

Pythonine snakes (Boidae) from the Miocene of Australia

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Two new species of pythonine snake (Boidae) are described from middle to late Miocene local faunas at Riversleigh (Queensland) and Bullock Creek (Northern Territory). To date, they are the oldest records

of snakes in Australia, and their age implies that snakes entered Australia in the late Cretaceous or early Tertiary, before the break up of Gondwanaland.

Introduction

A.A. Öpik played a role, albeit a rather indirect one, in the discovery of both snakes described in this paper. His early work in northern Queensland was concerned, amongst many other things, with Cambrian biostratigraphy and the early Middle Cambrian faunas of the Thornton Limestone. During the course of field work in the Lawn Hill-Camooweal area in the late 1940s and 1950s, the Tertiary Carl Creek Limestone near Riversleigh (Fig. 1) was examined and some unsuccessful attempts were made to collect vertebrates from it. Cameron (1901) had recorded the presence of gastropods, mammals, and reptiles, but no serious attempts were made to collect them until Tedford visited the area in 1963 during his search for geochronological data to assist with the interpretation of the Cainozoic history of the area (Tedford, 1967). Subsequent collections have been made by Plane, in 1968, and Archer, during 1976-1984.

In 1966, C.G. Gatehouse, an associate of Öpik, was working on the early Middle Cambrian Montejinni Limestone, 20 km southeast of Camfield homestead in the north central Northern Territory (Fig. 1). In low but extensive mesas, previously mapped as Cambrian, but now known to be Tertiary and mapped as the Camfield beds, he discovered fossil mammals (Plane & Gatehouse, 1968). Several fossil sites in the Camfield Beds have produced Gastropoda, Osteichthyes, Aves, Reptilia, and Marsupialia. Collecting by Plane in 1981 unearthed interesting new marsupials (Flannery & others, 1982; Truswell & Plane, 1983) and some of the snake material described here.

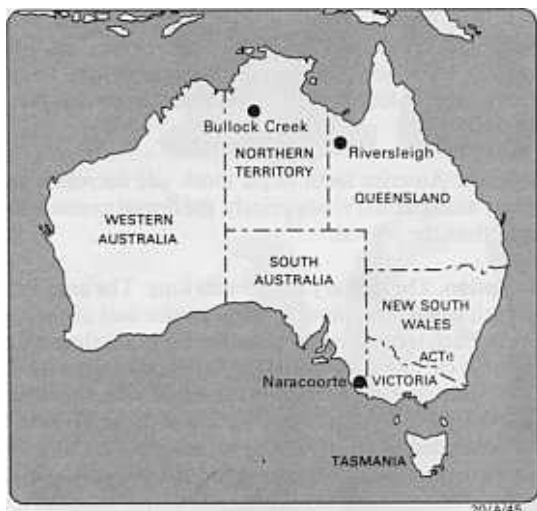


Figure 1. Locality map.

Australia has a diverse and interesting living snake fauna. However, fossil evidence for the development of snakes on the continent is scanty. The Elapidae, the most numerous and

venomous family, with 25 genera and 75 species currently recognised (Cogger & others, 1983), is not represented by fossils older than Pleistocene. The 'possibly elapid' vertebra from the early Pleistocene Bluff Downs fauna (Archer & Wade, 1976) has low-set paradiapophyses, which suggest that it is from an achrochordid (file snake); if so, it is the only known Australian fossil of that family. The Colubridae, with 10 extant species, are unknown as fossils here (Molnar, 1982), as are the Typhlopidae (blind snakes) and Hydrophiidae (sea snakes). The Boidae (constricting snakes), with 4 genera and 13 extant species, all in the subfamily Pythoninae, are represented in the fossil record by an unnamed python ('?Morelia sp.') from the Bluff Downs fauna (Archer & Wade, 1976) and by the Pleistocene species *Wonambi naracoortensis*, from Naracoorte (Fig. 1), which, interestingly, shows relationships with the extinct subfamily Madtsoiinae from North Africa and South America (Smith 1976).

