

***Aspidites* and the Phylogeny of Pythonine Snakes**

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ABSTRACT. Twenty-four extant species of snakes, usually referred to as pythonines (*sensu* Underwood, 1976), are compared in terms of 121 behavioural and external and internal morphological characters. A cladistic analysis of 194 synapomorphies confirms the monophyly of the group, and provides a partially resolved, well-corroborated hierarchy of lineage relationships. That hypothesis obtains without regard to assumptions of additivity or nonadditivity, and only those synapomorphies which delimit clades unambiguously are used to diagnose taxa. *Aspidites* is demonstrated to be the sister lineage of all other pythonines, and the remaining Australia-New Guinea taxa constitute a paraphyletic assemblage. The South-east Asia-Africa *Python* forms a highly derived clade. The following binominal monophyletic taxonomy is proposed: *Antaresia childreni*, *A. maculosus*, *A. perthensis*, *A. stimsoni*, *Apodora papuana* (n.gen.), *Aspidites melanocephalus*, *A. ramsayi*, *Bothrochilus boa*, *Leiopython albertisii*, *Liasis mackloti*, *L. olivaceus*, *Morelia amethystina*, *M. boeleni*, *M. carinata*, *M. oenpelliensis*, *M. spilota*, *M. viridis*, *Python anchietae*, *P. curtus*, *P. molurus*, *P. regius*, *P. reticulatus*, *P. sebae*, *P. timoriensis*. The extinct Miocene *Morelia antiqua* and *Montypythonoides riversleighensis* from Australia are referred to the synonymy of extant *Liasis olivaceus* and *Morelia spilota*, respectively.

KLUGE, A.G., 1993. *Aspidites* and the phylogeny of pythonine snakes. Records of the Australian Museum, Supplement 19: 1-77.

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Introduction

Twenty-four extant species of pythonine snakes are recognised currently (see below). The group is restricted to the Old World, where it is found today in Sub-Saharan Africa, and from Pakistan eastward to the Solomon Islands (Stafford, 1986). Eighteen species occur in Australia and New Guinea, and nine of those are unique to Australia (McDowell, 1975; Cogger, 1976). The habitat preference of pythonines varies from desert to rainforest, between sea level and 1,828 m elevation (Stafford, 1986; Ross & Marzec, 1990; Shine, 1991). Some species are terrestrial, while others are arboreal. The group contains some of the smallest and largest extant species of snakes; they range from an average adult total length of 45 cm to one with individuals that are reported to exceed 10 m. The principle food of pythonines consists of frogs, crocodiles, squamates (some pythonines are cannibalistic), birds and mammals. The females of most, if not all, species incubate their eggs, the average clutch size varying from five to 21. Male-male combat also appears to be typical of all pythonines. While most species are different shades of brown, some are black, green, red or yellow. Colouration is nearly uniform, spotted, variegated to some degree, or strikingly banded. Well-developed labial-rostral scale thermoreceptive pits are present in some species, and head shields vary from uniformly small scales to a few large plates. The dentary, maxilla, palatine, premaxilla and pterygoid have teeth, at least during some stage in ontogeny, and the length and number of teeth varies considerably.

While pythonines are usually recognised as a clade (Underwood & Stimson, 1990:566; Kluge, 1991:fig.4), there have been few attempts to identify actual diagnostic states of the group, and among those contributions there is little consensus as to the nature of the evidence. For example, Underwood (1976:169) thought the following conditions delimited the pythonine assemblage: "Prefrontals approach one another in midline. Movable articulation between snout and braincase. Dorsal end of postorbital bilobed. Levator anguli oris muscle lost. Body of pancreas lobed. Minimum adult length more than 1 m. Labial pits within labial scales. Transverse scale-rows double on flank." In contrast, McDowell (1975:28-29) listed the following features as distinguishing most, or all, pythonines (including *Calabaria*; see however, Kluge, 1993) from other boids: supraorbital bone is present; medial process of the maxilla (articulating with the prefrontal and

palatine) is broad anteroposteriorly and is anterior to palatine-pterygoid articulation; palatine surrounds the maxillary nerve to define a palatine [sphenopalatine] foramen; palatine is produced back along the flat medial surface of the pterygoid in a simple overlap; palatine teeth closely resemble those of the maxilla, and when the anterior maxillary teeth are excessively enlarged..., so are the anterior palatine teeth; the palatine and pterygoid tooth-rows are continuous and closely aligned with each other; paroccipital process is recognisable as a distinct protruberence, dorsal to the fossa containing the fenestra ovalis and base of the stapes; basiptyergoid process has a distinct and flattened distal facet for the pterygoid; Meckelian cartilage is extended forward beyond the dentary onto the skin of the symphyseal region; exoccipital has a flange articulating directly with the atlas, lateral to the occipital condyle-atlantal joint. Still further (Kluge, 1991:fig.4), I conjectured that the following conditions diagnose the pythonine clade, without regard to the assumption of multistate character additivity or nonadditivity: supraorbital bone present; prokinetic joint involves a dorsal contact between the nasal and frontal; basioccipital participates in the *apertura lateralis*; anterior and posterior portions of the descending lamella of the nasal are conspicuously deep and nearly absent, respectively; left vidian canal is larger than the right; nasal process of the premaxilla is long and separates a considerable portion of the nasals; *intermandibularis anterior* muscle is undivided. Given the little consensus in these findings, I believe it is necessary to continue to test pythonine monophyly, and the aforementioned variables will be among those examined for phylogenetic information in the present study.

Several species of pythonines have received considerable study, and many recent investigators have concluded that subgroups of these snakes are weakly differentiated (Brongersma, 1953:319; McDowell, 1975:30; Underwood, 1976; L.A. Smith, 1981a,b, 1985:273-275; Banks & Schwaner, 1984; Storr *et al.*, 1986:34; Underwood & Stimson, 1990). In a particular case, Schwaner & Dessauer (1981) were able to distinguish African *regia* from New Guinea pythonines using transferrin immunodiffusion, but they found no detectable differences among New Guinea *albertisii*, *amethistina* and *papuanus*.

In addition to the claims that there is little divergence between groups of pythonines, there is general disagreement concerning species relationships. For example, McDowell's (1975) conclusions, extrapolated from his general discussion of species and species-group

affinities, can be summarised as the nested series of lineage relationships illustrated in Figure 1¹, Underwood's (1976:168, fig.8) branching diagram of genera is presented in Figure 2, according to the species he examined, and Underwood & Stimson's (1990: figs 7,8) preferred hypothesis is reproduced as Figure 3. The sister group relationships of *amethystina* and *boeleni* and *spilotus* and *viridis* are the only clades consistently present in these hypotheses. Other phylogenetic propositions have been published (eg, Frazzetta, 1975: fig.2) and might also be illustrated here, but they would only serve to further emphasise the general lack of agreement among investigators.

Aspidites is of particular interest because in all of the aforementioned species hypotheses of relationship it (represented by *A. melanocephalus*) is the sister lineage of some or all of the Australia-New Guinea pythonines. Moreover, special *ad hoc* arguments have been required to discount the evidence which suggested *Aspidites* is the sister lineage to all pythonines, not just a subgroup of pythonines. For example, McDowell (1975:30,32) assumed *a priori* that *Aspidites* secondarily acquired the horizontal part of the nasal bone lying above the nostrils, and that it lost (as opposed to never had) premaxillary teeth, a sphenoid keel, most or all divided subcaudals, and thermoreceptive pits (see also Underwood & Stimson, 1990:596). These characters are discussed in considerable detail below (see nos 1, 8, 56

(and/or 59), 93, 98, 101-105).

I seek the best fitting phylogenetic hypothesis and taxonomy based on all the available evidence (Kluge, 1989a), and in that search I investigate the accuracy of the claims that there is little evidence to individuate pythonines into clades. The sister group relationship of *Aspidites* is of particular concern. I will also examine the reason(s) why previous authors have found pythonine relationships so difficult to resolve. Possible explanations include natural processes (homoplasy), absence of synapomorphies, and methodological artifact.

Pythonine Terminal Taxa and Nomenclature

There have been many changes in pythonine taxonomy since Stimson's (1969) checklist (Wilson & Knowles, 1988:367). For example, *amethystina* has been placed in the genus *Python* (McDowell, 1975; see also Boulenger, 1893), *Liasis* (Underwood, 1976; see also Gray, 1842), *Morelia* (Cogger, 1986; Welch, 1988; Underwood & Stimson, 1990) and *Australiasis* Wells & Wellington (1984). Further, none of the authors using these binominal combinations consistently employed monophyletic taxa. I frequently cite this taxonomically variable and inconsistent literature, especially in the Character Descriptions section, and to avoid confusing the reader with various binominal combinations and different spellings of species names, I adopt the species nomenclature in the following list. Moreover, I use only the species names, without generic designation, to

¹ The spelling of species names follows the usage set forth in the Pythonine Terminal Taxa and Nomenclature section.

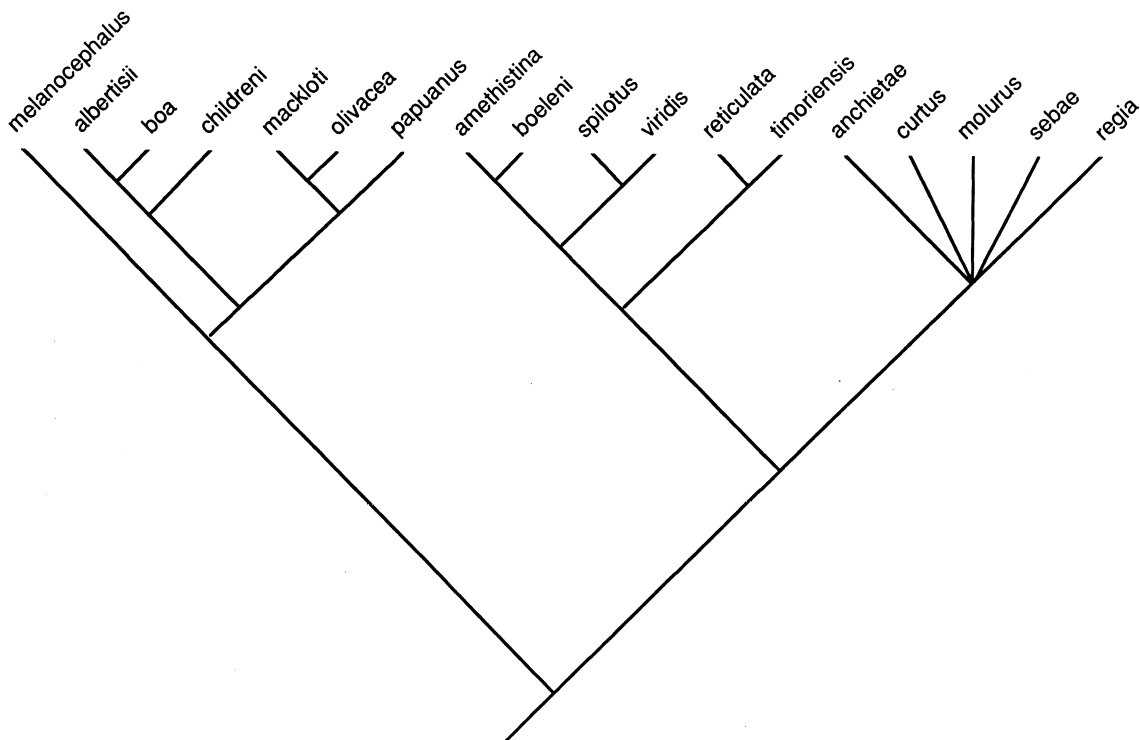


Fig.1. Pythonine relationships extrapolated from McDowell's (1975) general discussion of species and species-group affinities. Compare to Figure 22.

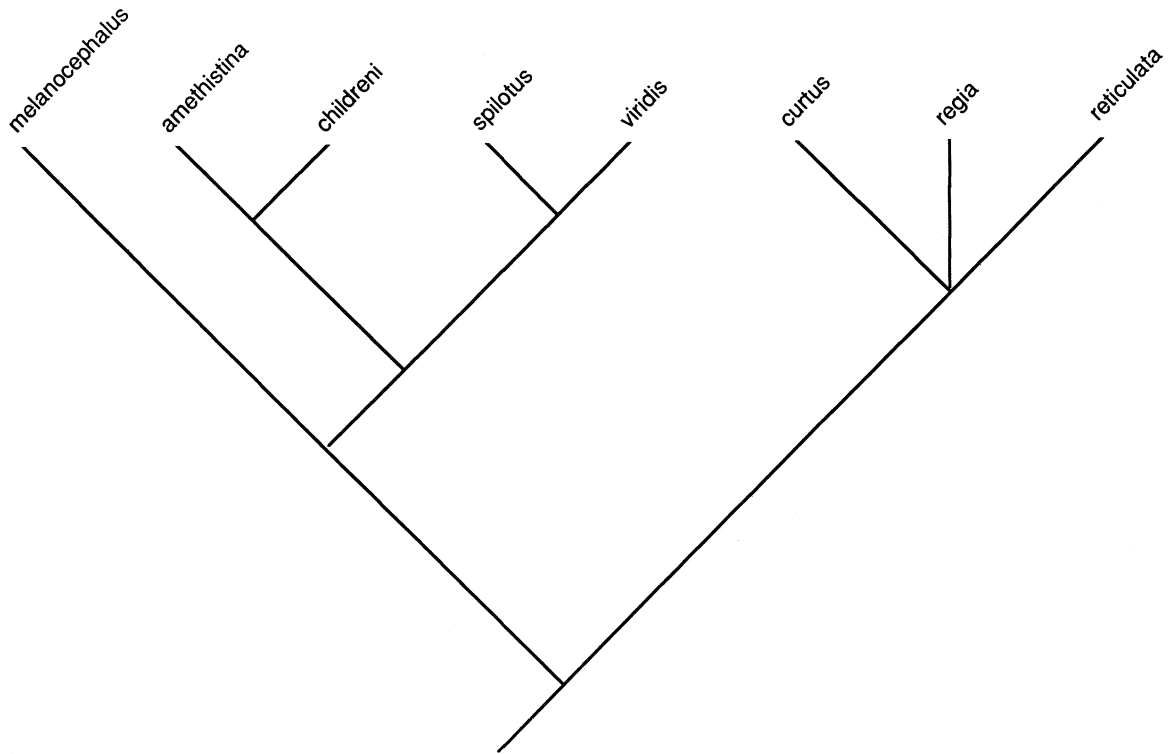


Fig.2. Pythonine relationships according to the species Underwood (1976:168,fig.8) examined. Compare to Figure 22.

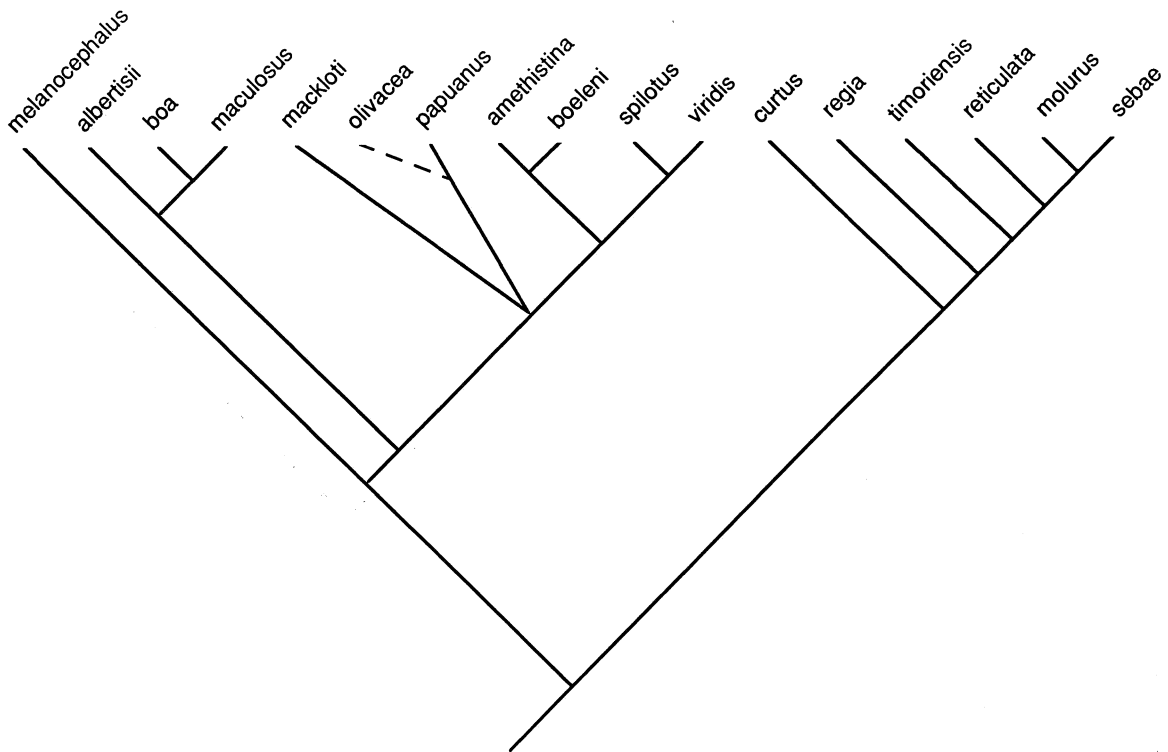


Fig.3. Underwood & Stimson's (1990:figs 7,8) preferred hypothesis of pythonine species relationships. According to Underwood & Stimson (p.570), *olivacea* is the sister group of *papuanus*. Compare to Figures 22 and 27.

avoid biasing the reader toward any particular phylogenetic hypothesis. While this uninominal form of presentation is a significant departure from taxonomic tradition, any possible ambiguity can be eliminated by referring to the species list below (eg, *boa* is a pythonine, whereas *Boa* is a boine genus group taxon). A strictly binominal monophyletic taxonomy derived from an analysis of all of the available evidence will be presented later in this paper.

Wells & Wellington (1984, 1985) proposed many new genus and species group names for Australian and New Zealand amphibians and reptiles, including several for pythonines. The International Commission on Zoological Nomenclature (1991) has refused to rule on an application (case 2531) requesting suppression of their works for nomenclatural purposes. It is the Commission's intention to consider particular nominal taxa in future submissions, and to settle whatever differences the zoological community might have, according to the criteria of usage and nomenclatural stability. Thus, where appropriate, I recognise Wells & Wellington names.

The present research is not a study of tokogenetic relationships (Kluge, 1990:fig.2) or pattern classes (*sensu* subspecies of Mayr & Ashlock, 1991). The focus is on the historical relationships of those lineages termed species (Frost & Hillis, 1990; Kluge, 1990; Frost *et al.*, 1992). It is not concerned with the discovery of the limits of those lineages, and in fact I have assumed the individuality of each species. The species I recognise are those accepted in the majority of the recent papers on pythonines. My few comments on geographic variation and the subspecific taxonomic category, in the species' Remarks sections to follow, emphasise where the current consensus of opinion may require further research. Complete synonymies are in Stimson (1969) and Cogger *et al.* (1983).

albertisii

Liasis Albertisii W. Peters & Doria, 1878: 401.

SYNTYPES. MSNG 29989 (near Andai) and 29990 (Kapaor).

TYPE LOCALITY. Near Andai and Kapaor, Irian Jaya, Indonesia.

SYNONYM. *Leiopython gracilis* Hubrecht (1879).

TYPE OF GENUS GROUP NAME. *Leiopython gracilis* Hubrecht for *Leiopython* Hubrecht (1879), by monotypy.

GEOGRAPHIC RANGE. New Guinea, Mussau Island (but not other Bismarck Archipelago islands; S. McDowell, personal communication), and offshore islands in Torres Strait (Cogger, 1986).

REMARKS. Subspecific taxa have not been recognised in *albertisii*; however, specimens from the vicinity of Wau are distinctive "in having the loreal divided into two or three scutes and often having a small pair of [posterior] prefrontals" and in lacking a

"whitish spot behind [the] eye" (McDowell, 1975:33,44-45).

amethystina

Boa Amethystina Schneider, 1801: 254.

HOLOTYPE. ZMB 1485 (presumed lost).

TYPE LOCALITY. Unknown.

SYNONYMS. *Aspidopython Jakati* Meyer (1874); *Liasis duceboracensis* Günther (1879); *Hypaspistes dipsadides* Ogilby (1891); *Liasis clarki* Barbour (1914); *Liasis amethystinus kinghorni* Stull (1933).

TYPE OF GENUS GROUP NAMES. *Simalia* (*part.*) Gray (1849); *Aspidopython Jakati* Meyer for *Aspidopython* Meyer (1874), by monotypy; *Hypaspistes dipsadides* Ogilby for *Hypaspistes* Ogilby (1891), by monotypy; *Australiasis* Wells & Wellington (1984), by original designation.

GEOGRAPHIC RANGE. Molucca Islands and Timorlaut Island in the west, through New Guinea, to Rossel Island, Louisiade Archipelago; New Ireland, New Britain, Trobriand Islands, north-eastern Queensland, and islands in Torres Strait.

REMARKS. The geographically variable characteristics described by McDowell (1975:56, 58) do not appear to covary, and therefore I assume only one species lineage is present (*sensu* Kluge, 1990).

anchietae

Python Anchietae Bocage, 1887: 87.

SYNTYPES. MBL 89-1206-7 (destroyed).

TYPE LOCALITY. Catumbela, near Lobito, Angola.

GEOGRAPHIC RANGE. Southern Angola and northern Namibia (Finkeldey, 1963).

boa

Tortrix Boa Schlegel, 1837: 22.

HOLOTYPE. MHNP 7172.

TYPE LOCALITY. New Ireland, Papua New Guinea.

SYNONYM. *Nardoa Schlegelii* Gray (1842), *nomen substitutum*.

TYPE OF GENUS GROUP NAMES. *Nardoa Schlegelii* Gray for *Nardoa* Gray (1842), by subsequent designation (Stimson, 1969:5); *Bothrochilus* Fitzinger (1843), by original designation; *Nardoana* Berg (1901), *nomen substitutum pro Nardoa* Gray.

GEOGRAPHIC RANGE. Bismarck Archipelago, Umboi, New Britain, Duke of York, Mioko, Gasmata, New Ireland, New Hannover and Tatau Islands, and the Nissan Atoll (McDowell, 1975), and Bougainville Island in the Solomons.

boeleni

Liasis boeleni Brongersma, 1953: 317.

HOLOTYPE. RMNH 9651.

TYPE LOCALITY. Dimija (3°56'S 136°18'E), Wissel Lakes, Irian Jaya, Indonesia, about 1750 m.

SYNONYM. *Liasis taronga* Worrell (1958)

GEOGRAPHIC RANGE. New Guinea.

carinatus

Python carinatus L.A. Smith, 1981a: 220.

HOLOTYPE. WAM R45352.

TYPE LOCALITY. Mitchell River Falls (14°50'S 125°42'E), WA, Australia.

GEOGRAPHIC RANGE. Northern coastal area of Western Australia.

childreni

Liasis Childreni Gray, 1842: 44.

HOLOTYPE. BMNH 1946.1.16.78.

TYPE LOCALITY. Unknown.

SYNONYM. *Nardoa Gilbertii* Gray (1842).

TYPE OF GENUS GROUP NAME. *Nardoa gilbertii* Gray from *Antaresia* Wells & Wellington (1984), by original designation.

GEOGRAPHIC RANGE. Northern Australia.

REMARKS. Wells & Wellington (1984) placed four species of small Australian pythonines, *childreni*, *gilbertii* (resurrected from the synonymy of *childreni*), *maculosus* and *perthensis*, in *Antaresia*. L.A. Smith's (1985) revision of that assemblage provided little more diagnostic evidence for the four lineages he recognised, *childreni*, *maculosus*, *perthensis* and *stimsoni*. Occasionally, I find it convenient to refer to these four taxa as the *childreni* complex.

curtus

Python curtus Schlegel, 1872: 54.

HOLOTYPE. RMNH 3782.

TYPE LOCALITY. Sumatra, Indonesia.

SYNONYMS. *Python Breitensteini* Steindachner (1881); *Python curtus brongersmai* Stull (1938).

TYPE OF GENUS GROUP NAME. *Aspidoboa* Sauvage (1884), by monotypy.

GEOGRAPHIC RANGE. Malaya, peninsular Thailand, Sumatra, Borneo.

mackloti

Liasis Mackloti Duméril & Bibron, 1844: 440.

LECTOTYPE. MHNP 1625.

TYPE LOCALITY. Timor, Indonesia.

SYNONYMS. *Python timorensis* Müller (1844); *Python timoriensis* Müller (1857); *Liasis fuscus* W. Peters (1873); *Liasis corwallisius* Günther (1879); *Nardoa crassa* Macleay (1885); *Liasis mackloti dunnii* Stull 1932); *Liasis mackloti savuensis* Brongersma (1956).

TYPE OF GENUS GROUP NAMES. *Liasis* Gray (1842), by designation under the plenary powers of the Commission on Zoological Nomenclature (Stimson & McDowell, 1986); *Simalia* (part.) Gray (1849).

GEOGRAPHIC RANGE. Sawoe, Samao, Timor, and Wetar Islands, in the Lesser Sundas, to southern New Guinea, and coast and adjacent area of northern Australia.

REMARKS. Cogger (1986) recognised the Australian form as a different species, *fuscus*, but McDowell (1975) did not. Conspicuous geographic variation in scalation and colour exist in *mackloti* (eg, Stull, 1932); however, there appear to be no covarying patterns of synapomorphies which would suggest the presence of two or more historical entities, ie, species (Kluge, 1990). For example, the Savu Island variant (*savuensis*; Brongersma, 1956), like the nominate form from the Lesser Sundas, has a marbled colour pattern due to "an irregular mottling of dark brown and light brown scales" (McDowell, 1975:36; see however, Stafford, 1986:63). Further, McDowell (1975:36) noted that "all New Guinea specimens are iridescent black above in life, rather than brown as in Australian material". But, he went on to state that New Guinea specimens "have only the first of the supralabials pitted," whereas all the Australian specimens seen by him "have a dent or dimple on the second supralabial, as well, thus resembling Lesser Sunda *L. mackloti*." Still, the widespread nature of *mackloti*, in more areas of endemism than any other species of pythonine (see Biogeography section), suggests a detailed study of geographic variation is warranted.

maculosus

Liasis maculosus W. Peters, 1873: 608.

SYNTYPES. ZMB 5860 (Rockhampton), 5948 (Port Mackay) and 7513 (Port Clinton for Port Bowen; see Cogger, *et al.*, 1983 and *melanocephalus* type locality).

TYPE LOCALITY. Rockhampton, Port Mackay and Port Bowen, Qld, Australia.

GEOGRAPHIC RANGE. Eastern Queensland, from Torres Strait south to border of New South Wales.

melanocephalus

Aspidiotes melanocephalus Krefft, 1864: 20.

HOLOTYPE. BMNH 1946.1.8.2.

TYPE LOCALITY. Bowen (for Port Denison, see Cogger *et al.*, 1983 and *maculosus* type locality), Qld, Australia.

TYPE OF GENUS GROUP NAMES. *Aspidiotes* Krefft (1864), by monotypy; *Aspidites* W. Peters (1876a) *nomen novum pro Aspidiotes* (non Bouche, 1834; non Schoenherr, 1847).

GEOGRAPHIC RANGE. Northern third of Australia, except for extremely arid regions.

molurus

Coluber Molurus Linnaeus, 1758: 225.

HOLOTYPE. NHRM 5 (no. Lin.).

TYPE LOCALITY. "Indiis".

SYNONYMS. *Boa Ordinata* Schneider (1801); *Boa Cinerea* Schneider (1801); *Boa Castanea* Schneider (1801); *Boa Albicans* Schneider (1801); *Boa Orbiculata* Schneider (1801); *Coluber Boaeformis* Shaw (1802); *Python bora* Daudin (1803); *Python tigris* Daudin (1803); *Python bivittatus* Kuhl (1820); *Python Jamesonii* Gray, 1842; *P[ython] trivittatus* Jerdon (1853), *ex errore pro Python bivittatus* Kuhl; *Python molurus ocellatus* Werner (1899); *Python molurus intermedia* Werner (1899); *Python molurus sondaica* Werner (1899); *Python molurus pimbura* Deraniyagala (1945).

TYPE OF GENUS GROUP NAMES. *Python tigris* Daudin for *Python* Daudin (1803), by subsequent designation (Stimson, 1969); *Python tigris* Daudin for *Asterophis* Fitzinger (1843), by original designation.

GEOGRAPHIC RANGE. Pakistan, India, Sri Lanka, Burma, from southern China to Thailand, Java, Borneo, Sulawesi; appears to be absent from Malay Peninsula (M.A. Smith, 1943).

oenpelliensis

Python oenpelliensis Gow, 1977: 133.

HOLOTYPE. NTM R0840.

TYPE LOCALITY. 6.5 km south-west of Oenpelli (12°21'S 133°01'E), NT, Australia.

TYPE OF GENUS GROUP NAME. *Nyctophilopython* Wells & Wellington (1985), by original designation.

GEOGRAPHIC RANGE. Western Arnhem Land, NT.

olivacea

Liasis olivacea Gray, 1842: 45.

HOLOTYPE. BMNH 1946.1.1.56.

TYPE LOCALITY. Port Essington, NT, Australia.

SYNONYM. *Liasis olivaceus barroni* L.A. Smith (1981b).

TYPE OF GENUS GROUP NAME. *Lisalia* Gray (1849), by monotypy.

GEOGRAPHIC RANGE. Coast and hinterland of northern Australia, from north-western Western Australia to western Queensland.

papuanus

Liasis papuanus W. Peters & Doria, 1878: 400.

HOLOTYPE. MSNG 29988.

TYPE LOCALITY. Romoi, near Soron, Irian Jaya, Indonesia.

SYNONYMS. *Liasis Tornieri* Werner (1897); *Liasis maximus* Werner (1936).

GEOGRAPHIC RANGE. Misool Island, through most of New Guinea, to Fergusson Island in d'Entrecasteaux Islands.

REMARKS. I follow McDowell (1975) in tentatively referring *Liasis maximus* to the synonymy of *papuanus*.

perthensis

Liasis childreni perthensis Stull, 1932: 26.

HOLOTYPE. MCZ 24426.

TYPE LOCALITY. Perth, WA, Australia.

GEOGRAPHIC RANGE. Pilbara region, and adjacent rocky areas, of Western Australia.

ramsayi

Aspidiotes ramsayi Macleay, 1882: 813.

HOLOTYPE. MMUS, lost (Cogger *et al.*, 1983; G. Shea, personal communication).

TYPE LOCALITY. Fort Bourke, NSW, Australia.

SYNONYM. *Aspidites collaris* Longman (1913).

GEOGRAPHIC RANGE. Arid areas, including desert sand hills, of central Australia.

regia

Boa Regia Shaw, 1802: 347.

SYNTYPES. Not traced (= Seba, 1734, vol.1:pl.62 fig.1,

and Seba, 1734, vol.2:pl.102).

TYPE LOCALITY. Unknown.

SYNONYM. *Python Bellii* Gray (1842).

TYPE OF GENUS GROUP NAME. *Boa Regia* Shaw for *Enygrus* Wagler (1830), by subsequent designation (Fitzinger, 1843).

GEOGRAPHIC RANGE. Senegal, east to Uganda.

reticulata

Boa Reticulata Schneider, 1801: 264.

HOLOTYPE. Presumed lost.

TYPE LOCALITY. Unknown.

SYNONYMS. *Boa Rhombeata* Schneider (1801); *Boa Phrygia* Shaw (1802); *Coluber Javanicus* Shaw (1802); *Python Schneideri* Merrem (1820).

GEOGRAPHIC RANGE. Thailand, Burma, Nicobar Islands, much of Indo-China, Malaya, Philippines, Indo-Australian Archipelago from Sumatra to Ceram, Halmahera, and Timorlaut.

sebae

Coluber Sebae Gmelin, 1789: 1118.

HOLOTYPE. Uppsala University.

TYPE LOCALITY. "Guiara, Brazil".

SYNONYMS. *Coluber Speciosus* Bonnaterre (1789); *Boa Hieroglyphica* Schneider (1801); *Python Houttuyni* Daudin (1803); *Python natalensis* A. Smith (1840); *Heleionomus variegatus* Gray (1842); *Python Liberiensis* Hallowell (1845); *Python jubalis* Pitman (1936), *nomen nudum*.

TYPE OF GENUS GROUP NAMES. *Heleionomus variegatus* Gray for *Heleionomus* Gray (1842), by monotypy; *Python natalensis* A. Smith for *Hortulia* Gray (1842), by monotypy.

GEOGRAPHIC RANGE. Senegal, east to Sudan and Uganda, and south to Cape.

REMARKS. Broadley (1983, 1984) treated *natalensis* as a subspecies of *sebae*. The two parapatric entities can be readily delimited, and they might be considered separate species under Frost & Hillis' (1990; see also Kluge, 1990) definition of the categorical rank species.

spilotus

Coluber spilotus Lacépède, 1804: 209.

HOLOTYPE. MHNP 3272.

TYPE LOCALITY. Australia.

SYNONYMS. *Coluber Arges* Linnaeus (1758) [see Stimson (1969:28)], *nomen dubium*; *Python punctatus*

Merrem (1820); *Python Peronii* Wagler (1828); *Morelia variegata* Gray (1842); *Morelia argus fasciolata* Jan (1864); *Python spilotes macrospila* Werner (1909); *Python bredli* Gow (1981); *Python spilotus imbricatus* L.A. Smith (1981a); *Morelia cheynei* Wells & Wellington (1984); *Morelia mcdowellii* Wells & Wellington (1984); *Morelia metcalfei* Wells & Wellington (1985).

TYPE OF GENUS GROUP NAME. *Morelia* Gray (1842), by subsequent designation (McDowell, 1975).

GEOGRAPHIC RANGE. Continental Australia, except southern Victoria and arid west-central region of Western Australia; Merauke region of Irian Jaya, and southern Western District, and Port Moresby region of Central District, including Yule Island, Papua New Guinea.

REMARKS. Some authors (eg, Cogger, 1986; Underwood & Stimson [1990]) have considered the allopatric *bredli*, which is restricted to the arid southern parts of the Northern Territory and south-western Queensland (Ingram & Raven, 1991), to be a distinct species (see however, L.A. Smith, 1985:275 and Fyfe, 1990). The south-western *imbricata* is quite distinct from *variegata* in number of ventral scales and shape of dorsal scales (Schwaner *et al.*, 1988:18). Additional study is required to establish the historical individuality of these and other entities within the *spilotus* complex (Kluge, 1990).

stimsoni

Liasis stimsoni L.A. Smith, 1985: 267.

HOLOTYPE. WAM R63108.

TYPE LOCALITY. 15 km south-east of Nullagine (21°58'S 120°12'E), WA, Australia.

SYNONYMS. *Liasis stimsoni orientalis* L.A. Smith (1985); *Antaresia saxacola* Wells & Wellington (1985).

GEOGRAPHIC RANGE. Coastal Western Australia throughout arid interior of most of Australia.

timoriensis

Liasis amethystinus timoriensis W. Peters, 1876b: 533 (*non* Müller, 1843, 1857).

HOLOTYPE. ZMB 8927.

TYPE LOCALITY. Kupang, Timor, Indonesia.

SYNONYM. *Liasis petersii* Hubrecht (1879).

GEOGRAPHIC RANGE. Flores, Lomblen and Timor Islands.

REMARKS. See Brongersma (1968) for a review of the names *timorensis* (Müller, 1844; Boulenger, 1893) and *timoriensis* (Müller, 1857; W. Peters, 1876b).

viridis

Python viridis Schlegel, 1872: 54.

SYNTYPES. RMNH 4672 (2 specimens).

TYPE LOCALITY. Aru (as Aroe) Islands, Indonesia.

SYNONYMS. *Chondropython azureus* Meyer (1874); *Chondropython pulcher* Sauvage (1878).

TYPE OF GENUS GROUP NAME. *Chondropython azureus* Meyer for *Chondropython* Meyer (1874), by monotypy.

GEOGRAPHIC RANGE. Rainforests of north-eastern Cape York Peninsula, Qld; New Guinea, and Aru Islands (McDowell, 1975:72).

Methods and Materials

The same methods used in my investigation of boine and ericine phylogeny (Kluge, 1991, 1993) are employed in this study. I adopt the principles of cladistics: special similarity (Hennig, 1966; Farris, 1977:836), monophyly (Hennig, 1966), and character congruence (Kluge, 1989a). Further, I do not prejudge the phylogenetic informativeness of relevant classes of characters by differential exclusion. Rather, I pursue the ideal of total evidence, which in a practical sense amounts to seeking the best fitting cladogram for a data matrix consisting of all the available evidence (Kluge, 1989a). Additions and corrections to the matrix are expected, and hopefully subsequent cycles of research concerning pythonine phylogeny (Kluge, 1991) will focus on that enlarged and refined body of data.

I began my search for relevant evidence on pythonine relationships with a review of the literature. The following articles provided background information on many potential characters: Zacharias (1897), Beddard (1904a,b, 1906), H.M. Smith & Warner (1948), Bellairs & Boyd (1950), Johnson (1955), Hoffstetter (1962, 1968), Gasc (1974, 1981), Kamal & Hammouda (1965), Underwood (1967, 1976), Langebartel (1968), Hoffstetter & Gasc (1969), McDowell (1972, 1975, 1987), Rage (1972), Rieppel (1976, 1977, 1978a,b, 1979a,b,c,d, 1980, 1987, 1988), Groombridge (1979a,b,c, 1984), Bellairs & Kamal (1981), Jayne (1982), Shine (1985), Underwood & Stimson (1990). Genetic distances (eg, Dessauer *et al.*, 1987) were rejected because they cannot be analysed in terms of character congruence and total evidence (see above). Relatively conservative and independent characters with few discrete states were sought, and autapomorphies excluded. The cladistically informative characters are summarised below in the approximate order in which I found it convenient to observe them and score their states in the data matrix (Table 31). A similar order is found in my other studies of alethinophidian relationships (Kluge, 1991, 1993).

Synapomorphies were sought at three levels of taxonomic generality: within pythonines, pythonines as a group, and pythonines and relevant outgroups (see below). The results of the latter survey will be published

elsewhere. I emphasise the concept of synapomorphy instead of homology, the former being viewed as an estimator, the latter the parameter. I do so because synapomorphy does not presuppose common ancestry whereas homology does. Homology is dealt with only indirectly by maximum character congruence, the ultimate arbiter of character history (Patterson, 1982). Thus, synapomorphy and homology are connected by parsimony, and bridging the present with the past is the context in which parsimony must be justified (for review, see Sober, 1988).

The anatomical nomenclature employed follows that of Frazzetta (1959, 1966, 1975), Hoffstetter & Gasc (1969), Bellairs & Kamal (1981), Cundall & Irish (1989), and Kluge (1991, 1993). The issue of which anatomical name to apply arises repeatedly in my studies of the higher classification of snakes (Kluge, 1991, 1993), especially when the outgroups are distantly related lineages. As a rule, I have given the same name to anatomically similar structures, synapomorphies, even though a phylogenetic hypothesis might suggest the identically named structures are not homologues. In my opinion, most phylogenetic hypotheses are still too weakly corroborated to realise an stable anatomical nomenclature based on descent. Structures are given different names only when they are obviously dissimilar and are likely to have had an independent history. I have taken the liberty of renaming some structures whose infrequently used nomenclature does not describe anatomical location accurately. I give synonyms in those cases where I break from an obvious tradition. My renaming follows either of two conventions, anatomical location (eg, anterodorsal process of the ...) or the structure it contacts (eg, the maxillary process of the palatine).

When a quantitative character, such as number of teeth, varied in an ingroup terminal taxon, the modal or median condition is considered representative. In this regard, my use of species terminal taxa may overlook significant intraspecific variation (eg, the reasonably well differentiated subspecies of *curtus*, *molurus* and *sebae*). All frequently observed qualitative variants in a terminal taxon are separated by a slash in the data matrix (eg, 1/2; Table 31); however, single or infrequently observed states are not recorded. A variable character in a terminal taxon (eg, 1/2) is treated analytically as unknown. A character state that is not applicable or not yet observed is recorded in the data matrix as N or ?, respectively. Outgroup variation is discussed under each character, and the ambiguous condition in the ancestor is recorded as ? in Table 31. Characters involving bones and scales of the same name (eg, parietals, etc.) are distinguished by adding the term scale to the scale variable.

A quantitative character can present a coding problem because numerous states are evident in the variation. Often, that number is greater than phylogenetic inference software will allow (0-9 states), and stands in sharp contrast to the binary subdivision of most qualitative variables. I employ five quantitative characters in the

present study, the number of premaxillary (character 1), maxillary (12), palatine (50), pterygoid (57), and dentary (64) teeth, which have the following observed ranges of variation among pythonines: 0-3, 13-25, 2-9, 6-24, and 13-26, respectively (Table 1). Even using the mode, or median, number of teeth to characterise each pythonine species, there are spans of 3, 9, 6, 14 and 10 integers, respectively. As an objective basis for their recoding, I use a character's pooled within-group standard deviation (times three) to define the interval to which an integer state is applied (Farris, 1990). Only samples greater than ten are analysed, and the coefficient of variation is required to adjust for a significant relationship between mean and variance. The interval is one for premaxillary, two for maxillary and palatine, and three for pterygoid and dentary teeth characters. The intervals for the premaxillary, palatine, and pterygoid teeth characters were initialised at zero. The intervals for the maxillary and dentary teeth characters were initialised at one, in order to minimise the loss of information, ie, reducing the number of taxa recorded as having two or more states. Additional quantitative characters (77, 81, 86-87, 89-90, 92, 96-99, 106 and 121) are employed; however, my attempt to maintain comparability to others' research (eg, McDowell, 1975; Underwood, 1976; Underwood & Stimson, 1990) governed the number of states recognised. Future studies must strive to establish a more uniform and nonarbitrary basis for coding multistate quantitative characters.

The snout of pythonines is often damaged, and care was taken to record observations on only normal premaxillary bones and rostral scales. Many of the characters employed are qualitative, and the alternative states were judged relative to one another; representatives of all species were at hand when each character was scored. The alcoholic and skeletal material studied in detail is listed in Appendix I. All hemipenes noted in that section are everted. Repository abbreviations are: AM – Australian Museum, Sydney; AMNH – American Museum of Natural History; ANWC – Australian National Wildlife Collection, CSIRO Division of Wildlife Research, Canberra; BMNH – Natural History Museum, London; BPBM – Bernice P. Bishop Museum, Honolulu; CAS – California Academy of Sciences; FMNH – Field Museum of Natural History; KU – Museum of Natural History, University of Kansas, Lawrence; MBL – Universidade Lisboa; MCZ – Museum of Comparative Zoology, Harvard University; MHNP – Muséum National d'Histoire naturelle, Paris; MMUS – Macleay Museum, University of Sydney; MSNG – Museo Civico di Storia Naturale di Genova; MVZ – Museum of Vertebrate Zoology, University of California, Berkeley; MZB – Museum Zoologicum Bogoriense, Bogor; NHRM – Naturhistoriska Riksmuseet, Stockholm; NTM – Northern Territory Museum, Darwin; QM – Queensland Museum, Brisbane; RMNH – Rijksmuseum van Natuurlijke Historie, Leiden; SDSNH – San Diego Natural History Museum; SAM – South Australian Museum, Adelaide; UF – Florida Museum of Natural History, University of Florida; UMMZ – University of Michigan Museum of Zoology;

UMMVP – University of Michigan Museum of Vertebrate Paleontology; USNM – United States National Museum; UTACV – University of Texas at Arlington Collection of Vertebrates; WAM – Western Australian Museum, Perth; ZMB – Zoologisches Museum, Universität Humboldt, Berlin.

The outgroup criterion (Farris, 1982; Maddison *et al.*, 1984) was used to infer polarity because it provides the most parsimonious hypothesis of character evolution, where the number of synapomorphies interpretable as independent evolutionary events is minimised. This criterion provided an unambiguous hypothesis of plesiomorphy for most characters (only nos 4, 36, 53, 60, 65, 68, 78-82, 84, 88, 92, 101, 105 and 107 remain unpolarised). The relevant, alethinopidian, outgroup taxa examined are listed in Kluge (1991, 1993). The informal term booids is used for all alethinopidians, except caenophidians (Rieppel, 1988). The binominal nomenclature for erycines follows Stimson (1969), with the exception of my not recognising *Gongylophis* as distinct from *Eryx*. Other major changes in erycine nomenclature are published elsewhere (Kluge, 1993). The nomenclature for boines follows Kluge (1991), and that of other booids is from Stimson (1969).

I do not accept Rieppel's (1978a:202) use of Marx & Rabb's (1970:531) "Morphological specialization" criterion for determining polarity because that rule requires hypotheses of adaptive specialisation which are difficult to evaluate critically. I did not discard unpolarised characters because all matches can count in the application of parsimony algorithms (Donoghue, 1990). Some aspects of the snake phenotype are subject to considerable ontogenetic variation (Kluge, 1989a), the increasing size of bony crests and processes being the most obviously correlated with age. In the absence of developmental series of most pythonines (some newborn and juvenile specimens of *molurus* and *spilotus* were available), I have accepted the largest individuals available for each taxon as comparable semaphoronts.

According to my preliminary study (Kluge, 1991:fig.4), pythonines are the sister group to boines (Fig.4). In terms of the strict consensus of the best fitting hypotheses, that clade is the sister group to the erycine, (tropidophiine (bolyeriine (*Acrochordus*, higher snakes))), or (erycine (tropidophiine (bolyeriine (*Acrochordus*, higher snakes)))) clades.² Thus, the erycine and (tropidophiine (bolyeriine (*Acrochordus*, higher snakes))) assemblages share equally, as the second outgroup, in estimating the plesiomorphic state in pythonines. In order to simplify the following text, the (tropidophiine (bolyeriine (*Acrochordus*, higher snakes))) lineage may be referred to as the 'advanced snake' clade. My preliminary research on the higher classification of snakes also indicated that *Loxocemus*, *Xenopeltis*, and (*Anilius* (*Cylindrophis*, uropeltines)) are the third, fourth, and fifth outgroups to pythonines, respectively. The

² The content of the "higher snake" group is equivalent to Marx & Rabb's (1970) definition of colubroids (see also Rieppel, 1981)

(*Anilius* (*Cylindrophis*, uropeltines)) clade is usually abbreviated as anilioids in the text to follow, and it does not include *Anomochilus* (see review by Cadle *et al.*, 1990). The hypothesised common ancestral state of the advanced snake clade was usually a function of the condition observed in bolyeriines (*Bolyeria*, *Casarea*) and tropidophiines ((*Exiliboa*, *Ungaliophis*) (*Trachyboa*, *Tropidophis*)), rarely *Acrochordus*, and never higher snakes (caenophidians of some authors; eg, Underwood, 1967). Polarity is estimated on a character-by-character basis, given the complicated dichotomous and trichotomous pattern of booid relationships discovered in my preliminary study (Fig.4), and therefore a brief statement of outgroup variation is included in each of the following character descriptions. The inferred common ancestral condition is listed in the data matrix (Table 31).

