more precisely: AR 17402, 17432, 17435 with pzw 8-9 mm; AR 17434, QMF 22795, 22800, 22801, 24140 with pzw 5-7 mm.

Phylogeny and Biogeographic Origin of Australian Pythons

Any phylogenetic hypothesis makes testable predictions for what would be observed in a complete fossil record. On the 'Gondwanan' model of python origin, we could expect to find fossil pythons only in Australia (or Antarctica or South America) until some time in the middle Tertiary when dispersal to Asia (and thence Europe and Africa) became possible. The genus *Python* would have originated at, or after, the dispersal from Australia to south-east Asia, but Australian fossil pythons could belong to any of the other extant lineages and could also include more primitive, extinct sister lineages to one or more of the extant genera.

On the 'Laurasian' model, pythons would be absent from Australia prior to the mid-Tertiary dispersal, and would never have been present in South America or Antarctica. Assuming an origin in Europe, Africa or Asia (within or adjacent to the range of the genus *Python*), *Python* would be either the sister group to the remaining (Australasian) taxa, or a paraphyletic stem group. The Australasian lineages most resembling *Python* spp. (e.g. *Morelia*) would then be relatively basal, and could appear earlier (closer to the time of arrival in Australia) than more distinctively Australian taxa such as *Antaresia* and *Aspidites*. Dispersal of pythons and other terrestrial vertebrates from Asia could have been facilitated by globally lowered sea-levels for several million years during the late Oligocene, beginning before 30 Ma (Frakes *et al.* 1987), which corresponds to the time-scale suggested by Cogger & Heatwole (1981) for pythonine and other Australian radiations.

Kluge's (1993a) support for an origin of pythons within Australia (one version of the 'Gondwanan' hypothesis) followed from the basal position of Australian endemics (*Aspidites* and lineages within *Liasis* s.l.) with respect to the rest of the group. *Aspidites* had formerly been regarded

as a highly derived taxon whose ancestors would have resembled species of *Liasis* s.l. (McDowell 1975, Shine & Slip 1990). The lack of premaxillary teeth and labial thermoreceptive pits, relatively thick neck, strengthening modifications of the bones of the snout and braincase (more strongly developed in *A. melanocephalus* than *ramsayi*), and relatively short, robust and uniform teeth, can be readily understood as adaptations to 'fossoriality' (digging behaviour associated with foraging, rather than living within self-constructed tunnels) and mainly reptilian diet which characterises both species of *Aspidites* (McDowell 1975, Shine & Slip 1990, Shine 1991). On the other hand, *Python*, apparently regarded as a paraphyletic stem-group of other pythonines by McDowell (1975) or the monophyletic sister-group to the Australasian radiation by Underwood & Stimson (1990), is indicated by parsimony analysis to be monophyletic, but derived within the Australasian group as the sister taxon to *Morelia* (Kluge 1993a; Fig. 16). The two biogeographic hypotheses thus correspond to two different general positions of the root for a cladogram of pythons: within/adjacent to *Python*, or adjacent to *Aspidites*.

At present, the number of characters and populations represented by fossils is very small, but already conflict is apparent. Preliminary answers can be given to the questions posed at the end of the Introduction. Mid-Tertiary diversity appears to be much less than might have been expected; there is no evidence for more than a single species among all python material from Australia's late Oligocene and Miocene. Moreover, rather than being a 'primitive' species, it is closely related to one particular lineage among extant *Morelia*. Indeed, all Miocene pythons in Australia and elsewhere, can be referred to *Morelia* and *Python* which, according to cladistic analysis, form a single lineage which should have appeared relatively late in pythonine history.

If Kluge's (1993a) cladogram were correct, there must have been one or more species of each of *Aspidites*, *Antaresia*, *Bothrochilus*, *Leiopython*, *Liasis* and *Apodora* extant in Australasia during the whole history of *Morelia*. To be sure, negative evidence cannot prove that they did not exist somewhere. However, if this situation persists with further discoveries, the absence of evidence of all six 'basal' extant lineages would have to be seen as a significant problem for Kluge's hypothesis of phylogeny, and for the Gondwanan hypothesis of pythonine origins. Strictly speaking, the Gondwanan hypothesis is untestable

(unfalsifiable) by the late Oligocene and Miocene Australian fossil record, whereas the Laurasian one is vulnerable but as yet unhurt. Conversely, the European fossil record does provide a test for the Gondwanan (Australian) model, and python-like snakes from Germany and France (Szyndlar & Böhme 1993, Duffaud & Rage 1997) may, when better known, justify its rejection.

Python phylogeny is increasingly coming under investigation using genetic sequencing methods (Rawlings 2001, S. Donnellan pers. comm.), though no genetic resolution of the 'origin' question is yet available. Well designed genetic studies are, of course, critical to fully understanding the history of extant lineages, but can never replace the information on extinct and primitive taxa available in the fossil record.