The two new pythonine snakes described here are from rocks much older than any other Australian deposits that have yielded snake fossils. Species names of modern Australian boids are after Cogger & others (1983); all measurements are in millimetres; CPC is the Commonwealth Palaeontological Collection, and QMF is the Queensland Museum Fossil Collection.

Systematic palaeontology

Class Reptilia
Order Squamata
Family Boidae
Subfamily Pythoninae
Montypythonoides gen. nov.

Type species. *Montypythonoides riversleighensis* gen. et sp. nov.

Generic diagnosis. Maxilla with a prominent bulge on the labial surface about half way along its length; maxillary teeth curved near base, a weakly developed cutting ridge on labial side of tooth, no cutting ridge on lingual side of tooth.

Origin of the generic name. The genus is named *Montypythonoides* as it was found on a small hill or monti, and is like the pythons sensu lato.

Montypythonoides riversleighensis sp. nov.

Holotype. QMF 12926, right maxilla fragment with 9 teeth, most having broken tips, and alveoli for two other teeth.

Specific diagnosis. Same as for genus.

Paratypes. Seven vertebrae were found in the same block of matrix as the holotype. All are to be lodged in the Queensland Museum (QMF12927 - 12933). Other specimens found at Riversleigh localities are three vertebrae (AR3190 - Site D, AR3526 - Site GAG, AR398A - Site GAG), 3 isolated teeth (AR3936, AR4015 - Site GAG, AR4133 - Henks Hollow).

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Type locality and lithology. The type locality is known as Henk's Hollow, and was found in 1983 by M. Archer and his party from the University of New South Wales. It and the GAG site are approximately 3.6 km southwest of Tedford's (1967) Site B. The lithology at this locality is a dirty white to grey limestone. It breaks down readily in acetic acid.

Stratigraphic position and age. The previously known fossil mammal localities in the Carl Creek Limestone (Tedford, 1967; Flannery & others, 1982) are known as the Riversleigh local fauna, and believed to be middle Miocene. At present, the stratigraphic relationships of the Henk's Hollow and GAG localities and the previously known sites to the northeast are not known. However, on the basis of similarities in the fauna, a middle Miocene assignment is probably warranted.

Description. The incomplete right maxilla, QMF12926, is 42.9 mm long, has a maximum height of 8.4 mm, and, near the anterior end, is 3.2 mm wide. Nine teeth are fused to the bone and there are alveoli for two more (Fig. 1). Although several teeth lack the distal portion, enough remain to show that the teeth decreased in size evenly from front to back. The anterior teeth are directed vertically, with the tips directed posteriorly. The more posterior teeth are directed increasingly ventrolaterally, the most posterior tooth showing the greatest divergence from vertical. The teeth are slender, each one being curved near its insertion into the bone, but with the distal half of the tooth straight. A weak cutting ridge is present on the labial surface of the four most complete teeth, but a cutting ridge could not be detected on the lingual surface of any tooth. The maxilla is high and narrow anteriorly. Posteriorly, it is compressed dorsoventrally to form a facet for articulation with the ectopterygoid. In this region of dorsoventral compression, posteriorly from the level of the fifth tooth position, the bone bulges outwards, i.e. labially. The labial surface of the maxilla has two foramina, one at the level of the first tooth position, the other at the third tooth position. The labial, ventral edge of the maxilla is not straight, but is curved upwards, slightly anteriorly from the fifth tooth position. The medial process of the maxilla is incomplete and lacks part of the medial edge. However, the curved anterior edge of the medial process shows that the process was much longer than wide. Two foramina open through the dorsal surface of the medial process. On the dorsal surface of the maxilla, the facet for contact with the prefrontal is an ill-defined planar area, extending anteriorly from the level of the fourth tooth position. The facet for contact with the ectopterygoid is similarly ill-defined; it appears to extend anteriorly to the back of the sixth tooth position.