The importance of outgroup relationships cannot be overemphasised in phylogenetic inference (Hennig, 1966). For example, Underwood & Stimson's (1990: illustrated here as Fig.3) and my hypothesis (Fig.22) of pythonine affinities are markedly different, although our studies employ many of the same characters. The hierarchy of outgroup history employed by Underwood & Stimson (as explicitly illustrated by Underwood, 1989) can be summarised as follows: (*Calabaria* (((*Charina*, *Eryx*, *Lichanura*) (boines, *Exiliboa*, *Ungaliophis*)) (bolyeriines (*Trachyboa*, *Tropidophis*))) ((*Anilius* (*Anomochilus*, *Cylindrophis*, uropeltines, *Xenopeltis*)) (*Loxocemus*

(pythonines (*Acrochordus*, all other snakes)))))). Thus, our character polarities stand a good chance of being different, and it should come as no surprise that many of our conclusions concerning relationships among pythonine terminal taxa are also in conflict.

While I analyse the phylogenetically informative multistate character evidence (Table 31) as additive and nonadditive, only those synapomorphies unambiguously delimiting the same clade under both assumptions of character state history are interpreted as diagnostic. Further, I distinguish between diagnostic states that are unique and unreversed and those which exhibit some form of homoplasy, as a way of describing the strength of the evidence for a clade. In this context, the attributions of homology and homoplasy apply only to the states in question, not to the other conditions in the transformation series.

All cladistic analyses are performed with Farris' (1988) phylogenetic inference software, Hennig86. The large number of taxa and characters (Table 31) rendered the exact "implicit enumeration" (ie) algorithm inefficient, and the heuristic routines, with limited (mhennig*, m*) and extended branch-swapping (bb*), are used to find the best-fitting phylogenetic hypotheses. This combination of algorithms begins with the discovery of several cladograms, each by a single pass through the data, adding terminal taxa in several different sequences. The shortest topologies are retained, and branch-swapping is applied to each of these initial cladograms, retaining no

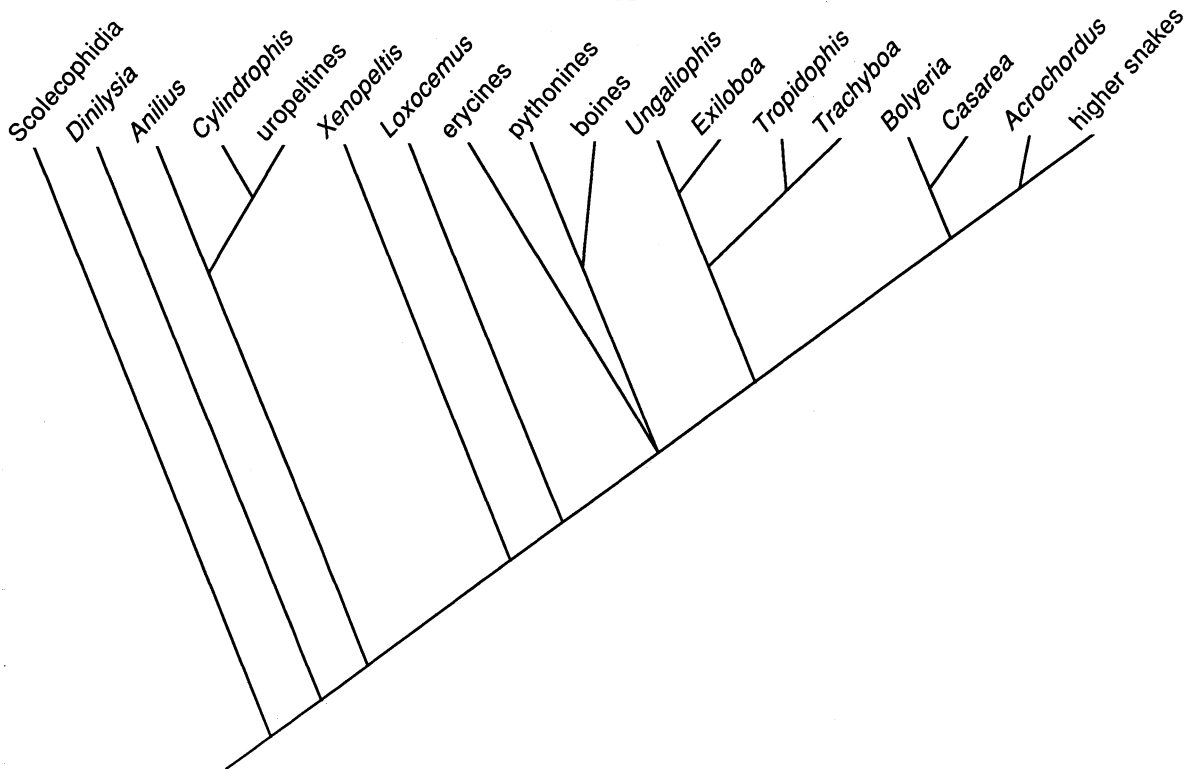


Fig.4. Preliminary hypothesis of relationships of the major groups of snakes ($C = 0.75$, $R = 0.86$). See Kluge (1991:fig.4) for information on the evidence for this hypothesis, and further resolution of boines, erycines, and Scolecophidia. The sister groups discovered among pythonines were (*melanocephalus* ((*albertisii*, *boa*, *childreni*, *mackloti*) (*spilotus*, *viridis*) (*amethistina*, *boeleni*, *curtus*, *molurus*, *regius*, *reticulata*, *sebae*, *timoriensis*))).

more than one topology for each initial one (m^*). Then, extended branch-swapping is applied to these topologies, retaining all the shortest cladograms that can be found (bb^*). Fit to data is measured in terms of consistency and retention indices. Character consistency – c – is defined as m/s , where s is the minimum number of steps a character can exhibit on a particular tree hypothesis, and m is the minimum number of steps that character can show on any tree hypothesis (Kluge & Farris, 1969). Character retention – r – is defined as $(g-s)/(g-m)$, where g is the greatest number of steps a character can have on any tree (Farris, 1989; Seberg, 1989; Steve Farris, personal communication). The ensemble consistency – C – and ensemble retention – R – indices used to choose among alternative phylogenetic hypotheses are simply the quantities for a single character, m , g and s , summed over all characters in the matrix, thus yielding corresponding totals, M , G and S . Therefore, $C = M/S$, and $R = (G-S)/(G-M)$.

The successive weighting algorithm employed ($xs w$ in Hennig86) is based on the concept of “cladistic reliability” (Farris, 1969:374) – those characters which are highly consistent are given the most weight. Platnick’s (1989:149; see also Carpenter, 1988) reason for using this weighting technique, “to determine which of the equally parsimonious cladograms found are best supported by the most consistent characters”, does not take account of the fact that $xs w$ can lead, if only rarely, to a novel branching pattern (Farris, 1969). In other words, $xs w$ is employed because it increases accuracy, as well as precision. In successive weighting, a character’s weight is the product of its rescaled consistency and retention indices (times 10), where the smallest s is used (not the “average value” [Carpenter, 1988:292]). The effectiveness of this weighting procedure, in finding the cladogram(s) supported by the most cladistically reliable characters, is owing to the fact that it closely approximates a concave bounded function (see Farris, 1969:fig.4). In the present study, successive weighting is applied to additive multistate characters that have undergone additive binary coding so that each step in the data matrix is evaluated separately (Farris, 1969:382; see also Carpenter, 1988:294-295). J.S. Farris’ MST program (Lipscomb, 1992) was used to transform the multistate characters into their additive binary factors. Unfortunately, efficient parsimony algorithms are unavailable for analysing multistate characters that have been nonadditively recoded (Sankoff & Rousseau, 1975), and therefore successive weighting is not performed on that class of data. Swofford & Olsen’s (1990:499-500) negative comments concerning the *a posteriori*, successive approximations, form of weighting used herein seem to be ill-founded (Farris *et al.*, 1993), particularly their charge of circularity. In any case, Swofford & Olsen’s (p.499) “extreme [counter] example” does not relate to the $xs w$ algorithm.

I have not employed the techniques which use only length (S) test statistics to measure structure in cladistic data because they are known to produce spurious

conclusions (Källersjö *et al.*, 1992). For example, Hillis’ (1991) skewness method can be influenced more by the frequencies of states within characters than the congruence among characters, and Archie’s (1989; see also Faith & Cranston, 1991) permutation approach can suggest a highly significant departure from randomness where the data do not show an unambiguous hierarchic structure.

All tables are listed in Appendix II.

Pythonine Phylogeny

Character Descriptions

The following 121 characters are employed in my study of pythonine phylogeny (Tables 1-31, Figs 5-19). Characters 1 to 72 are skeletal in nature, and the remainder concern various aspects of the external and internal soft anatomy and behaviour. There are 76 binary (nos 2-8, 10, 13-15, 17, 19, 21-26, 28-34, 36-37, 40-47, 49, 51, 54, 60-63, 65-70, 72, 78-80, 83, 88-89, 91, 93-95, 98-101, 103-104, 108-111, 113, 116-120), 31 three state (nos 1, 9, 11, 16, 18, 20, 27, 35, 38-39, 48, 50, 52-53, 55-56, 58-59, 71, 73, 82, 84-87, 90, 92, 107, 112, 114, 121), seven four state (nos 64, 75-77, 81, 96, 115), two five state (nos 12, 57), one six state (no.97), two seven state (nos 74, 102), one eight state (no.106), and one 10 state (no.105) characters. Not all of the recognised states are recorded for three characters because no taxon unequivocally exhibits all recognised conditions; states 6, and 0, 5 and 9, and 6 and 7 are not recorded in Table 31 for characters 102, 105, and 106, respectively. Character 92 is also exceptional because it cannot be polarised unambiguously, nor can its state 0 be attributed unambiguously to any particular ingroup terminal taxon (Tables 31,32). Thus, the total size (M) of the data set is 194. The hypothesised histories of three state characters 12, 16, 50, 55-57, 59, 64, 74, 90 and 112 are coded in an unusual manner because state 1 is hypothesised to be plesiomorphic, with state 0 being an apomorph. Some of the ambiguous variation within the ingroup terminal taxa is described in the character descriptions, and it is summarised in Table 31.

1. *Premaxilla*. The modal, or median, number of premaxillary teeth in an adult is none (0), one (1), or two (2) per ramus. Variation in the ingroup terminal taxa is summarised in Table 1 (see also Fig.5). This compilation agrees with McDowell’s (1975) observations on *albertisii*, *amethystina*, *mackloti*, *papuanus*, *spilotus*, and *viridis*; however, Cogger (1986:406) incorrectly stated that *viridis* has no premaxillary teeth. Curiously, Underwood (1976:156) considered this variable (his character 35) in his study of booid relationships, but Underwood & Stimson (1990) did not do so in their investigation of pythonine phylogeny. Adult premaxillary teeth are found elsewhere among snakes only in *Anilius* (1-3 per ramus; usually 1), *Loxocemus* (1-2; usually 1; not 2 as recorded by Underwood, 1976;

see also McDowell, 1975:fig.1), and *Xenopeltis* (3-4; usually 4). Given these observations and the outgroup hypothesis of relationships illustrated in Figure 1, the most parsimonious interpretation of polarity is that state 0 is plesiomorphic in pythonines.

Aside from egg-tooth development, two types of premaxillary tooth ontogeny have been observed in snakes. M.A. Smith *et al.* (1953) found the number of rudimentary premaxillary teeth to increase from two to four to six during *molurus* embryogenesis, and then decline postnatally to the usual two adult teeth. I have almost always found one erupted (functional) premaxillary tooth per ramus in neonate *melanocephalus* and *ramsayi*. That premaxillary tooth usually co-occurs with an egg-tooth (eg. *melanocephalus*: AM R127417-21), the two kinds of teeth being easily distinguished on the basis of shape and orientation (de Beer, 1949:pl.13[2]). The premaxillary teeth are then lost in *melanocephalus* and *ramsayi* as the rostral shield grows posteroventrally to form the distinctive spatulate snout of the adult. On the basis of the number of adult teeth (Table 1) and the subadult conditions observed in *melanocephalus*, *molurus*, and *ramsayi*, I suspect there are at least three ontogenetic trajectories in pythonines. All three sequences begin with an early phase of increasing numbers of rudimentary tooth buds, followed by reduction which leaves either two, one, or no adult teeth. While M.A. Smith *et al.*'s (1953:262) observations suggest the early phase of increasing numbers of rudimentary tooth buds does not occur among caenophidians, further survey work is obviously required. As those authors noted (p.262) it is not clear which trajectory applies to other booids, such as boines and erycines. The most important reason I have for scoring the number of premaxilla teeth only in terms of the adult semaphoront, and thus *melanocephalus* and *ramsayi* as state 0, is the absence of developmental series of most of those outgroup taxa which lack teeth in the adult. Ideally, species characterisations should reflect the entire lifecycle (Hennig, 1966; Kluge, 1988a), and I look

forward to that time when there are sufficient developmental series to allow for that possibility. The available ontogenetic series of pythonines might suggest the absence of teeth in adult *melanocephalus* and *ramsayi* represents an evolutionary reversal; however, the caenogenetic evolution of teeth is an alternative process explanation. Such competing propositions will be evaluated later in this paper, in the context of the phylogenetic hypothesis based on all the available evidence (see Diagnoses section, clade C). For example, if *melanocephalus* and *ramsayi* are highly apomorphic relative to other pythonine sister lineages, then the reversal hypothesis may be the most parsimonious explanation.

2. *Premaxilla.* The middle third of the anterior margin of the premaxilla is slightly convex or straight (0) or concave (1). A largely dorsal view is necessary to correctly identify the states of this character; a strictly anterior-posterior perspective is too severe. At least in pythonines, state 1 (Fig.5) appears to reflect the enlarged area of the premaxilla from which the premaxillary teeth originate. *Anilius*, *Casarea*, erycines (all species but a few *Eryx*), *Loxocemus*, *Trachyboa* and *Xenopeltis* are characterised by state 0. State 1 occurs in *Bolyeria*, *Exiliboa*, *Tropidophis* and *Ungaliophis*. Boines cannot be delimited unambiguously, at least part of the problem being the confounding presence of the novel ascending process which may or may not exhibit an indentation on its outer surface. Thus, it appears that state 0 is plesiomorphic in pythonines.

3. *Premaxilla.* The lateroposterior margin of the maxillary process of the premaxilla is gradually rounded (0) or curved markedly upward to form a long, narrow prominence (1). State 1 is most evident in large, adult specimens. For example, the lateroposterior margin is only turned upward slightly in subadult *viridis*, and in that regard those specimens are like neonate *reticulata*. However, adults of both species clearly exhibit state 1.

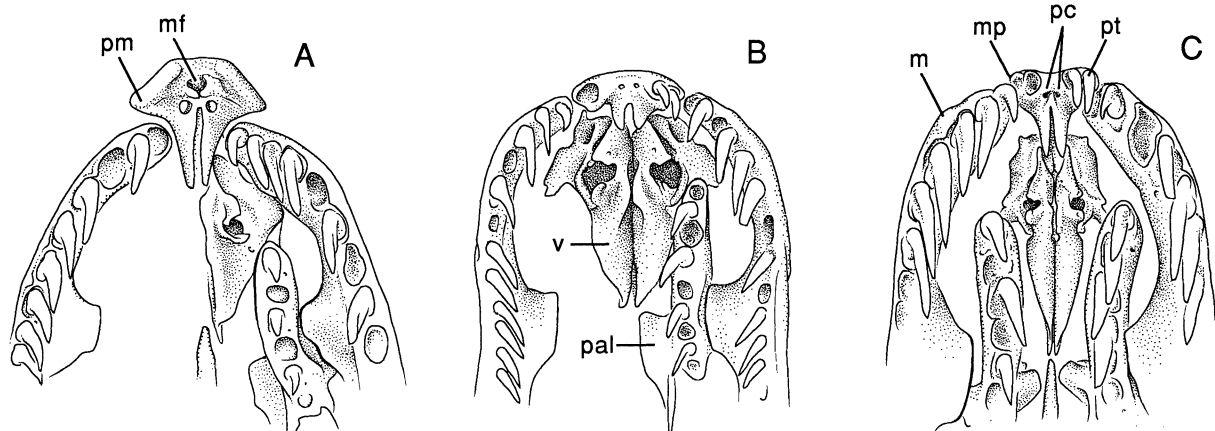


Fig.5. Ventral view of the skeleton making up the palate, including the premaxilla and the anterior tips of right and left maxillae. A - *melanocephalus* (UMMZ 190781); B - *boa* (UMMZ 190704); C - *reticulata* (UMMVP 82). See also Figure 11. m - maxilla, mf - median fenestra, mp - maxillary process, p - premaxilla, pal - palatine, pc - premaxillary channels, pm - posterior margin of maxillary process, pt - premaxillary tooth, v - vomer.

One specimen of *anchietae* exhibits a slightly curved condition (UMMZ 190773), while the only other available skull exhibits the opposite (AMNH 50501). State 1 appears to be restricted to some pythonines (Table 31) among booids, and therefore I assume the gradually rounded condition is plesiomorphic.

4. *Premaxilla. The posterior margin of the maxillary process of the premaxilla is nearly perpendicular to the midline (0) or it slopes posteriorly (1).* The character state observations are made from a dorsal view, and state 1 (Fig.5) suggests the premaxilla has an overall triangular appearance, whereas state 0 looks more rectangular in pythonines. The margin is crenelated in some *boa*, which gives the false appearance of state 1 (eg, UMMZ 190704). Both 0 and 1 states occur in *mackloti* (eg, MCZ 37244 and AM R41872, respectively). Among the outgroups, state 0 occurs in anilioids, *Loxocemus* and *Xenopeltis*. Tropicodphiines and erycines have an extremely narrow and pointed lateral process, respectively, but are nonetheless more like state 0 than 1. Bolyeriines exhibit state 1, and the fact that *Candoia* and *Corallus* also have that condition suggests the boine lineage can be diagnosed by that condition as well. Thus, the plesiomorphic condition in pythonines must be considered ambiguous, state 0 or 1 being most parsimoniously optimised.

5. *Premaxilla. The ventral openings for the premaxillary channels (Frazzetta, 1959:fig.3) are located posterior (0) or anterior (1) to the posterior margin of the premaxillary teeth.* The channels in *albertisii* (particularly AM R16796) and *reticulata* lie relatively far forward for those taxa scored as state 0 (Fig.5). The latter species is also peculiar in that the channels are close to the midline, which in some specimens gives the appearance of a single opening. One channel is present in both specimens of *timoriensis* available. One specimen of *boa* (AM R132966) has no channels; however, all other representatives of that species exhibit state 1 (Fig.5). While adult *melanocephalus* and *ramsayi* have lost their premaxillary teeth, the channels are nonetheless conspicuously posterior in position. All of *olivacea* examined, but one (WAM R77667), exhibit the anterior position, and therefore that common state is considered representative of the taxon. This character cannot be scored in those outgroups which lack adult teeth; however, state 0 clearly obtains in *Anilius* and *Xenopeltis*. Even the condition in *Loxocemus* is difficult to judge because the lateral processes of the premaxilla, on which the teeth are located, curve posteriorly, far beyond the channel openings. Thus, it is only on the basis of *Anilius* and *Xenopeltis* that I assume state 0 is plesiomorphic in pythonines.

6. *Premaxilla. A median fenestra is absent (0) or present (1) on the ventral surface of the premaxilla, anterior to the premaxillary channels.* Most species of snakes have tiny foramina in the region in question, but these are not to be confused with the extremely large

depression in *melanocephalus* and *ramsayi*, which receives two or more foramina (Fig.5). Further, the fenestra is not to be confused with the small foramina that occasionally lie closer to (actually within, in some cases) the premaxillary channels (eg, *anchietae* and *regia*). The fenestra is located approximately where the egg tooth attached; however, I suspect the opening is an anterior extension of the foramen that occurs in the vicinity of the incisive process (Oelrich, 1956:fig.4) in *melanocephalus* and *ramsayi* (see however, *viridis* [UMMZ 128060, 151090]). The fenestra appears to be restricted to some pythonines among booids, and therefore I assume state 0 is plesiomorphic.

7. *Premaxilla. The maxillary process of the premaxilla is located immediately anterior to or within (0) or well beyond (1) the arc formed by the anterior ends of the maxillae (Fig.5).* In most other primitive snakes the premaxilla is located between the ends, within the arc, of the maxillae. Only erycines, and perhaps bolyeriines, exhibit state 1. The premaxilla is set slightly anterior to the arc in some boines (*Candoia* and some *Epicrates*). Thus, I assume state 0 is plesiomorphic in pythonines.

8. *Nasal. The anterodorsal region of the nasal, between the nostrils, is wide (0) or narrow (1).* The narrow state consists of the descending lamella, with little or no horizontal plate of bone. Some of the *childreni* complex (L.A. Smith, 1985), such as *pertensis* (SAM R4094, UMMZ 190842), have a noticeable horizontal lamella, but nothing that approaches the extreme condition found in *melanocephalus* and *ramsayi*. I have tentatively recorded state 0 for *boa* because it is more like the latter two species than it is any example from the *childreni* complex. Among the outgroups, state 0 occurs in anilioids, erycines, *Loxocemus* and *Xenopeltis*, while both conditions seem to occur in bolyeriines (wide in *Bolyeria*, narrow in *Casarea*) and tropicodphiines (wide in *Trachyboa* and *Ungaliophis*, narrow in *Exiliboa* and *Tropidophis*). Both conditions also occur in boines (Kluge, 1991); however, the plesiomorphic condition for that group appears to be state 0 (eg, *Candoia* and *Corallus*). Thus, the most parsimonious interpretation is that a wide plate of bone is plesiomorphic in pythonines. McDowell's (1975:30-31) suggestion that wide "horizontal subcutaneous plates extending all the way forward between the nostrils" distinguishes the group consisting of *melanocephalus* and *ramsayi* is inconsistent with this hypothesis of polarity. The horizontal plate between the nostrils does not appear to be preceded by state 1 during *melanocephalus*' ontogeny, which is also inconsistent with McDowell's (1975) hypothesis.

9. *Nasal. The anterolateral margin of the horizontal portion of the nasal, opposite the anterior end of the prefrontal, is more or less gradually curved anteriorly (0), or sharply directed medially (1) or posteriorly (2) toward a narrow shelf above the internarial septum.*

Conditions 1 and 2 in adults give the impression that the region anterior to the nasal is wider than it is when condition 0 obtains. Further, this character (and character no. 8, to a lesser degree) affects the amount the septomaxilla is exposed (Frazzetta, 1959:466). The gradually curved state characterises anilioids, *Casarea*, erycines, tropidophiines, *Loxocemus* and *Xenopeltis*, while *Bolyeria* appears to be described best by state 1. There is considerable variation among boines: state 0 applies to *Candoia*, and *Corallus*, and states 1 or 2 accurately describe all other taxa in that group. Thus, the most parsimonious explanation is that the gradually curved condition is plesiomorphic in pythonines.

10. *Nasal*. The lateroposterior margin of the nasal is covered by the prefrontal (0) or it is exposed (1). The exposed state, which was illustrated by McDowell (1975:fig.17), is probably a function of both a narrow nasal and prefrontal. In fact, this character might be defined entirely in terms of the shape of the lateroposterior margin of the nasal (U- and V-shaped; Frazzetta, 1966:fig.13, and Dowling & Duellman, 1978:fig.101.1, respectively). All specimens of *olivacea* exhibit only a small area of overlap, a large area of exposure, and therefore it seems appropriate to score that species as state 1. Among the outgroups, the covered condition is present in anilioids, boines (except *Boa manditra*), erycines, *Loxocemus* and *Xenopeltis*. While the bolyeriine and tropidophiine condition might be viewed as state 1, I have little confidence that it is strictly comparable to that condition in pythonines because of the different shapes and sizes of the nasal and prefrontal bones in those taxa (Anthony & Guibé, 1952:figs 2,4). In any case, the most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

11. *Nasal*. The posterior end of the nasal, in the vicinity of the frontonasal joint, is largely vertical (0), nearly equally horizontal and vertical (1), or mostly horizontal (2). The nasal should be removed to accurately interpret its condition. Frazzetta (1959:469, fig.4A,B) recognised only two states, vertical (*viridis*) and horizontal, whereas Underwood (1976; his character 40) used three, dorsal, dorsoventral and ventral contact. These states are only approximately correlated with the points of articulation between the nasal and frontal. State 1 applies to anilioids, *Calabaria*, *Charina*, *Exiliboa*, and *Ungaliophis*. State 0 typifies boines (except most *Candoia* which exhibit state 2), bolyeriines, *Eryx*, *Lichanura*, *Loxocemus*, *Trachyboa*, *Tropidophis*, and *Xenopeltis*. While there is considerable variation among the outgroups, state 0 appears to be plesiomorphic in pythonines.

12. *Maxilla*. The modal or median number of maxillary teeth per ramus in an adult is 15-16 (0), 17-18 (1), 19-20 (2), 21-22 (3), or 23 or more (4). Variation in the ingroup terminal taxa is given in Table 1. The following summarises McDowell's (1975), Underwood's (1976, his character 52), and Underwood & Stimson's (1990, their character 30, as inferred from their appendix

I) observations, respectively: *albertisii* (22-24, -, 13-17), *amethystina* (13-18, 15, 20-24), *boa* (19-21, 21, 18-19), *boeleni* (18, -, 13-17), *curtus* (-, 20, 13-17), *mackloti* (20-21, -, 13-17), *maculosus* (-, 23, 13-17), *melanocephalus* (-, 14, 20-24), *molurus* (-, -, 20-24), *papuanus* (14-17, -, 18-19), *regia* (-, 17, 13-17), *reticulata* (-, 17, 20-24), *sebae* (-, -, 20-24), *spilotus* (16-18, 17, 20-24), *timoriensis* (-, -, 13-17), and *viridis* (15-19, 17, 20-24). All of McDowell's (1975) counts are closely correlated with those in Table 1, and all but one, *regia*, of Underwood's (1976) are as well. I believe the City of London Polytechnic specimen cited as an example of *regia* by Underwood ("C.L.P. 1 specimen, skeleton") was misidentified, and that individual is *reticulata* (now BMNH 1988.600).

Underwood & Stimson's (1990) records of maxillary teeth number are substantially different from all other published data. A general difference in character state coding, where maxillary tooth counts 20-24, 18-19, and 13-17 should actually have been recorded as apomorphic, intermediate and plesiomorphic states, respectively, seems to explain most, but not all, of the discrepancies in Underwood & Stimson's "data file" (1990, appendix I). Underwood & Stimson's differences in *curtus*, *molurus*, *papuanus*, and *spilotus* require another explanation. In any case, comparing what those authors recorded in their appendix I and table VI for most taxa, better reveals the extent of the errors: *albertisii* (13-17, 22), *amethystina* (20-24, 16), *boa* (18-19, 21), *boeleni* (13-17, 18), *curtus* (13-17, 20), *mackloti* (13-17, 22), *maculosus* (13-17, 24), *melanocephalus* (20-24, 15), *molurus* (20-24, 17), *regia* (13-17, 19), *reticulata* (20-24, 16), *sebae* (20-24, 17), *spilotus* (20-24, 17), *timoriensis* (13-17, 20), and *viridis* (20-24, 16).

The outgroups can be characterised as follows: advanced snake clade 17, boines 17, erycines 17, *Loxocemus* 20, and *Xenopeltis* 34, and therefore I assume state 1 is plesiomorphic in pythonines (see also Kluge, 1993). I disagree with Underwood & Stimson's (1990) choice of 20-24 maxillary teeth (my states 2-4) as plesiomorphic.

13. *Maxilla*. The anterior maxillary teeth are short to moderately long and curved (0) or extremely long and relatively straight (1). Length is determined without respect to tooth curvature and changes in the level of the dental margin of the maxilla. The longest and straightest anterior maxillary teeth of any pythonine are exhibited by *carinatus*, with *viridis* being extremely similar. State 1 is present among the outgroups only in *Corallus*, and therefore I assume state 0 is plesiomorphic in pythonines. The teeth are quite long, but curved, in *Boa manditra*.

14. *Maxilla*. The anterior maxillary foramen on the lateral surface of the maxilla is small (0) or large (1). Foramen size concerns the height of the opening, not its length, and size should not be assessed relative to the depth of the maxilla in the vicinity of the foramen because the shape of that region varies considerably among pythonines. I measure foramen size relative to

the length of the base of the maxillary tooth which lies immediately below the foramen, states 0 and 1 being much less than and equal to, or more than, the size of that tooth, respectively. Of all those pythonines scored as having state 1 (Fig.6), *spilotus* seems to consistently exhibit the smallest foramen. The states recorded for this character (Table 31) are moderately correlated with the absence/presence of the rostral pit (character 100), but surprisingly much less so with the number of supralabial pits (character 102); however, a strong impression of functional dependence does not exist in either case. The foramen appears to be absent in *Eryx*, *Lichanura*, *Trachyboa* and *Tropidophis*, and small among all other relevant outgroups. Thus, I assume state 0 is plesiomorphic in pythonines.

15. *Maxilla. A lateral bulge is absent (0) or present (1) in the maxilla.* This variation is best judged from a dorsal view, the emphasis being on the contour of the maxilla. The bulge (Fig.6) is evident in the conspicuous indentation that occurs opposite the lateral foot process of the prefrontal (Frazzetta, 1966:fig.18). There is a slight bulge in *curtus* and *timoriensis*; however, it is not consistently present, nor nearly so prominent, as it is in some other pythonines (eg, *amethystina* and *spilotus*). State 0 occurs among the outgroups, and therefore it is assumed to be plesiomorphic in pythonines. M.J. Smith & Plane (1985) noted the presence of a lateral bulge in the extinct *Montypythonoides riversleighensis* (see discussion in Fossils section below).

16. *Maxilla. The dorsolateral margin of the suborbital region of the maxilla is oriented nearly vertically (0) or horizontally, and projects moderately (1) or markedly (2) laterally.* States 1 and 2 (Fig.6) are characterised by a ledge that extends lateral to the tooth row, often with a sharp edge, and which from above gives the appearance that the suborbital area of the maxilla is wider and flatter

than usual. The maxilla must be in its natural anatomical position, and viewed posteriorly, when scoring this character. In very large *amethystina* and *reticulata*, the outer margin becomes deeper and more rounded, thereby giving the appearance of the vertical state. Some specimens of *spilotus* have only a small, rounded ledge, whereas it is especially prominent and sharp in all *carinatus* and *viridis*. The suborbital region tends to be much shallower in *curtus* compared to most other pythonines. State 0 typifies anilioids and *Loxocemus*, while state 1 characterises boines (at least the basal lineages), bolyeriines, most erycines (except some species of *Eryx*), and most tropidophiines (except *Exiliboa*). The suborbital region of the maxilla is so flattened in *Xenopeltis* that it is difficult to score the variable for that taxon. Thus, the most parsimonious explanation appears to be that state 1 is plesiomorphic in pythonines. While characters 15 and 16 focus on the same general region of the maxilla, they attempt to describe different, independent, aspects of variation (compare their state distributions in Table 31).

17. *Maxilla. The palatine process of the maxilla (the medial process of McDowell [1975:30]) is narrow (0) or wide (1) at its origin from the body of the maxilla (Underwood, 1976).* The medioposterior edge of the process gradually curves anteriorly in most taxa recorded as state 1, whereas in the alternative form the edge is notched, the direction being anterior, then noticeably curving posteriorly where the process contacts the palatine (Frazzetta, 1959:469). The margin is definitely notched in almost all of the specimens belonging to the *childreni* complex. A narrow process is present in anilioids, boines (except *Corallus enydris*), bolyeriines, erycines, *Loxocemus* and tropidophiines. The process is absent in *Xenopeltis*. Thus, state 0 is assumed to be plesiomorphic in pythonines.

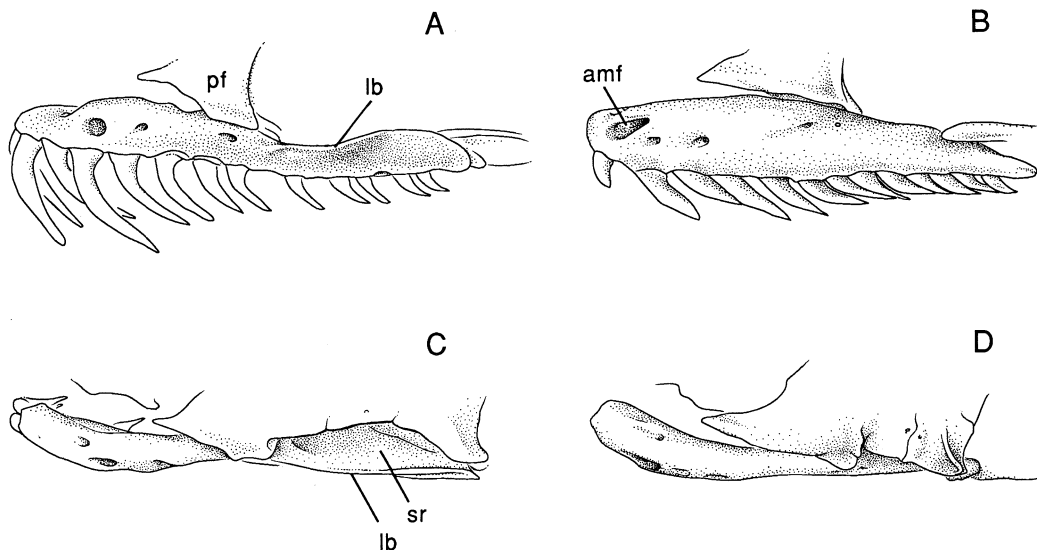


Fig.6. Lateral (A,B) and dorsal (C,D) views of the left maxillary bone. A,C – *viridis* (UMMZ 151090). B,D – *reticulata* (UMMVP 82). amf – anterior maxillary foramen, lb – lateral bulge, pf – prefrontal, sr – suborbital region.

18. *Maxilla*. The medioposterior corner of the palatine process of the maxilla lies opposite (0), or slightly (1) or far (2) anterior to the palatine-ptyergoid joint (McDowell, 1975:32; Underwood, 1976:fig.4). Among the outgroups, state 0 occurs in boines, *Calabaria*, most *Eryx*, *Exiliboa* and *Lichanura*; state 1 in *Charina*, some *Eryx*, some *Trachyboa*, *Tropidophis* and *Ungaliophis*; state 2 in anilioids, *Loxocemus*, and some *Trachyboa*. The process is absent in *Xenopeltis*. It is not clear which state applies to bolyeriines (Anthony & Guibé, 1952:figs 3,4) because the intramaxillary hinge of these snakes appears to have perforated the palatine process (S. McDowell, personal communication). Thus, the most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

19. *Prefrontal*. The lachrymal foramen is incompletely (0) or completely (1) enclosed by bone (Fig.7; see also Frazzetta [1959:fig.6]). A completely enclosed foramen occurs in *Anilius*, *Rhinophis* (only *R. sanguinaeus*; BMNH 1930.5.8.59), and the (*Acrochordus*, higher snakes) clade. While the foramen is completely encircled by bone in alethinophidians, a few specimens exhibit an incomplete fusion of the ventral bar of bone to the lateral pedicle of the prefrontal. The condition in *Loxocemus* is obviously affected by age (size) because small individuals have the open state, whereas the largest specimens have the ventral margin of the opening formed by a thin bar of the prefrontal, which contacts, but does not fuse to, the lateral pedicle. An open foramen characterises all other anilioids, boines (except *Corallus caninus*), bolyeriines, *Dinilysia* (Estes *et al.*, 1970:42), erycines (see *Calabaria* discussion below), tropidophiines, and *Xenopeltis*. Frazzetta (1959:469) stated that the foramen is completely enclosed by bone in one of two specimens of *Calabaria* he examined, and Underwood (1967:69) reported it as variable in that taxon. In 1976 (p.43), Underwood stated that the foramen formed a "partly closed notch" in *Calabaria*. I have examined 13 skulls of *Calabaria*, and it is completely closed (both sides) in only one specimen (UF 54072). There is a wide, open notch on both sides in eight specimens, an open, but narrow notch on both

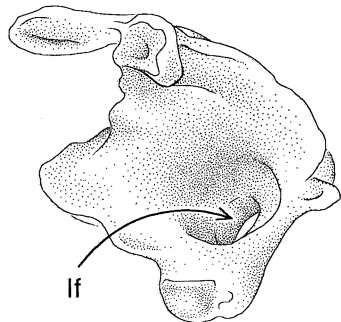


Fig.7. Anterior view of the right prefrontal bone in *melanocephalus* (UMMZ 190781) illustrating the completely enclosed nature of the lachrymal foramen. See also Figure 9. lf – lachrymal foramen.

sides in one specimen, and in three individuals the foramen is wide open on one side and narrowly open on the other. Thus, *Calabaria* ordinarily exhibits state 0, rarely state 1. Thus, the most parsimonious interpretation is that an open lachrymal foramen is plesiomorphic in pythonines.

20. *Prefrontal*. The floor of the prefrontal, the more or less horizontal sheet of bone lying dorsal and anterior to the lachrymal foramen, is absent (0), or present and with a broad (1) or narrow (2) upturned medial margin. The area of bone in question is easily damaged and extra care must be taken during skeletal preparation. The floor of the prefrontal rests on top of the maxilla, and is best viewed in situ, from within the nasal cavity, because other perspectives give the impression of a larger floor than is actually present. The shape of the medial edge of the floor conforms closely to the curvature of the palatine process of the maxilla, and states 1 and 2 are distinguished in terms of how long the process remains narrow. The projection in state 1 is often pointed but that narrow terminus originates gradually from a broad base, whereas state 2 is narrow throughout much of the length of the process. The upturned medial edge is narrow in small *reticulata*, but the largest specimens examined of that species (eg, BMNH 1972.2169, SVL = 21'6", TL = 2', and BMNH 1972.2170, "21 feet long") exhibit state 1. I suspect there is a strong ontogenetic shape change in pythonines, except perhaps in the *childreni* complex. A floor is absent in all outgroups, except *Boa*, *Calabaria*, and *Xenopeltis*; however, it is flat in those taxa, and does not rest on the maxilla in the latter two. Thus, I assume state 0 is plesiomorphic in pythonines.

21. *Prefrontal*. The dorsal recess (Frazzetta, 1966:fig.18) of the prefrontal is broad (0) or narrow (1). The opening in question is where the nasal and frontal laminae meet dorsolaterally, the apex being the place of articulation between the prefrontal and frontal. The ledges of bone near the apex, on which the frontal rests or is covered, are highly variable and they are not part of the definition of this character. While the prefrontal must be removed to accurately assess the character states, a reasonably good indication can be obtained from the angle of the posterior edge of the nasal lamina, an anterior orientation indicating a broad opening (Fig.8B), whereas a more medial position represents the narrow condition. Among the outgroups, the open form was only observed in the boine *Candoia bibroni*, and therefore I assume state 0 is plesiomorphic in pythonines.

22. *Frontal*. The frontal is narrow (0) or wide (1) relative to its length. Only the width (W) of a single frontal is considered, and length (L) does not include the nasal ledge above the olfactory canal openings; however, otherwise both measurements involve maximum distances. Only adults are employed because there is significant ontogenetic variation. Quantitatively, the character is W/L, and the states are .74 or less (0) or

.75 or greater (1). One out of six specimens of *olivacea* exhibit state 1, as do one out of four *sebae*, and both are recorded as having a narrow frontal. McDowell (1975:32,50) concluded that a wide frontal delimited New Guinea *Python* from *Liasis* (*sensu* McDowell), except for the extralimital *curtus*. My observations (Table 31) substantially confirm McDowell's. Among the outgroups, only *Boa*, *Charina*, *Corallus*, and *Epicrates* exhibit state 1, all others have the narrow condition. *Bolyeria* is not comparable because the frontals and parietal are coossified into a single element in the only specimen available to me (BMNH 70.11.30.4A; see however, Anthony & Guibé, 1952: fig.4). Thus, the most parsimonious explanation is that the narrow state (0) is plesiomorphic in pythonines.

23. *Frontal*. The anterodorsal margin of the frontal, the area overlapped by the nasal and prefrontal, is approximately even with (0) or lies below (1) the general horizontal level of the dorsal surface of the frontal. The nasal and prefrontal bones must be removed to judge these states accurately. The ledge on which the nasal and prefrontal rest appears to be absent in boines, bolyeriines (*Casarea* may be an exception), erycines, and tropidophiines, and present in anilioids, *Loxocemus*, and *Xenopeltis*. Thus, the most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

24. *Frontal*. The prefrontal process of the frontal projects either anteriorly or nearly laterally (0) or anterolaterally (1). The process in question originates from the lateral margin of the olfactory canal. The process is directed anteriorly in *Bolyeria* (small; probably absent in *Casarea*), *Loxocemus* and *Xenopeltis*, laterally in those boines possessing the projection (eg, *Boa* and *Corallus*), *Exiliboa*, most *Tropidophis* species, and *Ungaliophis*, and anterolaterally in erycines, *Trachyboa*

and *Tropidophis taczanowskyi*. Based on these observations, and the hypothesis illustrated in Figure 4, the most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

25. *Frontal*. A groove is absent (0) or present (1) between the prefrontal process and the anterodorsal margin of the frontal. The groove is horizontal and is probably the result of the prefrontal process originating farther posteriorly beneath the roof of the frontal, and/or the anterodorsal margin of the frontal extending anteriorly above and beyond the process. The prefrontal must be removed if this character is to be judged accurately. Such a groove appears to be absent among the outgroups, and therefore I assume state 0 is plesiomorphic in pythonines.

26. *Frontal*. The lateral margin of the frontal is convex or nearly straight (0) or conspicuously concave (1). The indentation is deep in most pythonines (Fig.8), with *boa* being most like state 0, and *curtus* exhibiting what I believe is an incomparable triangular shape. Most of the outgroups, boines, bolyeriines, erycines, and tropidophiines, exhibit nearly straight sides, which gives the frontal region a decidedly rectangular appearance. The condition in anilioids, *Loxocemus* and *Xenopeltis* is difficult to determine because of the adjacent nature of the parietal; however, in general it is more convex than straight. Thus, I assume state 0 is plesiomorphic in pythonines.

27. *Frontal*. The anterior and posterior corners of the frontal extend laterally nearly equally (0), or the anterior corner projects slightly (1) or much (2) beyond the posterior (Fig.8). These states can be quantified according the relative width of the frontal anteriorly (A) and posteriorly (P), as P/A, the states being defined as

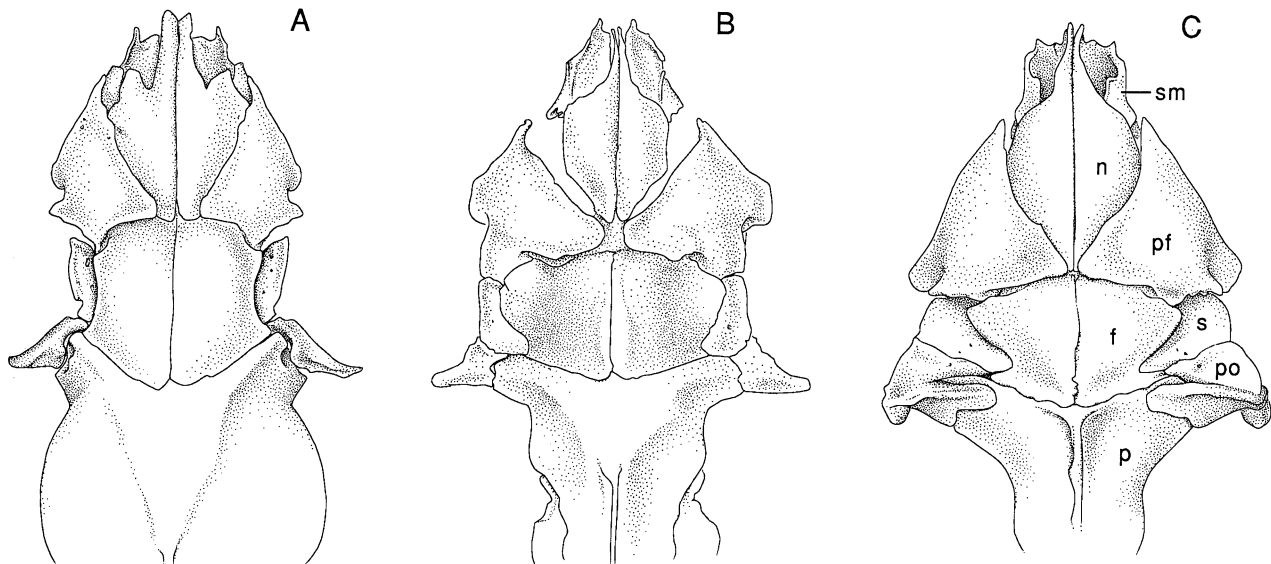


Fig.8. A dorsal view of the mid-skull region. A – *boa* (UMMZ 190704); B – *viridis* (UMMZ 151090); C – *reticulata* (UMMVP 82). f – frontal, n – nasal, p – parietal, pf – prefrontal, po – postorbital, s – supraorbital, sm – septomaxilla.

0 = 0.94 or more, 1 = 0.79-0.91, and 2 = 0.76 or less. Characters 26 to 27 do not appear to be correlated (see Table 31). All of the relevant outgroups with distinct anterior and posterior corners exhibit a ratio of approximately 1.0, and therefore, I assume state 0 is plesiomorphic in pythonines.

28. *Frontal*. The suture between the frontal and parietal, as it arises from the dorsal margin of the optic foramen, is oriented dorsally or only slightly (0) or markedly (1) anteriorly. This transformation series can be readily determined from either a ventral or lateral view, with the sphenoid held horizontally. An extremely large *boa* (AMNH 44002) approaches the angle typical of state 1, whereas all other representatives of that species clearly have a dorsally oriented suture. The suture is oriented anteriorly in *Anilius*, *Cylindrophis*, *Exiliboa*, *Loxocemus* and *Xenopeltis*, but it is more like state 0 in boines, *Casarea*, erylinae, and the remaining tropidophiines. While the condition in *Bolyeria* cannot be observed directly, because of the frontal-parietal fusion in the only available specimen (BMNH 70.11.30.4A), the approximate location of the groove is indicated by a depression above the optic foramen, which suggests state 0 applies to this taxon as well. Thus, I assume state 0 is plesiomorphic in pythonines.