It could even be suggested, based on the apparent retention of interfertility and weak recognition barriers in this group (Banks & Schwaner 1984, Hoser 1989, Ehmann 1992, Greer 1997, A. Thorne pers. comm.), that some of the character conflict evident in the data is due to one or more hybridisation events (reticulations) among lineages of pythons. If this is the case, no (strictly upwardly branching) cladogram could accurately summarise their relationships (Scanlon 1996, Doolittle 1999). Methods of detecting and describing reticulation in phylogeny have not been a wildly popular area of research in phylogenetic systematics (but see e.g. Sneath 1975, Nelson 1983, Funk 1985, Hillis *et al.* 1996, Reiseberg 1997, Dowling & Secor 1997, Wiens 1998), although such an approach appears to be fully consistent with the principle of parsimony and the goals of recovering evolutionary history and producing a monophyletic taxonomy.

Reticulate evolution aside, there are two plausible explanations for the basal position of *Aspidites* in a parsimony analysis of pythons: either it is actually the most basal lineage, or its fossorial habits have produced adaptive modifications which are evolutionary reversals (resembling ancestral states) or convergences (resembling similarly derived outgroups) and outweigh the true phylogenetic signal (cf. Lee 1998). We still lack any knowledge of primitive fossil pythons (as this work has shown), or adequate knowledge of early members of the other booid lineages, which could have important effects on estimates of character polarity for pythons (cf. Gauthier *et al.* 1988, Donoghue *et al.* 1989). Well-preserved skeletons are known from the Eocene of Messel (probable boines, tropidophiid-like snakes, and possible pythons; Keller & Schaal

1988, Szyndlar & Böhme 1993) and Oligocene of Wyoming (complete skeletons attributed to the extinct and poorly known erycines *Calamagras* and *Ogmophis*; Breithaupt & Duvall 1986). When these are fully studied, phylogenetic analysis of all macrostomatan lineages will be placed on a firmer footing and estimates of relationships within and between lineages may change significantly.

In conclusion: the question of the biogeographic origin of pythons may be conclusively resolved in the near future, either by study of known European fossils, or sequencing of genes in extant species; but I do not expect a definite answer from the Australian fossil record. In terms of positive evidence, the phylogenetic analysis of Kluge (1993a), and its corollary the Gondwanan origin of pythons, are currently better supported than the alternatives. Nevertheless, I would be betting on an Afro-Eurasian origin and a relatively young (about 30 Ma) radiation of pythons in Australasia (as proposed by Cogger & Heatwole 1981). I give some weight to the negative evidence (lack of New World pythons of any age, and of primitive fossil pythons in Australia) and some to the apparent (but unproved) pythonine affinities of some Eocene fossils in Europe. Moreover, during the late Oligocene and Miocene (at least at Riversleigh), Australia's snake fauna was dominated by a different group of 'boid-like', presumably constricting snakes, the madtsoiids. Like the modern pythonines, Riversleigh madtsoiids included terrestrial or semiaquatic forms up to about 6 metres long, probable arboreal forms of about half that length, and terrestrial lizard-eating species less than a metre long (Scanlon 1992, 1996, 1997, Scanlon & Lee 2000). There is no direct evidence of a comparably diverse pythonine radiation at that time, and it may simply not have existed.

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APPENDIX

Recent skeletal material examined:

Aspidites melanocephalus QMJ30786 (complete skeleton)

A. ramsayi QMJ23629 (skull), AMR132964 (skull)

Liasis childreni R132962 (skull, premaxilla missing), SAMR 26973 (complete skeleton)

L. maculosus QMJ132961 (skull, premaxilla missing)

L. stimsoni uncatalogued specimen (incomplete skeleton)

L. sp. (childreni or stimsoni orientalis) QMJ28416 (skull)

L. boa AMR132966 (skull)

L. albertisii AMR16796 (skull)

L. mackloti AMR41872 (skull), R.Shine unnumbered specimen (skull and partial skeleton)

L. olivaceus AMR132963 (skull); AR 8422, 9373, 9374 (partial skulls) and AR unnumbered specimen (complete skull)

L. papuanus AMR16488 (complete skeleton)

Morelia amethystina QMJ51148 (skeleton), AMR4908 (skull), AR uncatalogued specimens (partial skull and several mandibles, articulated sections of vertebral column)

M. oenpelliensis AMR93417 (skull)

M. spilota AMR132965 (skull), QMJ 22191 (skull); JS 94 (damaged skull); JS unnumbered specimen (partial skeleton)

Python molurus AMR366 (complete skeleton), MMR1243 (partial disarticulated vertebral columns)

P. reticulatus AR unnumbered specimen (complete skull)