The largest vertebra, QMF12927, is 12.0 mm long from the ventral lip of the cotyle to the posterior surface of the condyle. Across the outermost points of the postzygapophyses it is 23.8 mm wide and across the tops of the paradiapophyses, 19.7 mm. The neural spine is broken, showing an oval cross-section; its length near the base (6.1 mm) is about half the length of the centrum. The zygosphenes are robust with maximum width 10.6 mm; in dorsal view its anterior edge is concave. The zygosphenal facets are upturned at approximately 55° from horizontal; each facet is oval shaped with height 6.8 mm and width 4.5 mm (Fig. 2). Within the zygantrium, on each side, there is a roundish depression, through the bottom of which open two large foramina. The cotyle is round with a diameter of 8.0 mm; the condyle is 7.4 mm high and 7.8 mm wide. The prezygapophyses are slightly upturned (about 5° from horizontal); no other characteristics of the prezygapophyses can be determined. The paradiapophyses are set on the sides of the centrum and project very slightly below the centrum. Each paradiapophysis is simple, rounded oblong in shape, with a constriction in the middle; it is 7.6 mm high, and 4.5 mm wide above the constriction and slightly narrower below. There is no parapophysial process. The

postzygapophysis is rounded triangular in shape (Fig. 2). The margo lateralis and margo ventralis are present. The low haemal keel ends posteriorly in a sharp point. The foramina on the centrum are one pair of subcentral, one pair of lateral, and one pair (very small) at the base of the neural spine. Paracotylar foramina are not present.

The next largest vertebra (AR4059) is unusual in having two pairs of subcentral foramina. The neural spine is crumbling, but appears to be quite low (height above centrum approx. 9.1 mm). Of the five nearly complete dorsal vertebrae, only two have intact prezygapophyses. The prezygapophysial facet is rounded triangular in shape; the small accessory process is anteroposteriorly compressed and extends only slightly laterally to the prezygapophysis.

Only one vertebra from the anterior, hypapophysial region was recovered, and it has the hypapophysis broken. Other than in the presence of a hypapophysis, it differs from the more posterior vertebrae in having a higher neural spine and narrower zygosphenes.

Morelia antiquus sp. nov.

Holotype. Commonwealth Palaeontological Collection 20577, right dentary with 12 teeth, four of them having broken tips, and spaces for six other teeth.

Other material. None known.

Type locality and lithology. The holotype was found at the 'small hills locality' in the Camfield beds, 20 km southeast of Camfield homestead, on the Wave Hill 1:250 000 Sheet area. The snake mandible was found in association with *Balbaroo camfieldensis* (Potoroidae), and a skull of *Wakaleo vanderleuri* (Thylacoleonidae). Specimens of *Neohelos* (Diprotodontidae) have also been recovered from this locality, where the dominant lithology is a white, fine-grained, black-speckled limestone, which breaks down readily in acetic acid.

Stratigraphic position and age. The mammal faunal assemblage, known as the Bullock Creek local fauna, is believed to be middle to late Miocene (Woodburne & others, 1984) or, in relative terms, younger than the Riversleigh local fauna, but older than the Alcoota local fauna from the central Northern Territory.

Diagnosis. Anterior teeth large; tooth size decreases sharply midway along dentary; posteriorly, the dorsal ramus is slightly deeper than the ventral.

Description. The dentary is 46.5 mm long. The anterior teeth are much larger than those in the posterior half of the dentary (Fig. 3). Each tooth is curved near the base and almost straight distally. A cutting ridge is weakly developed on the labial and lingual sides of each tooth. On the labial side, the dentary is deeply divided posteriorly for insertion of the compound bone, which extended anteriorly for more than 1/3 of the length of the dentary, to the level of the eleventh tooth. In this divided region, the dorsal ramus is slightly thicker and deeper than the ventral. The ventral ramus is incomplete posteriorly, and relative length cannot be determined. On the labial side, the Meckelian groove is completely open. The facet for insertion of the splenial extends anteriorly, approximately to the level of the fourteenth tooth.