29. *Supraorbital*. The supraorbital is absent (0) or present (1). This is equivalent to Underwood's (1976) character 44 (his "postfrontal" bone; see Kluge, 1993 for review). State 1 applies only to *Calabaria*, *Dinilysia*, *Loxocemus* and pythonines (Fig.8). If the bone in *Calabaria* is not homologous, as suggested by Kluge (1993), then state 0 is most parsimoniously interpreted as plesiomorphic relative to the condition which is typical of all pythonines.

30. *Supraorbital*. The supraorbital is narrow (0) or wide (1). The states of this character can be quantified in terms of the width of the posterior margin of the supraorbital, along the parietal-postorbital edge, and the length of the lateral margin of the supraorbital, between the prefrontal and postorbital; the former measurement is shorter than or equal to the latter in state 0, whereas the former measurement is longer than the latter in state 1 (Fig.8). McDowell (1975:31) claimed that his *Liasis* group of species, *albertisii*, *boa*, *childreni*, *mackloti*, *olivacea* and *papuanus*, could be delimited by the supraorbital being "longer than wide, underlapping [the] frontal bone only narrowly, [and being] slightly movable." He claimed (p.50) that the bone is "broader than long in adults of New Guinea forms [*amethystina*, *boeleni*, *spilotus*, *viridis*] (but longer than broad in the extralimital *P. anchietae*, *P. curtus* and *P. regius*)". The only skeletal material representative of *mackloti dunni* (AMNH 32264; the paratype) exhibits state 1 (all other *mackloti* examined have state 0), which suggests this island form (Wetar, Indonesia) has undergone considerable differentiation. Assuming the supraorbital is present in *Loxocemus* and *Calabaria*, the narrow

condition (state 0) is most parsimoniously interpreted as plesiomorphic in pythonines. This hypothesis of polarity casts doubt on the usefulness of the narrow state in diagnosing the *Liasis* group of species (McDowell, 1975:31). The size of the supraorbital seems to covary exactly with its mobility and underlying and/or abutting the frontal, and I have not scored those conditions as separate variables because of the implied lack of independence.

31. *Supraorbital*. The supraorbital contacts or is narrowly (0) or broadly (1) separated from the parietal. The anterior head of the postorbital noticeably separates the supraorbital and parietal in state 1 (Fig.8). The broad contact with the parietal exhibited by *Calabaria* and *Loxocemus*, assuming those taxa actually possess the supraorbital, suggests state 0 is plesiomorphic in pythonines (Fig.8).

32. *Postorbital*. The dorsomedian end of the postorbital is undivided (0) or divided into two heads (1) (Frazzetta, 1959:461, fig.7A-C; see also Underwood [1976; his character 45]). McDowell (1975:30) appears to have defined state 1 in terms of the cleft dorsal end of the postorbital embracing a "salient formed by frontal and parietal." *In situ*, the cleft which divides the postorbital into two heads, anterior and posterior, is only seen clearly from above. State 0 is recorded for *childreni*, *maculosus*, *perthensis*, *regia* and *stimsoni*; however, a distinct, broad, indentation occurs along the posterior margin of the postorbital in the last species, which may be a remnant of the cleft. Among the outgroups which possess a postorbital (the bone is absent in *Anilius*, *Charina*, uropeltines, and *Xenopeltis*), a cleft is absent in most boines, *Bolyeria* (Anthony & Guibé, 1952: fig.4), *Casarea*, *Cylindrophis*, erylinae, *Exiliboa*, *Loxocemus* and *Ungaliophis*, and present in *Candoia carinata* (especially distinct in BMNH 1964.1609), *Trachyboa* and *Tropidophis*. Thus, the most parsimonious explanation is that state 0 is plesiomorphic in pythonines.

33. *Postorbital*. The anterior head of the dorsomedian end of the postorbital under- or overlaps (0) or abuts (1) the postorbital process of the parietal. I have recorded state 1 (Fig.9) only in *childreni*, *maculosus*, *perthensis*, and *stimsoni*; however, there are traces of the alternative condition in some specimens. The conspicuously underlying projection in all other pythonines is usually rectangular, rarely does it decrease in width toward a rounded, medial end. Further, the amount the anterior head underlays the parietal appears to be positively correlated with the width of the process. This character is nearly perfectly correlated with the distribution of character 32's states; however, it is on the basis of the exceptional condition in *regia* (Table 31) that I employ both variables in my analysis of pythonine relationships. While the dorsomedian end of the postorbital is not obviously divided by a cleft into anterior and posterior heads in *Calabaria*,

Cylindrophis and *Loxocemus*, it is fair to say that the orbital portion of the postorbital underlays slightly the parietal in all three taxa, and even so in the absence of a postorbital process of the parietal. In tropidophiines, the orbital portion of the postorbital completely underlays the postorbital process of the parietal in *Trachyboa* and *Tropidophis*, and slightly overlaps the parietal in *Exiliboa* and *Ungaliophis*. The condition in *Bolyeria* cannot be determined with the available material, or from Anthony & Guibé (1952), but in *Casarea* the postorbital seems to underlay most, if not all, of the postorbital process of the parietal (like *Trachyboa* and *Tropidophis*). In the remaining erylacines with a postorbital, the anterior extension of that element either overlaps the parietal in *Eryx* or abuts its anterior edge in *Lichanura*. The boine postorbital appears to overlap much of the postorbital process of the parietal. Thus, the most parsimonious explanation is that state 0 is plesiomorphic in pythonines, with state 1 being derived from either the underlap or overlap position.

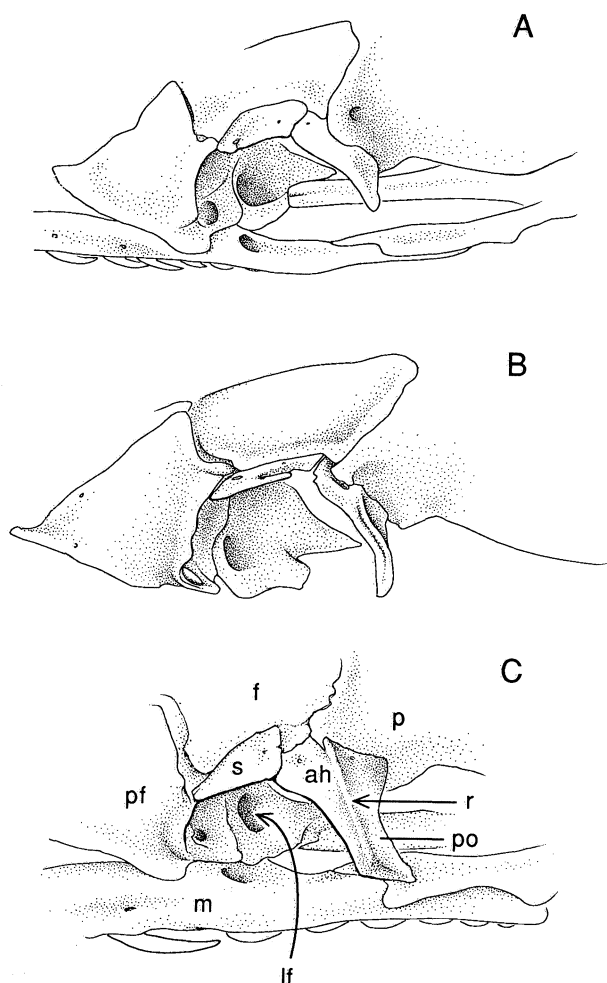


Fig.9. Dorsolateral view of the left mid-skull region. A – *childreni* (UMMZ 190779); B – *boa* (UMMZ 190704); C – *olivacea* (UMMZ 190780). ah – anterior head, f – frontal, lf – lachrymal foramen, m – maxilla, p – parietal, pf – prefrontal, po – postorbital, r – ridge, s – supraorbital.

34. *Postorbital.* The anterior head of the dorsomedian end of the postorbital, as observed ventrally from within the orbit, is in extensive contact with (0) or nearly, or completely, separated from (1) the frontal. Among the outgroups, which have a postorbital, state 0 applies to bolyeriines, *Cylindrophis*, *Eryx*, *Lichanura* and tropidophiines, whereas the contact is absent in *Calabaria* and *Loxocemus*. The following distribution among boines suggests that state 0 is plesiomorphic for that group (see Kluge, 1991: character 27, fig.7): the bones are in contact in *Boa constrictor*, *Candoia aspera*, *C. carinata*, *Corallus enydris*, *Epicrates* and *Eunectes*, and separated in all other taxa. Thus, the most parsimonious interpretation is that contact between the postorbital and frontal is the plesiomorphic condition in pythonines.

35. *Postorbital.* A crest is absent along the mid-dorsal surface of the median end of the postorbital (0), and when present it is either a low and relatively rounded (1) or tall and sharp edged (2) ridge. The most accurate way to assess this variation is to examine the postorbital from either a dorsal or ventral view so that the cross-sectional profile is revealed. The posterior head appears to be absent in *regia*, and the crest appears to be located along the posterior margin of the postorbital of that species (Fig.9). Among the outgroups, the area of the postorbital in question is flat or concave, almost never convex to any appreciable extent. The posterior margin of the bolyeriine postorbital is deeply grooved, and this novelty gives the impression of a crest in that taxon, similar to the condition in *regia*. Thus, the plesiomorphic condition in pythonines appears to be state 0.

36. *Postorbital.* The postorbital contacts (0) or is separated from (1) the ectopterygoid and/or maxilla. An argument for actual contact is difficult to make in most cases because skull preparation has altered the natural positions of the elements. Nonetheless, the ventral end of the postorbital is almost always expanded in state 0, whereas it narrows to a point in the alternative condition. The postorbital, when present among the outgroups, exhibits state 0 in boines, *Calabaria*, *Eryx*, *Trachyboa* and *Tropidophis*, and state 1 in bolyeriines, *Cylindrophis*, *Exiliboa*, *Lichanura* and *Ungaliophis*. It appears that it is equally parsimonious to consider states 0 or 1 to be plesiomorphic in pythonines.

McDowell (1975:31-32) referred to the postorbital-ectopterygoid (maxilla) contact as a “joint”, and he used (see also Worrell, 1956) this transformation to distinguish the *Lisalia* group (*olivacea*, *mackloti*, *papuanus*) from the *Liasis* group (*albertisii*, *boa*, *childreni*). Until this character can be polarised it is impossible to say which of these groups is diagnosable. This variable also constituted part of Underwood & Stimson’s (1990) character 28, although they emphasised just the contact between the postorbital and the maxilla. In polarising their transformation series, Underwood & Stimson, without justification, accepted the 0 state as primitive “although the postorbital is small

in *Xenopeltis* and *Loxocemus*" (p.582), which are the two taxa they ordinarily relied on to establish polarity. Aside from this questionable inference, the postorbital appears to be absent in *Xenopeltis* (McDowell, 1975: fig.6; see also Underwood, 1976: character 44).

37. *Postorbital*. The plane of the blade-like ventral portion of the postorbital is more or less directed anteriorly (0) or anterolaterally (1). This character cannot be scored on taxa which have no postorbital or where it is very short (see character 36). State 0 characterises the outgroups which have a postorbital, and therefore that condition is assumed to be plesiomorphic in pythonines.

38. *Ectopterygoid*. Two distinct anterior processes are absent from the maxillary end of the ectopterygoid (0), or when present the medial anterior process is obviously longer than the lateral anterior process (1) or the two processes are nearly equal in length (2). It is important to judge this character from a dorsal view, with the postorbital removed. One or both processes are well developed in almost all pythonines (states 1 and 2, respectively). Even though most specimens of *viridis* have little, if any, lateral process, I believe it is reasonable to score that species as state 1 because the asymmetrical shape of that end of the ectopterygoid is indicative of two processes. One specimen of *reticulata* exhibited state 2; however, all other individuals examined of that taxon had the medial process longer than the lateral. According to McDowell (1975:51), "in the *reticulatus* Group, the medial anterior process of the ectopterygoid is produced far in advance of the lateral anterior process; in the *molurus* Group, except for *P. curtus*, the two anterior processes of the ectopterygoid are subequal or (*P. sebae* and *P. anchietae*) the ectopterygoid is only gently concave anteriorly so that the medial and lateral anterior processes are poorly distinguished from each other".

There is considerable variation in the outgroups, which makes my polarity assessment tentative. A single-headed condition characterises *Anilius*, *Boa*, *Charina*, *Corallus annulatus*, *C. caninus*, *Epicrates*, *Eryx*, *Lichanura*, *Trachyboa* and *Tropidophis*. Those taxa with extremely short processes form two groups, the medial process being slightly longer than the lateral in *Cylindrophis* and *Xenopeltis*, or of nearly equal length in *Candoia*, *Eunectes*, *Exiliboa* and *Ungaliophis*. I consider all of aforementioned outgroups to be state 0 because there is little or no indentation on the anterior end of the ectopterygoid. The fact that distinct processes are present only in bolyeriines, *Calabaria*, *Corallus enydris* and *Loxocemus* (state 1) suggests that the single headed condition is plesiomorphic in pythonines. While McDowell (1975; see also Frazzetta, 1966) also indicated state 2 is apomorphic in pythonines, additional research on this character is obviously required. For example, there is some indication that the medial process is very slightly longer than the lateral in *Boa madagascariensis*, *B. manditra*, *Candoia carinata*,

Corallus caninus and *Lichanura*, and the lateral very slightly longer than the medial in *Charina* and *Eunectes*.

39. *Ectopterygoid*. The ectopterygoid completely covers the posterior end of the maxilla (0), or the maxilla is exposed laterally (1) or at its tip (2). This character should be judged from a dorsal view, with all the bones *in situ*, except for the removal of the postorbital. The ectopterygoid, posterior to the lateral and medial processes, narrows considerably in *olivacea* and slightly so in *papuanus*, thereby exposing the margin of the maxilla, and therefore those taxa are scored as state 1. The exposure of the maxilla is not correlated with the size of the prominence that occurs at the posterolateral corner of the ectopterygoid. I have not attempted to score the variation in that prominence as a character because of extreme individual variation, not all of which appears to be due to ontogenetic differences. State 0 typifies at least some anilioids (eg, *Cylindrophis*), bolyeriines, erycines, *Loxocemus* and tropidophiines, whereas state 1 occurs in *Xenopeltis*. Boines vary considerably: state 0 occurs in *Candoia* and the more plesiomorphic sister taxa of *Epicrates*, while state 1 or 2 occurs in all other taxa. Thus, the implication is that the covered condition is plesiomorphic in pythonines.

40. *Ectopterygoid*. The ectopterygoid contacts the pterygoid dorsolaterally (0) or dorsally (1). While the ectopterygoid is dorsal to the pterygoid in *papuanus*, it is not so extreme as it is in *melanocephalus* and *ramsayi* where there is considerable overlap. The contact is dorsolateral in all of the relevant outgroups, with the following exceptions, where the juncture is more dorsal or anterodorsal: *Exiliboa*, *Trachyboa* and *Tropidophis* (Kluge, 1991). Thus, the most parsimonious interpretation is that the plesiomorphic condition is state 0 in pythonines.

41. *Supraoccipital*. Lateral crests on the supraoccipital are absent or weakly developed (0) or prominent (1). Prominent crests are present when they project both laterally and dorsoposteriorly (Fig.10). The condition in *sebae* is quite similar to that of boines. This variable seems to be a combination of Underwood's (1976) characters 49-50, which he used to diagnose pythonines. Frazzetta's (1959:464) distinction between boines and pythonines in terms of number of crests, one and two, respectively, requires qualification. Supraoccipital crests are absent or weakly developed in all of the relevant outgroups except *Bolyeria* (the condition in *Casarea* requires further study) and tropidophiines. Therefore, the absence of those ridges is considered plesiomorphic in pythonines.

42. *Exoccipital*. The supratemporal (squamosal, tabular or paroccipital) process of the exoccipital is small or absent (0) or large (1). When the process is large (state 1) it extends from the dorsal margin of the fossa forming the *fenestra ovalis* to the underside of the supratemporal, and projects posteriorly or

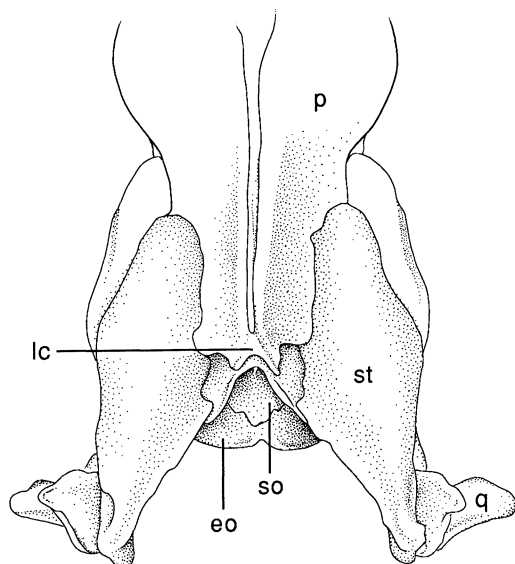


Fig.10. Dorsal view of the posterior end of the skull of *regia* (UMMZ 149660). eo – exoccipital, lc – lateral crest, p – parietal, q – quadrate, so – supraoccipital, st – supratemporal.

lateroposteriorly well beyond the fenestra. The presence of a large supratemporal process creates a deep groove in the exoccipital, seen in ventral view, adjacent to the foramen magnum. While the groove is shallow in *stimsoni*, it is sufficiently deep, more so than any other species in the *childreni* complex, to qualify as state 1. McDowell (1975:29) referred to this protuberance as the “paroccipital process”, and in so doing implied that it is homologous with the paroccipital process of other squamates (ie, “lizards”). I think his interpretation is highly unlikely to be correct because such a process is absent among more primitive ophidians, and I therefore choose a different name for the structure found in more derived snake lineages. I cannot confirm McDowell’s (1975) claim that all pythonines, except *Aspidites*, possess this structure, although it is smaller in *ramsayi* than *melanocephalus*. The groove is absent or only weakly developed in all of the relevant outgroups, and therefore I assume state 0 is plesiomorphic in pythonines.

43. Exoccipital. *The atlantal flange on the exoccipital, adjacent to the occipital condyle, is inconspicuous (0) or prominent (1).* McDowell (1975:29-30) considered state 1 to be characteristic of pythonines; however, the flange is recorded as absent in *anchietae*, *childreni*, *maculosus*, *perthensis*, *regia* and *stimsoni*. In most other pythonines, the flange is sufficiently long to contact a swelling on the neural arch, and thereby form an accessory joint, one per side. The process is absent in the outgroups, except bolyeriines where it is especially well developed in *Bolyeria*. I assume state 0 is plesiomorphic in pythonines.

44. Quadrate. *The anterodorsal end of the quadrate is narrow (0) or very wide (1).* The dorsal end of the quadrate is conspicuously triangular in shape in state 1,

especially in large specimens, as opposed to being more nearly oval in state 0. Moreover, the body of the quadrate is to some degree concave anteriorly in state 1, the depression being formed by a ridge leading to the stapedial facet, while the shaft of the quadrate is approximately of equal thickness throughout its length in state 0. The quadrate does not have to be removed to judge the state accurately, providing connective tissue does not cover the supratemporal-quadrate area of contact. Among the outgroups, only anilioids (*Anilius* and *Cylindrophis*) and *Calabaria* have a quadrate that even approaches state 1. *Boa* and *Candoia carinata* have a triangular condition; however, unlike pythonines, there is no ridge between the inner corner of the triangle and the stapedial facet. All other boines clearly exhibit state 0. Thus, the most parsimonious explanation is that state 0 is plesiomorphic in pythonines.

45. Quadrate. *The quadrate is tall (0) or short (1).* In quantitative terms, the states are approximately more than 21% or less than 22%, respectively, relative to the total length of the lower jaw. Frazzetta (1959:461; see also Underwood, 1967:69) appears to have been the first to recognise the systematic importance of this variation. The relatively longest quadrate observed among pythonines is *viridis*, at about 29%. Anilioids exhibit particularly short quadrates (15% in both *Anilius* and *Cylindrophis*). Boines and erycines range between 23-30%, and *Loxocemus* and *Xenopeltis* are 21% and 19%, respectively. *Bolyeria* has a relatively long quadrate (23%), whereas that of *Casarea* is short (18%). Long quadrates occur generally among tropidophiines, particularly in *Trachyboa* at 32%, except for *Exiliboa* which exhibits state 1. The most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

46. Vomer. *The ventral, horizontal, fluted wing of the vomer, posterior to the septomaxilla, is uniformly wide or varies in width (0) or is uniformly narrow (1).* In the former state, the horizontal wing nearly meets the palatine, whereas it does not in the latter condition (Fig.11). The uniform narrowness of the latter state is accentuated in pythonines by the extraordinary length of the wing. While there is considerable variation, I believe state 0 applies to all of the relevant outgroups, except the *Corallus caninus* and *C. cropanii* clade. A wide vomer is present in *Loxocemus* and all other boines (Frazzetta, 1959:469). State 0 applies to anilioids and all tropidophiines, except *Ungaliophis*, which has a narrow, but very short, wing. State 0 also appears to characterise bolyeriines; however, the available material was damaged somewhat in preparation and a significant amount of interpolation is required. The wing in erycines is variable. The wide state occurs in *Eryx*, whereas the opposite condition characterises *Calabaria*, *Charina* and *Lichanura*. However, in the latter three taxa, the wing is not only narrow but extraordinarily short, unlike pythonines. Thus, I assume state 0 is plesiomorphic in pythonines.

47. *Vomer*. The posterior portion of the vomer, from the middle of the vomeronasal fenestra to the posterior tip of the vomer, is 76% or less (0) or 77% or more (1) of the total length of the vomer (Fig.11). Curiously, relative length of the posterior portion of the vomer of the three available specimens of *stimsoni* is 77%, whereas all other taxa in the *childreni* complex are considerably less than 76%. All of the relevant outgroups, except *Xenopeltis* (78%), exhibit state 0: anilioids (55-69%), boines (65-76%), bolyeriines (63-65%), erycines (58-72%), *Loxocemus* (51%), and tropidophiines (59-69%). Therefore, I conclude that state 0 is the plesiomorphic condition in pythonines.

48. *Septomaxilla*. Anterior to the vomeronasal fenestra, the anterodorsal margin of the septomaxilla is even and the vertical lamina is without a fenestra (0), or there exists a fenestra completely enclosed by bone or narrowly (1) or broadly (2) continuous with the dorsal margin (Fig.12). The frequently fenestrated or notched anteroventral margin of the septomaxilla is not at issue in this transformation series. The fenestra is completely enclosed in *mackloti*, *olivacea*, and *viridis*, but narrowly notched in *papuanus*. The condition in bolyeriines does not appear to be comparable because of the reduced nature of the anterior portion of the septomaxilla. All other relevant outgroups exhibit state 0, and therefore it is considered plesiomorphic in pythonines.

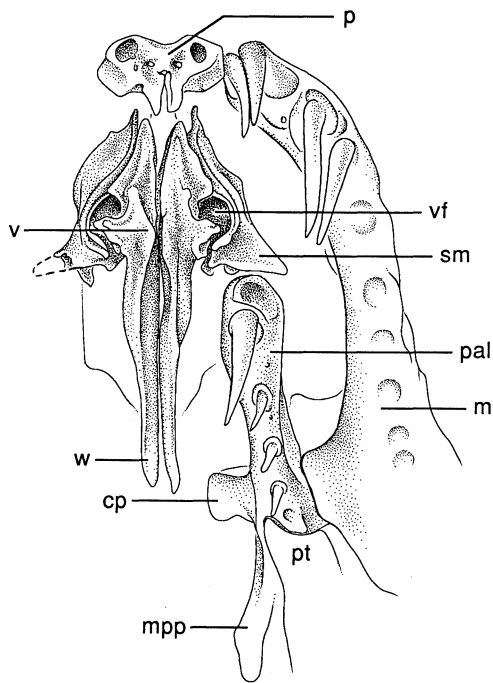


Fig.11. Ventral view of the vomer and palatine bones in *viridis* (UMMZ 151090). See also Figure 5. cp – choanal process, m – maxilla, mpp – medial pterygoid process, p – premaxilla, pal – palatine, pt – pterygoid, sm – septomaxilla, v – vomer, vf – vomeronasal fenestra, w – wing of vomer.

49. *Septomaxilla*. The dorsolateral process of the septomaxilla, which projects posteriorly beneath the nasal and/or prefrontal, is present (0) or barely noticeable or absent (1). The process is fragile and easily broken during preparation, and quantification may make it impossible to consistently distinguish additional states. The condition of the process must be assessed from a dorsolateral view, which requires that the septomaxilla be removed from the nasal cavity, or that the nasal and prefrontal bones be removed. Length pertains only to the free portion of the process, regardless of its angle (Fig.12). In *melanocephalus* and *ramsayi*, there is extensive contact between the dorsolateral margin of the septomaxilla and the superficial bones roofing the nasal capsule, and there is little if any of the dorsolateral process of the septomaxilla present. Frazzetta (1959:469) concluded that the lateral process is present in all pythonines (excluding *Loxocemus*), but absent in boas, in which he included erycines and tropidophiines. As the following summary indicates, I do not agree with Frazzetta's conclusion concerning outgroup variation. I believe the process is absent only in anilioids and *Eryx*. It is extraordinarily long in many boines, such as *Boa constrictor*, *Candoia* and *Corallus enydris*. Therefore, I assume the presence of a dorsolateral process is plesiomorphic in pythonines.

50. *Palatine*. The modal, or median, number of palatine teeth per ramus in an adult is four or less (0), five or six (1), or seven or eight (2). Variation in the ingroup terminal taxa is given in Table 1. The following summarises McDowell's (1975), Underwood's (1976, his character 58), and Underwood & Stimson's (1990, their character 31, table VI) observations, respectively: *albertisii* (7-8, -, 8), *amethystina* (-, 5, 5), *boa* (8-9, 7, 8), *boeleni* (5, -, 5), *curtus* (-, 6, 6), *mackloti* (6, -, 7), *maculosus* (-, 11, 9), *melanocephalus* (-, 6, 6), *molurus* (-, -, 7), *papuanus* (6, -, 5), *regia* (-, 7, 7), *reticulata* (-, 7, 7), *sebae* (-, -, 6), *spilotus* (6, 6, 6), *timoriensis* (-, -, 6), and *viridis* (5, 5, 5). All of McDowell's and all but one of Underwood's counts are closely correlated with those in Table 1. Nine palatine teeth is the largest number I observed in any pythonine, and I assume Underwood's (1976) claim that *childreni* (= *maculosus*; BMNH 77.3.3.6) has 11 is erroneous. Underwood & Stimson (1990:585) did not use palatine teeth number as a character because it was not significant according to their compatibility test method. Nonetheless, they summarised their observations in table VI. The outgroups can be characterised as follows: advanced snake clade 7-9, boines 5-6, erycines 5, *Loxocemus* 7, and *Xenopeltis* 13. Thus, I assume state 1 is plesiomorphic in pythonines (see also Kluge, 1993).

51. *Palatine*. The anterior palatine teeth are short (0) or long (1). Considerable variation is covered by both states, the extremes being *boa* and *viridis*, respectively. Moreover, this character does not take into account variation in tooth curvature or circumference. The length of the maxillary (character 13), dentary (character 65)

and palatine teeth are not correlated (see Table 31), and therefore these tooth length characters are treated as independent. State 0 characterises anilioids, bolyeriines, *Loxocemus*, tropidophiines and *Xenopeltis*. Boines and erycines cannot be characterised unambiguously. Thus, I tentatively assume the short condition is plesiomorphic in pythonines.

52. *Palatine*. The choanal process of the palatine makes extensive (0), little (1), or no (2) contact with the vomer (Fig.11). There are two other aspects of choanal process variation (see characters 53-54), and the only variation considered in this character is the extent of contact between the two bones. In state 0, the palatine either extensively overlaps the vomer, or it is wedged into a notch in the vertical and/or horizontal laminae of the vomer. State 0 typifies anilioids, boines, bolyeriines, erycines, *Loxocemus*, tropidophiines and *Xenopeltis*. In *Candoia*, *Epicrates*, *Eryx* and *Eunectes* the contact exists, but only by means of a thin, disconnected, portion of the choanal process (Kluge, 1991, 1993). Among the outgroups, state 2 appears to apply only to *Boa*. Thus, extensive contact between the choanal process of the palatine and the vomer is assumed to be plesiomorphic in pythonines.

53. *Palatine*. The posterior margin of the choanal process, from the end of the medial pterygoid process of the palatine, is straight or slightly convex (0), or slightly (1) or deeply (2) concave (Fig.11). The convexity occurs opposite the palatine-ptyergoid joint, and the variation in this character must be determined from a dorsomedial view. This variable appears to be equivalent to Underwood & Stimson's (1990:582) character 27. State 0 is present in *Anilius*, boines, bolyeriines, erycines (not applicable to *Eryx* because the basal portion of the choanal process is absent), some specimens of *Loxocemus*, and tropidophiines, state 1 in some *Loxocemus*, and state 2 in *Cylindrophis* and *Xenopeltis*. Thus, the straight or convex posterior margin is assumed to be the plesiomorphic condition in pythonines.

54. *Palatine*. The rostral margin of the choanal process of the palatine is oriented anteromedially or medially (0) or posteromedially (1), relative to the long

axis of the dentulous ramus of the palatine. The apex of the choanal process is fragile and easily damaged during preparation. State 0 involves considerable variation in the shape of the dorsomedian margin of the choanal process. However, it is difficult to distinguish consistently among the various types, and I have left the recognition of additional states to future studies which measure the shape of the anterior margin. State 0 characterises all of the relevant outgroups, except for those few taxa with a reduced choanal process (eg, *Boa*). Therefore, I assume state 0 is plesiomorphic in pythonines.

55. *Palatine*. The maxillary process is broad (0), narrow (1), or absent (2). This character can only be determined accurately when the palatine is removed. The area in question lies ventrally and lateroposteriorly to the palatine (sphenopalatine) foramen; it does not include the lateral pterygoid process. The maxillary process is usually relatively thin and thick in states 0 and 1, respectively. Also, the lateral wall of the palatine (sphenopalatine) foramen is oriented much more posteriorly in state 1 than it is in state 0. Among the outgroups, state 0 is found in anilioids, bolyeriines, and some erycines (*Calabaria*, *Charina* and *Lichanura*), and state 1 occurs in some erycines (*Eryx*) and tropidophiines. While *Loxocemus* and *Xenopeltis* also exhibit state 1, the process is peculiar in being much longer than in any other booid. Boines, as a group, appears to be characterised by state 2; however, a few taxa exhibit state 1 (*Candoia carinata*, *Epicrates*, *Eunectes*). Thus, the most parsimonious explanation is that state 1 is plesiomorphic in pythonines.

56. *Palatine*. The medial pterygoid process of the palatine is short (0), of modest length (1), or long (2). The length of the process is assessed from the anterior end of the pterygoid joint, as seen in ventral view. Size can be judged relative to the length of the base of an anterior pterygoid tooth (a posterior maxillary tooth is used in *Calabaria* because it lacks pterygoid teeth): two or less tooth lengths is state 0, three to four lengths is state 1, and five or more is state 2. Frazzetta (1959:469) noted the short process in *amethystina*, which provides an attachment for the *retractor pterygoideus*

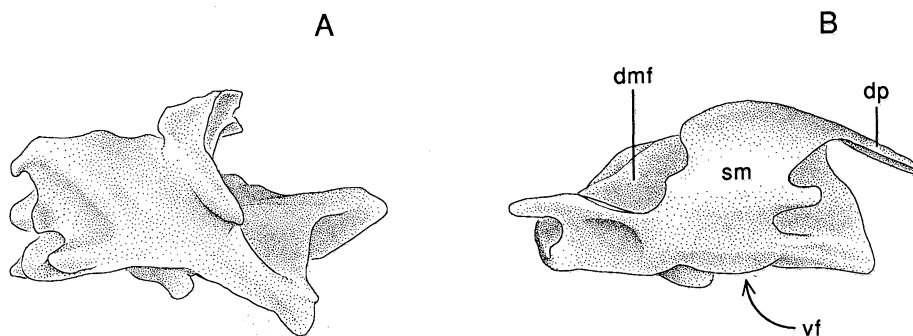


Fig.12. Lateral view of the left septomaxillary bone. A – *melanocephalus* (UMMZ 190781); B – *boa* (UMMZ 190703). dp – dorsolateral process, dmf – dorsal margin fenestra, sm – septomaxilla, vf – vomeronasal fenestra.

muscle (McDowell, 1975:58). This character is equivalent, in part, to Underwood & Stimson's (1990:582) character 26. The long condition does not appear to be present in the outgroups. However, state 0 is present in *Exiliboa*, *Ungaliophis* and *Xenopeltis*, and probably characterises boines as well (the Madagascan species of *Boa* being the only exceptions), and state 1 is found in anilioids, bolyeriines, erycines, *Loxocemus*, *Trachyboa* and *Tropidophis*. The most parsimonious explanation is that state 1 is plesiomorphic in pythonines.

57. *Pterygoid*. The modal, or median, number of pterygoid teeth per ramus in an adult is 9 or less (0), 10-12 (1), 13-15 (2), 16-18 (3), or 19 or more (4). Variation in the ingroup terminal taxa is given in Table 1. The following summarises McDowell's (1975), Underwood's (1976, his character 59), and Underwood & Stimson's (1990, their character 32, as inferred from their appendix I) observations, respectively: *albertisii* (13-19, -, 18), *amethistina* (-, 12, 15), *boa* (12-13, 14, 14-19), *boeleni* (12-14, -, 13), *curtus* (-, 9, 12-13), *mackloti* (14-15, -, 14), *maculosus* (-, 18, 17), *melanocephalus* (-, 8, 10-11), *molurus* (-, -, 9), *papuanus* (9-10, -, 14-19), *regia* (-, 8, 19), *reticulata* (-, 8, 9), *sebae* (-, -, 9), *spilotus* (-, 11, 12-13), *timoriensis* (-, -, 14-19), and *viridis* (12, 13, 14-19). All of McDowell's (1975) counts are closely correlated with those in Table 1, and all but one, *regia*, of Underwood's (1976) are as well. I suspect the discrepancy associated with *regia* represents a taxonomic misidentification (see character 12 for further discussion).

Underwood & Stimson's (1990) determinations are reasonably close to those in Table 1, except for *papuanus* (see also McDowell, 1975), a discrepancy which is probably due to their using a skull of *olivacea* for internal features of *papuanus* (p.570). Unfortunately, six of the species Underwood & Stimson (1990) included in their data matrix, *albertisii*, *amethistina*, *boeleni*, *mackloti*, *maculosus* and *regia*, were given a character state code (see their appendix I) for which no interpretation was provided in the character description (see p.586). Moreover, comparing their appendix I and table VI, there are considerable differences in the tooth counts they recorded for other taxa, *curtus* (12-13, 10), *melanocephalus* (10-11, 9), *molurus* (9, 8), *papuanus* (14-19, 13), *reticulatus* (9, 8), *sebae* (9, 7), *spilotus* (12-13, 11), *timoriensis* (14-19, 12), and *viridis* (14-19, 13).

The number of teeth in the outgroups is as follows: advanced snake clade 11, boines probably 11 (highly variable, from 7 in *Corallus cropanii* to 29 in *Candoia carinata*; see Kluge, 1991, 1993), erycines 10-12, *Loxocemus* 9, and *Xenopeltis* 11-14. Thus, I assume state 1 is plesiomorphic in pythonines. This proposition is different from Underwood & Stimson's choice of state 0 (9 teeth).

58. *Sphenoid*. The ventral surface of the cultiform process of the parasphenoid, anterior to the basipterygoid processes and between the trabeculae

cranii, is flat (0), or elevated slightly (1) or markedly (2). States 1-2 cover considerable variation, which ranges from oval to narrow, deep and sharply keeled (Fig.13). There appears to be an ontogenetic effect to keel size. Further, the elevated area in question is not to be confused with McDowell's (1975:31; see character 61) "sphenoid keel", which lies posterior to the basipterygoid processes (his "basitrabecular" processes; see character 59), and to which the *protractor pterygoideus* attaches. Anilioids, bolyeriines, erycines (except a few species of *Eryx*), *Loxocemus*, tropidophiines and *Xenopeltis* exhibit the flat condition. While the flat condition also applies to *Candoia*, states 1 or 2 characterise all other boines. Thus, I assume state 0 is plesiomorphic in pythonines.

59. *Sphenoid*. The pterygoid process of the sphenoid is absent (0), short (1), or tall (2). The term basipterygoid process (Fig.13) has been employed for the process in question (McDowell, 1975:29); however, that usage suggests a homologous relationship with the basipterygoid process found in other squamates (ie, "lizards"; Oelrich, 1956). It is likely that such a projection was lost early in snake history, and the prominence in more derived snakes requires a different name in order to underscore its independent history. Thus, Bellairs & Kamal's recommendation (1981:11) that basitrabecular process be synonymised with basipterygoid process may be premature. Final resolution of this nomenclatural issue must also consider the homology of the basipterygoid meniscus (Bellairs & Kamal, 1981:fig.2) and the "nodule sub-trabéculaire" (Genest-Villard, 1966:234,fig.4). For example, while Bellairs & Kamal (1981) imply that the nodule is an apomorphic state of the process (compare their figures 61-62), that interpretation does not pass the test of conjunction (Patterson, 1982) because both the process and the nodule occur in the same organism (Genest-Villard, 1966:fig.4).

S. McDowell (personal communication) has offered what he terms the "standard" interpretation, that the basitrabecular process is the endochondral component of the basipterygoid process, and that it is represented in "boas" by the cartilaginous nodule, as reported for *Eryx* by Kamal & Hammouda (1965) and *Boa manditra* by Genest-Villard (1966). In addition, he claimed that the nodule is partially ossified in "boas", and lies in a ligament extending from the sphenoid (including the parasphenoid) to the pterygoid. Further, according to McDowell, what is called "basipterygoid" or "pterygoid" process of the sphenoid in "boas" is a muscular scar on the parasphenoid part of the sphenoid (the *retractor vomeris* arises from its anterior face), comparable to a much less conspicuous muscle scar in "pythons", which runs anteromedially from the basitrabecular facet and similarly marking the rear of the *retractor vomeris*. Still further, he maintained that the basitrabecular process of "pythons" (and *Calabaria*) has a facet that articulates with the dorsal surface of the pterygoid, whereas the so-called basipterygoid process of "boas", even when large

(eg, *Boa constrictor*), does not, the *levator pterygoideus* insertion covering the pterygoid in that region. To my way of thinking, this interpretation does not resolve the issue, in light of the occurrence of a process and a nodule in the same individual.

According to my evaluation, state 0 characterises some outgroup taxa, such as *Boa manditra*, *Calabaria*, *Casarea*, *Charina*, *Lichanura* and tropidophiines. State 1 occurs in anilioids, *Bolyeria*, *Eryx*, *Loxocemus* and *Xenopeltis*. I believe most boines, except *Boa manditra*, exhibit state 1 or 2, and the most parsimonious explanation appears to be that a short process characterises the group. Therefore, state 1 is assumed to be plesiomorphic in pythonines.

60. *Sphenoid*. The anterior-posterior width of the ventral surface of the pterygoid process of the sphenoid (Fig.13), that closest to the pterygoid bone, is broad (0) or narrow (1). Those taxa without a process (see character 59) are scored as N. The process is broad in anilioids, a few boines (*Boa madagascariensis* and *Eunectes*), and *Eryx*, and state 1 applies to most boines, *Bolyeria* and *Loxocemus*. A state cannot be scored for those outgroup taxa which exhibit state 0 in character 59. Thus, the plesiomorphic condition is ambiguous for pythonines.

61. *Sphenoid*. The median keel on the basisphenoid region of the sphenoid, posterior to the pterygoid processes, is absent or slight (0) or deep (1). While I have recorded *anchietae* and *boa* as state 1, their keels are of only modest height. McDowell (1975:31) claimed that a "strong median keel" on the sphenoid (basisphenoid

region) was typical of the members of his *Liasis* assemblage (*albertisii*, *boa*, *childreni*, *mackloti*, *olivacea* and *papuanus*); however, my observations do not support that conclusion (Table 31). For example, there is very little, if any, elevation on the sphenoid of *childreni*, *maculosus*, *perthensis* and *stimsoni*, and the keel is present in all other pythonines (Fig.13), except *melanocephalus* and *ramsayi*. Anilioids, *Casarea*, erycines, *Exiliboa*, *Ungaliophis* and *Xenopeltis* have little, if any, keel, while all boines, except some *Corallus* (eg, *C. caninus*), *Loxocemus*, *Trachyboa* and *Tropidophis* exhibit a slight keel. Only *Bolyeria* possesses an extremely deep keel; however, its thickness and shape are unique among booids, which indicates convergence to those pythonines with state 1. Thus, it appears that state 0 is plesiomorphic among pythonines.

62. *Sphenoid*. The basisphenoid fenestra is tiny and hidden by the overlapping pterygoid process (0) or exposed and relatively large (1). The opening in question lies immediately anterior and dorsal to the anterior vidian foramen, and it is situated between the parietal, parasphenoid, and basisphenoid. The fenestra is oriented dorsoventrally, unlike the anterior vidian foramen which is directed anteroposteriorly.

The basisphenoid fenestra may have been referred to by Estes *et al.* (1970:fig.5) as the "unknown foramen" and "cid" by Rieppel (1979c:fig.8B). The "fenestra x" of Haluska & Alberch (1983:fig.18; see also McDowell, 1987:fig.1-1) does not appear to be comparable to the basisphenoid fenestra because it is an embryological state of all snakes, a lysis of the cartilage in the basal plate, which is subsequently filled by membrane bone.

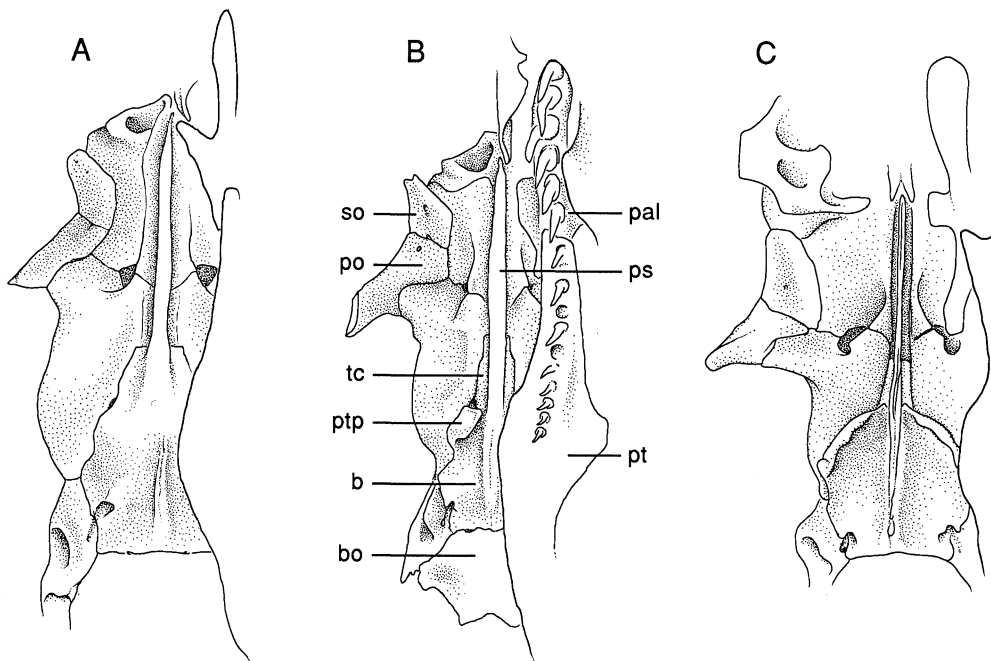


Fig.13. Ventral view of the sphenoid bone complex. A - *childreni* (UMMZ 190779); B - *mackloti* (AM R41872); C - *viridis* (UMMZ 151090). b - basisphenoid region, bo - basioccipital, mk - median keel, pal - palatine, pf - prefrontal, po - postorbital, ps - cultiform process of parasphenoid, pt - pterygoid, ptp - pterygoid process, so - supraorbital, tc - trabeculae cranii.

S. McDowell (personal communication) has suggested the basisphenoid fenestra transmits a nerve from the trigeminal ganglion to join the palatine ramus of VII (= "greater superficial petrosal nerve"), while G. Underwood (personal communication) has claimed it is for the exit of the *retractor vomeris* and *retractor pterygoidei* branches of the *constrictor internus dorsalis* branch of nerve V (cf. Rieppel, 1979c:424-5). There seems to be no real disagreement here because the nerve is both sympathetic and the *levator bulbi* nerve. In other squamates ("lizards"), the *levator bulbi* component splits off before the sympathetic (greater superficial petrosal) joins the palatine ramus of VII to form the vidian. However, in snakes the *levator bulbi* component extends all the way to the palatine ramus of VII, along with the sympathetic (deep petrosal) component, and the nerves to the *levator bulbi* derivatives (*retractor vomeris* and *retractor pterygoidei*) come off the vidian nerve just anterior to the palatine ramus of the VII-deep petrosal anastomosis. According to Rieppel (1979c:420, figs 7A, 9A), the basicranial fenestra is occupied by the "cid-nerve (innervating the *constrictor-internus-dorsalis* musculature)", which "enters the groove of the Vidian canal anteriorly. It leaves the skull through the secondary anterior opening of the Vidian canal. It then gives off a branch to the *retractor pterygoidei* muscle and subsequently fuses with the palatine nerve."

A large, exposed fenestra is also present in *Boa* (including the Madagascan species), most adult *Epicrates* (except *E. cenchria*), and *Eunectes* (eg, BMNH 1952.1.2.58), and a slightly smaller and less exposed opening is present in *Loxocemus*. Otherwise, the fenestra in question appears to be absent in all other outgroup lineages examined, and therefore I assume that state 0 is plesiomorphic in pythonines.

63. *Sphenoid*. The left and right common canals in the basisphenoid region of the sphenoid are approximately equal in size, or the right is larger than the left (0) or the left is larger than the right (1). Most authors refer to the common canals as posterior vidian canals (eg, Underwood, 1967:13), or parbasal canals (not to be confused with the vidian or pterygoid canals of mammals). However, usually, as in pythonines, the cerebral artery and palatine nerve enter a common opening (as Liem *et al.*, 1971:76 described for *Azemiops*), whereupon the artery turns medially and the nerve continues into the posterior vidian canal proper. Rarely (eg, *Xenopeltis*, see below, and one *boeleni* examined by S. McDowell, personal communication) do the cerebral artery and vidian nerve enter the cranial vault separately, and therefore I have chosen the term common canal for the usual case. This character is easily quantified, and measurements were taken so as to find the greatest width of the canals. Underwood (1976:163-164; see also Rieppel, 1977; Groombridge, 1984) pointed out that the left vidian canal is larger in pythonines and *Loxocemus*; however, there is considerable variation within the former group, as the following range of observations indicate (the number of times the width of the left canal can be divided

by that of the right in a given specimen): *albertisii* 1.7-2.5; *amethystina* 1.3-1.9; *anchietae* 1.8-2.3; *boa* 1.7-2.1; *childreni* 2.0-2.7; *curtus* 1.2-1.4; *mackloti* 1.7-2.3; *maculosus* 1.9-2.4; *melanocephalus* 1.8-2.8; *molurus* 1.4-2.0; *oenpelliensis* 2.5; *olivacea* 1.6-1.9; *papuanus* 1.8; *perthensis* 2.4; *ramsayi* 1.6-1.8; *regia* 1.7; *reticulata* 1.2-2.1; *sebae* 1.5-2.1; *spilotus* 1.1-2.2; *stimsoni* 2.0-2.7; *timoriensis* 1.4-1.5; *viridis* 1.0-1.6. Presumably, the differences are also reflected in the size of the cerebral artery located in the canal (Underwood & Stimson, 1990:567). Among the outgroups, only *Loxocemus* has state 1 (left greater than right, 1.5-2.3), and it is most parsimoniously explained as convergence. There are two foramina just beyond the level of the posterior openings in *Xenopeltis*, the more anterior opening leads to the anterior vidian canal, the other foramen proceeds to the center of the cranial vault. On the basis of either the width of the common opening or the more anterior foramen, I record *Xenopeltis* as state 0 (left=right, or right greater than left, 0.9). Therefore, state 0 is assumed to be plesiomorphic in pythonines.

64. *Dentary*. The modal, or median, number of dentary teeth per ramus in an adult is 16 or less (0), 17-19 (1), 20-22 (2), or 23 or more (3). Variation in the ingroup terminal taxa is given in Table 1. The following summarises McDowell's (1975), Underwood's (1976, his character 60), and Underwood & Stimson's (1990, their character 33, as inferred from their appendix I) observations, respectively: *albertisii* (23-24, -, 20-24), *amethystina* (-, 17, 16-19), *boa* (19-20, 21, 16-19), *boeleni* (17-19, -, 20-24), *curtus* (-, 19, 16-19), *mackloti* (-, -, 20-24), *maculosus* (-, 23, 20-24), *melanocephalus* (-, 17, 16-19), *molurus* (-, -, 16-19), *papuanus* (-, -, 16-19), *regia* (-, 17, 16-19), *reticulata* (-, 17, 16-19), *sebae* (-, -, 16-19), *spilotus* (17-21, 20, 16-19), *timoriensis* (-, -, 20-24), and *viridis* (16, 16, 16-19). All of these counts, except that of *regia*, are closely correlated with those in Table 1, and I suspect the exception is due to taxonomic misidentification (for further discussion see character 12). Except for *boa* (16-19, 20) and *boeleni* (20-24, 18), Underwood & Stimson's (1990, appendix I and table VI) separately summarised results are consistent. The outgroups can be characterised as follows: advanced snake clade 21, boines 17-19, erycines 17-19, *Loxocemus* 19, and *Xenopeltis* 34. Given these numbers, the most parsimonious interpretation is that state 1 is plesiomorphic in pythonines.

65. *Dentary*. The anterior dentary teeth are short (0) or long (1). State 0 obtains when there is little, if any, difference in the height of the anterior and posterior sets of dentary teeth. State 1 covers considerable variation, some of which is due to the appearance of short teeth merely as a reflection of their being markedly curved posteriorly. Among the outgroups, only boines, some *Eryx* (eg, *E. conicus*), and *Ungaliophis* have long teeth. Thus, it is not possible to unambiguously polarise this character in pythonines.

66. *Dentary*. There is a slight (0) or marked (1) change in the height of the dentary teeth (Fig.14). If the decreasing height of teeth 4-6 (counting anterior to posterior) forms a nearly continuous line, or shallow angle, with teeth 9-11 then the state is 0; if there is an abrupt and significant change in the heights of the two sets of teeth then state 1 applies. Also, the perception of a significant change in height appears to be affected by all the teeth in the posterior series being of uniform height (except for the last one or two, which are curved inward to a considerable degree in most snakes). The teeth must be oriented vertically, and the dentary examined from a lateral view when recording this character. Further, it is important to emphasise that the variable at issue is change in height of the two sets of teeth; the length of the anterior or the posterior teeth and dentary shape are not considerations.

McDowell (1975:32; see also Worrell, 1956) claimed that "[i]n the *Liasis olivaceus* Group, the mandibular dentition is as in *Python molurus*, and there is a gradual decrease from the long anterior teeth to the short teeth at the rear of the dentary; but in the *Liasis boa* Group there is a rapid decrease in length behind the enlarged first six (or so) teeth, followed by a subequal series of short teeth extending to the rear of the dentary." While I agree with McDowell's assessment that *mackloti* and *olivacea* (also *papuanus*) and the *boa* group exhibit different states, I believe the taxa in the "*Liasis olivaceus*" group exhibit some tendency toward having posterior

teeth of nearly equal length, more so than other species recorded as state 0 (see discussion of Fossils below). This transformation series appears to be identical to Underwood & Stimson's (1990:582) character 29, and our taxonomic observations are consistent. State 0 applies to all the outgroup taxa, except *Candoia carinata*, *Corallus caninus*, *C. cropanii*, *C. enydris* and *Ungaliophis*, and perhaps some species of *Eryx* (eg, *E. conicus*). Therefore, I assume state 0 is plesiomorphic in pythonines.

67. *Coronoid*. The dorsal end of the coronoid lies slightly below (0) or at or above (1) the apex of the surangular process of the composite (compound) bone. Curiously, the largest *amethistina* and *reticulata* appear to have a shorter coronoid than do subadults of those species. State 1 is attributed to *ramsayi*; however, one specimen (UMMZ 190782) exhibits the reduced condition. Among the outgroups, state 0 is present in most boines, bolyeriines (even though the surangular process is effectively absent), *Calabaria*, some *Eryx* (eg, *E. colubrinus*), *Lichanura*, *Loxocemus* and *Xenopeltis* (the surangular process is also absent in this taxon), and state 1 occurs in anilioids, a few boines (*Boa*), and most *Eryx*. Tropicophiines appear to have lost the coronoid; however, a tiny ridge of bone located between the angular, dentary, and splenial may represent a remnant. If the coronoid is absent in tropicophiines, then this character is not applicable to the group; if it is

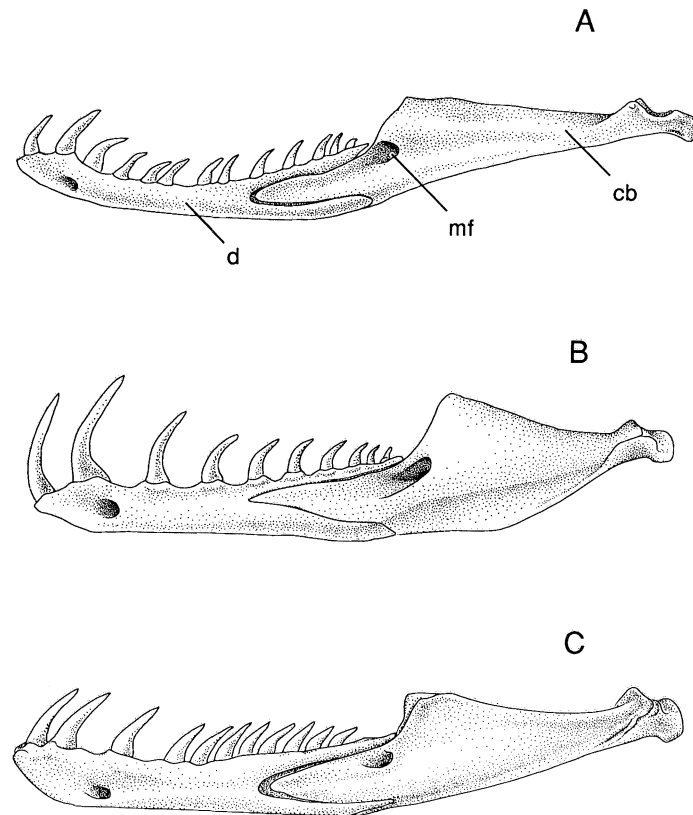


Fig.14. Lateral (labial) view of the left lower jaw. A – *boa* (UMMZ 190704); B – *viridis* (UMMZ 151090); C – *reticulata* (UMMZ 82). cb – composite bone, d – dentary, mf – mandibular foramen. Not all teeth illustrated.

considered present, then state 0 applies. The bone is absent in *Charina bottae* (Kluge, 1993). Thus, it appears that the plesiomorphic condition in pythonines is state 0.

68. *Coronoid*. From a lateral view, the entire anterodorsal margin of the coronoid is exposed (0) or completely hidden (1) beyond the edge of the surangular portion of the composite bone. The exposure in *boa* often occurs only at the dorsal end of the coronoid, and only a thin part of the coronoid is evident in *childreni*. State 0 is present in most boines (except *Candoia bibroni*; variable in *Epicrates*), bolyeriines, *Calabaria* (narrowly exposed), *Cylindrophis*, and most *Eryx*, and state 1 in *Anilius*, some *Eryx* (eg, *E. colubrinus*), *Lichanura* and *Loxocemus*. The coronoid is absent in *Charina bottae* (Kluge, 1993). If the bone is present in tropidophiines, then state 1 applies; however, if that element is absent this character is not applicable (see discussion in character 67). In any case, the plesiomorphic condition cannot be determined unambiguously for pythonines.

69. *Coronoid*. From an anterior view, the portion of the coronoid adjacent to the surangular process of the composite bone is thick and of even width, or expands dorsally, (0) or thin and narrows toward its apex (1). There is considerable ontogenetic variation in this character, and only the largest representatives of each taxon are scored. State 0 occurs in boines, *Calabaria*, *Cylindrophis* and *Eryx*. Bolyeriines and *Lichanura* do not obviously represent either state, and this character is definitely not applicable to *Anilius*, *Charina*, *Loxocemus*, tropidophiines (see discussion under character 67), and *Xenopeltis*. Thus, it is on the basis of very little evidence that I assume state 0 is plesiomorphic in pythonines.

70. *Composite Bone*. The height of the surangular process of the composite bone is 15% or less (0) or 16% or more (1) of the total length of the lower jaw. Height is measured as the greatest vertical distance across the composite bone, but does not include the coronoid or angular. The anteriormost tooth is not recorded in the length measurement. There is a strong ontogenetic component to this variation, and therefore only the largest individuals available were scored for each taxon. I suspect my record of state 0 for *molurus* may be due to not having any maximum size adult skeletal material. State 0 is found in *Boa constrictor*, *B. madagascariensis*, bolyeriines, *Candoia*, *Eryx*, *Lichanura*, *Loxocemus*, tropidophiines (the process is effectively absent in *Trachyboa* and *Tropidophis*, and small in *Boa manditra*, *Exiliboa* and *Xenopeltis*), while state 1 occurs in *Anilius*, *Calabaria*, *Charina*, *Corallus*, *Cylindrophis*, most *Epicrates*, and *Eunectes*. A most parsimonious optimisation suggests state 0 is plesiomorphic in pythonines.

71. *Composite Bone*. The posterior margin of the mandibular foramen lies posterior to (0), even with (1)

or anterior to (2) the posterior end of the tooth bearing portion of the dentary (Fig.14). State 0 occurs in boines, bolyeriines, erycines and tropidophiines, state 1 in *Anilius*, and 2 in *Cylindrophis*, *Loxocemus* and *Xenopeltis*. Therefore, the most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

72. *Composite Bone*. The mandibular foramen is relatively shallow (0) or deep (1). Height of the aperture is the variable in question (Fig.14). The foramen in *albertisii* is open laterally, which gives the appearance of a deep opening (Worrell, 1956), and which McDowell (1975:37) claimed is a restatement of the difference "in degree of development of the infralabial pits" (see character 107). All of the outgroups exhibit state 0, with the possible exception of *Corallus*. Thus, the plesiomorphic condition is assumed to be state 0 in pythonines.

73. *Neck*. The neck is approximately as wide as (0), or slightly (1) or markedly (2) narrower than the head in adults (Wilson & Knowles, 1988:367). It is important to judge this character on specimens that have the head and neck extended in a straight line, and only on adults because of significant ontogenetic variation. The head/neck area is only slightly, if at all, differentiated in *Boa madagascariensis*, *Bolyeria*, *Epicrates* (the more plesiomorphic sister lineages), erycines, *Eunectes*, *Loxocemus* and *Xenopeltis*, whereas the contrast between the two regions is quite noticeable in *Boa manditra*, *Casarea*, most *Corallus*, *Trachyboa*, and a few species of *Tropidophis*. A slightly narrow neck (state 1) is present in *Boa constrictor*, *Candoia*, *Corallus cropanii*, *Exiliboa*, most *Tropidophis* species, and *Ungaliophis*. Assuming an unordered transformation series, the plesiomorphic condition for the advanced snake and boine (Kluge, 1991) clades is state 0 and 1, respectively. Thus, given this outgroup variation, the most parsimonious interpretation is that state 0 is plesiomorphic in pythonines.

74. *Tail*. Average adult tail length (TL, from the cloacal opening to the tip of the tail) expressed in relation to head length (HL, from the intermandibular symphysis to end of retroarticular process), and expressed as TL/HL is 2.4 or less (0), 2.5-2.9 (1), 3.0-3.4 (2), 3.5-3.9 (3), 4.0-4.4 (4), 4.5-4.9 (5), or greater than 5.0 (6). Measurements were taken only on specimens with undamaged tails. Some species, like *ramsayi*, have a relatively high proportion of incomplete, damaged tails, which is believed to be due to the appendage being used as a predator lure (Wilson & Knowles, 1988:368). The following summarises the average TL/HL relation, and sample size, in parentheses, for each species: *albertisii* 3.6 (17), *amethystina* 5.3 (26), *anchietae* 2.9 (2), *boa* 3.7 (14), *boeleni* 3.4 (9), *carinatus* 3.8 (2), *childreni* 2.7 (21), *curtus* 1.6 (15), *mackloti* 4.5 (22), *maculosus* 2.6 (19), *melanocephalus* 3.6 (14), *molurus* 3.5 (7), *oenpelliensis* 7.1 (3), *olivacea* 4.6 (18), *papuanus* 5.0 (15), *perthensis* 2.5 (20), *ramsayi* 2.7 (19),

regia 2.0 (14), *reticulata* 3.6 (14), *sebae* 3.2 (14), *spilotus* 4.3 (25), *stimsoni* 2.8 (24), *timoriensis* 3.6 (6), *viridis* 3.8 (19). There is considerable variation among the outgroups, as the following survey documents: anilioids 0.4-1.2, boines 1.8-7.6, bolyeriines 8.0-8.7, erycines 1.3-4.1, *Loxocemus* 3.2, tropidophiines 1.9-3.0, *Xenopeltis* 2.3. The plesiomorphic condition for boines, erycines and tropidophiines appears to be state 1, and if those three taxa are correctly characterised the most parsimonious explanation is that same condition is also plesiomorphic for pythonines.

75. *Tail. The cross-sectional appearance of the tail, as measured by the average adult tail depth (TD) and tail width (TW), and expressed as TD/TW, is 1.0 (0), 1.1 (1), 1.2 (2), or 1.3 (3).* TD and TW were taken at one-half TL (see character 74) on undamaged. This shape character varies from round (state 0) to highly compressed (state 3). The following summarises the average TW/TD relation, and sample size, in parentheses, for each pythonine species: *albertisii* 1.0 (18), *amethystina* 1.2 (27), *anchietae* 1.0 (2), *boa* 1.0 (14), *boeleni* 1.1 (11), *carinatus* 1.1 (2), *childreni* 1.0 (21), *curtus* 1.1 (13), *mackloti* 1.0 (22), *maculosus* 1.0 (19), *melanocephalus* 1.0 (14), *molurus* 1.0 (4), *oenpelliensis* 1.1 (3), *olivacea* 1.0 (18), *papuanus* 1.0 (16), *perthensis* 1.0 (20), *ramsayi* 1.0 (19), *regia* 1.0 (13), *reticulata* 1.2 (14), *sebae* 1.1 (14), *spilotus* 1.1 (25), *stimsoni* 1.0 (22), *timoriensis* 1.0 (6), *viridis* 1.3 (19). McDowell (1975) used tail shape and function as measures of arboreal behaviour, which he believed delimited two groups of pythonines: (a) *amethystina*, *boeleni*, *spilotus* and *viridis*, and (b) *albertisii*, *boa*, *mackloti* and *papuanus*. He claimed (p.30) the former group has a "tail that is highly muscular and slightly compressed to its tip, with strong prehensile function", and he amplified and confirmed this distinction with "tail strongly prehensile; stout and muscular to the tip, distinctly deeper than broad distally", which appeared in one of the couplets in his key to the genera. I agree with McDowell that all of the species in his first group have a compressed tail, at least to some degree (states 1-3); however, the following additional species must be considered similar: *carinatus*, *curtus*, *oenpelliensis*, *reticulata* and *sebae*. A round tail (state 0) characterises all of the outgroups, and therefore I assume it is plesiomorphic in pythonines. Many more observations are required to confirm McDowell's suggestion that function can be inferred from shape.

76. *Scales. The parietal region is covered with small, asymmetrical scales which are indistinguishable from the nuchals and temporals (0), or one pair of large scales separated (1) or in contact (2) on the midline, or two or more pairs of large scales (3).* Most pythonines, except *molurus* and *perthensis*, exhibit a single, reasonably strong, mode (see individual variation summarised in Table 2). A second pair of enlarged scales occurs posterior to the parietals in a few *albertisii* (Underwood & Stimson, 1990:fig.1b) and one *maculosus* (AM R17108); however, they do not make contact on

the midline. Thus, none of those specimens were scored as state 3. My multistate characterisation of parietal scale variation attempts to represent the sense of two of Underwood & Stimson's (1990:573) binary characters, 4 and 5, in part; however, the little correlation between our recordings (compare my Table 2 to their appendix I) suggests I have not been entirely successful. The fact that Underwood & Stimson's codings do not cover my state 0 may be partly responsible for our differences. Minimally, their form of coding leads to a contradiction, namely, a scale of any size is a parietal (their character 4) but median contact between parietals (their character 5) is not applicable to those taxa with small parietals (see their appendix I, eg, *viridis*). Parietals are present in *Loxocemus* and *Xenopeltis*, and absent in all boines (except a few apomorphic sister lineages of *Epicrates*; Kluge, 1989a, 1991), bolyeriines, erycines, and tropidophiines (except *Tropidophis*; Zacharias, 1897; Bogert, 1968b). Given this pattern of outgroup variation, the most parsimonious interpretation is absence of parietals (state 0) is plesiomorphic in pythonines. It is not surprising, given our different codings, that Underwood & Stimson (1990:573) came to another conclusion, viz., the single pair of separated parietals found in *Loxocemus* and *Xenopeltis* is plesiomorphic.

77. *Scales. The number of postocular scales, those bordering the posterior margin of the eye, is one or two (0), three (1), four (2), or five or more (3).* Subocular and supraocular scales (characters 79-80, respectively) are not included in the postocular count, which is summarised in Table 3. This variable is equivalent to Underwood & Stimson's character 11 (1990:576; see also McDowell, 1975:37), and our observations are in general agreement, with the exception of those made on *molurus* (their state 1 versus my 2) and *sebae* (3 versus 1). Underwood & Stimson stated that two postocular scales occur in *Loxocemus* and *Xenopeltis*, and "[t]he great majority of other snakes have either one or two" (p.576). From these claims they assumed the plesiomorphic state in pythonines to be state 0. I can confirm that *Loxocemus* and *Xenopeltis* exhibit state 0; however, the variation recorded for the other relevant outgroups (Zacharias, 1897; Bogert, 1968b; McDowell, 1979) suggests choosing that condition as plesiomorphic for pythonines must be tentative. For example, the boine clade can be diagnosed by state 2 or 3 (probably the latter), bolyeriines 2, erycines 0 or 2-3, and tropidophiines 0.

78. *Scales. The parietal scale contacts (0) or is separated from (1) the postocular scale.* The observed variation is summarised in Table 4; N was recorded when the parietal is absent (see character 76). This variable is equivalent to Underwood & Stimson's (1990:574) character 6, and the conditions we attribute to species are in agreement, with the following exceptions: *albertisii* (their state 0 versus my 1), *mackloti* (1 versus 0), *melanocephalus* (1 versus 0), and *reticulata* (1 versus N). Underwood & Stimson assumed parietal-postocular

contact is the plesiomorphic state in pythonines because that state occurs in *Loxocemus* and *Xenopeltis*; however, if the absence of parietals is plesiomorphic in pythonines (see character 76), then logically N must be recorded as the plesiomorphic state of parietal-postocular contact.

79. Scales. A complete series of subocular scales is absent (0) or present (1). Scales between the eye and supralabials are termed suboculars. State 1 obtains when one or more supralabials are excluded from the border of the orbit. This character is equivalent, in part, to Underwood & Stimson's character 8 (see character 90). The variation I observed in this character is summarised in Table 5. Only two pythonine species, *anchietae* (Broadley, 1983:69) and *sebae* (Broadley, 1984), appear to be fixed for the presence of suboculars. Four taxa, *curtus*, *molurus*, *ramsayi*, and *regia*, exhibit considerable intraspecific variation (Table 5). The patterns of variation in *curtus* (Stull, 1938; Brongersma, 1947) and in *molurus* (M.A. Smith, 1943; de Rooij, 1917:23) have long been recognised as geographically nonrandom and correlated with other scale and colour (pattern) characters, and subspecies have been defined on the basis of such combinations of characters. The subocular variation I observed (Table 5) suggests that *curtus brongersmai* (absent) and *molurus bivittatus* (present) predominated in my samples of those nominate forms. In any case, I am forced to treat *curtus* and *molurus* as variable for this character (Table 31) because relationships within these terminal taxa remain unresolved. Both Lesson (1950) and Pitman (1974) indicated that suboculars are usually present in *regia*, and I record that species as state 1, even though my sample mode suggests otherwise (Table 5). Suboculars are absent in bolyeriines, *Loxocemus*, tropidophiines and *Xenopeltis*, and present in most boines (*Boa manditra*, *Candoia carinata*, and most *Epicrates* species are exceptions) and all ercines but *Calabaria* (see however Villiers, 1963:fig.100). Thus, the plesiomorphic condition in

pythonines cannot be inferred unambiguously.

80. Scales. A single, large supraocular scale is present (0) or absent (1). This character is equivalent to Underwood & Stimson's (1990:571) character 1.3, which they described as single (plesiomorphic) or greater than one. The supraocular region is covered by three scales in *carinatus* (Fig.15), the middle being the largest. I always observed two or more supraoculars in *sebae* (Table 6; see also Broadley, 1983, 1984), never one, which Pitman (1974; see also Zacharias, 1897) implied occurs occasionally, and which Underwood & Stimson (1990, appendix I) concluded always obtains. Both *carinatus* and *sebae* are recorded as apomorphic because a single scale covering that region is absent. Further, I accept Broadley's (1983) suggestion that *anchietae* usually has two or more scales covering the supraocular region, and record that species as having state 1 (Table 31). State 0 occurs in bolyeriines, *Loxocemus*, all tropidophiines (except *Trachyboa*), and *Xenopeltis*, while state 1 characterises all boines (except the [*Epicrates*, *Eunectes*] clade) and ercines. Thus, the plesiomorphic state of pythonines cannot be inferred unambiguously.

81. Scales. The number of preocular scales is one (0), two (1), three (2), or four or more (3). Preoculars are those scales bordering the anterior margin of the eye (Fig.16). The subocular and supraocular scales (see characters 79-80) are not counted. Further, this character may be confounded with the presence of sublorals (character 88) because that row of small scales extends occasionally into the orbit (eg, *childreni*). The number of preocular scales is equivalent to Underwood & Stimson's (1990:576) character 10. Our observations agree for the most part; however, I recorded more variation in *molurus* and *sebae*, and a different state for *regia* (Table 31; state 2, as opposed to their 3). Underwood & Stimson assumed one preocular represented the primitive state because it occurs in the

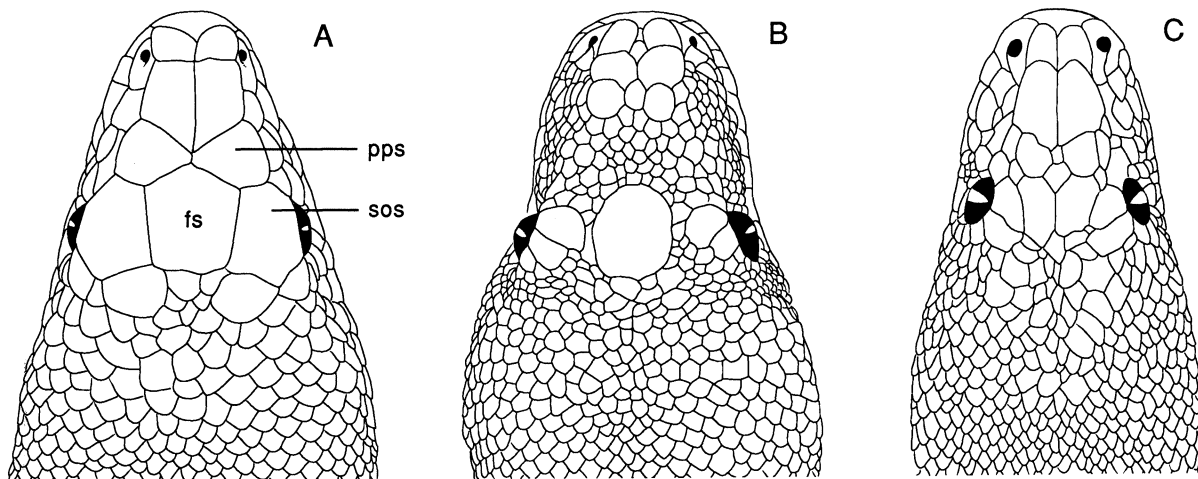


Fig.15. Dorsal view of the snout scalation. A – *ramsayi* (UMMZ 192811); B – *carinatus* (WAM R45352, holotype); C – *sebae* (modified after de Witte, 1962: fig.27). fs – frontal scale, pps – posterior prefrontal scale, sos – supraocular scale.

“great majority” of snakes, including *Loxocemus* and *Xenopeltis*. However, one preocular scale characterises only *Loxocemus*, tropidophiines (except *Trachyboa* and at least two species of *Tropidophis* – *T. melanurus* and *T. taczanowskyi*) – and *Xenopeltis* (Kluge, 1993). Two or more such scales typifies bolyeriines, and all of the more plesiomorphic boine lineages (Kluge, 1991). The alternative states of one or more preocular scales could not be optimised unambiguously on the best fitting hypothesis of erycine relationships (Kluge, 1993). Thus, the polarity of this character cannot be inferred unambiguously in pythonines.

82. Scales. A large frontal scale is present, either undivided (0) or divided (1) along the midline, or the interocular region is covered with three or more smaller, irregularly shaped scales (2). Partial division anteriorly or posteriorly, or some combination of the two, amounting to one-half or more of the length of the frontal (eg, *reticulata*, SAM R15920, R22450) is recorded

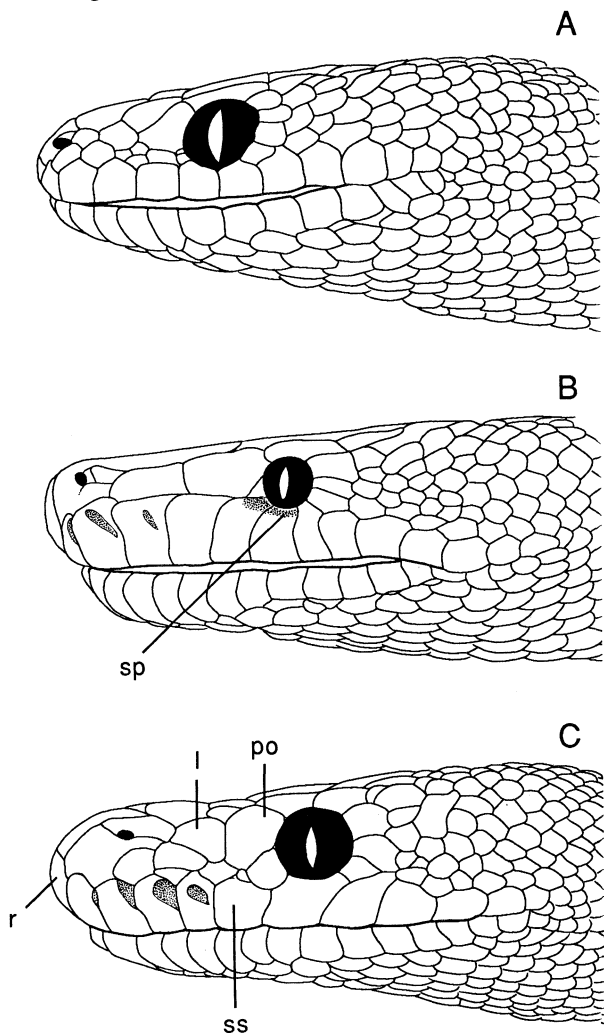


Fig.16. Left lateral view of the snout scalation. A – *childreni* (AM R32615); B – *albertisii* (BMNH 1986.1174); C – *timoriensis* (WAM R105148). l – loreal, po – preocular, sp – subocular pit, r – rostral, ss – supralabial scale. Infralabial pits not illustrated.

as state 1. A few specimens have the frontal divided transversely but those are not counted as state 1 because it does not characterise any taxon identified on the basis of other evidence. The variation in *sebae* occurs between subspecies, the nominate form exhibits state 1 (Fig.15) and *sebae natalensis* state 2 (Broadley, 1984; Underwood & Stimson, 1990:571). I have recorded *sebae* as variable for this character (Table 31) because it cannot be decided unambiguously which state is plesiomorphic for that terminal taxon. This character is equivalent to Underwood & Stimson's (1990:571) variables 1 (only the 1.3 additive binary recoded portion) and 2, which they described as differentiated (plesiomorphic) versus broken and undivided (plesiomorphic) versus divided, respectively. I prefer my use of a single transformation series because it avoids the appearance of having logically redundant states, broken and divided, and recording *spilotus* and *viridis* as inapplicable for character 2. The frontal scale conditions I record for pythonines (Tables 8,31) are in complete agreement with those of Underwood & Stimson (1991, appendix I), with the exception of *reticulata*, to which I attribute state 1 and they consider variable (1 and 2). A large unpaired frontal is present in *Loxocemus*, all tropidophiines (except *Trachyboa*), and *Xenopeltis*. It is absent in all boines (except a few apomorphic species of *Epicrates*), *Casarea*, and erycines (except *Charina* and *Calabaria*, which exhibit state 0), and divided in *Bolyeria*. Thus, given this pattern of outgroup variation, it cannot be determined unambiguously whether state 0 or 2 is plesiomorphic for pythonines.

83. Scales. The frontal scale is separated from (0) or contacts (1) the preocular scale. N is recorded for those taxa without a frontal (see character 82, state 2). This character is identical to Underwood & Stimson's (1990:573) character 3, except I have reversed the order of the state definitions. Nonetheless, the conditions we record for pythonines are mostly the same (Table 9), except I claim that frontal-preocular contact in *boa* and *boeleni* is present and absent, respectively, and they considered *amethystina*, *curtus* and *papuanus* to be variable, whereas I attribute states 1, 0, and 0 to those species, respectively. Underwood & Stimson noted that frontal-preocular contact occurs in *Loxocemus* and *Xenopeltis*, and from this distribution alone they assumed that condition to be plesiomorphic in pythonines (p.572). I believe the opposite state is the more parsimonious explanation, given the following outgroup variation: the absence of contact occurs in *Bolyeria*, *Calabaria*, *Charina*, *Exiliboa* and *Tropidophis*, whereas contact obtains in *Loxocemus*, *Ungaliophis* and *Xenopeltis*. The condition cannot be determined for the plesiomorphic sister lineages of boines, *Casarea*, *Eryx* and *Lichanura* because the frontal is interpreted as absent.

84. Scales. An anterior prefrontal scale is large (0), small (1), or absent (2). Large, almost always paired (see however, *Ungaliophis* Bogert, 1968a) and symmetrical,

scales in contact with the nasal series (including the internasals) are referred to as anterior prefrontals. I prefer anterior prefrontal for the scale in question, instead of McDowell's (1975:35; see also Stafford, 1986:52) "medial prefrontal", because it more accurately reflects the relative positions of the two sets of prefrontals that I recognise, anterior and posterior (characters 84-85, respectively). State 0 obtains when the anterior prefrontal and frontal(s) are in broad contact (as in *albertisii*; see Underwood & Stimson, 1990:fig.1a,b,d) or closely approach the interocular plane (eg, *melanocephalus*; Zacharias, 1897:fig.53); however, when these conspicuous scales are separated by much smaller scutes (Underwood & Stimson, 1990:fig.1c), the anterior prefrontal is said to be small (state 1). The anterior prefrontal is also considered small when the posterior prefrontals are in broad contact on the midline, as always occurs in *curtus* (see character 85). The anterior prefrontal is considered absent (state 2) when the region is covered with asymmetrical scales not much, if at all, larger than those surrounding the snout.

This character is equivalent, at least in part (see also character 85), to Underwood & Stimson's (1990:571, appendix I) character 1.1. These authors recognised only two states – two (plesiomorphic) and greater than two prefrontal scales – which I interpret to mean a pair of large anterior prefrontal scales is present or absent, respectively. The character states Underwood & Stimson (1990, appendix I) and I record for pythonines (Tables 10, 31) disagree in several instances: they attributed state 1 to *amethystina*, *mackloti*, *melanocephalus*, *papuanus* and *boeleni*, whereas I record state 0 for the first four species, and consider the fifth species variable (0/1). According to Underwood (1976:fig.8), state 2 delimits the (*spilotus*, *viridis*) clade.

A large anterior prefrontal scale is present (state 0) in bolyeriines, *Exiliboa* (according to Bogert, 1968b:fig.1), *Loxocemus*, *Tropidophis taczanowskyi*, *Ungaliophis* (unpaired) and *Xenopeltis*, whereas it is small (state 1) in *Calabaria*, *Charina*, *Lichanura*, *Trachyboa*, and all other *Tropidophis*. A large anterior prefrontal is absent (state 2) in most *Boa* species, all *Candoia*, and all other erycines. *Corallus*, *Epicrates* (except the more apomorphic clades which exhibit state 1; Kluge, 1989a), *Eunectes*, and *Boa manditra* have slightly enlarged postnasal scales on the dorsal surface of the snout; however, their irregular shape and variable size among conspecifics indicates that state 2 should be attributed to them, like all other boines. This pattern of variation among the outgroups suggests equally parsimonious estimates of the plesiomorphic condition in pythonines, not the single large anterior prefrontal unequivocally recognised by Underwood & Stimson (1990:571).

85. Scales. A posterior prefrontal scale is absent (0), or when present it is separated from (1) or contacts (2) its counterpart on the midline (Fig.15). The posterior prefrontal, which is equivalent to McDowell's lateral prefrontal (1975:35; see also Stafford, 1986:52), occurs between the preocular, frontal, anterior prefrontal, and

loreal, and much of it lies above the *canthus rostralis*. The posterior prefrontal might be confused with a large posterior loreal; however, the latter usually occurs below the *canthus*. A slightly enlarged scale occurs on, or just above, the *canthus* in some pythonines (eg, *regia* Pitman, 1974:pl.A2 and *reticulata* Underwood & Stimson, 1990:fig.1e); however, the status of those scales, as loreals or posterior prefrontals, does not affect the determination of the states of the present character.

I believe my definition of postfrontal variation is not accounted for in Underwood & Stimson's (1990:571) character 1.1. As noted in my discussion of the anterior prefrontal scale (character 84), these authors recognised only two states – two (plesiomorphic) and greater than two prefrontal scales – which does not speak to the presence of large postfrontals and the nature of their contact on the midline. However, Cogger's (1986:406) attributing one pair of prefrontals (anterior) to *albertisii* and two pairs (anterior and posterior) to *fuscus* (= *mackloti*) and *olivacea* is consistent with my prefrontal character definitions and observations, as is McDowell's (1975:33) "two pairs of prefrontals". While my recognising two areas of prefrontal scale variation (characters 84-85) provides more synapomorphies than Underwood & Stimson's single binary variable (their character 1.1), the problem of independence increases (compare however Tables 10 and 11). Moreover, when only one prefrontal is present, I assume it is the anterior because the rostral field of scalation (in particular, the nasal and internasals) appears to exhibit less variation than the interocular field among booids (Zacharias, 1897:figs 1-57).

According to McDowell (1975:33, 44), specimens of *albertisii* from near Wau often have a posterior prefrontal, but that geographic variation is not obviously represented in my sample (Table 11). In *papuanus*, the small posterior prefrontal is absent occasionally, and the fact that the preocular projects into the area ordinarily occupied by that scale suggests its absence is due to fusion.

State 2 is present in *Calabaria*, *Charina*, *Lichanura* (the remaining erycines exhibit small, mostly asymmetrical, scales, which are most accurately described as state 0), *Trachyboa*, and most species of *Tropidophis*. State 0 occurs in bolyeriines, *Exiliboa*, *Loxocemus*, at least one species of *Tropidophis* (*taczanowskyi*), *Ungaliophis* and *Xenopeltis* because the anterior prefrontal is large (character 84, state 0). Also, state 0 is attributed to all boines, with the exception of a few apomorphic sister species of *Corallus* and *Epicrates* (Kluge, 1991), because the dorsal surface of the snout is generally covered by small, asymmetrical scales (Zacharias, 1897). Thus, the most parsimonious explanation is that state 0 is plesiomorphic for pythonines.

86. Scales. The number of posterior sutures in the nasal scale is none (0), one (1), or two or more (2). Scale subdivision must be longer than half the width of the nasal, between the nostril and the outer margin of

the nasal scale, to count as a suture. For example, partial subdivisions and dorsal and ventral folds occur in the nasal scale of *olivacea*, but these conditions are not scored as sutures. Occasionally, *viridis* exhibits an indentation in the posterior margin of the nasal scale or a partial suture; however, neither case is scored as present. This character is equivalent to Underwood & Stimson's (1990:576) character 12. Our observations (compare Tables 12 and 31 to their appendix I) are in almost perfect agreement, except for *regia* (1 versus 0/1/2) and *spilotus* (0/1 versus 1). They concluded that the absence of a suture is primitive because that is the condition observed in *Loxocemus* (the state of *Xenopeltis* could not be decided because the nostril is extremely large). Variation among other outgroup taxa, as provided by the review of Zacharias (1897) and Bogert (1968a,b), seem to support Underwood & Stimson's hypothesis of pythonine plesiomorphy. I accept that hypothesis of polarity.

87. Scales. There is none or one (0), two (1), or three or more (2) scales present in the loreal region (Fig.16; Table 13). This count is made at the level of the middle of the orbit and nostril, between the preocular(s) and posterior nasal scales. Anterior and posterior prefrontal scales are included in the count when they intersect that line, and therefore this character does not attempt to identify the presence of loreal scales as such. For example, state 0 applies to *Loxocemus*, where the anterior prefrontal contacts the supralabials between the preocular and nasal scales, and to *Xenopeltis*, where the preocular and nasal scales are in contact. Thus, I assume this definition is unlike Underwood & Stimson's (1990:571) character 1.2, which they described as a single (plesiomorphic) or broken loreal.

I agree with Cogger (1986:409), that *albertisii*, *fuscus* (= *mackloti*), and *olivacea* have one loreal, and two or more occur in *childreni* and *perthensis*. McDowell (1975:33, 44) noted that specimens of *albertisii* from near Wau have the loreal divided into two or three scales; however, most of my sample comes from other geographic regions (Table 13). Further, McDowell (1975:32) seems to have used a combination of loreal and subloreal variation (characters 87-88) to differentiate Papuan *Liasis* and *Python*.

State 0 applies to bolyeriines, *Calabaria*, *Charina*, *Loxocemus*, all tropidophiines (except *Trachyboa*, which exhibits state 1), and *Xenopeltis*. The remaining erycines, *Eryx* and *Lichanura*, usually have state 1, rarely 2, and state 2 applies to the most plesiomorphic sister lineages of boines (the [*Epicrates*, *Eunectes*] clade may be diagnosed by state 0). Thus, the most parsimonious interpretation for the plesiomorphic condition in pythonines appears to be state 0.

88. Scales. A series of small scales adjacent to the dorsal margin of the supralabials is absent (0) or present (1). Two or more small scales along the supralabials constitute a series (Fig.16; Table 14). A survey of the variation in the loreal region, along two axes, between

the middle of the orbit and the nostril, and immediately dorsal to the supralabials, suggests characters 87-88 are independent (compare Tables 13-14). State 0 is exhibited by bolyeriines, *Calabaria*, *Charina*, *Exiliboa*, *Loxocemus*, *Tropidophis*, *Ungaliophis* and *Xenopeltis*, whereas state 1 delimits boines, *Eryx*, *Lichanura*, and *Trachyboa*. It appears that the plesiomorphic state in pythonines is equivocal.

89. Scales. The number of supralabial scales, between the rostral and the anteriormost subocular scale (Fig.16), is four or less (0) or five or more (1). This character is equivalent to Underwood & Stimson's (1990:574) character 7, and our observations are in close agreement (compare Table 15 to their appendix I), with the exception of *melanocephalus* and *papuanus*. Their records for these species are 0 and 1, whereas mine are 0/1 and 0, respectively. Underwood & Stimson's selection of a plesiomorphic state seems to have been based on the commonest number in the outgroup, and they did not place much confidence in their assessment of polarity. My review of outgroup variation is as follows: state 0 delimits bolyeriines, *Calabaria*, *Charina*, some *Eryx*, *Loxocemus*, tropidophiines and *Xenopeltis*; state 1 characterises boines, some *Eryx* species, and *Lichanura*. Thus, the plesiomorphic condition in pythonines appears to be state 0.

90. Scales. The number of supralabial scales entering the orbit is one (0), two (1), or three (2). This character (Table 16) is equivalent, in part, to Underwood & Stimson's (1990:574; see also McDowell, 1975:37) character 8, except for our treatment of individuals whose supralabials are excluded from the orbit by subocular scales. I treat subocular scales as a separate character (see no. 79), and here record an N for those specimens whose supralabials are excluded by the presence of subocular scales. Underwood & Stimson did not recognise subocular scale variation as a separate character, and they recorded the absence of supralabials entering the orbit in their character 8 as a separate state (0). Underwood & Stimson assumed two supralabials meeting the eye (state 1) is plesiomorphic in pythonines because it "is clearly the commonest number in the outgroup" (p.574), and the other conditions, one (state 0) and three (state 2), as apomorphic. My review of outgroup variation is as follows: state 0 delimits bolyeriines, state 1 applies to *Calabaria* (all other erycines are recorded as N), *Loxocemus*, all tropidophiines (except *Ungaliophis panamensis* Bogert, 1968a), and *Xenopeltis*. Boines are highly variable, either N or state 1 applies to the plesiomorphic sister taxa, and state 2 only occasionally and to more apomorphic clades. Thus, I agree with Underwood & Stimson's inference that two supralabials entering the orbit is the plesiomorphic condition in pythonines.

91. Scales. The first, anteriormost, genieal scale is short (0) or long (1) compared to other throat scales, particularly the posterior genieals (Fig.17). Genieals (=

genials, postmentals; J.A. Peters, 1964) are the large chin shields that border the mental groove, and are not otherwise infralabials. It is often difficult to decide which scales are geneials in *carinatus*, *spilotus*, and *viridis* because the scales are small and continue into the fundus of the mental groove (see character 93 for further discussion). According to McDowell (1975:31), the size of the anteriormost geneial (his “pregeneial”, p.22) is supposed to distinguish the *Liasis* group (*albertisii*, *boa*, *childreni*) from the *Lisalia* group (*olivacea*, *mackloti*, *papuanus*), long and short, respectively, and my observations confirm this distinction (Table 17). The following variation among the outgroups suggests that the short condition is plesiomorphic in pythonines: state 0 is typical of almost all boines (*Corallus caninus* is exceptional), erycines (where a mental groove is present), and tropidophiines (*Tropidophis taczanowskyi* being an obvious exception), and state 1 characterises bolyeriines, *Loxocemus* and *Xenopeltis*. Under this assumption of polarity, the *Liasis*, but not the *Lisalia*, group can be delimited by the size of the first geneial scale.

92. Scales. The anteriormost geneial scale contacts three (0), two (1), or one (2) infralabial scales (Table 18). Contact with the mental scale is not counted, and characters 91-92 appear to be independent (compare Tables 17 and 18). This character is equivalent to Underwood & Stimson’s (1990:577, appendix I) character 14, and our results are in good agreement, with the following exceptions: they recorded *albertisii* and *boa* as state 0 (I treat them as variable, 0/1), and *boeleni* and *melanocephalus* as variable, 0/1/2 and 1/2, respectively (I record both species as state 1). McDowell (1975:22) erroneously claimed that state 2 applies to all pythonine species in New Guinea, *albertisii*, *amethystina*, *boa*, *boeleni*, *mackloti*, *papuanus*, *spilotus* and *viridis*, whereas I believe that state is characteristic of only the last two taxa (Table 31). The fact that I have been unable to score unequivocally any pythonine terminal

taxon as state 0 (Table 31) means that condition does not appear in the analysis. Underwood & Stimson based their polarity decision on anilioids, *Loxocemus* and *Xenopeltis*, where the anterior geneial contacts three labials. I agree that *Xenopeltis* has state 0; however, I record *Loxocemus* as variable (states 0 and 1 seem to occur with nearly equal frequency). Additionally, the following variation exists among the other relevant outgroups which have a mental groove and obvious geneials: state 0 is exhibited by *Eunectes* and some *Tropidophis taczanowskyi*, state 1 by *Boa*, *Bolyeria*, *Charina*, *Corallus*, *Epicrates*, *Exiliboa*, *Lichanura*, most *Tropidophis*, and *Ungaliophis*, and state 2 by *Candoia*, *Casarea*, *Eryx* and *Trachyboa*. Thus, while it is equally parsimonious to choose state 1 or 2 as the plesiomorphic state for pythonines, state 0 is not such a candidate based on parsimony optimisation (*contra* Underwood & Stimson, 1990).