Discussion.

Before the relationships of the fossil pythons can be discussed, it is necessary to comment on the taxonomy of extant species.

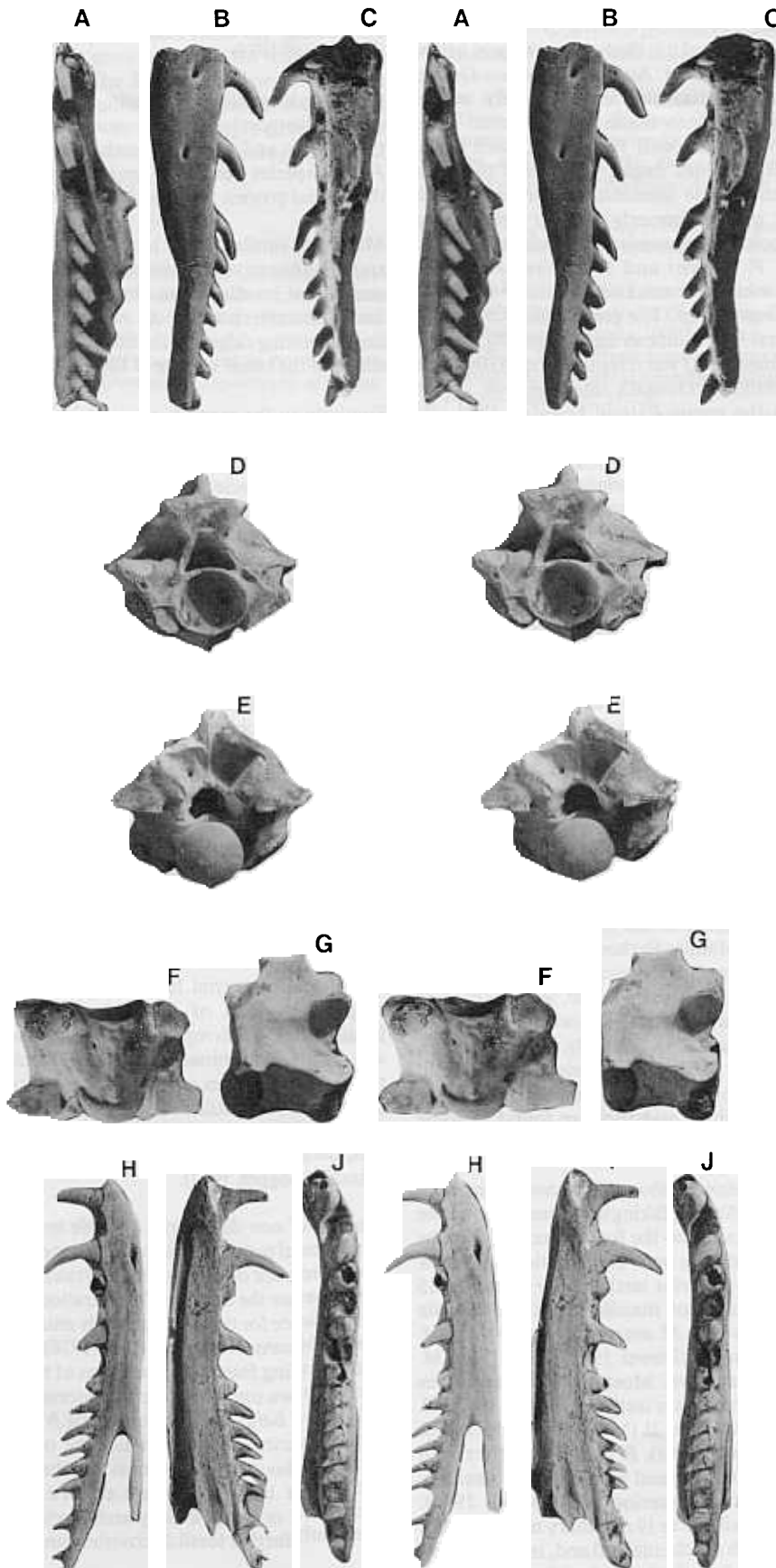


Figure 2. Stereopairs of right maxilla (QMF12926) and dorsal vertebra (QMF12927) of *Montityphonoides riversleighensis*, and right dentary of *Morelia antiquus* (CPC20577).