93. Scales. Several small scales are absent (0) or present (1) on the fundus of the mental groove (Fig.17; Table 19). The longitudinal ridges of soft skin that often occur along the bottom of the mental groove are not recorded as state 1. The (*carinatus*, *spilotus*, *viridis*) clade seems to have an extra row of elongate scales on the wall of the groove, adjacent to the geneials, as well as smaller oval scales on the fundus (state 1). While characters 92-93 appear to be independent (compare Tables 18 and 19), the presence of scales on both the wall and floor of the mental groove seem to be strongly correlated. McDowell (1975) made several observations on pythonines, which I assume concerns variation in this character: (1) “a few small scales may lie in [the] groove” of *amethystina* (p.57), (2) *spilotus* “sometimes with some smaller scales in fundus of groove” (p.65), and (3) *viridis* is “basically an exaggeration of the condition in *Python spilotus*, where a number of rather small gulars usually lie medial to the gulars forming the margins of the mental groove, but quite different in degree and in

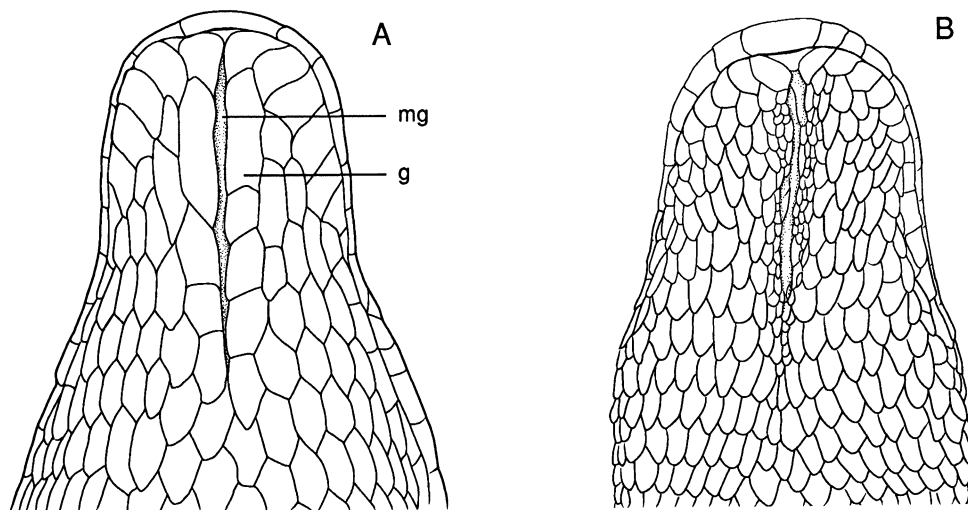


Fig.17. Ventral view of the throat scalation. A – *albertisii* (BMNH 1986.1174); B – *viridis* (AM R127472).
g – geneial scale, mg – mental groove.

general appearance" (p.67). I agree with McDowell's conclusions concerning *pilotus* and *viridis*; however, I doubt the implication that *amethystina* has state 1 (see Table 19). Given that state 0 is observed among all outgroups (state 1 was observed only in *Corallus caninus*), I assume it is plesiomorphic in pythonines.

94. *Scales. Apical, sensory, organs (the scale pits of McDowell, 1975:30) are absent (0) or present (1) on many of the posterior upper-body scales (Table 20).* There is considerable individual variation in this character and I examined several specimens before determining each species' state. Moreover, I have been unable to characterise consistently the organs as "pits" represented by "colorless spots on the pigmented stratum corneum when the latter is removed and viewed by transmitted light" (McDowell, 1975:31), nor as "thin spots in the epidermal keratin without sharply defined edges ... 0.2 mm or more in diameter" (Underwood & Stimson, 1990:579). More often, I have used the presence of a pair of small, ovoid concentrations of pigment near the free edge of the scale as evidence of sensory organs. In some species (eg, the *savuensis* form of *mackloti*), the latter characterisation will not always reveal the organs in the absence of dark pigmentation on the dorsal surfaces. Thus, I have little confidence that my definition is any better than McDowell's or Underwood & Stimson's (see below), and I urge the further study of this character. Sonification (Chiasson & Lowe, 1989:110) will almost certainly be required to remove epidermal debris that might fill the depressions, in order to decide unambiguously when pits are absent. Scanning electron microscopy may be required as well. Further, I believe several scales should be examined from snakes of different sizes and reproductive condition, and from both sexes. My impression is that if the pits are present they will be found in the dorsal and lateral body scales, immediately anterior to the anal opening.

According to McDowell (1975:31,50,66), the (*albertisii*, *boa*, *childreni*, *mackloti*, *olivacea*, *papuanus*) group is diagnosed by the presence of pits, whereas pits are usually absent in *amethystina*, *boeleni*, *pilotus* and *viridis*. He stated (p.33) that *childreni*, based mainly on Northern Territory specimens (the *childreni* and *stimsoni* species of L.A. Smith, 1985), has a "single, terminal scale pit (rather than a pair of subapical pits...)." Underwood & Stimson's (1990:579) character 20 "mostly confirm and extend" McDowell's (1975) observations concerning paired pits in pythonines; however, they were unable to confirm his claim that pits occur in *boa*.

I too have been unable to identify pits in *boa*, nor have I observed them in any *albertisii* (*contra* McDowell, and Underwood & Stimson). Perhaps, this should not be too surprising because S. McDowell (personal communication) acknowledged that they are much smaller and less conspicuous than they are in other species. Of all the specimens of the four species in the *childreni* complex that I examined, *childreni*, *maculosus*, *perthensis* and *stimsoni*, only several representatives of *maculosus* exhibited pits; however, in these examples the

actual posterior margin of the dorsal body scale is emarginate on both sides of the apex. While these cases are clear, other *maculosus* possess no such marks. Only two specimens of *stimsoni* possess pits (Table 20; it is single in AM R92327). I did not observe any single or double pits in *childreni* or *perthensis* (Table 20). Underwood & Stimson (1990, appendix I) recorded *melanocephalus* and *papuanus* as having pits (as did McDowell, 1975); however, I have never seen anything that would pass for a pit in the former species, and only very rarely were pits present in the latter taxon. I was unable to find pits in the scales of *melanocephalus* (BMNH 1931.12.2.2) provided by G. Underwood (personal communication), nor do they exist in more recently collected material of that species (eg, UMMZ 201036, 201038). Further, I was unable to verify S. McDowell's claim (personal communication) that all AMNH specimens of *papuanus* clearly show pits. According to my criterion, pits are rarely present in that species; however, the stratum corneum is loosely attached in *papuanus* and may have been lost in the AMNH material. One specimen of *oenpelliensis* (Table 20) has especially large dark spots near the tip of many scales (AM R55009), which suggest the presence of sensory pits, but no such marks occur in a second specimen (AM R93417). I have been unable to identify sensory pits in any of the relevant outgroup taxa, and therefore I conclude that state 0 is plesiomorphic in pythonines.

95. *Scales. Most subcaudal scales are single (0) or paired (1).* This character is defined in terms of frequency, the simple majority, to account for the fact that almost every specimen I examined has both single and paired subcaudals (Table 21). While it is always quite clear which of the two states applies, the proportion does approach 50:50 in some specimens. Most troublesome was *boa*, where I observed only a few more divided than undivided scales (eg, BMNH 77.2.24.11 has 21 undivided and 30 divided scales). The proportions even change considerably among taxa held traditionally to be sister species. For example, *melanocephalus* usually has a few paired subcaudals, whereas *ramsayi* rarely possesses any. Among the outgroups, boines, bolyeriines, erycines and tropidophiines have mostly undivided subcaudals, while they are divided in *Loxocemus* and *Xenopeltis*. Stafford (1986:159) incorrectly stated that subcaudals are divided in *Calabaria*. Thus, I assume state 0 is plesiomorphic for pythonines. McDowell (1975:30) acknowledged that *Aspidites* has entire subcaudals, but he concluded that state was not plesiomorphic for pythonines (he viewed *Aspidites* as derived among pythonines, secondarily so in the case of thermosensitive pits).

96. *Scales. The number of subcaudal scales is 63 or less (0), 65-66 (1), 68-72 (2), or 79 or more (3).* This character is identical to Underwood & Stimson's (1990:586) character 35. I had considerable difficulty in confirming the states Underwood & Stimson attributed to the terminal taxa they investigated (their appendix I),

and I include this variable (and 101-102) only so that its phylogenetic informativeness can be further judged in terms of all the available evidence (Kluge, 1989a). Also, I have employed Underwood & Stimson's character state coding and hypothesis of polarity.

97. Scales. The minimum number of rows of neck scales is 44 or less (0), 45 (1), 46 (2), 47 (3), 48-50 (4), or 56 or more (5). This character is identical to Underwood & Stimson's (1990:586) character 36 (see character 96 for further discussion).

98. Scales. The maximum number of midbody scale rows is 50 or less (0) or 54 or more (1). This character is identical to Underwood & Stimson's (1990:586) character 37 (see character 96 for further discussion).

99. Scales. The number of posterior trunk scale rows is 22-33 (0) or 34-44 (1). This character is identical to Underwood & Stimson's (1990:586) character 38 (see character 96 for further discussion).

100. Thermoreceptive Pits. A pair of thermoreceptive pits is absent (0) or present (1) in the rostral scale (Fig.18; Table 22; Shine, 1991:20). Pit variation (Table 22) was determined macroscopically (microanatomical details are not considered; Maderson, 1970; Meszler, 1970; Gamow & Harris, 1973; Gopalakrishnakone, 1984), and a particular neurophysiology is not implied. Barrett (1970) and de Cock Buning *et al.* (1978, 1981) have ascribed a thermoreceptive function to the rostral-labial pits, in terms of the pits' special sensitivity to infrared radiation of relatively long wavelengths. However, the fact that *ramsayi* feeds on birds and mammals (Fyfe & Harvey, 1981), 4% and 48%, respectively (Shine, 1991: appendix), suggests that thermoreception *per se* is not necessary for prey location in pythonines. Moreover, some pythons with well developed pits feed on prey with body temperatures at or near ambient (eg, *viridis*; Shine, 1991: appendix). Among the outgroups, pits are absent in bolyeriines, erycines, *Loxocemus*, tropidophiines and *Xenopeltis*. Boines are variable; some form of rostral-labial pits are present only in *Boa manditra*, *Corallus* (including *C. cropanii*), and the most plesiomorphic sister lineages in *Epicrates*, *E. cenchria* and the West Indian clade (Maderson, 1970; Kluge, 1989a). Underwood's (1967:78) implication that *Boa constrictor* possesses pits may be in error (Maderson, 1970:301), and his phyletic analysis of boid snakes (1976:fig.8) may also be interpreted as incorrectly implying that *Boa dumerili*, *B. madagascariensis*, and *Eunectes* have pits. The situation in *Boa constrictor* requires further study because at least some specimens of that species (eg, UMMZ 114663) have shallow depressions located between infralabial scales (Kluge, 1991: table 1), that position being peculiar to those boines which do have well developed pits. The absence of pits is interpreted as plesiomorphic in pythonines. Also, Underwood & Stimson (1990:577) "infer with confidence that absence of pits is primitive."

101. Thermoreceptive Pits. A suture originating from the dorsal margin of a rostral thermoreceptive pit is absent (0) or present (1). An N is entered in the data matrix when the rostral pit is absent. This character is equivalent to Underwood & Stimson's (1990:578) character 16, and most of our characterisations of terminal taxa are in agreement. However, they recorded *albertisii* as state 0, whereas I consider that taxon to be variable (Table 23). Further, they attributed state 0 to *mackloti*, whereas I record that species as N. Their attribution gives the erroneous impression that pits are present in *mackloti*. See character 100 for discussion of rostral-labial pit variation and polarity (Fig.18).

Underwood & Stimson (1990:578) also considered the absence/presence of a suture originating from the narrow lower extremity of a rostral thermoreceptive pit and continuing laterally (their character 17). Many of our characterisations of terminal taxa are in agreement; however, they claimed that a lower rostral pit suture is absent in *albertisii*, *boeleni*, *molurus* and *viridis*, whereas I believe it exists in all of the specimens of those species I examined (Table 24). As with the dorsal suture, this variation cannot be considered when the rostral pit is absent (eg, as in *mackloti*; see discussion immediately above). I have not considered the ventral rostral pit suture an additional character because only *papuanus* exhibits state 0 (Table 24) and the transformation cannot be polarised unambiguously (see character 100 for

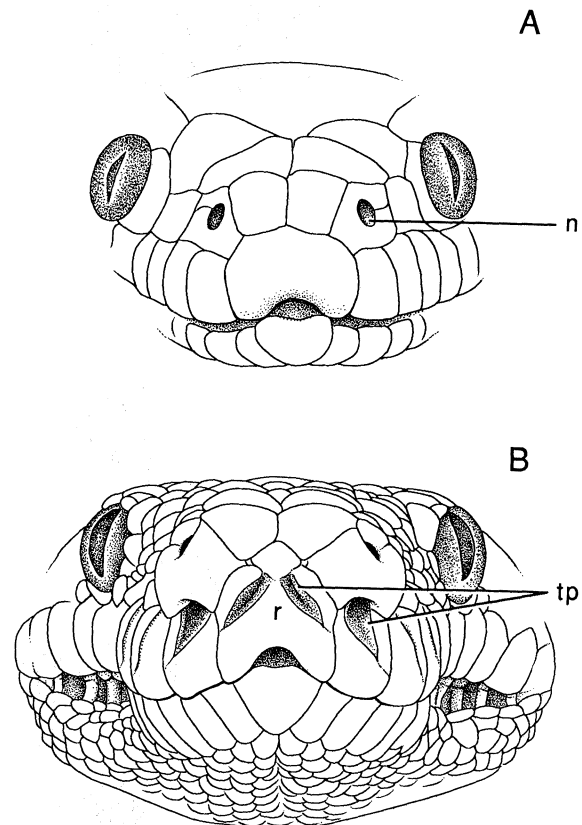


Fig.18. Posterior view of the rostral scale. A – *mackloti* (UMMZ 132865); B – *spilous* (modified after Shine, 1991:20). n – nostril, tp – thermoreceptive pit, r – rostral scale.

discussion of rostral-labial pit variation and polarity).

102. *Thermoreceptive Pits.* A thermoreceptive pit is absent (0), or present in the first (1), second (2), third (3), fourth (4), fifth (5) and sixth (6) supralabial scales (Table 25). In some species (eg, the *childreni* complex), this set of pits is represented by a shallow depression located between the upper margin of the first supralabial and the lower edge of the nasal. This cavity is usually horizontally oriented, except in some large individuals where it is more dorsoventrally elongate, and is thus unlike the supralabial pits of other pythonines. The supralabial containing the sixth pit lies below the eye; however, it is not to be confused with the subocular series of pits (see character 103). Underwood & Stimson (1990:577) focused on the degree of development of the first pit (their character 15) because it "afforded a clearer partition into discrete states than a count of their number." While I hold the opposite opinion, the general sense of their character 15 seems to be included in my characters 102-103. Occasional specimens of *melanocephalus* (eg, AM R65983) have a faint depression in the dorsal part of the first supralabial scale, which may suggest a concentrated thermoreceptive function in that area. See character 100 for discussion of rostral-labial pit variation and polarity.

103. *Thermoreceptive Pits.* One or more pits are absent (0) or present (1) in the supralabial scale(s) below the eye (McDowell, 1975:37). These shallow depressions lie near the upper margin of the subocular supralabial scales, and occasionally the posteroventral corner of the lower preocular scale (Fig.16), and are therefore readily distinguished from supralabial pits (see character 102). I have no evidence that the subocular depressions function in thermoreception (Barrett, 1970; de Cock Bunning *et al.*, 1978, 1981), however, they are superficially similar to rostral-labial pits in shape and pigmentation. McDowell (1975:43) stated that these pits are not sensory, "but rather a suborbital depression associated with a distinct preorbital concavity of the head". The pits are particularly obvious in *albertisii* as horizontal, oval cavities. Shallower depressions, often evident as a dense concentration of pigment, particularly in the anteriormost subocular supralabial and the preocular, are found in some *boa*, *mackloti* and *olivacea*. Not all specimens of each of these taxa have obvious subocular modifications (Table 26), and McDowell (1975:37) stated that "no such groove is present in *L. mackloti*", and that (p.39) *olivacea*'s "supralabials below [the] eye and preocular [are] gently convex, without suborbital groove or depression". Further effort must be put toward accurately defining state 1. See character 100 for discussion of rostral-labial pit variation and polarity.

104. *Thermoreceptive Pits.* A shallow thermoreceptive pit is absent (0) or present (1) in the second through fourth or fifth infralabial scales. Faint dimples have been observed in some of those scales in a few of the largest specimens of *amethystina*, *oenpelliensis* and *papuanus*

(two, one and one, respectively). Such pits are not much better developed in *sebae*; however, they appear to be present throughout the series of anterior infralabial scales and in all examples of that taxon. Accordingly, I have recorded *sebae* as apomorphic, but *amethystina*, *oenpelliensis* and *papuanus* as plesiomorphic. This character is equivalent to Underwood & Stimson's (1990:579) character 18, and our characterisations of the terminal taxa are in close agreement (Table 27). While I consider pits absent in *amethystina* and *boeleni*, they recorded those species as variable and state 1, respectively. See character 100 for discussion of rostral-labial pit variation and polarity.

105. *Thermoreceptive Pits.* The anteriormost thermoreceptive pit in the posterior infralabial series occurs in scale 6 (0), 7 (1), 8 (2), 9 (3), 10 (4), 11 (5), 12 (6), 13 (7), 14 (8), or 15 or more (9). See character 100 for discussion of rostral-labial pit variation (Table 28) and polarity. This character cannot be polarised because the absence of pits is plesiomorphic in pythonines.

106. *Thermoreceptive Pits.* There is none (0), 3 (1), 4 (2), 5 (3), 6 (4), 7 (5), 8 (6), or 9 (7) thermoreceptive pits in the posterior infralabial series of scales. See character 100 for discussion of rostral-labial pit variation and polarity (Table 29).

107. *Thermoreceptive Pits.* The rostral-supralabial thermoreceptive pits are deeper (0), approximately equal in depth (1), or shallower (2) than the infralabial pits. According to Branch (1986:296), shallower pits are found in *anchietae*, *curtus*, *molurus*, *regia* and *sebae*, with the infralabial pits much less deeply impressed than the rostral and supralabial pits (McDowell, 1975:51). McDowell (1975:43) described *albertisii* as exhibiting the opposite extreme (state 2). While most *reticulata* and *timoriensis* examined exhibit state 0, the sets of pits appear to be approximately equal in depth in a few specimens. See character 100 for discussion of rostral-labial pit variation (Table 30). This character cannot be polarised because it does not apply to the outgroups. Likewise, N is scored for those ingroup taxa, *boa*, *melanocephalus* and *ramsayi*, which have no rostral-supralabial and/or infralabial pits (Table 31).

Underwood & Stimson (1990:579) characterised variation in the posterior infralabial thermoreceptive pits (their character 19). The states they recognised refer to two sets of conditions, depth (absent, shallow, deep) and appearance (gutter or pit-like). While their notion of infralabial pit depth is presented in absolute terms, and my characterisation is relative to the depth of the rostral-supralabial pits, it is surprising that there is little correlation between our observations (compare Table 30 to their appendix I). I did not attempt to score the aspect of appearance because it is unclear how they defined gutter-like.

108. *Muscles.* The levator anguli oris muscle is

present (0) or absent (1). I accept Underwood's (1976: fig.8) opinion that this muscle has been lost in pythonines.

109. *Muscles. The intermandibularis anterior muscle is divided (0) or undivided (1).* I accept Groombridge's claim (1979b; see also Rieppel, 1988:86-87) that pythonines are diagnosed by the undivided state. The group may also be characterised by a distinctly developed *pars anterior* separation (Groombridge, 1979b).

110. *Viscera. The pancreas is undivided or partially (0) or fully (1) lobed.* According to Underwood (1976; see his character 27), pythonines are apomorphic, and I accept his conclusion.

111. *Blood Vascular System. Each posterior trunk intercostal artery usually supplies blood to one (0) or more (1) body segments.* My choice of an intercostal artery character and polarity hypothesis, and the states I record, depend largely on the research of F.E. Beddard and G. Underwood. Like Underwood (1976), I restrict my character definition to the posterior trunk, specifically the last 10%. I have found that dissections are easier to make in that area, conclusions are less ambiguous, and, most importantly, those vessels appear to be more conservative.

Beddard (1904a,b, 1906, 1908) described considerable intercostal artery variation in snakes, and he tried unsuccessfully to use certain aspects of that variation to define boines and pythonines (1908:153-154). Setting aside the complications added by the presence of the anterior, posterior, and superficial vertebral arteries (1904a:362), I briefly review his observations concerning the intercostals *per se*. Beddard's (1904a:362-363) dissections of *spilotus* showed that there is serial variation in the number of segments (1-7) an intercostal supplies. He also observed that it supplied more than one segment in *Boa* and *Eunectes*, and *Corallus* (Beddard, 1906:515, 1908:143, respectively). Beddard (1904b:110) claimed that "each intercostal bifurcates close to the parietes and supplies but a single intervertebral area" in *sebae* and *Eryx (conicus, jaculus and johni)*. He (Beddard, 1906:515; 1908:143) then noted that *Boa manditra* (his *Corallus madagascariensis*) is similar to *sebae*, but appears to have contradicted his earlier statement that *Eryx* is like *sebae* (pp. 515,517). I believe Beddard's investigations of intercostal artery variation in booid snakes can be effectively summarised as a single transformation series, the number of body segments an intercostal artery supplies.

There are many other vessels in the dorsal body cavity of snakes, and subsequent authors may have mistaken them for intercostals (see below). Thus, I believe it is worth emphasising that the intercostal arteries are small, usually vertical, not always paired, penetrate the intercostal muscle masses immediately adjacent to the vertebral column, and originate from the dorsal aorta, which is thick walled and lies outside the peritoneal cavity on the midline ventral to, but not always in

contact with, the vertebral column. Further, assessing the number of segments an intercostal supplies is made especially difficult by the fragile and transparent nature of the vessels. Doubtless, latex injected specimens would improve the accuracy and ease of making observations. The presence of serial change may also contribute significantly to sample variation. Underwood & Stimson (1990:579-580) noted that "In some pythons and most boas, in the anterior trunk, vessels arise from the dorsal aorta at intervals of three or four body segments and then divide to give rise to several pairs of intercostal arteries ... [and towards the cloaca] the number of pairs arising from one primary vessel dwindles to one and the two intercostals of a pair arise separately from the aorta."³

Curiously, Underwood (1976:155-156), citing Beddard's research, recognised two intercostal artery variables (his characters 23-24): "Average number of body segments, in posterior trunk, supplied by each [intercostal artery] from dorsal aorta" and "Anastomoses between intercostal arteries in posterior trunk: present between all ..., between some ... or absent ..." (my italics). Although Underwood recorded the states of these two characters in a wide variety of primitive snakes, he only used the information to diagnose two assemblages of pythonines. "Intercostal arteries arise in groups from dorsal aorta" was the uncorroborated state delimiting the (*amethistina, boa, childreni, melanocephalus, spilotus, viridis*) clade from *curtus, regia* and *reticulata*, the other pythonines he examined, and "Intercostal arteries anastomose" was the single state setting off the (*amethistina, boa, childreni, spilotus, viridis*) group (p.168-169, fig.8). Until recently, Underwood (1989; also personal communication) has remained firm in his conclusion that groups of intercostal arteries is a derived feature linking together all Australian pythonines. Underwood & Stimson (1990:579-580) did not cite Underwood (1976), and they used only one of the two aspects of intercostal artery variation he employed. The reason G. Underwood (personal communication) has given for discounting the second variable is that he "found anastomoses in *Aspidites melanocephalus* (two specimens) and decided that it should not be scored primitive to the others in this respect." Effectively, Underwood & Stimson's simplified character state description (no. 21), "Intercostal artery pairs arise: in groups", diagnosed the same, more inclusive, Australia-New Guinea lineage Underwood (1976) identified, (*albertisii, amethistina, boa, boeleni, childreni, mackloti, melanocephalus, papuanus, spilotus, viridis*). This character is equivalent to Beddard's (see also Brongersma, 1961; Underwood, 1967:33-34), and deserves careful reconsideration because it seems to provide evidence for *melanocephalus* (and presumably *ramsayi*) being the sister group of other Australian pythonines, but not pythonines in general. It may be recalled (see

³ While Underwood and Stimson's use of the term intercostal for more distal vessels is unusual (see Beddard, 1904a,b, 1906, 1908), their description of the anatomy is accurate

Introduction) that McDowell (1975:30, 32) resorted to *ad hoc* arguments concerning character evolution to avoid having to treat *melanocephalus* as the sister lineage of all other pythonines. More recently, G. Underwood (personal communication) reported that he re-examined the two *melanocephalus* he and Stimson had studied. With respect to the smaller of the specimens (BMNH 1931.12.2.2), he was unable to discover any anastomoses in the anterior trunk, but in the larger individual (BMNH 1976.1588) he found two or three. Neither specimen exhibited any linked series of anastomoses, like Beddard's "posterior vertebral artery".

In addition to the pythonine species examined by Underwood (1976) and Underwood & Stimson (1990), I dissected *anchietae* (UMMZ 190758), *maculosus* (UMMZ 190774), *oenpelliensis* (AM R93417), *olivacea* (UMMZ 190768), *perthensis* (UMMZ 190789), *ramsayi* (AM R76042, UMMZ 190769), and *stimsoni* (UMMZ 190766). My sample of *melanocephalus* consisted of two specimens (AM R65983, UMMZ 190770), and several outgroup taxa, including *Calabaria reinhardti* (UMMZ 61660), *Candoia bibroni* (UMMZ 100015), *Eryx jaculus* (UMMZ 130590), and *Boa manditra* (UMMZ 126088), were also dissected. The intercostal arteries are short, the dorsal aorta rests against the vertebral column, and there is but one per segment in *melanocephalus* and *ramsayi*; most of the intercostals are completely paired in the latter species, whereas most are paired throughout about 90% of their length in the former species. Thus, my observations indicate that *melanocephalus* (and *ramsayi*) are like the African-Asian pythonines, not the Australia-New Guinea species (*contra* Underwood, 1976 and Underwood & Stimson, 1990). *Boa (manditra)*, *Calabaria*, and *Eryx* are similar to *melanocephalus* and *ramsayi*, and I accept Underwood's (1976) and Underwood & Stimson's (1990) hypothesis of polarity. *Candoia bibroni* exhibits the derived state and is like all other congeners (*contra* Underwood, 1976).

112. *Hemipenes*. The hemipenis is feebly bilobed or undivided (0), or shallowly (1) or deeply (2) forked. Branch (1986:295) stated that *anchietae* and *regia* have undivided hemipenes, *curtus*' is shallowly forked, whereas other *Python* species have more strongly lobed hemipenes. In most species of pythonines, the awn (character 115) is slender and restricted to the center of the lobe (Ross & Marzec, 1990:45), whereas in *childreni*, *maculosus*, *perthensis*, *reticulata*, *sebae* and *stimsoni* the awn has a broad base and appears to originate from the outer margin of the lobe. The latter condition gives the appearance of deeper lobation than may actually exist. The lobes appear to be slightly more deeply forked in *mackloti* and *olivacea* than other Australia-New Guinea species; however, I still interpret their state as 1 because their organs are not nearly as markedly divided as *sebae*'s (Branch, 1986:fig.3A), which is scored as state 2. I would not be surprised, with a more detailed survey of well prepared hemipenes, that state 1 cannot be consistently distinguished from 2. McDowell's (1975) and Underwood & Stimson's (1990:580; character 22)

surveys of hemipenial lobation disagree considerably, and therefore I put little reliance on their character state assessments. Among the outgroups, only *Calabaria* and *Eryx* have undivided hemipenes, while most other booid hemipenes are usually noticeably forked (Branch, 1986). Thus, I assume state 1 is plesiomorphic in pythonines.

113. *Hemipenes*. An oblique distal capitation of the hemipenis is absent (0) or present (1). According to Branch (1986:fig.3B,C), state 1 is exhibited by *anchietae*, *curtus*, and *regia*. Oblique capitation does not seem to apply to *viridis*, the other species with reduced lobation, which suggests characters 112-113 may be independent. Branch (1986) appears to have concluded that the oblique distal capitation of the hemipenis is a specialisation, and therefore state 0 would be assumed to be plesiomorphic in pythonines.

114. *Hemipenes*. The sulcus spermaticus branches proximal to (0), or at a point level with the upper margin of (1), or distal to (2) the proximal flounce. This variable is like Underwood & Stimson's (1990:580) character 23, except that it pertains to the level of sulcus branching relative to a conspicuous landmark, like the proximal flounce (see character 117). I tentatively accept their opinion that state 0 is plesiomorphic in pythonines.

115. *Hemipenes*. An awn is absent (0), or gradually (1) or abruptly originates from a hemipenial lobe and forms a short (2) or long (3) process (Fig.19; Ross & Marzec, 1990:45). The longer awns (= papillae *sensu* McDowell, 1975) are often curled and occasionally form complete loops. The awn, if actually present (see character 112), originates from the outer margin of the hemipenial lobe (state 1) in *childreni*, *maculosus*, *perthensis*, *reticulata*, *sebae* and *stimsoni*. The absence of an awn is assumed to be plesiomorphic in pythonines because that condition is widespread among other booids (Cope, 1895; Stull, 1928; Dowling & Gibson, 1970; Dowling,

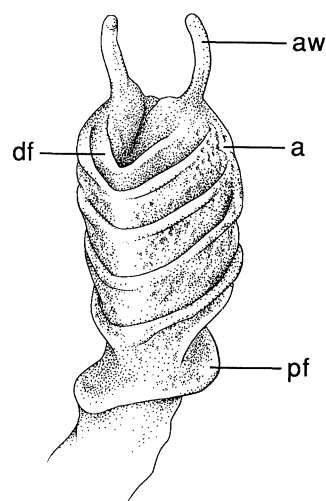


Fig.19. Absulcal view of the hemipenis of *albertisii* (modified after Ross & Marzec, 1990:45). a – anastomosis, aw – awn, df – distal flounce, pf – proximal flounce.

1975; McDowell, 1975, 1979; Dowling & Duellman, 1978; Branch, 1981, 1986). The distinction between states 2 and 3 appears to be easily obscured by the nature of the hemipenial preparation, and I predict considerable character incongruence due to investigator error.

116. *Hemipenes*. Calyces are generally distributed over most of the hemipenis, distal to the bifurcation of the sulcus spermaticus, (0) or limited to the distal end of the hemipenial lobes (1). The calyces usually extend to the bifurcation of the sulcus in the plesiomorphic state. According to Branch (1986), a weakly developed calyculate zone occurs on the distal portion of the arms of the hemipenes of *anchietae*, *curtus*, *molurus* and *regia*. I interpret Branch's discussion to mean that state 1 is apomorphic in pythonines.

117. *Hemipenes*. The proximal flounce is absent (0) or present (1). The protuberance in question is different from other flounces in that it is fleshier, much thicker and protruding, and limited to the center of the absculcal side of the hemipenis (Fig.19; see character 118; Ross & Marzec, 1990:45). I suspect that Underwood & Stimson (1990:581) included the proximal flounce in their character 24 count. The proximal flounce appears to be absent among the relevant outgroups (Cope, 1894; Stull, 1928; Dowling & Gibson, 1970; Dowling, 1975; McDowell, 1975, 1979; Dowling & Duellman, 1978; Branch, 1986), except perhaps the Madagascan *Boa* (Branch, 1981:figs 1,2), and therefore I assume state 0 is plesiomorphic among pythonines.

118. *Hemipenes*. There are four or more (0) or three or less (1) complete or incomplete distal flounces on the hemipenis. These narrow bands of tissue occur on the absculcal side of the intromittent organ, between the proximal flounce and the point of origin of the lobes (see character 117; Ross & Marzec, 1990:45). A lateral view is often necessary to distinguish flounces from calyces. This character is partially equivalent to Underwood & Stimson's (1990:580-581) variable 24 (see also Branch, 1986; McDowell, 1975), and I tentatively accept their opinion that the larger number is plesiomorphic in pythonines.

119. *Hemipenes*. An anastomosis of distal flounces (Fig.19) is absent (0) or present (1). According to Branch (1986:295), the anastomosis forms a fine reticulum of calyces in *Liasis*, *Morelia* and *Python* (and elsewhere, presumably only, in the Madagascan *Boa*). I accept Branch's opinion that state 0 is plesiomorphic in pythonines.

120. *Behaviour*. Shivering thermogenesis is absent (0) or present (1). Egg brooding females shiver and provide metabolic heat to their eggs, and it has been suggested that this activity is diagnostic of pythonines (Shine, 1985; Charles *et al.*, 1985; Shine & Slip, 1990). Thus, Branch's (1988:51) statement that *sebae* does not incubate eggs by shivering requires confirmation.

121. *Size*. Maximum total length (in meters), in either sex, is approximately 1.4 or less (0), 1.5-3.9 (1) or 4.0 or more (2). Estimating the "maximum", the extreme of a distribution, is fraught with sampling problems, not the least of which concerns the bias in this example of not collecting and preserving extremely large individuals. While an average adult length is a more defensible parameter to try to estimate, there are too few data (see however, Shine & Slip, 1990). All records were taken from the literature, and confirmed by two or more sources, which included de Rooij (1917), M.A. Smith (1943), Pitman (1974), McDowell (1975), Begg & Martin (1980), L.A. Smith (1981a,b, 1985), Parker (1982), Broadley (1983), Cogger (1986), Stafford (1986), Storr *et al.* (1986), Shine & Slip (1990), and Shine (1991: appendix). I have been unable to confirm rumors of *childreni* (*sensu lato*) attaining more than 1.5 meters total length. Further, Underwood & Stimson's (1990:595) reference to *timoriensis* as "small" is misleading (eg, MZB is recorded as 270 cm total length). Small size appears to characterise bolyeriines, erycines, *Loxocemus*, tropidophiines, and *Xenopeltis*. Even though boines cannot be diagnosed unequivocally (state 0 or 1), it is most parsimonious to assume that small size is plesiomorphic in pythonines.

Other Variation

McDowell (1975:31) stated that *Liasis* has a narrow premaxilla; however, I have been unable to find a clear-cut distinction between that assemblage and other pythonines in the width of the maxillary processes. While it is obvious that the *childreni* complex has a narrow premaxilla and other pythonines a somewhat longer maxillary processes, I have been unable to discover a break among the species in the variation that might be reasonably attributable to different character states. Further, there is considerable variation in the width of the premaxilla in the outgroup, and it seems unlikely that an unambiguous hypothesis of polarity is attainable.

Underwood (1967:69) described most pythonines as not having the ascending process of the premaxilla (Frazzetta, 1959:fig.3). That process seems to be restricted to boines (Kluge, 1991), and its widespread absence among other alethinopidians and their sister taxa (aniiloids, bolyeriines, erycines, *Loxocemus*, pythonines, tropidophiines and *Xenopeltis*) suggests that state is most parsimoniously interpreted as plesiomorphic (Underwood, 1967; see also Kluge, 1991:17). The considerable variation in the depth and shape of the nasal process of the premaxilla (Kluge, 1991:fig.9) in pythonines requires further study. Consistent character states may be revealed with a multivariate quantitative analysis (eg, Lombard *et al.*, 1986).

M.J. Smith & Plane (1985:191) called attention to a weakly developed cutting ridge on the labial side of maxillary teeth in their study of pythonine fossils (see

Fossils section for further discussion). Such a ridge is present in many extant pythonines; however, a further survey is necessary to document the scope of that variation. The considerable ontogenetic variation must be taken into account, as should variation according to position in the dental arcade. In any case, my preliminary review suggests the cutting edge occurs in other booids (eg, boines), and that the condition is plesiomorphic in pythonines.

Underwood (1976: table 1, his character 42) pointed out that the prefrontal and "postfrontal" (= supraorbital) are in contact in all pythonines, and that condition might be interpreted as diagnostic of pythonines. However, in the three taxa with a "postfrontal", *Calabaria*, *Dinilysia* (Estes *et al.*, 1970) and *Loxocemus*, contact exists only in the latter taxon. Given the working hypothesis of relationships among the outgroups, polarity is ambiguous. Moreover, the globally most parsimonious explanation is that the supraorbital evolved independently in each of these lineages (see character 29).

McDowell (1975) and Underwood (1976:fig.8; see also Frazzetta, 1966:fig.18) stated that the prefrontal bones approach one another on the midline in pythonines (eg, they are in broad contact in *reticulata*, SAM R27307). However, as described, this condition does not diagnose pythonines because it occurs widely among the outgroups. The prefrontal bones are more widely separated in bolyeriines, erycines, *Loxocemus*, tropidophiines, and *Xenopeltis* than they are in pythonines, but the primitive condition in boines (eg, *Candoia* species) is not unlike the pythonine state (Kluge, 1991). Thus, it seems that prefrontal bones approaching one another on the midline may delimit the (boine, pythonine) clade, with actual contact of the prefrontal bones diagnosing boines.

Few synapomorphies have been discovered in the otic capsule (Kluge, 1991, 1993, and herein; Underwood, 1976; Underwood & Stimson, 1990), which is surprising because the capsule is rich in anatomical detail. There appear to be two reasons for this deficiency, extreme variability and subtle, and often hidden, differences. The wall between the vagus foramen and the *fenestra ovalis*, which varies from being complete to absent, is an example of the former reason – both conditions are present in the same individual, on opposite sides. Likewise, the laterosphenoid occasionally exhibits the same presence/absence variation within an organism. The second source of difficulty is illustrated with the *apertura lateralis*, where the exoccipital is continuous or discontinuous. Ordinarily, this variation is described in terms of the participation of the basioccipital in the *apertura lateralis*. However, the difficulty with the later description is the exoccipital can be narrowly discontinuous, as it is in most pythonines, but the basioccipital appears to be completely excluded because of the depth of the exoccipital below the *apertura*. Moreover, it is often difficult to assess the states of this character from a lateral view (through the *recessus scalae tympani*), even with the stapes removed. Rieppel (1979c:413; 1988:90) stated that the basioccipital is involved in the *fenestra rotunda* (viz., it underlays the

apertura lateralis of the *recessus scalae tympani*) in "lizards" and *Dinilysia* (see Estes *et al.*, 1970:40), but that "it is said to be excluded from the margin of the lateral aperture in snakes". Rieppel went on to say, however, that in his opinion the basioccipital also bordered the *apertura lateralis* "rather extensively" in anilioids, and more narrowly in *Bothrochilus*, *Casarea*, *Charina*, some (but not all) *Eryx*, *Morelia* and *Python* (Rieppel, 1979c:413). My observations are different. Observed through the *recessus scalae tympani*, I believe a broadly discontinuous state applies to "lizards" and *Dinilysia*. It is only narrowly separated in *Lichanura*, and variable in pythonines where the alternative conditions are weakly differentiated, except perhaps in *spilotus* and *viridis*. The exoccipital is only narrowly discontinuous in *mackloti*, *melanocephalus* and *molurus*. The exoccipital is obviously continuous in boines, bolyeriines, all other erycines, *Loxocemus*, tropidophiines (*Tropidophis* and *Trachyboa*) and *Xenopeltis*. In any case, regardless of how I characterise the *apertura lateralis*, it seems to be highly variable, both within and among individuals of the same species, and therefore I have not attempted to employ such a transformation series. Any attempt to formalise this, or related otic capsule, variation should be based on disarticulated basioccipital and prootic elements. Unfortunately, that class of material is available for few booids.

The supratemporal appears to be wide in most pythonines, and differs in that regard from some other booids (Frazzetta, 1959, compare figs 1 and 8). However, its shape is so variable, particularly among the outgroups, that I had no success in delimiting states and consistently scoring those conditions.

Frazzetta (1959:469; see also Underwood, 1967:69; McDowell, 1975:28-30,52,58) seems to have been the first to describe variation in the absence/presence of the palatine foramen among booids. According to McDowell (1975:29, 52), the foramen encloses the maxillary nerve (V_2), and Underwood & Stimson (1990:582) referred to the opening as the maxillary foramen. However, S. McDowell (personal communication) now claims that the nerve passing through this foramen is the conjoined V_2 and palatine ramus of VII, that is it seems to correspond to the sphenopalatine ganglion complex of *Anolis* (Willard, 1915) and, as in other snakes, may be called the sphenopalatine foramen. The foramen is present in almost all specimens examined of most pythonine species. Two species, *anchietae* (see also McDowell, 1975:29) and *ramsayi*, had an open foramen in one of two and approximately one/half of the specimens examined, respectively. Also, one specimen of each of the following had an open foramen, at least partially so: *melanocephalus*, *olivacea*, and *regia*. Aside from the single specimen of *olivacea*, I cannot confirm Underwood's (1967:70) claim that the foramen may be absent in *Liasis* species. Among pythonines, *amethystina* is the only species in which there is usually no hint of a foramen; however, a few specimens have the lateroventral, but rarely the dorsomedial, bony margin of the foramen present. I have been unable to confirm Underwood &

Stimson's (1990: character 25, appendix I) claim that *amethystina* and *reticulata* exhibit the same state. The foramen is absent in *Anilius*, boines, and erycines, and present in bolyeriines, *Cylindrophis*, *Loxocemus*, tropidophiines (tiny aperture in *Trachyboa* and *Tropidophis*, large completely and incompletely enclosed foramen in *Exiliboa* and *Ungaliophis*, respectively), uropeltines (completely encircled by bone, but distal margins unfused in most, if not all species), and *Xenopeltis*. Given this variation among the outgroups, it appears that the plesiomorphic condition in pythonines cannot be inferred unambiguously, and the transformation is considered uninformative.

In pythonines, the vidian canal is frequently open posterior to the pterygoid process (see character 59). However, there is considerable individual variation, and the character must be judged phylogenetically uninformative.

According to McDowell (1975:29), in pythonines (including *Calabaria*) Meckel's cartilage extends forward beyond the dentary onto a connective tissue pad located just beneath the mental scale, whereas in boines the tip of the cartilage does not extend beyond the dentary. I can confirm this distinction; however, the pythonine condition appears to be plesiomorphic. The apomorphic boine state is usually correlated with a Meckelian groove that does not reach the tip of the dentary (see my discussion of the extinct *antiquus* in the Fossils section below). The plesiomorphic form of the groove is especially well-developed in erycines.

Underwood & Stimson (1990:574) employed the number of posterior supralabial scales as a character, those labials between the posteriormost subocular and the corner of the mouth (their character 9). I have not included this character in the present analysis because several taxa were highly variable (6 of 19), and because Underwood & Stimson (1990:574) considered the polarity and character state coding "arbitrary".

Subdivision of the transverse rows of scales has been applied to pythonine phylogenetics in at least three different ways. First, Underwood (1976:169, fig.8) considered "[t]ransverse scale-rows double on flank" diagnostic of pythonines. However, Underwood & Stimson (1990:576) noted that "[s]imilar divisions of the transverse rows are found in many boas", which indicates greater taxonomic generality than previously thought (see also Underwood, 1976:169, fig.8, diagnosis of clade G). Underwood & Stimson (1990:576) went on to point out that the subdivision of the scale rows occurs higher on the flank in pythonines, "most commonly at the level of longitudinal rows 4 or 5, sometimes at row 3 or 6"; however, here again, the fact that this variation overlaps that observed in boines suggests greater taxonomic generality for the character than originally considered. Lastly, Underwood & Stimson (1990:577, fig.3, their character 13) focused on the serial distribution of the apomorph, on the trunk alone (state 1) or trunk and tail (state 2), but intraspecific variation seems to diminish, if not discount totally, the usefulness of this character in diagnosing parts of, or all, pythonines.

McDowell (1975) described several colour and colour pattern similarities in his survey of pythonine relationships; however, I have been unsuccessful in defining any such characters. For example, the conspicuous "shiny black" head of *albertisii* is similar to *boa* and *melanocephalus* (McDowell, 1975:45), but not all *albertisii* exhibit that condition. Even narrower definitions don't partition that variation entirely among species. For example, the colour of the postocular area may be defined as uniformly dark or light, and/or in terms of the presence of a broad or narrow bar. While these states are obvious and readily identified in most pythonines, there are some obvious problem species (eg, *amethystina* and *spilotus* are highly variable; McDowell, 1975:58).

Another definition of head colouration might apply just to the supralabials, they being nearly or completely uniformly coloured, or infrequently and irregularly or regularly covered with vertical bars. The definition can be made even more precise, in terms of where the greatest concentration of pigment occurs, near the center (eg, *maculosus*) or at the edge of each supralabial. For example, McDowell (1975:51) stated the *reticulata* group has the uniform state, whereas the *molurus* group (except *anchietae*) possesses a bar below the eye. He assumed that the latter condition applied to *curtus* and that it was expanded to cover most of the side of its head. Again, there appears to be greater within species variation than McDowell recognised, which defies a consistent application of these alternative character state codes to pythonines.

Another possible area of colour and colour pattern variation in pythonines is the dorsal midbody area, where it is a uniform brown or olive/gray, or there is a pattern of bands or subtle, small, blotches or conspicuous, large marks, usually rectangles, triangles or circles. However, the patternless state can involve an overall "speckled" appearance (eg, the *savuensis* form of *mackloti*), and the bands in *melanocephalus* and *ramsayi* are considerably less distinct than those in *boa*. Moreover, the small blotches typical of many specimens in the *childreni* complex (*childreni*, *maculosus* and *stimsoni*) are more band-like in other individuals. In some species (eg, *amethystina*), the pattern is faint, and may be easily lost in preservative. The problem is especially complicated in *spilotus*, where there are several different colour pattern types (Cogger, 1986), and none of these obviously apply to *viridis* (Ross & Marzec, 1990:161; Shine, 1991:24). There is also considerable colour pattern variation in *boa*; the conspicuously banded form is the most common in collections; however, there are uniformly dark (or nearly so) individuals (eg, AM R3149, R6596) and even broadly striped variants (eg, AM R6597). In fact, some of the exceptional *boa* exhibit a combination of banded, solid and striped areas on the body (eg, AM R3148, R6595, R6601). Further, McDowell (1975:45) pointed out that small specimens of *albertisii* may have a "ringed pattern", which underscores the need to study ontogenetic series of each species.

Underwood (1976:155) analysed four respiratory

variables in his study of booid snakes. Two of those, length of intrapulmonary bronchus as percentage of length of right lung (his character no.21) and level of junction of systemic arches in relation to tip of ventricle (no.22), exhibit variation within pythonines; however, in my opinion the nearly continuous nature of the variation makes it impossible to identify discrete character states. The fact that Underwood & Stimson (1990) did not include these two characters implies that they faced the same problem.

The diploid chromosome number ($2n = 36$) that occurs in all the pythonines examined thus far (*amethistina*, *boeleni*, *molorus* and *papuanus*) appears to be plesiomorphic (Kluge, 1991, 1993). However, Mengden & Stock (1980, fig.2) emphasised that all the pythonine species they examined (*amethistina*, *boeleni* and *papuanus*) had unique small interstitial regions of heterochromatin on the three largest chromosomes, as revealed with the C-chromosome banding technique. More observations on booids, and especially pythonines, are required before the phylogenetic informativeness of this variation can be judged. Such an assessment will be an important test of the conservative nature of banding patterns (King, 1985; see however Kluge, 1991:44).

According to Shaw & Campbell (1974), Shine (1985), Mehrrens (1987), and Shine & Slip (1990), acrochordids, anilioids (including *Anilius*, *Cylindrophis* and uropeltids; *Anomochilus* must be confirmed), all boines (*Corallus cropanii* is unknown), *Charina*, *Eryx*, *Lichanura* and tropidophiines (*Exiliboa* and

Ungaliophis require further study) are viviparous, whereas bolyeriines (*contra* Kluge, 1991, but following S. Tonge (personal communication) for *Bolyeria*, and Bloxam & Tonge, 1986, and Ross & Marzec, 1990 for *Casarea*), *Calabaria*, *Loxocemus*, all pythonines (eg, Charles *et al.*, 1985), and *Xenopeltis* are oviparous. The polarity is equivocal because equally parsimonious optimisations obtain on the accepted outgroup hypothesis (Fig.1). I have no reason to prefer one over the other; the pattern of variation among the more inclusive clades of snakes suggests both modes can evolve independently. Thus, at this time I am forced to treat this interesting aspect of life history variation as phylogenetically uninformative.

Data Analysis

Four equally most parsimonious hypotheses are obtained when the 121 characters summarised in Table 31 are analysed with the mhennig (**m***) and extended branch swapping (**bb***) algorithms, assuming additivity ($S = 474$, $C = 0.40$, $R = 0.63$). The strict consensus of those four hypotheses is illustrated in Fig.20 ($S = 479$, $C = 0.40$). The second iteration of character weighting applied to the additively binary coded multistate characters, which involves the **xs w** (see Methods and Materials section and Table 32 for **s** and **r** parameters), **m***, and **bb*** algorithms, led to two equally most parsimonious branching patterns, the strict consensus of which is

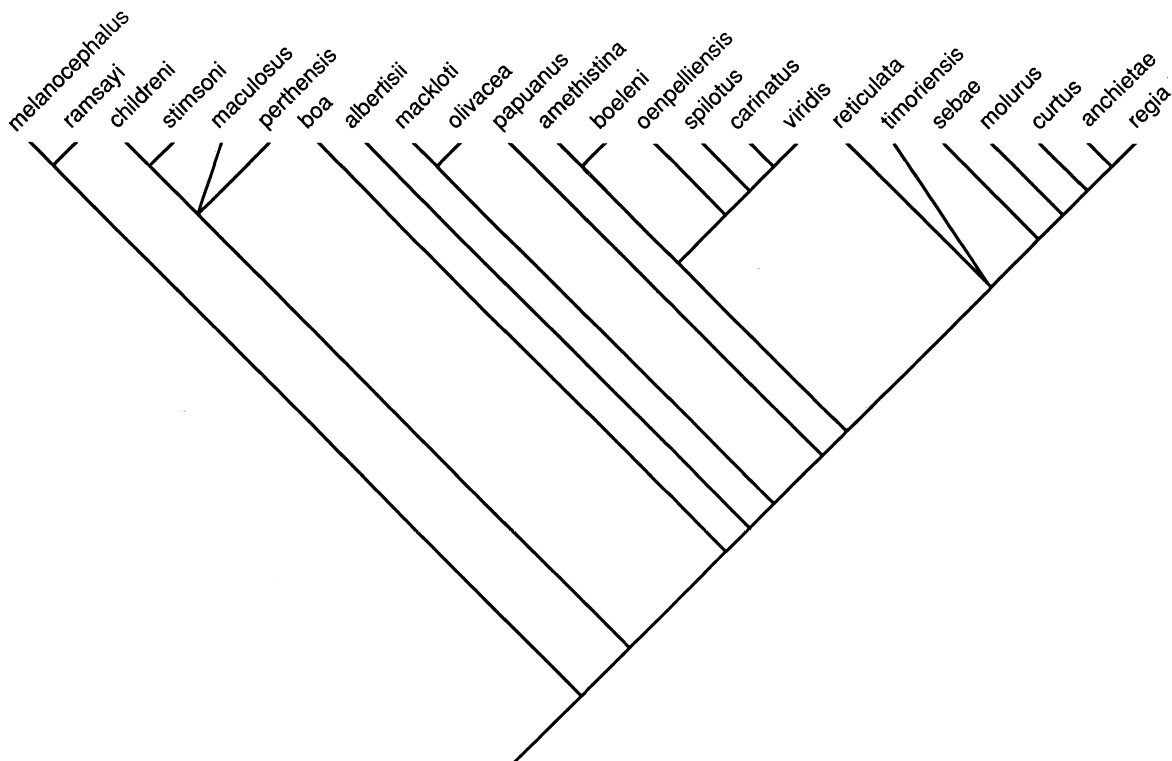


Fig.20. Strict consensus ($S = 479$, $C = 0.40$) of the four equally most parsimonious hypotheses of pythonine sister species relationships ($S = 474$, $C = 0.40$, $R = 0.63$) obtained from **m*** and **bb*** analyses of the 121 characters summarised in Table 31 (assuming additivity). The four cladograms form the basis for the weighted hypothesis illustrated in Figure 21.

shown in Figure 21 ($S=475$, $C=0.40$). This hypothesis requires 281 extra steps to explain the available evidence, whereas a completely unresolved topology requires 481 *additional* extra steps (Kluge, 1989a). Additional iterations of character weighting could not completely resolve the hypothesis of pythonine relationships.

When the multistate characters (Table 31) are treated as nonadditive and analysed with the m^* and bb^* algorithms, there are 17 equally most parsimonious hypotheses ($S = 409$, $C = 0.47$, $R = 0.63$), the strict consensus of which is illustrated in Figure 22 ($S = 452$, $C = 0.43$). This consensus hypothesis requires 258 extra steps to explain the available evidence, whereas a completely unresolved topology requires 338 *additional* extra steps (Kluge, 1989a). As noted in the Methods and Materials section, successive weighting could not be applied to nonadditively coded multistate characters because a computationally efficient algorithm for finding most parsimonious branching patterns is unavailable. Figures 21 and 22 have 13 clades in common in the ingroup, and I use those consistently resolved components as my most conservative hypothesis of pythonine sister group relationships (summarised in Fig.22).

As noted earlier, the data set in Table 31 consists of skeletal and nonskeletal characters, 72 and 49, respectively. The size of these two classes of evidence is nearly equal ($M = 99$ and 95 steps, respectively), and the effect of analysing all of the available characters at

one time (total evidence) can be investigated with separate analyses of the skeletal and nonskeletal characters (Kluge, 1989a). Underwood & Stimson's comparable study of pythonine relationships employed only 9 ($M = 14$) and 28 ($M = 56$) skeletal and nonskeletal characters, respectively.

When the 72 skeletal characters (1-72 in Table 31; 99 binary factors) are analysed separately and treated as additive, nine equally most parsimonious cladograms ($S = 210$, $C = 0.47$, $R = 0.70$) are obtained, which can be minimally resolved, after one iteration of character weighting, to two most parsimonious patterns, the strict consensus of which is presented in Figure 23 ($S = 211$, $C = 0.46$). Treated likewise, the 49 nonskeletal characters (73-121 in Table 31; 95 binary factors) result in 74 equally most parsimonious topologies ($S = 250$, $C = 0.37$, $R = 0.59$), which can be minimally resolved, after one iteration of weighting, to a single most parsimonious topology, which is reproduced in Figure 24 ($S = 252$, $C = 0.37$). The strict consensus of the 117 equally most parsimonious branching patterns ($S = 201$, $C = 0.49$, $R = 0.69$) obtained from the nonadditive treatment of the 72 skeletal characters is shown in Figure 25 ($S = 230$, $C = 0.42$). A comparable, nonadditive analysis was performed on the 49 nonskeletal characters, and the strict consensus of the 30 equally most parsimonious cladograms ($S = 197$, $C = 0.48$, $R = 0.60$) is presented in Figure 26 ($S = 201$, $C = 0.47$). Only two of 23 possible ingroup clades is consistently present in Figures 23-26,

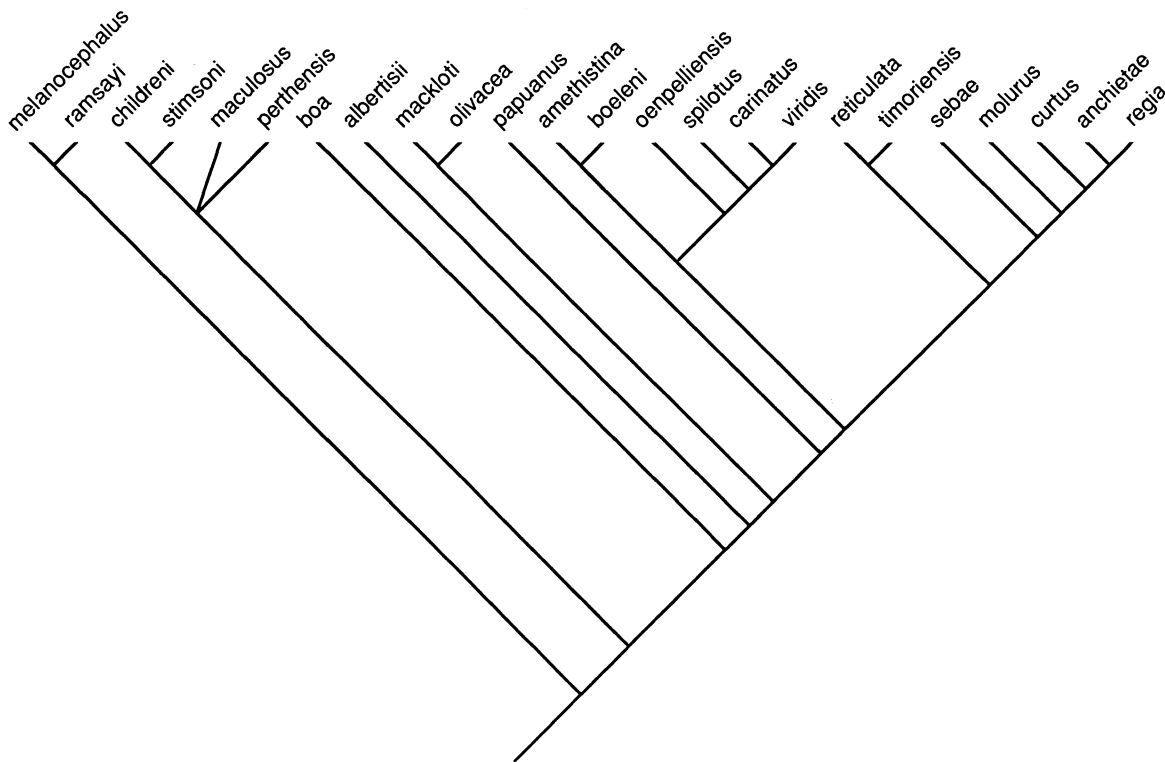


Fig.21. Strict consensus ($S = 536$, $C = 0.36$) of the two equally most parsimonious hypotheses of pythonine sister species relationships ($S = 475$, $C = 0.40$) obtained from m^* and bb^* analyses. This is the product of a second iteration of character weighting (the $xs w$ protocol; see Table 32 for parameters and values), applied to additively binary coded multistate characters, which began with the four equally most parsimonious hypotheses discussed in Figure 20.

(*melanocephalus*, *ramsayi*) and (*carinatus*, *spilotus*, *viridis*), whereas 13 are present when all of the available evidence is considered (Figs 21,22)⁴. These comparisons suggest considerable incongruence between the separate classes of evidence (compare Figs 23, 24 and 10, 11), but relatively little loss in consistency (C) when the data sets are combined. Unfortunately, the available quantitative methods seem incapable of consistently indexing the complex relation of incongruence within and between sets of characters (Swofford, 1991: 316-318). However, documenting exactly the proportion of synapomorphies that can be explained as homologues was not the only basis for promoting total evidence studies over those employing taxonomic congruence (Kluge, 1989a).

It is also important to emphasise that none of the consistency values obtained in this study are low, relative to the number of terminal taxa examined (Sanderson & Donoghue, 1989:fig.1). Moreover, most of the recognised clades can be diagnosed with two or more unique and unreversed synapomorphies (Fig.22).

Underwood & Stimson's (1990) recent account of

⁴ Nested parentheses designate clades of different levels of inclusiveness and exclusiveness; Wiley's (1981) sequencing convention does not apply to these examples.

pythonine relationships considered fewer species (16 of the 24 recognised herein), as well as fewer character transformations ($S = 70$). Their preferred hypothesis of species lineages (figs 7,8), redrawn here as Figure 3, is markedly different from that in Figure 21 (the comparable additive analysis of multistate characters), and provides a much less efficient explanation of the evidence summarised in Table 31. When only the terminal taxa in common are compared, the Underwood & Stimson proposition requires an additional 40 extra steps ($S = 444$ versus 404). Only four clades are present in both hypotheses: ((*amethistina*, *boeleni*) (*spilotus*, *viridis*)) and (*curtus*, *molurus*, *regia*, *reticulata*, *sebae*, *timoriensis*). Much of the difference in fit to data concerns the placement of *melanocephalus* because when it is considered the sister lineage to all other terminal taxa in Figure 3, the number of additional extra steps is 24 ($S = 428$).

Underwood & Stimson's (1990) research illustrates the effect analytical methods can have on discovering relationships. Those authors used a modified clique method (Gauld & Underwood, 1986: 569), which they admit "may not lead to a most parsimonious dendrogram" (see also Kluge, 1976). Thus, it should come as no surprise that my parsimony

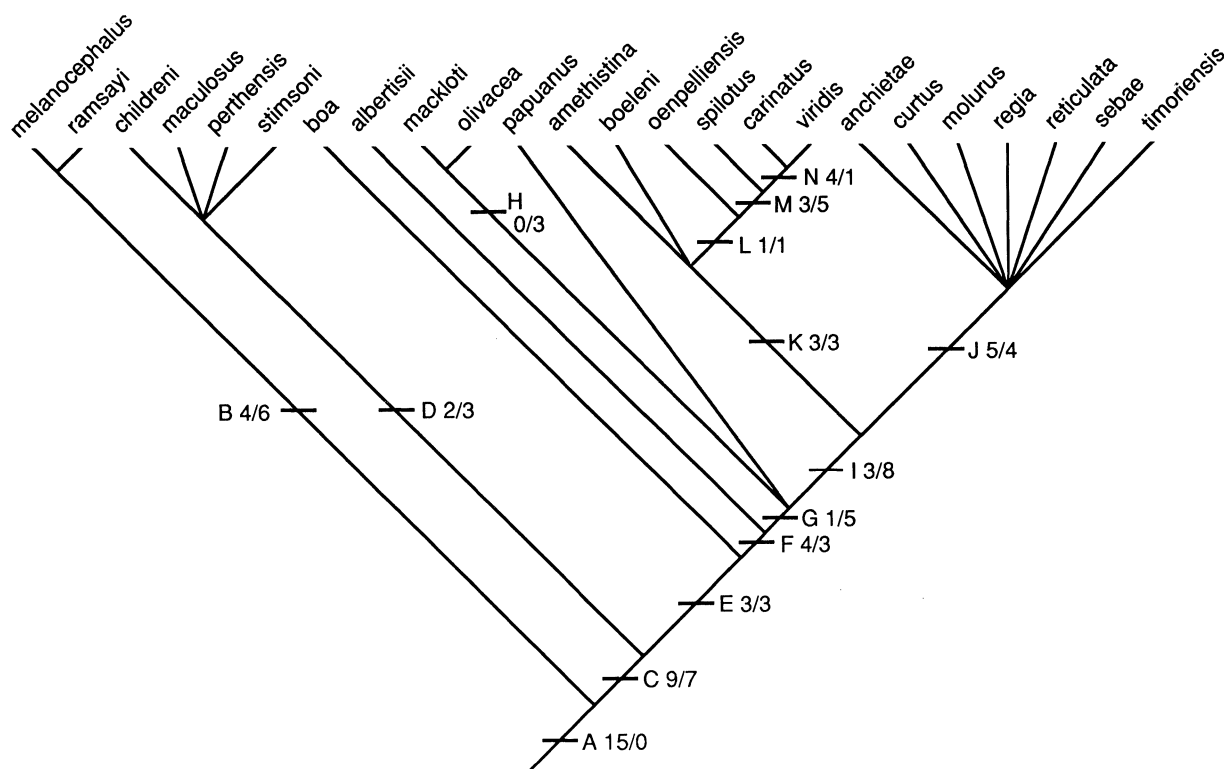


Fig.22. The strict consensus ($S = 452$, $C = 0.43$) of the 17 equally most parsimonious hypotheses of pythonine sister species relationships ($S = 409$, $C = 0.47$, $R = 0.63$) obtained from heuristic parsimony analyses, with limited (m^*) and extended (bb^*) branch-swapping, of the 121 characters summarised in Table 31 (assuming nonadditivity). A-N denote the clades cited in the Diagnoses section. The numbers of unique and unreversed and homoplasious synapomorphies diagnostic of a clade precede and follow the slash, respectively. Only those synapomorphies that can be unambiguously optimised under both assumptions of additivity and nonadditivity are included. Compare this preferred hypothesis to those of McDowell (1975), Underwood (1976), and Underwood & Stimson (1990), Figures 1 to 3, respectively. See also Figure 27.

analysis (using **m*** and **bb***) of their data (Underwood & Stimson, 1990, appendix I; *Loxocemus* excluded, as per their method [p.586]) yields a different result, presented here as the strict consensus of 13 equally most parsimonious cladograms ($S = 191$, $C = 0.36$, $R = 0.56$). However, it is noteworthy that their product (Fig.27) exhibits many striking similarities to my preferred hypothesis (Fig.22). In particular, there is the collateral placement of *melanocephalus* to all other pythonines, and the highly derived nature of the African and South-east Asian species. It is also worth pointing out, that my cladogram ($S = 204$; Fig.21; the comparable additive analysis of multistate characters) provides a better fit to Underwood & Stimson's data than does their estimate of pythonine species relationships ($S = 209$; Fig.3).

McDowell's (1975) hypothesis, illustrated in Figure 1, fares no better in explaining the evidence summarised in Table 31. Employing only the terminal taxa in common, Figure 1 requires an additional 49 extra steps compared to that in Figure 21 ($S = 484$ and 435 , respectively). While the difference in *melanocephalus*' position accounts for 20% of the extra homoplasy ($S = 474$), it is not so influential as Underwood & Stimson's placement of that species. Only four clades are in common between Figures 1 and 21 (the comparable additive analysis): (*mackloti*, *olivacea*) and ((*amethistina*, *boeleni*) (*spilotus*, *viridis*)).

Underwood's (1976) hypothesis, which is shown in

Figure 2, does the least well in explaining the evidence in Table 31. It requires an additional 55 extra steps compared to that pattern in Figure 21 ($S = 334$ and 279 , respectively), but *melanocephalus*' sister group relationship to all other pythonines investigated accounts for even less of that difference ($S = 314$). There are only two clades in common in Figures 2 and 21 (the comparable additive analysis of multistate characters): (*spilotus*, *viridis*) and (*curtus*, *regia*, *reticulata*).

The Reality of the Ingroup

The booid snakes traditionally referred to as pythonines, excluding *Calabaria* and *Loxocemus* (*sensu* Underwood, 1976:152-153; Fig.4), formed a highly corroborated clade in my preliminary study of relationships of the major groups of snakes (Kluge, 1991). *Calabaria*'s placement among erycines has been reconfirmed (Kluge, 1993), and *Loxocemus* continues to appear to be the sister lineage to the group consisting of advanced snakes, boines, erycines and pythonines. The following synapomorphies diagnosed unambiguously, under both assumptions of additivity and nonadditivity, the pythonine entity identified in my preliminary work: (1) ascending process of premaxilla absent; (2) horizontal lamella of nasal, between nostrils, narrow; (3) descending

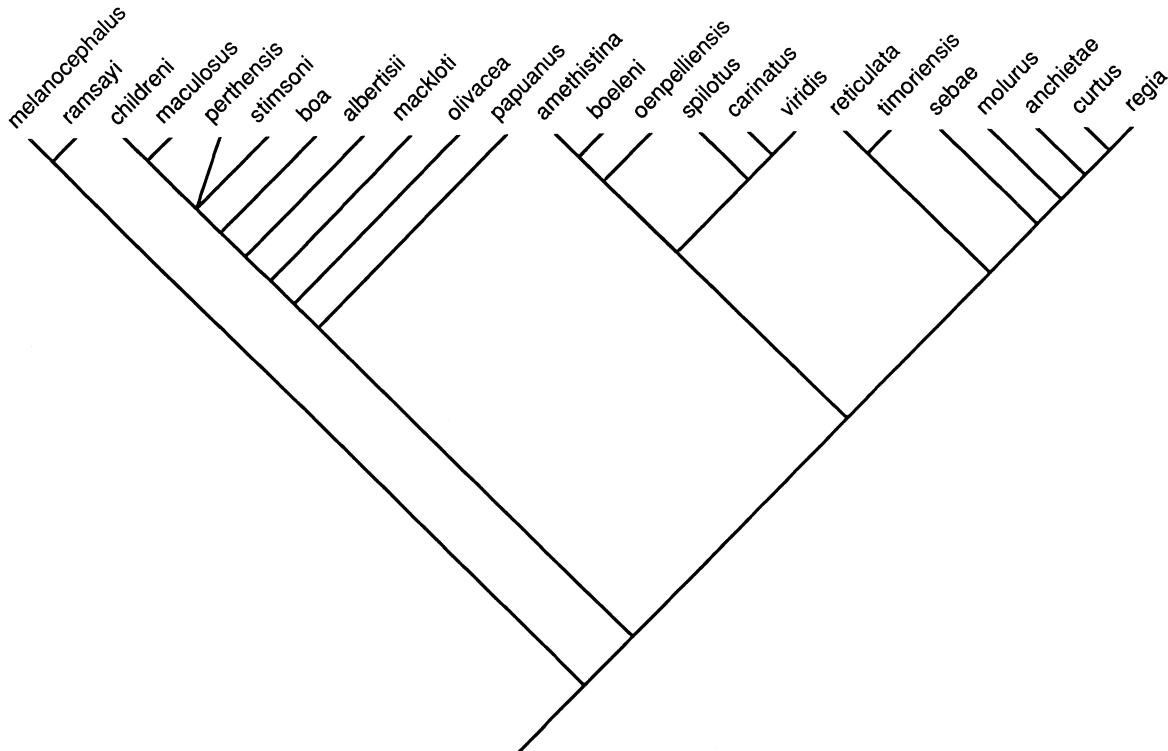


Fig.23. Strict consensus ($S = 211$, $C = 0.46$) of the two most parsimonious hypotheses of pythonine sister species relationships obtained from heuristic analyses, with limited (**m***) and extended (**bb***) branch-swapping, of the 72 skeletal characters summarised in Table 31 (1-72; applied to additively binary coded multistate characters). This pattern resulted from an analysis of the nine best-fitting hypotheses ($S = 210$, $C = 0.47$), after one iteration of character weighting.

lamella of nasal absent posteriorly; (4) dorsal contact between nasal and frontal; (5) presence of supraorbital; (6) basioccipital participates in *apertura lateralis* of *recessus scalae tympani*; (7) left posterior vidian foramen larger than right; (8) *intermandibularis anterior* muscle undivided.

Further study suggests that some of these features cannot be viewed as diagnostic of pythonines. As noted in the section on Other Variation, the absence of the ascending process seems to be best interpreted as plesiomorphic at the general taxonomic level of pythonines (Underwood, 1976:69). I have also considered the variation in the *apertura lateralis* to be so extensive as to be phylogenetically uninformative (see also above), and I have discovered that the level of taxonomic generality of a narrow anterodorsal nasal (character 8) cannot be interpreted unambiguously on Figure 22. Moreover, the depth of the descending lamella of the nasal and the place of contact between the nasal and frontal (items 3-4 above) have been expressed as a single character (no.11) in this study because they appear to be correlated logically. However, that variation, redescribed as narrow and shallow horizontal and descending lamellae, respectively, delimits pythonines only under the assumption of additivity. Such a reinterpretation of evidence is another example of the dynamic nature and importance of research cycles in cladistics (Kluge, 1991).

The presence of the supraorbital bone (postfrontal) has been the feature most often cited as diagnostic of pythonines (Frazzetta, 1959:469-470; Underwood, 1967:69-71, 1976:166-170; McDowell, 1975:30, 1987:28-29; Underwood & Stimson, 1990:567), and in some cases the only characteristic mentioned (Boulenger, 1893:74). As discussed under character 29, that bone is also present in *Calabaria*, *Dinilysia*, *Loxocemus*; however, given the pattern of relationships in Figure 4, that taxonomic distribution does not keep the presence of a supraorbital from diagnosing pythonines. Likewise, the larger left posterior vidian foramen (character 63) continues to diagnose pythonines, as does the presence of an undivided *intermandibularis anterior* muscle (character 109). The phylogenetic informativeness of characters such as supraorbital and vidian canal variables emphasises the importance of total evidence and character congruence. For example, Underwood & Stimson's (1990:566-567) conclusion that *Loxocemus* and pythonines are sister taxa is based in large part on these synapomorphies.

In the present study, I have identified an additional 13 characters diagnostic of pythonines, 19, 23-24, 26, 38, 44, 62, 108, 110, 114, 117 and 119-120 (see Diagnoses section). Thus, a total of 16 apomorphies delimit pythonines from all other booids (Figs 4,22), 9 skeletal and 7 nonskeletal. Such a large and varied amount of evidence is ample justification for

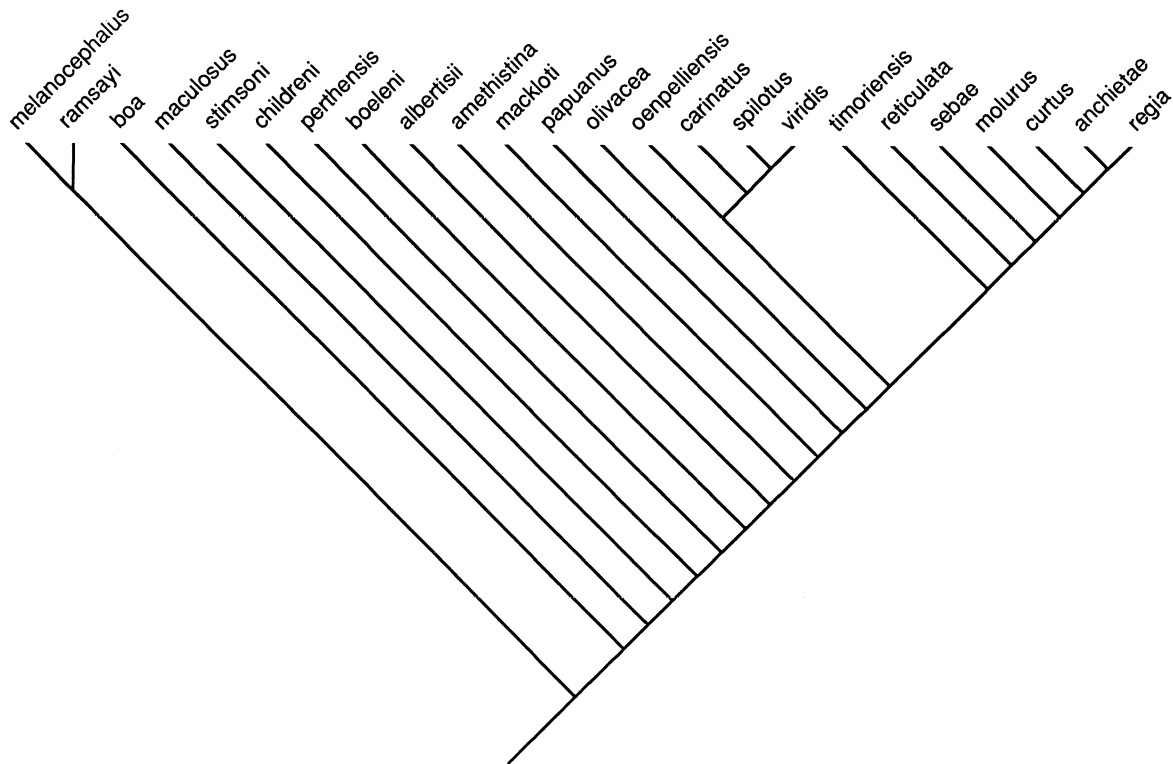


Fig.24. A most parsimonious hypothesis of pythonine sister species relationships ($S = 252$, $C = 0.37$) obtained from a heuristic parsimony analysis, with limited (**m***) and extended (**bb***) branch-swapping, of the 49 nonskeletal characters summarised in Table 31 (73-121; applied to additively binary coded multistate characters). This pattern resulted from an analysis of the 74 best-fitting hypotheses ($S = 250$, $C = 0.37$), after one iteration of character weighting.

continuing to treat pythonines as a monophyletic taxon. Also, characters 11, 18, 52 and 115 (states 1 or 2), and 12 (state 2) and 76 (state 2) can be added to that list, under the assumptions of additivity or nonadditivity, respectively.

Relationships Among the Parts of the Ingroup

While the data analysis indicates that a large number of characters, representing different classes of data, have to be investigated to realise substantial taxonomic resolution, pythonines appear to be no more prone to homoplasy than any other group of organisms (Sanderson & Donoghue, 1989). I suspect the reason many herpetologists (Brongersma, 1953: 319; McDowell, 1975:30; Underwood, 1976; Schwaner & Dessauer, 1981; L.A. Smith, 1981a,b, 1985:273-275; Banks & Schwaner, 1984; Storr *et al.*, 1986:34; Underwood & Stimson, 1990) have concluded that subgroups of pythonines are weakly differentiated is due to the few characters employed. However, methodological artifact cannot be ruled out as a contributing factor because none of these workers employed parsimony methods which attempt to find best fitting hypotheses for all of the available characters based solely on special similarity (synapomorphies).

One might infer weak differentiation from

interspecific crosses. For example, Mr Ray Field of Townsville, Queensland, successfully interbred *amethistina* and *spilotus* in captivity, the progeny (eg, AM R127423) being approximately intermediate in scalation between the two parents, whereas the colour pattern is more like the eastern *spilotus* parent (Banks & Schwaner, 1984). Banks & Schwaner (1984) reported on a more extraordinary cross, between a female *mackloti* and a male *spilotus*. The offspring from that mating appear to be more like *spilotus* in scalation, but they are a combination of the parents' colour patterns. Regardless of the apparent ease with which such matings take place in captivity, there remains the question as to the viability and reproductive success of the hybrid offspring. In any case, the ability to interbreed is the plesiomorphic condition, and my results suggest that delimiting groups of pythonines is no more difficult (see also Underwood & Stimson, 1990) than distinguishing clades of boines and erycines (Kluge, 1991, 1993).

Many previous hypotheses of pythonine relationships (eg, Figs 2,3; Underwood, 1976; Underwood & Stimson, 1990) recognise Australia-New Guinea and Africa-South-east Asia species as separate monophyletic entities. However, the cladogram that best fits the evidence in this study (Figs 22,28; Table 31) indicates that the Australia-New Guinea taxa form a taxonomic grade series of groups, with the (*melanocephalus*, *ramsayi*) lineage being collateral to all other

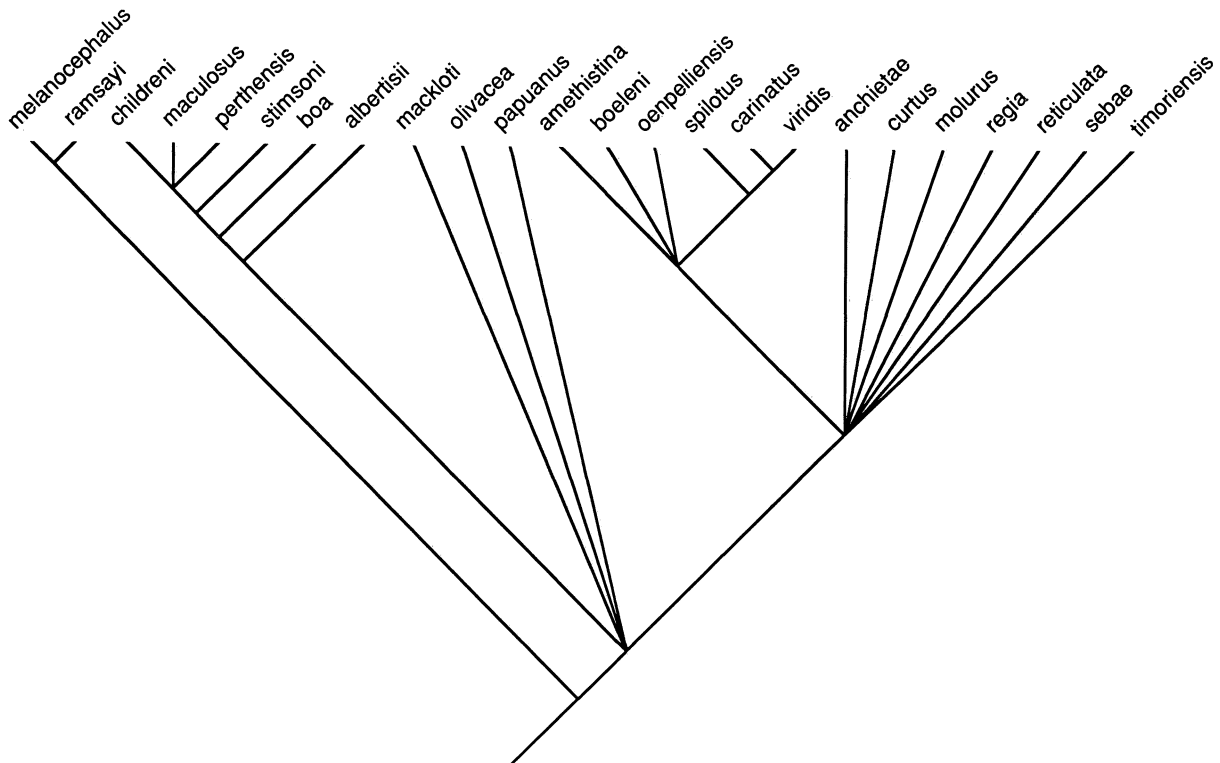


Fig.25. Strict consensus of the 117 equally most parsimonious hypotheses of pythonine sister species relationships ($S = 201$, $C = 0.49$) obtained from heuristic parsimony analyses, with limited (**m***) and extended (**bb***) branch-swapping, of the 72 skeletal characters summarised in Table 31 (1-72; assuming nonadditivity).

pythonines. To convert the pattern of relationships in Figures 22 and 28 into Australia-New Guinea and Africa–South-east Asia clades of species requires 33 ($S = 568$) and 21 ($S = 473$) additional extra steps under the assumptions of additivity ($S = 535$) and nonadditivity ($S = 452$), respectively. Thus, Figures 22 and 28 provide a considerably better fitting hypothesis, and it strongly suggests the pythonine radiation originated within the Australia-New Guinea region (see Biogeography section below).

A Monophyletic Taxonomy

Monophyly insures that sister group relationships are communicated accurately and efficiently, and I believe the following nomenclature (Fig.29) proposed for some of the least inclusive and most commonly referred to assemblages delimited in Figure 22 provides that taxonomy: (1) *Antaresia* Wells & Wellington is used for the (*childreni*, *maculosus*, *perthensis*, *stimsoni*) clade; (2) *Aspidites* W. Peters for (*melanocephalus*, *ramsayi*); (3) *Bothrochilus* Fitzinger for *boa*; (4) *Leiopython* Hubrecht for *albertisii*; (5) *Liasis* Gray for (*mackloti*, *olivacea*); (6) *Morelia* Gray for (*amethystina*, *boeleni*, *carinatus*, *oenpelliensis*, *spilotus*, *viridis*); and (7) *Python* Daudin for (*anchietae*, *curtus*, *molurus*, *regia*, *reticulata*, *sebae*, *timoriensis*).

Unfortunately, no genus group epithet is available for *papuanus*, and I take this opportunity to christen that species with the name *Apodora* (Greek; feminine; meaning “a peeling of the skin” [Brown, 1956:716]), which emphasises the peculiar nature of this species’ relatively thin and fragile integument. The unresolved relationships of *Apodora* and *Liasis* also requires those taxa be denoted *sedis mutabilis* (Wiley’s, 1981:211 convention 4). *Sedis mutabilis* means (L.) of changeable position, and that convention is useful in highlighting monophyletic groups in polytomous inter-relationships. There is no need for an additional convention, such as metataxon (Kluge, 1989b; *contra* Mishler, 1990:208). *Sedis mutabilis* will also have to be applied to the higher taxonomic name proposed for the (*Morelia*, *Python*) group.

If further research delimits the (*amethystina*, *boeleni*) clade, as per Figure 21, then I believe *Simalia* Gray (1849:91) should be used for the group because it is the oldest genus group name available. Of the two species Gray included under his new taxon, *amethystina* and *mackloti*, only the former was associated with *Simalia* in Boulenger’s (1893:81) subsequent comprehensive review of snake taxonomy. I interpret Boulenger’s action as restricting, by implication, the type species of *Simalia* to *amethystina*.

I suggest attributing names to more inclusive groups of pythonines await complete resolution of relationships and confirmation of that overall pattern

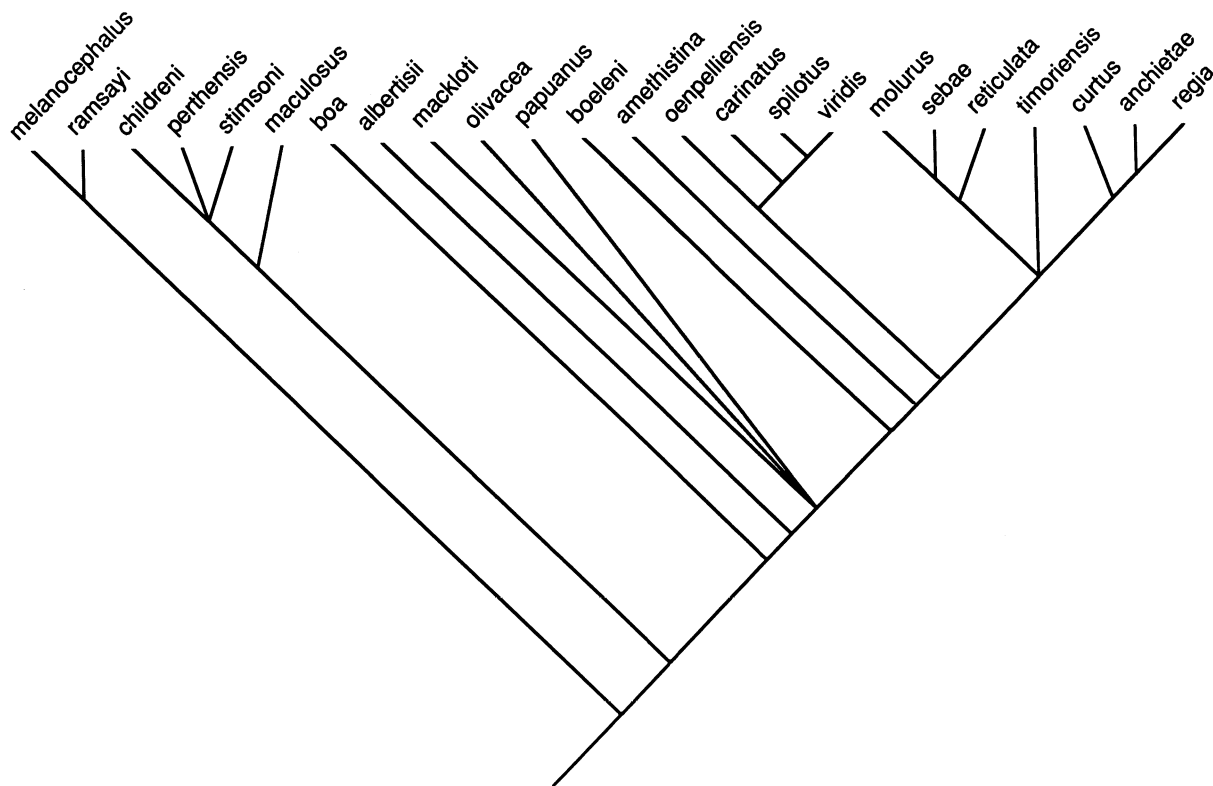


Fig.26. Strict consensus of the 30 equally most parsimonious hypotheses of pythonine sister species relationships ($S = 197$, $C = 0.48$) obtained from heuristic parsimony analyses, with limited (m^*) and extended (bb^*) branch-swapping, of the 49 nonskeletal characters summarised in Table 31 (73-121; assuming nonadditivity).

with additional evidence. Underwood & Stimson's (1990, appendix II) recently proposed higher classification exemplifies the importance of this suggestion, in light of the fact that their Morelini is paraphyletic on my hypothesis (Figs 22,29). For the time being, and with little diminished convenience, the branching pattern provided in Figures 22 and 29 can serve as the hierarchy from which monophyletic combinations of generic names

are extracted. I apply Wiley's (1981:209) sequencing convention to all levels of pythonine taxonomy, unless noted otherwise.

The following hierarchy of names summarises the monophyletic taxonomy of pythonines I recommend. The species names have been corrected for gender, and the new genus group name is indicated.

(*Antaresia*, *Apodora*, *Aspidites*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, *Python*)

Aspidites W. Peters (1876a)

A. melanocephalus (Krefft, 1864)

A. ramsayi (Macleay, 1882)

(*Antaresia*, *Apodora*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, *Python*)

Antaresia Wells & Wellington (1984)

A. childreni (Gray, 1842) *sedis mutabilis*

A. maculosa (W. Peters, 1873) *sedis mutabilis*

A. perthensis (Stull, 1932) *sedis mutabilis*

A. stimsoni (L.A. Smith, 1985) *sedis mutabilis*

(*Apodora*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, *Python*)

Bothrochilus Fitzinger (1843)

B. boa (Schlegel, 1837)

(*Apodora*, *Leiopython*, *Liasis*, *Morelia*, *Python*)

Leiopython Hubrecht (1879)

L. albertisii (W. Peters & Doria, 1878)

(*Apodora*, *Liasis*, *Morelia*, *Python*)

Apodora n.gen. *sedis mutabilis*

A. papuana (W. Peters & Doria, 1878)

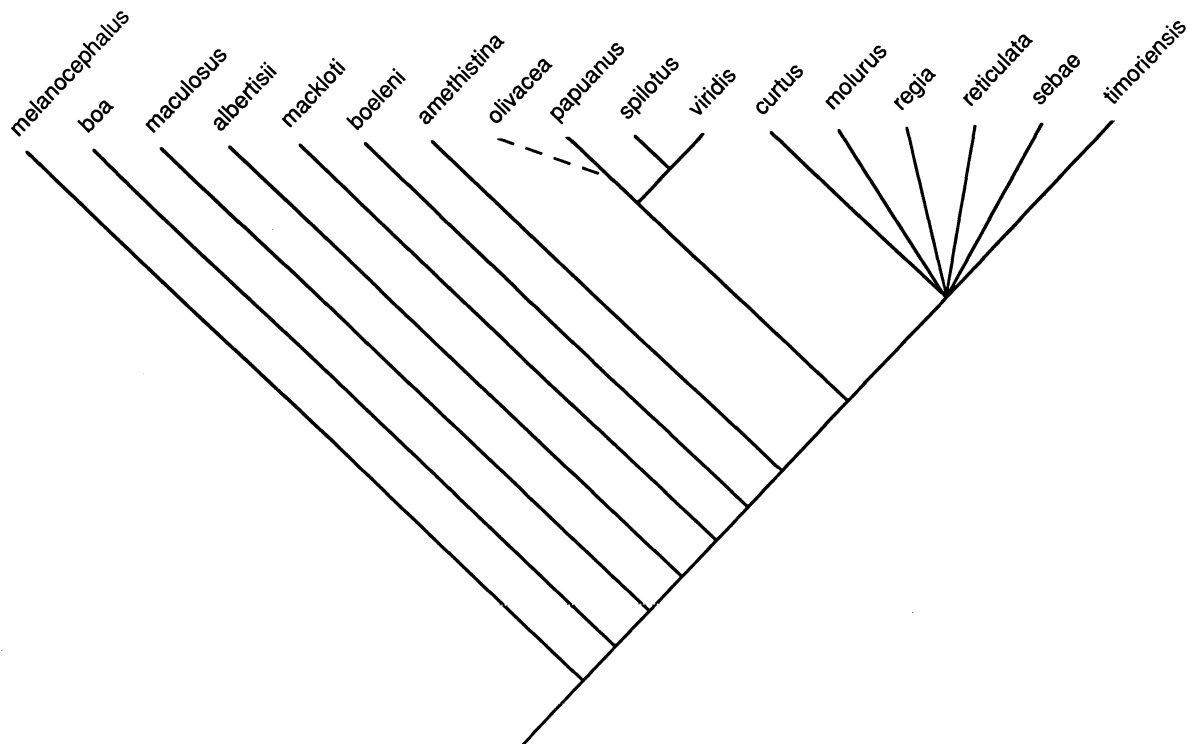


Fig.27. Strict consensus of the 13 most parsimonious hypothesis of pythonine species relationships obtained from heuristic parsimony analyses, with limited (**m***) and extended (**bb***) branch-swapping, of Underwood & Stimson's (1990, appendix I) data set (*Loxocemus* excluded; **S** = 191, **C** = 0.36, **R** = 0.56). According to Underwood & Stimson (p.570) *olivacea* is the sister group of *papuanus*. Compare to Figures 3 and 22.