QMF12926 – AA', occlusal view; BB', labial view; CC', lingual view. QMF12927 – DD', anterior view; EE' posterior view; FF', ventral view; GG', lateral view. CPC20577 – HH', labial view; II', lingual view; JJ', occlusal view.

The taxonomy of modern Australian boids is in a state of flux (compare, for example, Cogger, 1979, 1983; Cogger & others, 1983; and McDowell, 1975) and it is likely more changes will be made before stability is achieved. Australia and New Guinea share several python species, but, unfortunately, recent taxonomic revisions have been made on a regional basis (Cogger & others, 1983, McDowell 1975). McDowell (1975) working with the New Guinea fauna, recognised the close relationships between *Python amethystina* (formerly *Liasis amethystinus*) and *P. spilota* (formerly *Morelia spilotes*) and noted that on morphological grounds they could be grouped with *P. reticulatus*, *P. boeleni* and *P. timoriensis* as the 'reticulatus Group', while the remaining species could be grouped in the 'molurus Group'. The genus *Liasis* Gray, 1842 was retained for several New Guinean and Australian species, but *Bothrochilus* Fitzinger, 1843 was relegated to the synonymy of *Liasis*. Subsequently, McDowell's interpretation of the relationships within the genus *Python* Dawdon 1803 was supported by data from immunology (Schwaner & Dessauer 1981). In a catalogue of the Boidae in Australia, Cogger & others (1983) emphasised the close relationship between *P. amethystinus* and *P. spilota* by resurrecting the formerly monotypic genus *Morelia* to include *M. amethystina* and *M. spilota* together with three endemic Australian species, *M. bredli*, *M. carinata*, and *M. oenPELLIENSIS*. However, the morphological and immunological data show that the 'reticulatus Group' of species should be maintained. Hence Cogger & others concept of the genus *Morelia* should be expanded to include also *M. reticulata*, *M. boeleni*, and *M. timoriensis*. Cogger & others (1983) synonymously included *Liasis* with *Morelia*, and found *Bothrochilus* to be the correct genus name for the species *B. albertisii*, *B. childreni*, *B. fuscus*, *B. olivaceous*, and *B. perthensis* from Australia, and, by implication, *B. boa*, *B. mackloti*, and *B. papuanus* from New Guinea. The genus *Aspidites*, containing *A. melanocephalus* and *A. ramsayi*, and the monotypic *Chondrophython* have emerged unscathed from these taxonomic gyrations.

The fossil species *Montypythonoides riversleighensis* clearly can be assigned to the subfamily Pythoninae. In pythonines, the medial process of the maxilla is typically longer than wide, and this is the condition in *M. riversleighensis*, whereas in most boines the medial maxillary process is short and wide and 'swept' backward (Frazzetta, 1959). Similarly, in the vertebrae, the absence of paracotylar foramina is consistent throughout the Pythoninae, whereas their presence is characteristic in the extinct subfamily Madtsoiinae and they are found in some boines (Underwood, 1976).