- Liasis* Gray (1842) *sedis mutabilis*
L. mackloti Duméril & Bibron (1844)
L. olivaceus Gray (1842)
(*Morelia*, *Python*) *sedis mutabilis*
Python Daudin (1803)
P. anchietae (Bocage, 1887) *sedis mutabilis*
P. curtus (Schlegel, 1872) *sedis mutabilis*
P. molurus (Linnaeus, 1758) *sedis mutabilis*
P. regius (Shaw, 1802) *sedis mutabilis*
P. reticulatus (Schneider, 1801) *sedis mutabilis*
P. sebae (Gmelin, 1789) *sedis mutabilis*
P. timoriensis (W. Peters, 1876) *sedis mutabilis*
Morelia Gray (1842)
M. amethystina (Schneider, 1801) *sedis mutabilis*
M. boeleni (Brongersma, 1953) *sedis mutabilis*
M. oenpelliensis (Gow, 1977)
M. spilota (Lacépède, 1804)
M. carinata (L.A. Smith, 1981)
M. viridis (Schlegel, 1872)

Diagnoses⁵

The clades of terminal taxa (Fig.22) are diagnosed according to character and state numbers and in ordinary anatomical terms. The numbers provide ready access to additional information summarised in the Character Descriptions section and Tables 31 and 32. Diagnostic

features are not definitional, and a character's subsequent change within a clade must be considered when this information is used to place a specimen in the cladistic hierarchy.

A. (*Antaresia*, *Apodora*, *Aspidites*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, *Python*): 19 (Fig.7) – lachrymal foramen completely enclosed by bone; 23 –

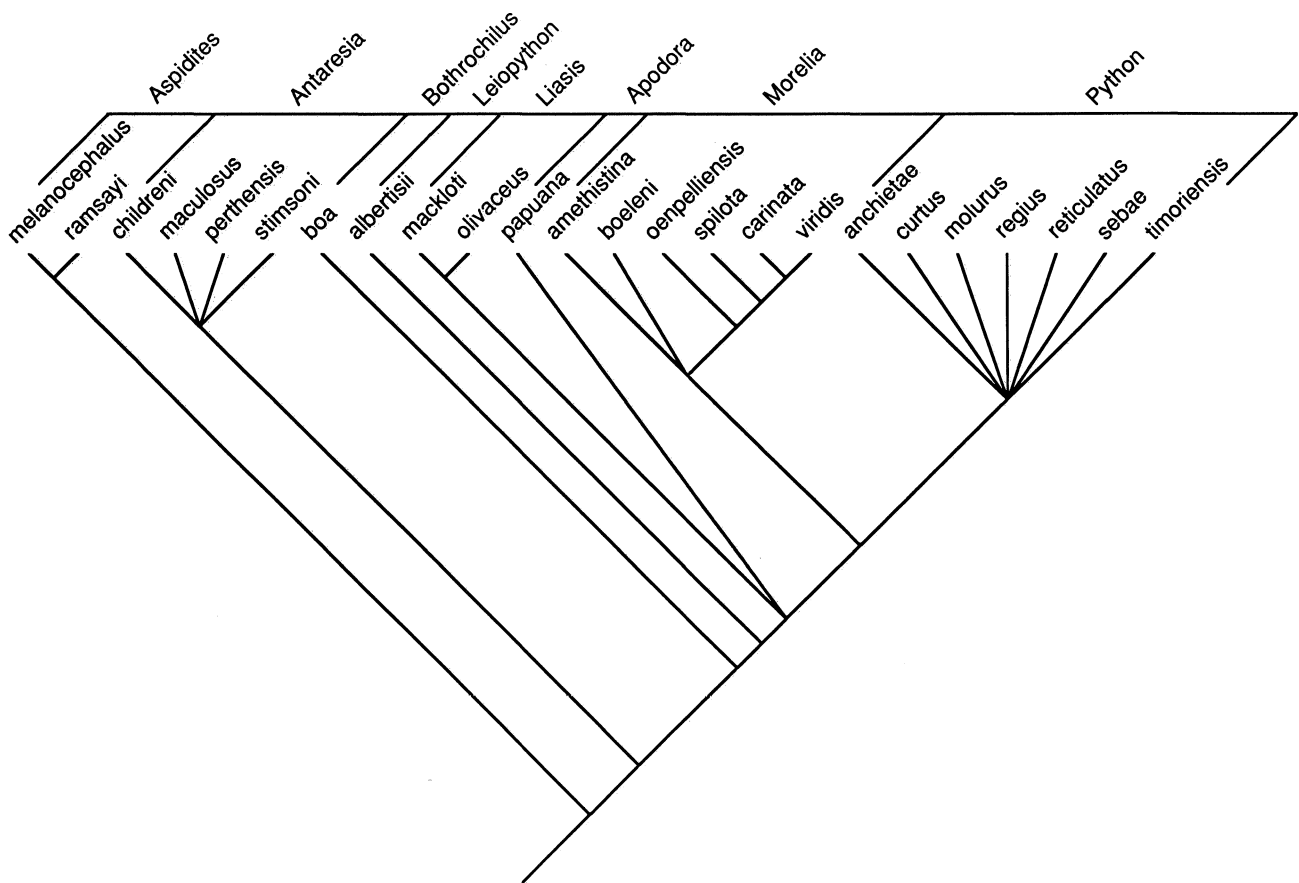


Fig.28. Adopted monophyletic generic taxonomy relative to the hypothesis of species relationships summarised in Figure 22.

anterodorsal margin of frontal, that area overlapped by nasal and prefrontal, lies below general horizontal level of dorsal surface of frontal; 24 – prefrontal process of frontal projects anterolaterally; 26 (Fig.8) – lateral margin of frontal conspicuously concave; 29 (Fig.8) – supraorbital present; 38 – medial anterior process obviously longer than lateral anterior process on maxillary end of ectopterygoid; 44 – anterodorsal end of quadrate very wide; 62 – basisphenoid fenestra exposed and relatively large; 63 – left common canal in sphenoid larger than right; 108 – *levator anguli oris* muscle absent; 109 – *intermandibularis anterior* muscle undivided; 110 – pancreas fully lobed; 114 – *sulcus spermaticus* branches at a point level with upper margin of primary flounce; 117 (Fig.19) – proximal flounce present on hemipenis;

119 (Fig.19) – an anastomosis of distal flounces present on hemipenis; 120 – shivering thermogenesis present during egg brooding.

B. *Aspidites*: 6c (Fig.5) – median fenestra present on ventral surface of premaxilla, anterior to premaxillary channels; 7 (Fig.5) – maxillary process of premaxilla located well beyond arc formed by anterior ends of maxillae; 27c (Fig.5; see also clade F) – anterior corner of frontal projects slightly beyond posterior corner; 28 – suture between frontal and parietal, as it arises from dorsal margin of optic foramen, oriented markedly anteriorly; 34c – anterior head of dorsomedian end of postorbital, as observed ventrally from within orbit, nearly, or completely, separated from frontal; 40c – ectopterygoid contacts pterygoid dorsally; 49 (Fig.12) – dorsolateral process of septomaxilla, that which projects posteriorly beneath nasal and/or prefrontal, barely noticeable or absent; 54 – rostral margin of choanal process of palatine oriented posteromedially, relative to long axis of dentulous ramus of palatine; 85(2)c (Fig.15) – posterior prefrontal scales in contact on midline; 121c – maximum total length 1.5-3.9 m.

C. (*Antaresia*, *Apodora*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, *Python*): 1(2) (Fig.5) – usually two adult premaxillary teeth per ramus; 5c (Fig.5) – ventral openings for premaxillary channels located anterior to posterior margin of premaxillary teeth; 31c (Fig.8) – supraorbital broadly separated from parietal; 41c (Fig.10)

⁵ The capitalised letter-index refers to the clades illustrated in Figure 22. The only diagnostic information summarised below is that which obtains without regard to the assumptions of multistate character additivity or nonadditivity. Numbers without parentheses refer to particular characters (1-121; see Character Descriptions and Table 31), those within parentheses specify character states. Character state 1 can be assumed, unless indicated otherwise. The lower-case letter c means convergence/parallelism, r equals reversal, and x signifies both c and r. Character state evolution can be assumed to be unique and unreversed in pythonines, unless indicated otherwise.

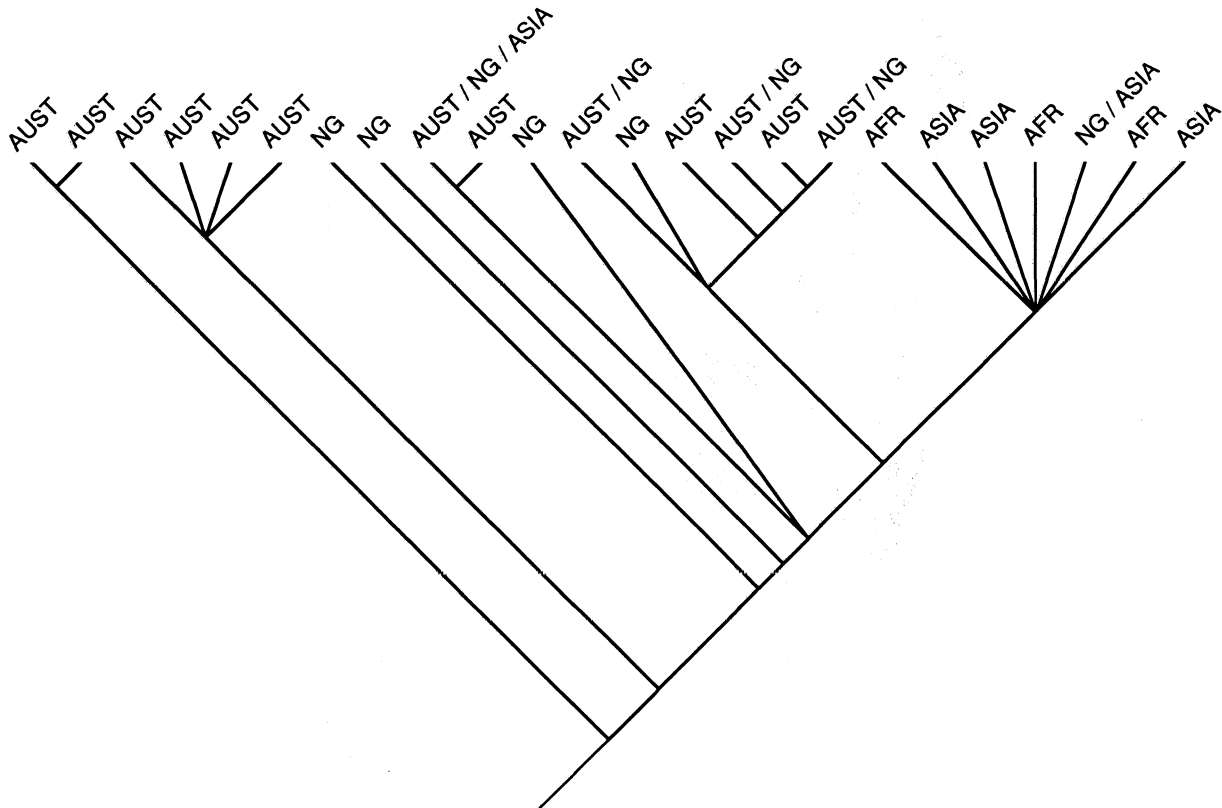


Fig.29. Area cladogram (Kluge, 1988b: fig.1) for pythonines derived from the taxon cladogram summarised in Figure 22. The four areas of endemism are defined as follows: AFR (Africa); ASIA (from Pakistan to the Lesser Sundas and Sulawesi); AUST (Australia, excluding Tasmania); NG (New Guinea region, from the Molucca and Timorlaut Islands in the west to Bougainville, Solomon Islands, in the east, and including islands in Torres Strait).

– prominent lateral crests present on supraoccipital; 45c – quadrate short; 46 (Fig.11) – ventral, horizontal, fluted wing of vomer, posterior to septomaxilla, uniformly narrow; 48(2) (Fig.12) – anterior to vomeronasal fenestra, anterodorsal margin of septomaxilla contains a fenestra broadly continuous with dorsal margin of septomaxilla; 50(2)c – usually seven or eight adult palatine teeth per ramus; 55(0) – maxillary process broad; 66c (Fig.14) – height of dentary teeth changes markedly; 73 – neck slightly narrower than head in adults; 86 – one posterior suture present in nasal scale; 91 (Fig.17) – first, anteriormost, genial scale long compared to other throat scales, particularly posterior genials; 95 – most subcaudal scales paired; 106(2)c – thermoreceptive pits present in four posterior infralabial scales; 111 – each posterior trunk intercostal artery usually supplies more than one body segment.

D. *Antaresia*: 12(3)c – adult maxillary teeth usually 21-22 per ramus; 33 (Fig.9) – anterior head of dorsomedian end of postorbital abuts postorbital process of parietal; 59(0) (Fig.13) – pterygoid process absent on sphenoid; 87c (Fig.16) – two scales present in loreal region; 88c (Fig.16; see also clade I) – series of small scales present adjacent to dorsal margin of supralabials.

E. (*Apodora*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, *Python*): 35(2) (Fig.9) – tall and sharp edged ridge present on mid-dorsal surface of median end of postorbital; 42c – exoccipital has large supratemporal process; 53c – posterior margin of choanal process, from end of medial pterygoid process of palatine, slightly concave; 61 (Fig.13) – deep median keel present on basisphenoid region of sphenoid, posterior to pterygoid processes; 74(3)c – adult tail length usually 4.0-4.4 times head length; 81(0) (Fig.16) – one preocular scale.

F. (*Apodora*, *Leiopython*, *Liasis*, *Morelia*, *Python*): 27c (Fig.8; see also clade B) – anterior corner of frontal projects slightly beyond posterior corner; 51 – anterior palatine teeth long; 58 (Fig.13) – ventral surface of the cultiform process of the sphenoid elevated slightly, anterior to basipterygoid processes and between trabeculae cranii; 67c – dorsal end of coronoid lies slightly at or above apex of surangular process of composite bone; 78c – parietal scale separated from postocular scale; 100 (Fig.18) – pair of thermoreceptive pits present in rostral scale; 102(3) – third supralabial scale possesses thermoreceptive pit.

G. (*Apodora*, *Liasis*, *Morelia*, *Python*): 36(0)c – postorbital contacts ectopterygoid and/or maxilla; 50r – usually five or six adult palatine teeth per ramus; 52(2)c (Fig.11) – choanal process of palatine makes no contact with vomer; 53(2) (Fig.11) – posterior margin of choanal process, from end of medial pterygoid process of palatine, deeply concave; 66(0)r (Fig.14) – height of dentary teeth changes only slightly; 91(0)r (Fig.17) – first, anteriormost, genial scale short compared to other throat scales, particularly posterior genials.

H. *Liasis*: 35c (Fig.19) – low and relatively round ridge present on mid-dorsal surface of median end of postorbital; 94c – apical, sensory, organ present on many posterior upper-body scales; 100(0)r (Fig.18) – rostral

scale without thermoreceptive pits.

I. (*Morelia*, *Python*): 2 (Fig.5) – middle third of anterior margin of premaxilla concave; 5(0)x (Fig.5) – ventral openings of premaxillary channels located posterior to posterior margin of premaxillary teeth; 14 (Fig.6) – large anterior maxillary foramen on lateral surface of maxilla; 30c (Fig.8) – supraorbital wide; 31(0)r (Fig.8) – supraorbital contacts, or is narrowly separated from, parietal; 45(0)r – quadrate tall; 59(2)c (Fig.13) – pterygoid process of sphenoid tall; 81(1)c (Fig.16) – two preocular scales; 87(2) (Fig.16) – three or more scales present in loreal region; 88c (Fig.16; see also clade D) – series of small scales present adjacent to dorsal margin of supralabials; 89c (Fig.16) – five or more supralabial scales between rostral and anteriormost subocular scale.

J. *Python*: 16(0)c (Fig.6) – lateral margin of suborbital region of maxilla oriented nearly vertically; 71 (Fig.14) – posterior margin of mandibular foramen lies even with posterior end of tooth bearing portion of dentary; 82 (Fig.15) – large frontal scale present and divided along midline; 97(5) – minimum number of rows of neck scales 56 or more; 98c – maximum number of midbody scale rows 54 or more; 101c – suture present in dorsal margin of rostral thermoreceptive pit; 104 – shallow thermoreceptive pit present in second through fourth or fifth infralabial scales; 107(0) – rostral-supralabial thermoreceptive pits deeper than infralabial pits; 111(0)r – each posterior trunk intercostal artery usually supplies one body segment.

K. *Morelia*: 15 (Fig.6) – lateral bulge present on maxilla; 37 – plane of blade-like ventral portion of postorbital more or less directed anterolaterally; 47c (Fig.11) – posterior portion of vomer, from middle of vomeronasal fenestra to posterior tip of vomer, 77% or more of total length of vomer; 56(0) – medial pterygoid process of palatine short; 70c – height of surangular process of composite bone 16% or more of total length of lower jaw; 75c – adult tail slightly compressed, depth 1.1 times greater than width.

L. *M. (carinata, oenpelliensis, spilota, viridia)*: 30(0)x (Fig.8) – supraorbital narrow; 93 (Fig.17) – several small scales present in fundus of mental groove.

M. *M. (carinata, spilota, viridis)*: 11(0)x – posterior end of nasal, in vicinity of frontonasal joint, largely vertical; 21 – triangular opening between nasal and frontal laminae of prefrontal narrow; 56(2)c – medial pterygoid process of palatine long; 58(2)c (Fig.13) – ventral surface of cultiform process of sphenoid elevated markedly, anterior to basipterygoid processes and between trabeculae cranii; 60 (Fig.13) – anterior-posterior width of ventral surface of pterygoid process of sphenoid narrow; 80c (Fig.15) – single large supraocular scale absent; 84(2) – anterior prefrontal scale absent; 85(0)x (Fig.15) – posterior prefrontal scales absent.

N. *M. (carinata, viridis)*: 1c – usually one premaxillary tooth per ramus; 13 – anterior maxillary teeth extremely long and relatively straight; 16(2) (Fig.6) – lateral margin of suborbital region of maxilla oriented laterally; 68 – from lateral view, entire anterodorsal margin of

coronoid completely hidden beyond edge of surangular portion of composite bone; 72 (Fig.14) – mandibular foramen relatively deep.

Fossils

Dunophis, *Palaeopython* and *Python* are the extinct taxa in Rage's (1984) review of fossil snakes that are referred to as, or likely to be, pythonines. However, the single species of *Dunophis*, *D. langi*, represented by "a badly preserved skeleton" from the Pliocene (Rage, 1984:18), appears to lack diagnostic characteristics of any one of the major alethinophidian clades. Furthermore, Rage's (1984:19; see also Rochebrune, 1880) summary of the "generic characters" of *Paleopython* (2-4 species, Eocene and Oligocene) casts serious doubt on its pythonine affinities. For example, the combination of a toothless premaxilla and an incompletely enclosed palatine (sphenopalatine) foramen is not found in any pythonine, and neither condition appears to diagnose that clade (see character no. 1, and the Other Variation and Diagnoses sections above). Lastly, Rage's (1976) *Python maurus*, from the Miocene of Morocco, may not be a pythonine because its toothed premaxilla without an ascending process is also typical of *Anilius* and *Loxocemus* (and probably *Xenopeltis*; Kluge, 1991: 18). The other extinct *Python*, *P. sardus* from the Miocene, maybe correctly identified to genus; however, a more detailed study of the only available material, an articulated palatine and anterior pterygoid fragment, is required to determine the presence of diagnostic features (see characters 50-57).

Two extinct Australian species, *Morelia antiqua* (corrected for gender from *M. antiquus*) and *Montypythonoides riversleighensis*, have been referred to as pythonines by M. J. Smith & Plane (1985). The fossils used in the original descriptions of *antiqua* and *riversleighensis* are from the Bullock Creek, Northern Territory (middle to late Miocene), and Riversleigh, Queensland (middle Miocene), local faunas, respectively. I have not examined the material used in the original descriptions of the species; however, the stereophotographs and detailed accounts provided by M. J. Smith & Plane (1985) appear to be sufficient to allow the following conclusions.

The holotype, and only known material, of *antiqua* consists of a nearly complete dentary, but there appear to be no diagnostic features of the pythonine clade evident on that bone. Even the "completely open" Meckel's groove exhibited by *antiqua* (M.J. Smith & Plane (1985:192), a feature used by McDowell (1975:29) to distinguish pythonines from boines, is not informative because that state appears to be plesiomorphic in pythonines (see discussion below). In any case, *antiqua*'s posterior dentary teeth appear to be of nearly equal length, allowing for an incomplete series and some broken teeth, and that feature may be characteristic of a group of pythonines (see character

66's discussion). While the posterior teeth in *albertisii*, *boa*, *childreni*, *maculosus*, *perthensis* and *stimsoni* are clearly of equal length, a derived feature in pythonines, they are of nearly equal length in *mackloti*, *olivacea* and *papuanus*. Thus, the fossil seems to have the tendency toward the special similarity exhibited by the later group, assuming there is a gradual apomorphic trend among pythonines in the length of the posterior teeth, from conspicuously unequal to equal. Further, the fossil dentary has the derived condition of a total of 18 teeth (see character 64). Of the aforementioned species with posterior teeth of equal, or nearly equal, length, only *boa* and *olivacea* have more or less than 18 dentary teeth (Table 1). The fossil dentary is 46.5 mm long, which is much bigger than any *boa*, but not unlike large *olivacea* (eg, AM R40648). That the fossil dentary seems devoid of autapomorphies leaves me no other choice but to synonymise *antiqua* with extant *olivacea*. Bullock Creek is within the geographic range of living *olivacea* (Cogger, 1986:410).

The type material of *riversleighensis* consists of a partial maxilla with nine teeth, and seven vertebrae, all taken from the same block of matrix, and three additional vertebrae and three isolated teeth. The wide palatine process of the fossil maxilla (see character 17) was correctly interpreted as evidence that *riversleighensis* is part of the pythonine clade, excluding the *childreni* complex; however, the absence of paracotylar foramina is not informative because that state is plesiomorphic in pythonines (M.J. Smith & Plane, 1985:194; see review in Kluge, 1991:40). The maxilla and associated teeth are supposed to have provided the authors with less general diagnostic characters, which were given as (p.191): "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." The bulge is also present in several extant pythonines (*amethistina*, *boeleni*, *carinatus*, *oenpelliensis*, *spilotus*, and *viridis*; see character 15), and the "shape of the labial surface of the maxilla" is therefore not peculiar to *Montypythonoides* (contra M.J. Smith & Plane, 1985:194). A weakly developed cutting edge is also present on the outer surface of the more anterior teeth of most, if not all, of the *amethistina* and *spilotus* examined (see Other Variation section above for additional discussion). Still further, none of the material referred to as *riversleighensis* in the original description exhibits autapomorphies. The type locality of Riversleigh is outside the geographic range of *amethistina*, but well within the range of *spilotus* (Cogger, 1986), and it is on the basis of syntopy that I tentatively refer *riversleighensis* to the synonymy of the latter species. An assessment of the vertebrae attributed to *riversleighensis* must await John Scanlon's (personal communication) detail study of ontogenetic and serial variation (LaDuke, 1991). Both *amethistina* and *spilotus* occur in a wide variety of habitats, including rain forest (Cogger *et al.*, 1983).

M.J. Smith (1976) described *Wonambi naracoortensis*

largely on the basis of vertebrae obtained from Pleistocene deposits in Victoria Cave, Naracoorte, South Australia. The material was compared to several extant Australian pythonines; however, she found it to be more similar to Patagonian and Madagascan *Madstoia* (Paleocene-Eocene and Cretaceous, respectively) and Egyptian *Gigantophis* (Eocene). I agree with Barrie (1990) that there are no synapomorphies which indicate the madtsoine group, including *Wonambi*, is part of the pythonine clade. Further discussion of madtsoine affinities will be published elsewhere.

Biogeography

Most students of pythonine biogeography have been guided to their conclusions using ecological and life history features as evidence (eg, Underwood, 1950; Storr, 1964). Underwood & Stimson's (1990) paper is a significant departure from building such untestable scenarios, in that their propositions seem to be constrained by the phylogenetic hypothesis they accept. In particular, they make three major claims: (1) there were two independent origins of *Python* in Africa (*anchietae* and *regius*, and *sebae*); (2) *Python* (their Pythonini) originated in South-east Asia; (3) the Australia-New Guinea radiation of pythonines (their Morelini) evolved from a South-east Asia pythonine stock. Claims 1 and 2 cannot be tested with the hypothesis set forth in Figures 22 and 29; however, I come to the opposite conclusion concerning claim 3. Optimising the current distributions on the area cladogram (Fig.29) suggests the earliest period of pythonine history occurred in Australia, a later interval involved radiations in New Guinea, as well as Australia, and the most recent divergences shifted to Africa and Asia. Thus, I hypothesise the African and South-east Asian *Python* evolved from the Australia-New Guinea radiation (*contra* Underwood & Stimson, 1990). Simply, my biogeographic interpretation is consistent with the Australia-New Guinea radiation (including *Antaresia*, *Apodora*, *Aspidites*, *Bothrochilus*, *Leiopython*, *Liasis* and *Morelia*) being plesiomorphic relative to *Python*. The Australia-New Guinea area of origin is also suggested by the sister group relationships between boines and pythonines, wherein one of the plesiomorphic sister lineages, *Candoia*, in the former clade is distributed from Sulawesi to Samoa (Kluge, 1991:8).

ACKNOWLEDGMENTS. I wish to thank the following persons and institutions for information on snakes and the loan of specimens: Adrienne Edwards and Mark Hutchinson, Herpetology Section, and Neville Pledge, Paleontology Section, South Australian Museum, and Marg Davies and Mike Tyler, Department of Zoology, University of Adelaide, Adelaide; Greg Schneider, Division of Amphibians and Reptiles, University of Michigan Museum of Zoology, and Phil Gingerich, University of Michigan Museum of Vertebrate

Paleontology, Ann Arbor; Jonathan Campbell, University of Texas at Arlington Collection of Vertebrates, Arlington; Barbara Stein and David Wake, Museum of Vertebrate Zoology, University of California, Berkeley; Mr Boeadi, Museum Zoologicum Bogoriense, Bogor, Java; Jeanette Covacevich and Patrick Couper, Department of Herpetology, and Ralph Molnar, Department of Paleontology, Queensland Museum, Brisbane; José Rosado, Museum of Comparative Zoology, Harvard University, Cambridge; Australian National Wildlife Collection, CSIRO Division of Wildlife Research, Canberra; Harold Voris, Alan Resetar, and Molly Ozaki, Division of Amphibians and Reptiles, Field Museum of Natural History, Chicago; John Barrie, Coonalpyn, South Australia; Joe Bailey, Duke University, Durham; David L. Auth, Florida Museum of Natural History, University of Florida, Gainesville; Allen Allison and Carla Kishinami, Bernice P. Bishop Museum, Honolulu; Marinus Hoogmoed, Division of Reptiles and Amphibians, Rijksmuseum van Natuurlijke Historie, Leiden; E.N. Arnold, Barry Clarke, Colin McCarthy, Andrew Stimson, and Garth Underwood, Department of Herpetology, Natural History Museum, London; William E. Duellman, Museum of Natural History, University of Kansas, Lawrence; Terry D. Schwaner, Virginia Museum of Natural History, Martinsville; Simon Tonge, Jersey Wildlife Preservation Trust, Channel Islands; Samuel B. McDowell, Department of Biological Sciences, Rutgers University, Newark; Margaret Arnold and Darrel Frost, Department of Herpetology, American Museum of Natural History, and Herndon G. Dowling, Department of Biology, New York University, New York; Ilaiah H. Bigilale, National Museum and Art Gallery, and John I. Menzies, Department of Biology, University of Papua New Guinea, Papua New Guinea; Don Bradshaw and Phil Withers, Department of Zoology, University of Western Australia, and Ken Aplin and Laurie Smith, Department of Ornithology and Herpetology, Western Australian Museum, Perth; Thomas A. Huff, Reptile Breeding Foundation, Picton, Ontario; Wulf Haacke, Transvaal Museum, Pretoria; Greg Pregill and R.M. Sullivan, Department of Herpetology, San Diego Natural History Museum, San Diego; Jens Vindum, Department of Herpetology, California Academy of Sciences, San Francisco; Hal Cogger, Allen Greer, Ross Sadler, and Glenn Shea, Department of Herpetology, Australian Museum, John Scanlon, Department of Zoology, University of New South Wales, Terry Boylan and Tim Hawkes, Reptile Department, Taronga Zoo, Rick Shine, Department of Zoology, University of Sydney, Sydney; Elyse Beldon and George Zug, National Museum of Natural History, Smithsonian Institution, Washington. Darrel Frost, Sam McDowell, and Garth Underwood kindly read the manuscript, and their detailed criticisms helped immeasurably to improve its content. Those errors of commission and omission remain mine alone. In addition to being an excellent travelling companion, Jean B. Kluge helped compile literature on booids and assisted with photography. Margaret Van Bolt provided the illustrations. This research was supported entirely by National Science Foundation grant BSR-8822656, and it was initiated during my sabbatical leave from the University of Michigan (1989-1990).

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Accepted April 5, 1993

APPENDIX I

Ingroup Specimens Examined

The specimen(s) are complete skeletons, unless indicated otherwise in parentheses. Abbreviations are: alc – alcoholic specimen, with or without skeleton; col(s) – column(s); comp. – complete; disart. – disarticulated; incomp. – incomplete; mand(s) – mandible(s); skel. – skeleton; vert. – vertebral; yg. – neonate.

- albertisii*: AM R8887 (alc.), R12242 (alc.), R14421 (alc.), R16796 (alc., skull, mand., incomp. vert. col.), R29919 (alc.), R33286 (alc.), R58744 (alc.), R123429 (alc.), R124481 (alc.), R124686 (alc.), R124798 (alc.); AMNH 66756 (skull, mand.), 104062; BMNH 92.3.15.1 (alc., skull, mand.), 97.12.10.108 (alc.), 1908.10.14.6 (alc.), 1926.5.31.4 (alc.), 1986.35 (skull, mand.), 1986.1174 (alc.); BPBM 11616 (alc.), 11612 (alc.), 11613 (alc.), 3277 (alc.); FMNH 218609; UTACV 970.
- amethystina*: AM R1087 (alc., holotype of *Hypaspistes dipsadides*), R43916 (alc.), R48320 (alc.), R4908 (skull, mand.), R7293 (skull, mand.), R62430 (alc.), R62431 (alc.), R62432 (alc.), R62433 (alc.), R62434 (alc.), R62435 (alc.), R62438 (alc., hemipenis), R62495 (alc.), R73745 (alc.), R76232 (alc.), R129577 (alc.), R129578 (alc., hemipenis), R129636 (alc.); AMNH 69300 (skull, mand., incomp. vert. col.), 69331 (skull, mand.), 71301 (skull, mand.), 77636, 84189, 117804-5; BMNH 1988.601 (skull, mand., incomp. vert. col.), 1988.604 (comp. vert. col.), 77.2.24.3-4 (alc., syntypes of *duceboracensis*), 77.3.3.1 (skull, mand.), 78.10.16.20-22 (alc.), 83.3.31.7-8 (alc.), 85.6.30.61 (alc., skull, mand.), 85.6.30.62 (alc.), 1909.4.30.9 (alc.), 1913.11.1.94-95 (alc.), 1946.1.10.34-35 (alc., syntypes of *duceboracensis*), 1966.308 (alc.), 1969.2908 (alc.); BPBM 6004 (skull), 11614 (alc.); FMNH 218599, 232744; QM J15815 (skull, mand., incomp. vert. col.), J45303 (skull, mand.), J47253 (incomp., disart. skel.), J50109; SAM R359 (skull, mand.); UF 60341 (skull, mand., incomp. vert. col.); UMMZ 132343, 132345, 190743 (vert.), 193250-52 (skull, mand., incomp. vert. col.), 201040 (alc.), 201041, 201042 (alc.), 201043 (vert. col.), 201044 (alc., hemipenes), 201045.
- anchietae*: AMNH 50501 (alc., skull, mand.); UMMZ 190758 (alc.), 190773 (skull, mand.).
- boa*: AM R3147 (alc.), R3148 (alc.), R3149 (alc.), R6593 (alc.), R6594 (alc.), R6595 (alc.), R6596 (alc.), R6597 (alc.), R6598 (alc.), R6600 (alc.), R6601 (alc.), R6602 (alc.), R129533 (alc.), R132966 (skull, mand., incomp. vert. col.); AMNH 44002 (skull, mand., incomp. vert. col.); BMNH 77.2.24.11 (skull, mand., incomp. vert. col.), 79.10.31.10-11 (alc.), 77.2.24.12 (alc.), 79.10.31.12 (skull disart., comp. vert. col.), 1903.6.29.33 (alc.); FMNH 13881 (alc.), 13882 (skull), 13916 (alc.), 21729; MCZ 26939 (skull, mand., incomp. vert. col.); UMMZ 170391 (alc.), 190703-4, 190744 (vert.).
- boeleni*: AM R15001 (alc., holotype of *taronga*); AMNH 113050 (alc.); BPBM 11618 (disart. skull, mand.), 11611 (alc.), 11615 (alc.); MCZ 118928 (alc., skull, mand., incomp. vert. col.); SDNHM 48507; UMMZ 190745 (vert.), 192809 (alc.); UTACV 11396 (alc.), 26148 (alc., hemipenis), 26712 (alc.), 26713 (alc.), 26714 (alc., hemipenes).
- carinatus*: WAM R45352 (holotype, alc., radiographs), R97959 (alc., radiographs).
- childreni*: AM R10226 (alc.), R11028 (alc.), R11029 (alc.), R31707 (alc.), R32615 (alc.), R48648 (alc.), R52364 (alc.), R53517 (alc.), R55321 (alc.), R55498 (alc.), R60301 (alc.), R60302 (alc.), R60303 (alc.), R63424 (alc.), R69086 (alc.), R72495 (alc.), R76510 (alc.), R97431 (hemipenis), R132962 (skull, mand., incomp. vert. col.); BMNH 72.10.11.3 (alc.), 44.6.13.60 (alc.), 51.2.12.10 (alc.), 85.6.20.5 (skull, mand.), 90.12.2.22 (alc.), 1946.1.16.69 (alc., holotype of *gilbertii*), 1946.1.16.78 (alc., holotype of *childreni*); SAM R26879 (alc., hemipenis), R26973; UMMZ 190746 (vert.), 190779 (skull, mand., incomp. vert. col.).
- curtus*: AMNH 50823 (alc.), 50993 (alc.), 50994 (alc.), 57802, 114495, 117806, 118694; BMNH 1988.598 (disart. skull, mand., comp. vert. col.), 91.7.24.1 (alc.), 1906.2.28.18 (alc.), 1915.12.2.31 (alc.), 1986.37-38 (skulls, mands.); FMNH 22472 (skull), 29479 (alc.), 55503 (alc.), 71586 (alc.), 71588 (alc.), 212308 (alc., comp. skel.), 222372 (alc., comp. skel.); UF 47853 (skull, mand.); UMMZ 145019, 153087; USNM 53427 (alc., paratype *Python curtus brongersmai*), 70942 (alc.), 89399 (alc.), 89400 (alc.), 94431 (alc.), 94432 (alc.); UTACV 732, 6693 (alc.), 7037 (alc.).
- mackloti*: AM R12885 (alc.), R21207 (alc.), R24417 (alc.), R25777 (alc.), R31886 (alc., syntype *Nardoa crassa*), R37499 (alc., hemipenis), R38486 (alc.), R39516 (alc.), R41862 (alc.), R41872 (skull, mand.), R48485 (alc.), R57288 (alc.), R76534 (alc.), R90337 (alc.), R93057 (alc.), R97509 (alc.), R105151 (alc.), R112429 (alc.), R131788 (alc., syntype *Nardoa crassa*); AMNH 32264 (skull, mand., paratype *Liasis mackloti dunnii*), 59904 (skull, mand.),

- 69334 (skull, mand.); BMNH 46.9.11.57 (alc.), 79.11.7.1 (alc.), 85.6.30.21 (alc.), 97.6.21.33 (alc., holotype of *savuensis*), 97.6.21.34-37 (alc., paratypes of *savuensis*), 1926.2.25.79 (alc.), 1946.1.10.41 (alc., holotype of *corwallisius*), 1986.36 (skull, mand.); KU 182381; MCZ 37244 (skull, mand.); QM J26898 (skull, mand., incomp. vert. col.), J28903 (disart. skull, mand.), J47919 (comp. skeleton, skull disart.); UF 58644; UMMZ 132865 (alc.), 190747 (vert.), 198427-28 (skull, mand.), 201039 (alc.).
- maculosus*: AM R9755 (alc.), R10424 (alc.), R11159 (alc.), R11520 (alc.), R16769 (alc.), R17108 (alc.), R36650 (alc.), R38309 (alc.), R47895 (alc.), R49831 (alc.), R54657 (alc.), R64072 (alc.), R69084 (alc.), R75174 (alc.), R92698 (alc.), R92699 (alc., hemipenis), R112860 (alc.), R120999 (alc.), R132961 (skull, mand., incomp. vert. col.); AMNH 69278 (skull, mand.); BMNH 77.3.3.6-8 (alc.); MCZ 4215 (skull, mand., incomp. vert. col.); QM J28425 (skull, mand.), J46070 (vert. col.); UMMZ 190774 (alc.), 190775 (skull, mand., incomp. vert. col.), 190777 (skull, mand., incomp. vert. col.), 190783, 201026-29 (alc.), 201030, 201031-32 (alc.), 201033 (alc., hemipenis), 201034-35 (alc.).
- melanocephalus*: AM R13049 (alc.), R37760 (alc.), R37761 (alc.), R40277 (alc.), R41877 (alc.), R53985 (alc., hemipenis), R59890 (alc.), R59924 (alc.), R60298 (alc.), R60299 (alc.), R65934 (alc.), R65983 (alc., hemipenis), R69260 (alc.), R84288 (alc.), R95321 (alc.), R127417-21 (alc.), R128317 (alc.), R131367 (alc.), R131388 (alc.); AMNH 69302 (skull, mand.), 76200; BMNH 66.2.13.27 (incomp. vert. col.), 1924. 1.24.15 (alc., skull, mand.), 1931.12.2.2 (alc.), 1946.1.8.2 (alc., holotype of *melanocephalus*), 1976.1588 (alc.); CAS uncatalogued (skull, mand., incomp. vert. col.); MVZ 77814 (skull, mand.); QM J5616 (skull, mand.), J30786 (skull, mand.); SDNHM 63812, 63814; UMMZ 190770 (alc.), 190781 (skull, mand., incomp. vert. col.), 192815 (skull, mand., incomp. vert. col.), 193249 (skull, man., incomp. vert. col.), 201036 (alc., hemipenis), 201037, 201038 (alc.); WAM R41655.
- molurus*: AM A10789 (skull, mand.); AMNH 7184 (skull, mand.), 7188 (skull, mand.), 27804 (alc.), 27806 (alc.), 27807 (alc.), 27809 (alc.), 27810 (alc.), 35231 (alc.), 36571, 36572-3 (skull, mand.), 36575 (skull, mand.), 57485 (skull, mand.), 57783 (disart. skel.), 57798 (skull, mand.), 57819, 57798 (vert. col.), 77081, 102176, 102281 (alc.); BMNH 1988.599 (disart. skull, mand.), 46.11.22.113 (alc.), 1924.12.9.158 (alc.), 1930.5.8.42 (skull, mand.), 1930.5.8.44-45 (skull, mand., incomp. vert. col.), 1940.4.28.1 (skull, mand., incomp. vert. col.), 1940.4.28.2 (skull, mand.), 1962.851 (alc.), 1972.2167-68 (skull, mand.); BPBM 11435 (skull, mand., incomp. vert. col.); FMNH 6734 (alc., skull, mand.), 6735 (alc.), 11171 (alc.), 11874 (alc.), 15930 (alc.), 31036 (alc.), 165096 (alc.), 207674 (skull, mand., incomp. vert. col.), 112000 (alc.), 211529 (alc.), 218576, 223198 (alc., comp. skel.); SAM R36021 (disart. skel.); UF 61300 (skull, mand., incomp. vert. col.); UMMZ 129407, 155835-6, 169895-6, 170385 (incomp. vert. col.), 181669-71.
- oenpelliensis*: AM R93417 (alc., skull, mand., incomp. vert. col.), R55009 (alc., paratype); ANWC R0363 (alc.).
- olivacea*: AM R10114 (alc.), R11043 (alc.), R11330 (alc.), R12334 (alc.), R12555 (alc.), R16489 (alc.), R20836 (alc.), R32632 (alc.), R33239 (alc.), R39518 (alc.), R39519 (alc., hemipenis), R40648 (alc.), R52363 (alc.), R58738 (alc.), R64772 (alc.), R76535 (alc.), R90338 (alc.), R111349 (alc.), R132962 (alc., hemipenis, skull, mand.); BMNH 57.10.24.51 (alc.), 58.10.25.18 (alc., skull, mand.), 1926.2.25.80-81 (alc.), 1946.1.1.56 (alc., holotype of *olivacea*); QM J47660, J47921 (incomp. vert. col.), J47975 (skull, mand., incomp. vert. col.); SAM R3906 (skull, mand., incomp. vert. col.), R22529 (hemipenis); UMMZ 190768 (alc.), 190780 (skull, mand., incomp. vert. col.); WAM R28277 (disart. comp. skel.), R33420 (comp. disart. skel.), R77667 (alc., skull, mand., incomp. vert. col.).
- papuanus*: AM R16488 (alc., skull, mand., incomp. vert. col.), R26236 (alc.), R33118 (alc.), R90353 (alc.); AMNH 57501 (alc.), 62019 (alc.), 62636 (alc., skull, mand., incomp. vert. col.), 66761 (alc.), 73989 (alc.), 73991 (alc.), 73992-3 (alc.), 101074 (alc.), 107151 (alc.); BMNH 80.9.23.4 (alc.), 95.4.26.45 (alc.), 1909.4.30.8 (alc.), 1986.1175 (alc.); QM J35387 (alc.).
- perthensis*: AM R75101 (alc.); BMNH 1980.26 (alc.); SAM R4094, R4096-9 (alc.); UMMZ 190789 (alc.), 190842 (skull, mand., incomp. vert. col.); WAM R6341 (alc.), R15109 (alc.), R15108 (alc., comp. skel.), R25229 (alc.), R99807 (alc.), R73616 (alc.), R100812 (alc.), R63165 (alc.), R63166 (alc.), R68113 (alc.), R75743 (alc.), R22738 (alc.), R87723 (alc.).
- ramsayi*: AM R1607 (alc.), R13902 (alc.), R18249 (alc.), R32748 (alc.), R46000 (alc.), R61093 (alc.), R76042 (alc., hemipenes), R91899 (alc.), R132964 (alc., skull, mand., incomp. vert. col.); MCZ 32807 (skull, mand.); QM J944 (alc., *collaris* holotype), J2260 (alc.), J7003 (alc.), J8674 (alc.), J10331 (alc.), J23629 (skull, mand.), J30171 (alc.), J32034 (alc.), J35386 (alc.), J40053 (alc.), J40943 (alc.), J41494 (alc.), J41661 (alc.), J41662 (alc.), J46850, J49952 (alc.); SAM R8110 (skull, mand., incomp. vert. col.), R19831 (hemipenis); UMMZ 190769 (alc.), 190782 (alc., skull, mand., incomp. vert. col.), 192811 (alc.).
- regia*: AMNH 31921 (skull, mand.), 73157, 75263; BMNH IV.3.3.b (alc.), 45.11.26.21 (alc.), 46.11.20.20 (alc.), 85.1.31.6 (alc.), 95.5.3.25 (alc.), 1916.5.20.1 (alc.), 1968.1216-8 (alc.), 1986.39 (skull, mand.), 1988.602 (skull, mand.), 1988.603 (comp. vert. col.); FMNH 20812 (alc.), 22464 (alc.), 28493 (alc.), 28497 (alc.), 31035 (skull, mand.), 34039 (alc.), 58354 (alc.), 154647 (alc.), 154665 (alc.), 223195; UF 57145 (skull, mand.); UMMZ 65958 (alc.), 116883 (alc.), 149660, 153033 (alc.), 155833, 176805, 186004, 188066, 190111, 190750 (incomp. vert. col.).
- reticulata*: AM R131363 (skull, mand., incomp. vert. col.); AMNH 77082, 102245, 116322; BMNH 78.1.31.1 (alc.), 83.3.31.6 (alc.), 91.5.1.13 (alc.), 97.6.21.38 (alc.), 1947.1.1.13 (skull, mand.), 1964.965 (mand.), 1964.1251 (disart. skull, mand.), 1972.2169 (skull, mand., incomp. vert. col.), 1972.2170 (skull, mand.), 1974.749 (alc.), 1986.40 (skull, mand.), 1988.600 (skull, mand.); BPBM 3131 (skull, mand.); FMNH 15678 (skull, mand., incomp. vert. col.), 26477 (alc.), 31281 (skull, mand.), 31324 (skull, mand.), 51631 (skull, mand., incomp. vert. col.), 53273 (alc.), 53274 (alc.), 53275 (alc.), 53280 (alc.), 53282 (alc.), 53284 (alc.), 53286 (alc.), 53287 (alc.), 98872, 131761 (alc.), 148974 (alc.), 211851-52; SAM R15920 (alc.), R22450 (alc., hemipenes), R25115 (hemipenis), R27307 (skull, mand., incomp. vert. col.); UF 65624 (skull, mand., incomp. vert. col.); UMMVP 82 (skull, mand.); UMMZ 55337 (alc.), 128051, 151095, 155332-3 (skulls, mands., incomp. vert. cols.), 173474; WAM R98426 (alc.).

sebae: AMNH 10087 (skull, mand., incomp. vert. col.), 10088 (skull, mand.), 11687 (skull, mand.), 11692-3 (skull, mand., incomp. vert. col.), 11694-5 (skull, mand.), 11696 (skull, mand., incomp. vert. col.), 50667 (skull, mand.), 73615 (skull, mand.), 74731 (vert. col.), 110444; BMNH uncatalogued (skull, mand.), IV.3.2c (alc.), 58.11.2.1 (alc.), 58.8.23.19 (skull, mand.), 58.8.31.1 (alc.), 97.6.9.83 (alc.), 1912.1.30.1 (alc.), 1913. 2.24.18 (alc.), 1946.1.8.3 (alc., presumed syntype of *natalensis*), 1946.1.17.13 (alc., presumed syntype of *natalensis*), 1952.1.2.59 (disart. skull, mand.), 1954.1.12.20 (alc.), 1964.1100 (skull, mand.), 1969.297 (alc.); BPBM 5962 (skull, mand.); SAM R26137 (skull, mand., incomp. vert. col.), R26954; FMNH 8545 (skull, mand.), 11161 (alc.), 11162 (skull, mand.), 11170 (skull, mand.), 13121 (skull, mand.), 17189 (alc.), 17190 (alc.), 17191 (alc.), 19789 (alc.), 20811 (alc.), 22366, 22497 (alc.), 196592 (skull, mand.); UF 61293 (skull, mand.); UMMZ 61190 (alc.), 61400 (disart. skull, mand.), 61410 (skull, mand.), 126992 (alc.), 132044 (alc.), 190751 (vert.).

pilotus: AM R11899 (alc., paratype of *bredli*), R19140 (alc.), R21210 (alc.), R24439 (alc.), R26273 (alc.), R31667 (alc.), R32633 (alc.), R33297 (alc., hemipenes), R38484 (alc.), R39517 (alc.), R39990 (alc.), R41648 (alc.), R48112 (alc.), R51929 (alc.), R57125 (alc.), R92357 (alc.), R95534 (alc.), R97661 (alc.), R97703 (alc.), R103069 (alc.), R103835 (alc.), R106325 (alc., hemipenis), R111989 (alc., holotype of *cheynei*), R116988 (alc., holotype of *metcalfei*), R116989 (alc., holotype of *mcdowellii*), R123971 (alc.), R131847 (alc.), R132965 (skull, mand., incomp. vert. col.); BMNH 51.2.20.23 (alc.), 63.6.2.2, 67.5.15.1, 84.9.13.20 (alc.), 88.10.27.2, 1964.934 (skull, mand.), 1974.744 (alc.), 1985.320 (alc.), 1987.2108 (skull, mand., incomp. vert. col.); BPBM 6003 (skull, mand.); FMNH 21714 (skull, mand.), 22234, 22380 (skull, mand., incomp. vert. col.), 22420 (skull, mand.), 218598; QM J4459 (disart. skull, mand.), J22191 (skull, mand.), J24566 (skull, mand.), J32743, J38107 (disart. skull, mand., incomp. vert. col.), J43802 (alc.), J43835 (incomp. skel.), J46066 (skull, mand.), J47078, J47249, J47442 (skull, mand., incomp. vert. col.), J47443 (incomp. vert. col.), J47643, J47979, J48450; SAM

R26878 (hemipenis), R26962, R26955, R27268 (hemipenis), R33495 (skull, mand., incomp. vert. col.); UMMZ 131714 (skull, mand., incomp. vert. col.), 132348, 190710-13, 190784-7, 190788 (skull, mand., incomp. vert. col.), 193253-55 (skull, mand., incomp. vert. col.), 201046-49 (alc.), 201050 (incomp. vert. col.), 201051 (alc.), 201052, 201053-54 (alc.), 201055 (incomp. vert. col.); WAM R26413, R40115, R47831.

stimsoni: AM R26020 (alc., skull, mand., incomp. vert. col.), R39063 (alc.), R39064 (alc.), R41676 (alc.), R60304 (alc., holotype of *saxacola*), R65229 (alc.), R69085 (alc.), R69087 (alc.), R72981 (alc.), R73910 (alc.), R73939 (alc.), R79124 (alc.), R84226 (alc.), R84375 (alc.), R90879 (alc., hemipenes), R92327 (alc.), R110596 (alc.), R101942 (alc.), R121003 (alc.), R128704 (alc., skull, mand., incomp. vert. col.), R128705 (alc.), R128706 (alc.); BMNH 1955.1.4.58 (alc.), 1955.1.4.60 (alc.); QM J28416 (skull, mand.), SAM R26996, R26998 (incomp. skel.); UMMZ 190766 (alc.), 190790 (alc.); WAM R36457-8 (skulls, mands.).

timoriensis: MZB 1205 (alc., uncatalogued (alc.)); FMNH 209468 (alc., hemipenis), 211934 (alc.), 218977 (alc.); KU 158546; UMMZ 190771-2 (skulls, mands.); UTACV 5699 (alc.), 6970; WAM R105148 (alc., radiographs), R105205 (alc., radiographs).

viridis: AM R12181 (alc.), R15059 (alc.), R66773 (alc., hemipenes), R66774 (alc.), R111058 (alc.), R115348 (alc.), R115349 (alc.), R115350 (alc., hemipenes), R115356 (alc.), R122363 (alc.), R122364 (alc.), R124531 (alc.), R127472 (alc.), R129204 (alc.), R129304 (alc.), R129716 (alc.); AMNH 59054 (skull, mand.), 59888 (skull, mand.), 106688, 110148; BMNH 76.7.18.10 (alc.), 80.9.23.1 (incomp. disart. skull, mand., incomp. vert. col.), 87.3.2.1 (alc.), 97.12.10.112 (alc.), 1922.11.24.32 (alc.), 1935.5.10.150 (alc.), 1986.34 (skull, mand.); BPBM 5010 (skull, mand.), 11617, 11618 (skull, mand., incomp. vert. col.); FMNH 21733 (skull, mand.), 207854, 211850, 213403; QM J2108, J22455 (skull, mand.); SAM R4803 (skull, mand., incomp. vert. col.); UMMZ 128025, 128060, 149644-5, 150698, 151090, 190734 (vert.).