Within the Pythoninae, *Montypythonoides* shows strong relationships with species of *Morelia*. Taking into consideration the position of the medial process on the fossil maxilla, it can be estimated that there would have been two additional anterior teeth and two additional posterior teeth to give a total of 15 maxillary teeth. The number of maxillary teeth in *Morelia* ranges from 13–18, usually 16 in *M. amethystina*, to 16–18 in *M. spilota*, 18 in *M. boeleni* (McDowell 1975), and 17 in *M. reticulata* (personal observation). Most *Bothrochilus* species have a higher number of maxillary teeth, e.g. *B. boa* 19–21, *B. albertisii* 22–24, *B. mackloti* 20 or 21 (McDowell 1975), and *B. childreni* 22 (personal observations). *B. papuanus* differs both in its few maxillary teeth (14–17) and in having the maxillary teeth very strongly enlarged anteriorly (McDowell 1975). *Chondrophython viridis*, with 15 to 19 maxillary teeth, also has the anterior maxillary teeth much enlarged and, in this respect, *Montypythonoides* differs from both. In *Aspidites ramsayi* the teeth are much shorter, relative to their width at base, than in *Montypythonoides*. *Morelia* species can be most readily distinguished from *Python* species by the form of the ectopterygoid, the medial anterior process of which is produced

far in advance of the lateral anterior process in *Morelia*, whereas, in *Python*, the two anterior processes are subequal (McDowell 1975).

On the information and specimens available to us, we cannot relate *Montypythonoides* more closely to *Python* or *Morelia*, the maxilla and maxillary teeth being similar in *Morelia* and *Python* species – except *P. anchietae* and *P. regius*, which have the medial process swept back as in boines (Frazzetta, 1959).

Moreover, similarities in tooth number or shape between *M. riversleighensis* and particular *Python* or *Morelia* species should not be allowed to obscure the more significantly different characteristics of *M. riversleighensis*, viz. the lack of lingual cutting ridges on the maxillary teeth and the distinctive shape of the labial surface of the maxilla.

Similarly to the maxilla, the vertebrae of *Montypythonoides* show strong resemblance to those of *Morelia* and *Python* species, but differ from *Aspidites* species and at least some *Bothrochilus* species in which the haemal keel and margo ventralis are more strongly developed.

The cutting ridges on the dentary teeth of *Morelia antiquus* clearly ally this species with the modern pythons rather than with *Montypythonoides*. It differs from *Aspidites* sp., in which the teeth are shorter, and from *Chondrophython viridis*, in which the posterior teeth are much reduced. It differs from all *Bothrochilus* species except *B. papuanus* in its dentary tooth count – most *Bothrochilus* species have 20 or more (McDowell 1975; personal observations) – and it can be distinguished from *B. papuanus* in not having a gradual decrease in dentary tooth length (McDowell 1975). The curvature of the teeth in *M. antiquus* is much less than in many species of *Python* and also much less than in *M. spilota*. *M. amethystina* and *M. boeleni* have dentary teeth only slightly curved (McDowell 1975). On the basis of the slight curvature of the dentary teeth, we consider the affinities of the Bullock Creek species to lie with *Morelia* rather than *Python*.

The living boids are a family of large constricting snakes of arboreal and terrestrial habit, and are found throughout the tropical regions of both the northern and southern hemispheres. All living species in Australia are classified in the sub-family Pythoninae. The genus *Morelia*, which is close to the new fossil species, is found in most of continental Australia and Papua New Guinea under an enormous variety of conditions, which vary from rain and monsoon forest to open savannah, coral cays, rocky outcrops, and burrows made by other animals (Cogger, 1983).

Whilst our new discoveries do little to assist in the palaeoenvironmental reconstruction of Miocene habitats, they do attest to the presence of pythons in Australia since the Miocene and hence, before the continent's separation from Antarctica. Further evidence for the probable early entry of snakes is provided *Wonambi naracoortensis* (Smith, 1976). This snake shares the distinguishing features of members of the sub-family Madtsoiinae known only from the Palaeocene–Eocene of Patagonia (*Madtsoia bai*), the Cretaceous of Madagascar (*Madtsoia madagascariensis*) and the Eocene of Egypt (*Gigantophis garstini*). This distribution hints that the ancestors of both sub-families of boids may have entered Australia in the late Cretaceous or early Tertiary and developed in isolation since then. Only further fossil discoveries can elucidate this scenario.

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