APPENDIX II

Table 1. Numbers of adult teeth. Abbreviations are: m – mode or median; n – number of specimens examined; ORV – observed range of variation (both right and left sides counted and used as the sample). See text for ontogenetic variation in premaxillary teeth in *melanocephalus* and *ramsayi*.

	Premaxillary			Maxillary			Palatine		
	n	ORV	m	n	ORV	m	n	ORV	m
<i>albertisii</i>	5	2-3	2	5	21-23	22-23	6	5-8	8
<i>amethistina</i>	20	1-2	2	27	13-19	16	27	2-5	4
<i>anchietae</i>	2	2	2	2	18	18	2	5-6	6
<i>boa</i>	9	1-2	2	8	19-22	20	8	8-9	8
<i>boeleni</i>	4	1-2	1	3	17-18	18	3	5	5
<i>carinatus</i>	2	1	1	2	15-17	15	1	3	3
<i>childreni</i>	4	1-3	2	4	20-24	22	4	6-9	7
<i>curtus</i>	13	2-3	2	12	19-22	19	13	5-7	6
<i>mackloti</i>	9	1-2	2	11	19-25	21	10	6-9	6
<i>maculosus</i>	6	1-2	2	6	20-23	22	5	6-9	7
<i>melanocephalus</i>	14	0	0	14	14-16	15	14	5-7	6
<i>molurus</i>	28	1-3	2	27	14-19	18	31	5-7	6
<i>oenpelliensis</i>	1	2	2	1	16-17	16-17	1	5	5
<i>olivacea</i>	9	1-2	2	9	18-20	19	9	5-6	6
<i>papuanus</i>	2	1	1	2	15-16	15	2	6	6
<i>perthensis</i>	3	2	2	3	21-23	23	3	7	7
<i>ramsayi</i>	6	0	0	6	17-21	19	6	6-8	6
<i>regia</i>	13	2	2	14	18-22	20	13	5-7	6
<i>reticulata</i>	19	1-2	2	25	15-19	17	25	6-8	7
<i>sebae</i>	26	1-2	2	25	16-18	17	23	5-7	6
<i>spilotus</i>	36	1-2	2	41	15-21	18	40	5-6	6
<i>stimsoni</i>	6	2	2	7	21-24	23	6	7-8	7
<i>timoriensis</i>	2	2	2	2	19-20	19-20	2	6	6
<i>viridis</i>	12	1-2	1	18	15-19	17	19	3-5	5

	Pterygoid			Dentary		
	n	ORV	m	n	ORV	m
<i>albertisii</i>	6	17-20	18	6	22-25	24
<i>amethistina</i>	25	9-15	12	26	14-20	17
<i>anchietae</i>	2	9-12	9	2	19	19
<i>boa</i>	8	12-15	14	8	17-21	19
<i>boeleni</i>	3	10-14	12	3	17-19	18-19
<i>carinatus</i>				1	16	16
<i>childreni</i>	4	12-18	17	4	21-23	23
<i>curtus</i>	13	8-13	11	13	18-21	19
<i>mackloti</i>	10	11-17	14	11	19-24	21
<i>maculosus</i>	5	15-18	16	6	21-23	22
<i>melanocephalus</i>	14	8-13	9	14	13-17	15
<i>molurus</i>	30	6-11	8	30	15-19	18
<i>oenpelliensis</i>	1	11	11	1	16	16
<i>olivacea</i>	8	10-16	14	9	17-20	19
<i>papuanus</i>	2	9-11	10	2	14-16	16
<i>perthensis</i>	3	13-16	15	3	22-23	22
<i>ramsayi</i>	6	8-11	9	6	17-20	18
<i>regia</i>	14	16-24	21	14	18-22	21
<i>reticulata</i>	25	7-11	10	26	15-19	17
<i>sebae</i>	24	7-11	9	24	16-18	17
<i>spilotus</i>	39	9-15	11	41	17-23	19
<i>stimsoni</i>	7	14-20	19	6	21-26	24
<i>timoriensis</i>	2	14-16	14	2	20-21	20
<i>viridis</i>	16	9-13	11	20	15-17	16

Table 2. Character 76: parietal scales.

	Character State Codes			
	0	1	2	3
<i>albertisii</i>		4	16	
<i>amethystina</i>				32
<i>anchietae</i>	2			
<i>boa</i>				20
<i>boeleni</i>				12
<i>carinatus</i>	2			
<i>childreni</i>		5	17	
<i>curtus</i>		1	18	4
<i>mackloti</i>			10	16
<i>maculosus</i>		8	13	
<i>melanocephalus</i>		7	15	
<i>molurus</i>	8	7	1	4
<i>oenpelliensis</i>	3			
<i>olivacea</i>		3	19	
<i>papuanus</i>		1	18	
<i>perthensis</i>		9	11	
<i>ramsayi</i>	1	23		
<i>regia</i>	3	17		
<i>reticulata</i>	20			
<i>sebae</i>	15	2		3
<i>spilotus</i>	29			
<i>stimsoni</i>		5	18	1
<i>timoriensis</i>			1	8
<i>viridis</i>	21			

Table 4. Character 78: parietal-postocular scale contact.

	Character N	State Codes	
		0	1
<i>albertisii</i>		2	9
<i>amethystina</i>		1	14
<i>anchietae</i>	2		
<i>boa</i>		13	3
<i>boeleni</i>		4	5
<i>carinatus</i>	2		
<i>childreni</i>		13	3
<i>curtus</i>		3	17
<i>mackloti</i>		10	6
<i>maculosus</i>		12	6
<i>melanocephalus</i>		18	
<i>molurus</i>	7		10
<i>oenpelliensis</i>	3		
<i>olivacea</i>		1	18
<i>papuanus</i>			15
<i>perthensis</i>		2	17
<i>ramsayi</i>	1	11	12
<i>regia</i>	3		8
<i>reticulata</i>	15		
<i>sebae</i>	7		3
<i>spilotus</i>	25		
<i>stimsoni</i>		18	4
<i>timoriensis</i>			9
<i>viridis</i>	16		

Table 3. Character 77: postocular scales.

	Character State Codes			
	0	1	2	3
<i>albertisii</i>	1	14	5	
<i>amethystina</i>	7	7	17	1
<i>anchietae</i>				2
<i>boa</i>	19	1		
<i>boeleni</i>	4	5	2	
<i>carinatus</i>				2
<i>childreni</i>	1	3	17	1
<i>curtus</i>	9	13	1	
<i>mackloti</i>	23	3		
<i>maculosus</i>	1	15	4	1
<i>melanocephalus</i>		3	19	
<i>molurus</i>		5	12	3
<i>oenpelliensis</i>				3
<i>olivacea</i>	2	10	9	3
<i>papuanus</i>	8	11		
<i>perthensis</i>	1	10	9	
<i>ramsayi</i>		9	12	3
<i>regia</i>		3	13	4
<i>reticulata</i>		9	11	
<i>sebae</i>	3	10	6	1
<i>spilotus</i>		3	16	10
<i>stimsoni</i>		3	18	3
<i>timoriensis</i>	1	7	1	
<i>viridis</i>				21

Table 5. Character 79: subocular scales.

	Character N	State Codes	
		0	1
<i>albertisii</i>	20		
<i>amethystina</i>	32		
<i>anchietae</i>			2
<i>boa</i>	20		
<i>boeleni</i>	12		
<i>carinatus</i>			2
<i>childreni</i>	22		
<i>curtus</i>	19		4
<i>mackloti</i>	26		
<i>maculosus</i>	21		
<i>melanocephalus</i>	21		1
<i>molurus</i>	5		15
<i>oenpelliensis</i>	3		
<i>olivacea</i>	24		
<i>papuanus</i>	19		
<i>perthensis</i>	20		
<i>ramsayi</i>	18		6
<i>regia</i>	12		8
<i>reticulata</i>	19		1
<i>sebae</i>			20
<i>spilotus</i>	29		
<i>stimsoni</i>	24		
<i>timoriensis</i>	9		
<i>viridis</i>	21		

Table 6. Character 80: supraocular scale.

	Character		Codes
	0	1	
<i>albertisii</i>	20		
<i>amethistina</i>	32		
<i>anchietae</i>	1	1	
<i>boa</i>	20		
<i>boeleni</i>	12		
<i>carinatus</i>		2	
<i>childreni</i>	22		
<i>curtus</i>	23		
<i>mackloti</i>	26		
<i>maculosus</i>	21		
<i>melanocephalus</i>	22		
<i>molurus</i>	20		
<i>oenpelliensis</i>	2	1	
<i>olivacea</i>	24		
<i>papuanus</i>	19		
<i>perthensis</i>	20		
<i>ramsayi</i>	24		
<i>regia</i>	19	1	
<i>reticulata</i>	19	1	
<i>sebae</i>		20	
<i>spilotus</i>	1	28	
<i>stimsoni</i>	24		
<i>timoriensis</i>	9		
<i>viridis</i>	1	20	

Table 8. Character 82: frontal scale.

	Character		
	0	1	2
<i>albertisii</i>	20		
<i>amethistina</i>	32		
<i>anchietae</i>			2
<i>boa</i>	20		
<i>boeleni</i>	12		
<i>carinatus</i>	2		
<i>childreni</i>	20	2	
<i>curtus</i>		23	
<i>mackloti</i>	26		
<i>maculosus</i>	21		
<i>melanocephalus</i>	22		
<i>molurus</i>		20	
<i>oenpelliensis</i>	2	1	
<i>olivacea</i>	24		
<i>papuanus</i>	19		
<i>perthensis</i>	19	1	
<i>ramsayi</i>	23	1	
<i>regia</i>		16	4
<i>reticulata</i>	4	15	1
<i>sebae</i>		15	5
<i>spilotus</i>	2	3	24
<i>stimsoni</i>	24		
<i>timoriensis</i>	9		
<i>viridis</i>			21

Table 7. Character 81: preocular scales.

	Character			
	0	1	2	3
<i>albertisii</i>	17	3		
<i>amethistina</i>		24	5	
<i>anchietae</i>				2
<i>boa</i>	20			
<i>boeleni</i>		11	1	
<i>carinatus</i>				2
<i>childreni</i>	1	21		
<i>curtus</i>		20	3	
<i>mackloti</i>	26			
<i>maculosus</i>	1	20		
<i>melanocephalus</i>		17	5	
<i>molurus</i>	1	10	9	
<i>oenpelliensis</i>			1	2
<i>olivacea</i>	22	2		
<i>papuanus</i>	19			
<i>perthensis</i>	1	19		
<i>ramsayi</i>		13	10	1
<i>regia</i>			13	7
<i>reticulata</i>		18	2	
<i>sebae</i>		12	8	
<i>spilotus</i>		3	19	7
<i>stimsoni</i>		20	4	
<i>timoriensis</i>		9		
<i>viridis</i>			4	17

Table 9. Character 83: frontal-preocular scale contact.

	Character		
	N	0	1
<i>albertisii</i>			11
<i>amethistina</i>		4	11
<i>anchietae</i>	2		
<i>boa</i>		2	14
<i>boeleni</i>		12	
<i>carinatus</i>		2	
<i>childreni</i>		16	
<i>curtus</i>		15	5
<i>mackloti</i>		16	
<i>maculosus</i>		18	
<i>melanocephalus</i>		18	
<i>molurus</i>		17	
<i>oenpelliensis</i>		3	
<i>olivacea</i>		18	1
<i>papuanus</i>		14	1
<i>perthensis</i>		19	
<i>ramsayi</i>		24	
<i>regia</i>	2	9	
<i>reticulata</i>		15	
<i>sebae</i>	2	8	
<i>spilotus</i>	25		
<i>stimsoni</i>		22	
<i>timoriensis</i>		8	1
<i>viridis</i>	16		

Table 10. Character 84: anterior prefrontal scale.

	Character		
	0	1	2
<i>albertisii</i>	20		
<i>amethystina</i>	20	12	
<i>anchietae</i>		2	
<i>boa</i>	20		
<i>boeleni</i>	5	7	
<i>carinatus</i>			2
<i>childreni</i>		22	
<i>curtus</i>		23	
<i>mackloti</i>	23	3	
<i>maculosus</i>	1	20	
<i>melanocephalus</i>	18	4	
<i>molurus</i>	2	18	
<i>oenpelliensis</i>		3	
<i>olivacea</i>	3	21	
<i>papuanus</i>	19		
<i>perthensis</i>	1	19	
<i>ramsayi</i>	3	21	
<i>regia</i>	1	18	
<i>reticulata</i>		20	
<i>sebae</i>		20	
<i>spilotus</i>		5	24
<i>stimsoni</i>	2	22	
<i>timoriensis</i>		9	
<i>viridis</i>			21

Table 12. Character 86: nasal scale sutures.

	Character		
	0	1	2
<i>albertisii</i>		10	
<i>amethystina</i>		15	
<i>anchietae</i>	1		1
<i>boa</i>	6	10	
<i>boeleni</i>		12	
<i>carinatus</i>		1	1
<i>childreni</i>		16	
<i>curtus</i>		4	16
<i>mackloti</i>	1	11	2
<i>maculosus</i>		17	
<i>melanocephalus</i>	18		
<i>molurus</i>		3	14
<i>oenpelliensis</i>		3	
<i>olivacea</i>	1	17	1
<i>papuanus</i>		12	3
<i>perthensis</i>		19	
<i>ramsayi</i>	21		
<i>regia</i>	2	8	
<i>reticulata</i>		12	3
<i>sebae</i>		10	
<i>spilotus</i>	12	13	
<i>stimsoni</i>		22	
<i>timoriensis</i>		8	1
<i>viridis</i>	16		

Table 11. Character 85: posterior prefrontal scale.

	Character		
	0	1	2
<i>albertisii</i>	19	1	
<i>amethystina</i>		31	1
<i>anchietae</i>	2		
<i>boa</i>	20		
<i>boeleni</i>		8	4
<i>carinatus</i>	2		
<i>childreni</i>		18	4
<i>curtus</i>			23
<i>mackloti</i>	1	25	
<i>maculosus</i>		9	12
<i>melanocephalus</i>		6	15
<i>molurus</i>		18	2
<i>oenpelliensis</i>		3	
<i>olivacea</i>		22	2
<i>papuanus</i>	4	15	
<i>perthensis</i>		20	
<i>ramsayi</i>		5	19
<i>regia</i>	15	4	
<i>reticulata</i>	7	7	6
<i>sebae</i>	4	7	9
<i>spilotus</i>	29		
<i>stimsoni</i>		23	1
<i>timoriensis</i>			8
<i>viridis</i>	21		

Table 13. Character 87: loreal scales.

	Character		
	0	1	2
<i>albertisii</i>	18	2	
<i>amethystina</i>		15	17
<i>anchietae</i>			2
<i>boa</i>	19	1	
<i>boeleni</i>		6	6
<i>carinatus</i>			2
<i>childreni</i>	7	13	2
<i>curtus</i>		2	21
<i>mackloti</i>	23	3	
<i>maculosus</i>	16	5	
<i>melanocephalus</i>	18	4	
<i>molurus</i>		5	15
<i>oenpelliensis</i>			3
<i>olivacea</i>	23	1	
<i>papuanus</i>	19		
<i>perthensis</i>	1	18	1
<i>ramsayi</i>		16	8
<i>regia</i>		1	19
<i>reticulata</i>		12	8
<i>sebae</i>		5	15
<i>spilotus</i>			29
<i>stimsoni</i>	2	14	8
<i>timoriensis</i>	8	1	
<i>viridis</i>			21

Table 14. Character 88: subloreal scales.

	Character		Codes
	0	1	
<i>albertisii</i>	20		
<i>amethistina</i>	8	24	
<i>anchietae</i>		2	
<i>boa</i>	20		
<i>boeleni</i>		12	
<i>carinatus</i>		2	
<i>childreni</i>	1	21	
<i>curtus</i>		23	
<i>mackloti</i>	26		
<i>maculosus</i>	1	20	
<i>melanocephalus</i>	22		
<i>molurus</i>		20	
<i>oenpelliensis</i>		3	
<i>olivacea</i>	24		
<i>papuanus</i>	19		
<i>perthensis</i>		20	
<i>ramsayi</i>	11	13	
<i>regia</i>		20	
<i>reticulata</i>	19	1	
<i>sebae</i>		20	
<i>spilotus</i>		29	
<i>stimsoni</i>		24	
<i>timoriensis</i>		9	
<i>viridis</i>		21	

Table 16. Character 90: subocular supralabial scales.

	Character			
	N	0	1	2
<i>albertisii</i>			3	8
<i>amethistina</i>			15	
<i>anchietae</i>	2			
<i>boa</i>			14	2
<i>boeleni</i>			10	
<i>carinatus</i>			2	
<i>childreni</i>			15	1
<i>curtus</i>	4	2	14	
<i>mackloti</i>			14	2
<i>maculosus</i>			18	
<i>melanocephalus</i>	1	8	10	
<i>molurus</i>	15	1		
<i>oenpelliensis</i>			1	2
<i>olivacea</i>			19	
<i>papuanus</i>			14	1
<i>perthensis</i>			19	
<i>ramsayi</i>	6	15	3	
<i>regia</i>	4	7		
<i>reticulata</i>	1	15		
<i>sebae</i>	10			
<i>spilotus</i>			19	6
<i>stimsoni</i>			22	
<i>timoriensis</i>		9		
<i>viridis</i>			16	

Table 15. Character 89: anterior supralabial scales.

	Character		Codes
	0	1	
<i>albertisii</i>	11		
<i>amethistina</i>	3	12	
<i>anchietae</i>		2	
<i>boa</i>	16		
<i>boeleni</i>	10		
<i>carinatus</i>		2	
<i>childreni</i>	14	2	
<i>curtus</i>	10	10	
<i>mackloti</i>	14	2	
<i>maculosus</i>	17	1	
<i>melanocephalus</i>	10	8	
<i>molurus</i>	3	14	
<i>oenpelliensis</i>		3	
<i>olivacea</i>		19	
<i>papuanus</i>	9	6	
<i>perthensis</i>	18	1	
<i>ramsayi</i>	4	20	
<i>regia</i>		11	
<i>reticulata</i>		15	
<i>sebae</i>		10	
<i>spilotus</i>		25	
<i>stimsoni</i>	14	8	
<i>timoriensis</i>		9	
<i>viridis</i>		16	

Table 17. Character 91: genaeal scale.

	Character	
	0	1
<i>albertisii</i>	4	16
<i>amethistina</i>	32	
<i>anchietae</i>	2	
<i>boa</i>		20
<i>boeleni</i>	12	
<i>carinatus</i>	2	
<i>childreni</i>	1	21
<i>curtus</i>	22	
<i>mackloti</i>	26	
<i>maculosus</i>	3	18
<i>melanocephalus</i>	18	4
<i>molurus</i>	19	1
<i>oenpelliensis</i>	3	
<i>olivacea</i>	23	1
<i>papuanus</i>	18	
<i>perthensis</i>	1	19
<i>ramsayi</i>	24	
<i>regia</i>	12	7
<i>reticulata</i>	15	4
<i>sebae</i>	14	5
<i>spilotus</i>	29	
<i>stimsoni</i>	5	19
<i>timoriensis</i>	9	
<i>viridis</i>	21	

Table 18. Character 92: genial-infralabial scale contact.

	Character State Codes		
	0	1	2
<i>albertisii</i>	6	5	
<i>amethistina</i>		12	3
<i>anchietae</i>		2	
<i>boa</i>	7	9	
<i>boeleni</i>		7	3
<i>carinatus</i>		2	
<i>childreni</i>		14	2
<i>curtus</i>		17	2
<i>mackloti</i>		16	
<i>maculosus</i>		18	
<i>melanocephalus</i>		16	2
<i>molurus</i>		15	1
<i>oenpelliensis</i>		2	1
<i>olivacea</i>		19	
<i>papuanus</i>		14	1
<i>perthensis</i>		19	
<i>ramsayi</i>		21	
<i>regia</i>		9	2
<i>reticulata</i>		13	1
<i>sebae</i>		9	1
<i>spilotus</i>		2	22
<i>stimsoni</i>		21	
<i>timoriensis</i>		6	3
<i>viridis</i>		3	13

Table 20. Character 94: apical body scale pits.

	Character State Codes		
	0	1	
<i>albertisii</i>	18		
<i>amethistina</i>	32		
<i>anchietae</i>	2		
<i>boa</i>	19		1
<i>boeleni</i>	12		
<i>carinatus</i>	2		
<i>childreni</i>	22		
<i>curtus</i>	23		
<i>mackloti</i>	8		16
<i>maculosus</i>	7		14
<i>melanocephalus</i>	14		
<i>molurus</i>	18		
<i>oenpelliensis</i>	1		2
<i>olivacea</i>	7		16
<i>papuanus</i>	17		2
<i>perthensis</i>	20		
<i>ramsayi</i>	21		
<i>regia</i>	19		
<i>reticulata</i>	17		
<i>sebae</i>	16		
<i>spilotus</i>	29		
<i>stimsoni</i>	22		2
<i>timoriensis</i>	9		
<i>viridis</i>	21		

Table 19. Character 93: mental groove scales.

	Character State Codes		
	0	1	
<i>albertisii</i>	20		
<i>amethistina</i>	32		
<i>anchietae</i>	2		
<i>boa</i>	20		
<i>boeleni</i>	10		1
<i>carinatus</i>			2
<i>childreni</i>	22		
<i>curtus</i>	22		
<i>mackloti</i>	26		
<i>maculosus</i>	21		
<i>melanocephalus</i>	21		
<i>molurus</i>	19		1
<i>oenpelliensis</i>	1		2
<i>olivacea</i>	24		
<i>papuanus</i>	18		
<i>perthensis</i>	20		
<i>ramsayi</i>	22		
<i>regia</i>	19		
<i>reticulata</i>	19		
<i>sebae</i>	17		1
<i>spilotus</i>	2		27
<i>stimsoni</i>	23		
<i>timoriensis</i>	9		
<i>viridis</i>			21

Table 21. Character 95: division of subcaudal scales.

	Character State Codes		
	0	1	
<i>albertisii</i>			19
<i>amethistina</i>			32
<i>anchietae</i>			2
<i>boa</i>			20
<i>boeleni</i>			12
<i>carinatus</i>			2
<i>childreni</i>			22
<i>curtus</i>			22
<i>mackloti</i>			25
<i>maculosus</i>			21
<i>melanocephalus</i>	15		
<i>molurus</i>			15
<i>oenpelliensis</i>			3
<i>olivacea</i>			22
<i>papuanus</i>			19
<i>perthensis</i>			20
<i>ramsayi</i>	22		
<i>regia</i>			19
<i>reticulata</i>			17
<i>sebae</i>			16
<i>spilotus</i>			29
<i>stimsoni</i>			24
<i>timoriensis</i>			9
<i>viridis</i>			21

Table 22. Character 100: rostral_pits.

	Character		Codes
	0	1	
<i>albertisii</i>			20
<i>amethistina</i>			32
<i>anchietae</i>			2
<i>boa</i>	19		
<i>boeleni</i>			12
<i>carinatus</i>			2
<i>childreni</i>	22		
<i>curtus</i>			20
<i>mackloti</i>	26		
<i>maculosus</i>	18		
<i>melanocephalus</i>	22		
<i>molurus</i>			19
<i>oenpelliensis</i>			3
<i>olivacea</i>	24		
<i>papuanus</i>	2		14
<i>perthensis</i>	20		
<i>ramsayi</i>	23		
<i>regia</i>			19
<i>reticulata</i>			20
<i>sebae</i>			20
<i>spilotus</i>			29
<i>stimsoni</i>	22		
<i>timoriensis</i>			9
<i>viridis</i>			21

Table 24. Ventral rostral pit suture.

	Character		
	N	0	1
<i>albertisii</i>			10
<i>amethistina</i>			13
<i>anchietae</i>			2
<i>boa</i>	14		
<i>boeleni</i>			7
<i>carinatus</i>			2
<i>childreni</i>	16		
<i>curtus</i>			11
<i>mackloti</i>	16		
<i>maculosus</i>	17		
<i>melanocephalus</i>	18		
<i>molurus</i>			16
<i>oenpelliensis</i>			3
<i>olivacea</i>	19		
<i>papuanus</i>	1	10	
<i>perthensis</i>	18		
<i>ramsayi</i>	24		
<i>regia</i>			10
<i>reticulata</i>			15
<i>sebae</i>			10
<i>spilotus</i>			23
<i>stimsoni</i>	22		
<i>timoriensis</i>			9
<i>viridis</i>			16

Table 23. Character 101: dorsal rostral pit suture.

	Character		
	N	0	1
<i>albertisii</i>		4	5
<i>amethistina</i>		9	
<i>anchietae</i>			2
<i>boa</i>	14		
<i>boeleni</i>		6	1
<i>carinatus</i>		2	
<i>childreni</i>	16		
<i>curtus</i>			11
<i>mackloti</i>	16		
<i>maculosus</i>	17		
<i>melanocephalus</i>	18		
<i>molurus</i>			16
<i>oenpelliensis</i>		3	
<i>olivacea</i>	19		
<i>papuanus</i>	1	10	
<i>perthensis</i>	18		
<i>ramsayi</i>	24		
<i>regia</i>			10
<i>reticulata</i>		15	
<i>sebae</i>			10
<i>spilotus</i>		8	15
<i>stimsoni</i>	22		
<i>timoriensis</i>		7	2
<i>viridis</i>		1	15

Table 25. Character 102: supralabial pits.

	Character						
	0	1	2	3	4	5	6
<i>albertisii</i>			5	15			
<i>amethistina</i>				1	26	4	1
<i>anchietae</i>						2	
<i>boa</i>	20						
<i>boeleni</i>				10	2		
<i>carinatus</i>				2			
<i>childreni</i>		22					
<i>curtus</i>			23				
<i>mackloti</i>		20	6				
<i>maculosus</i>	1	19					
<i>melanocephalus</i>	22						
<i>molurus</i>			19	1			
<i>oenpelliensis</i>				1	2		
<i>olivacea</i>		11	11	2			
<i>papuanus</i>			6	11			
<i>perthensis</i>	6	14					
<i>ramsayi</i>	24						
<i>regia</i>						20	
<i>reticulata</i>						17	3
<i>sebae</i>			19	1			
<i>spilotus</i>			4	24	1		
<i>stimsoni</i>		23					
<i>timoriensis</i>						9	
<i>viridis</i>			7	14			

Table 26. Character 103: subocular pits.

	Character State Codes	
	0	1
<i>albertisii</i>		20
<i>amethystina</i>	32	
<i>anchietae</i>	2	
<i>boa</i>	8	11
<i>boeleni</i>	12	
<i>carinatus</i>	2	
<i>childreni</i>	22	
<i>curtus</i>	23	
<i>mackloti</i>	19	7
<i>maculosus</i>	21	
<i>melanocephalus</i>	22	
<i>molurus</i>	20	
<i>oenpelliensis</i>	3	
<i>olivacea</i>	7	16
<i>papuanus</i>	18	
<i>perthensis</i>	20	
<i>ramsayi</i>	24	
<i>regia</i>	20	
<i>reticulata</i>	20	
<i>sebae</i>	20	
<i>spilotus</i>	29	
<i>stimsoni</i>	22	1
<i>timoriensis</i>	9	
<i>viridis</i>	21	

Table 28. Character 105: posterior infralabial pit position.

	Character State Codes											
	N	0	1	2	3	4	5	6	7	8	9	
<i>albertisii</i>		5	14	1								
<i>amethystina</i>			3	17	11	1						
<i>anchietae</i>					1	1						
<i>boa</i>		10	10									
<i>boeleni</i>		3	9									
<i>carinatus</i>					1	1						
<i>childreni</i>			11	8	3							
<i>curtus</i>						4	2	4	10	3		
<i>mackloti</i>					6	17	2	1				
<i>maculosus</i>			14	7								
<i>melanocephalus</i>	22											
<i>molurus</i>								5	9	5		
<i>oenpelliensis</i>										1	2	
<i>olivacea</i>						1	8	13	1	1		
<i>papuanus</i>							9	9				
<i>perthensis</i>				11	9							
<i>ramsayi</i>	24											
<i>regia</i>				10	5	5						
<i>reticulata</i>									11	7	1	
<i>sebae</i>										3	7	9
<i>spilotus</i>				2	15	11	1					
<i>stimsoni</i>				10	10	4						
<i>timoriensis</i>					2	5	2					
<i>viridis</i>		1	11	9								

Table 27. Character 104: anterior infralabial pits.

	Character State Codes	
	0	1
<i>albertisii</i>	20	
<i>amethystina</i>	32	
<i>anchietae</i>	2	
<i>boa</i>	20	
<i>boeleni</i>	11	1
<i>carinatus</i>	2	
<i>childreni</i>	22	
<i>curtus</i>	1	22
<i>mackloti</i>	26	
<i>maculosus</i>	21	
<i>melanocephalus</i>	22	
<i>molurus</i>		20
<i>oenpelliensis</i>	3	
<i>olivacea</i>	24	
<i>papuanus</i>	18	
<i>perthensis</i>	20	
<i>ramsayi</i>	24	
<i>regia</i>	20	
<i>reticulata</i>	1	19
<i>sebae</i>	1	18
<i>spilotus</i>	29	
<i>stimsoni</i>	24	
<i>timoriensis</i>	1	8
<i>viridis</i>	21	

Table 29. Character 106: number of posterior infralabial pits.

	Character State Codes							
	0	1	2	3	4	5	6	7
<i>albertisii</i>						12	7	1
<i>amethystina</i>					5	13	12	2
<i>anchietae</i>		1		1				
<i>boa</i>		2	17	1				
<i>boeleni</i>				3	6	3		
<i>carinatus</i>					2			
<i>childreni</i>				6	10	5	1	
<i>curtus</i>		3	11	6	2	1		
<i>mackloti</i>		14	9	3				
<i>maculosus</i>		3	16	2				
<i>melanocephalus</i>	22							
<i>molurus</i>		8	11	1				
<i>oenpelliensis</i>						1	2	
<i>olivacea</i>			2	10	12			
<i>papuanus</i>			8	10				
<i>perthensis</i>		17	1					
<i>ramsayi</i>	24							
<i>regia</i>		7	10	3				
<i>reticulata</i>				1	14	5		
<i>sebae</i>		7	8	2	1			
<i>spilotus</i>					3	20	6	
<i>stimsoni</i>				1	14	7	2	
<i>timoriensis</i>				2	6	1		
<i>viridis</i>						17	4	

Table 30. Character 107: size of pits.

	Character State Codes		
	N	0	1 2
<i>albertisii</i>			20
<i>amethystina</i>			10 22
<i>anchietae</i>		2	
<i>boa</i>	20		
<i>boeleni</i>			1 11
<i>carinatus</i>			2
<i>childreni</i>	1		21
<i>curtus</i>		23	
<i>mackloti</i>			26
<i>maculosus</i>	1		20
<i>melanocephalus</i>	22		
<i>molurus</i>		20	
<i>oenpelliensis</i>			3
<i>olivacea</i>			24
<i>papuanus</i>			18
<i>perthensis</i>	4		16
<i>ramsayi</i>	24		
<i>regia</i>		20	
<i>reticulata</i>		15	5
<i>sebae</i>		19	
<i>spilotus</i>			1 28
<i>stimsoni</i>			24
<i>timoriensis</i>		8	1
<i>viridis</i>			10 11

Table 31. Character X taxon matrix. Abbreviations are: a – ancestor; A – *albertisii*; B – *amethystina*; C – *anchietae*; D – *boa*; E – *boeleni*; F – *carinatus*; G – *childreni*; H – *curtus*; I – *mackloti*; J – *maculosus*; K – *melanocephalus*; L – *molurus*; M – *oenpelliensis*; N – *olivacea*; O – *papuanus*; P – *perthensis*; Q – *ramsayi*; R – *regia*; S – *reticulata*; T – *sebae*; U – *spilotus*; V – *stimsoni*; W – *timoriensis*; X – *viridis*.

	a	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	
1.	0	2	2	2	2	1	1	2	2	2	2	0	2	2	2	1	2	0	2	2	2	2	2	2	1	
2.	0	0	1	1	0	1	?	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1	1	
3.	0	0	0	0/1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	
4.	?	1	1	1	0	1	?	0	1	0/1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	
5.	0	0	0	0	1	0	?	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0	1	
6.	0	0	0	0	0	0/1	?	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0/1	0/1	
7.	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	
8.	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
9.	0	2	1	1	2	1	?	1	0	0	1	0	0	1	0	1	1	0	1	0	0/1	1	1	1	1	
10.	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	
11.	0	1	1	1	1	1	0	1	2	1	1	2	0	1	2	1	1	2	1	1	1	0	1	1	0	
12.	1	3/4	0	1	2	1	0	3	2	3	3	0	1	0/1	2	0	4	2	2	1	1	1	3	2	1	
13.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
14.	0	0	1	1	0	1	?	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	
15.	0	0	1	0	0	1	?	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	
16.	1	1	1	1	1	1	2	1	0	1	1	0	0	1	0/1	1	1	1	0	0	0	1	1	0	2	
17.	0	1	1	1	1	1	?	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	
18.	0	1	0	1	2	0	?	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1	0	
19.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
20.	0	1	2	1	1	1	2	0	1	1	0	1	1	2	1	1	0	1	1	1	1	2	0	1	2	
21.	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	
22.	0	0	1	1	0	1	?	0	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	
23.	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
24.	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
25.	0	0	0	1	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0/1	0	
26.	0	1	1	1	0	1	?	1	N	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
27.	0	1	2	1	0	2	?	0	2	1	0	1	1	0	1	1	0	1	2	1	1	1	0	1	1	
28.	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	
29.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
30.	0	0	1	0	0	1	?	0	1	0	0	0	1	0	0	0/1	0	0	1	1	1	0	0	1	0	
31.	0	1	0	0/1	1	0	?	1	0	1	1	0	1	1	1	0/1	1	0	0	0	0	0	1	0	0	
32.	0	1	1	1	1	1	?	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	0	1	1	
33.	0	0	0	0	0	0	?	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	
34.	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0/1	0	0	0	0	1	0/1	
35.	0	2	2	2	2	2	?	0	2	1	0	1	2	2	1	2	0	1	2	2	2	2	2	0	2	1
36.	?	1	0	0	1	0	?	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	
37.	0	0	1	0	0	1	1	N	0	0	N	0	0	1	0	0	N	0	0	0	0	0	N	0	1	
38.	0	1	1	2	1	1	?	1	1	1	1	1	2	1	1	1	1	1	2	1	2	1	1	1	1	
39.	0	0	0	2	0	0	?	0	2	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	
40.	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	

Table 31 (cont'd).

	a	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
41.	0	1	1	1	1	1	?	1	1	1	1	0	1	1	1	1	1	0/1	1	1	0	1	1	1	1
42.	0	1	1	0	1	1	?	0	0	1	0	1	1	1	1	1	0	0	0	1	1	1	1	1	1
43.	0	1	1	0	1	1	?	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	0	1	1
44.	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
45.	0	1	0	0	1	0	?	1	0/1	1	1	0	0	0	1	1	1	0	0	0	0/1	0	1	0	0
46.	0	1	1	1	1	1	?	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1
47.	0	0	1	0	0	1	?	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1
48.	0	2	2	2	2	2	2	2	2	1	2	0	2	2	1	1	2	0	2	2	2	2	2	2	1
49.	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
50.	1	2	0	1	2	1	0	2	1	1	2	1	1	1	1	1	2	1	1	2	1	1	2	1	1
51.	0	1	1	1	0	1	1	0	1	1	0	0	1	1	1	0	0	0	1	1	1	1	0	1	1
52.	0	1	2	2	1	2	?	1	2	2	1	2	2	2	2	2	1	2	2	2	2	2	1	2	2
53.	?	1	2	2	1	2	?	0	2	1	0/1/2	0	2	2	2	2	0	1/2	2	2	2	2	0	2	2
54.	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
55.	1	0	2	0	0	2	?	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1
56.	1	1	0	2	1	0	?	1	1	1	1	1	1	0	1	1	1	1	2	1	1	2	1	2	2
57.	1	3	1	0	2	1	?	3	1	2	3	0	0	1	2	1	2	0	4	1	0	1	4	2	1
58.	0	1	2	1	0	1	?	0	1	1	0	0	1	1	1	1	0	0	1	2	1	2	0	2	2
59.	1	2	2	2	1	2	?	0	2	1	0	1	2	2	1	1	0/1	1	2	2	2	2	0	2	2
60.	?	0	0	0	0	0	?	N	0	0	N	0	0	0	0	0	N/1	0	0	0	0	1	N	0	1
61.	0	1	1	1	1	1	?	0	1	1	0	0	1	1	1	1	0	0	1	1	1	1	0	1	1
62.	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
63.	0	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
64.	1	3	1	1	1	1	0	3	1	2	2	0	1	0	1	0	2	1	2	1	1	1	3	2	0
65.	?	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1
66.	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1
67.	0	1	1	1	0	1	?	0	1	1	0	0	1	1	1	1	0	1	1	1	1	1	0	1	0
68.	?	0	0	0	0/1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
69.	0	0	0	0	0	0	?	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70.	0	0	1	0	0	1	?	0	0	0	0	0	0	0	0	0/1	0	0	0	1	1	1	0	1	1
71.	0	0	0	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0	2	1	1	0	0	1	0
72.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
73.	0	2	2	1	1	1	2	1	1	1	1	0	1	2	1	1	1	0	1	1	1	2	1	1	2
74.	1	3	6	1	3	2	3	1	0	5	1	3	3	6	5	6	1	1	0	3	2	4	1	3	3
75.	0	0	2	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	2	1	1	0	0	0	3
76.	0	2	3	0	3	3	0	2	2	3	2	2	0/1	0	2	2	1/2	1	1	0	0	0	3	0	0
77.	0	1	2	3	0	0/1	3	2	0/1	0	1	2	2	3	1/2	0/1	1/2	1/2	2	1/2	1	2	2	1	3
78.	N	1	1	N	0	0/1	N	0	1	0	0	0	N/1	N	1	1	1	0/1	1	N	N	N	0	1	N
79.	?	0	0	1	0	0	0	0	0/1	0	0	0	0/1	0	0	0	0	0	1	0	1	0	0	0	0
80.	?	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1

Table 31 (cont'd).

	a	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
81.	?	0	1	3	0	1	3	1	1	0	1	1	1/2	3	0	0	1	1/2	2	1	1/2	2	1	1	3
82.	?	0	0	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1/2	2	0	0	2
83.	0	1	1	N	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N	0	0	N
84.	?	0	0	1	0	0/1	2	1	1	0	1	0	1	1	1	0	1	1	1	1	1	2	1	1	2
85.	0	0	1	0	0	1	0	1	2	1	1/2	2	1	1	1	1	1	2	0	0/1/2	0/1/2	0	1	2	0
86.	0	1	1	0/2	1	1	1/2	1	2	1	1	0	2	1	1	1	1	0	1	1	1	0/1	1	1	0
87.	0	0	1/2	2	0	1/2	2	1	2	0	0	0	2	2	0	0	1	1	2	1	2	2	1	0	2
88.	?	0	1	1	0	1	1	1	1	0	1	0	1	1	0	0	1	0/1	1	0	1	1	1	1	1
89.	0	0	1	1	0	0	1	0	0/1	0	0	0/1	1	1	1	0	0	1	1	1	1	1	0	1	1
90.	1	2	1	N	1	1	1	1	1	1	1	0/1	N	2	1	1	1	0	N/0	0	N	1	1	0	1
91.	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0
92.	?	0/1	1	1	0/1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2
93.	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
94.	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
95.	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1
96.	[0]	[2]	[3]	?	[0]	[0]	?	?	[0]	[3]	[0]	[1]	[1]	?	?	[3]	?	?	[0]	[3]	[1]	[3]	?	[?]	[3]
97.	[0]	[0]	[0]	?	[2]	[0]	?	?	[4]	[0]	[0]	[1]	[5]	?	?	[3]	?	?	[4]	[5]	[5]	[1]	?	[5]	[3]
98.	[0]	[0]	[0]	?	[0]	[0]	?	?	[0]	[0]	[0]	[0]	[1]	?	?	[1]	?	?	[1]	[1]	[1]	[0]	?	[1]	[1]
99.	[0]	[0]	[0]	?	[0]	[0]	?	?	[0]	[0]	[0]	[1]	[1]	?	?	[0]	?	?	[0]	[1]	[1]	[0]	?	[0]	[0]
100.	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	1	0	0	1	1	1	1	1	0	1
101.	N	0/1	0	1	N	0	0	N	1	N	N	N	1	0	N	0	N	N	1	0	1	1	N	0	1
102.	0	3	4	5	0	3	3	1	2	1	1	0	2	4	1/2	3	1	0	4	4	2	3	1	4	3
103.	0	1	0	0	0/1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
104.	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0
105.	N	1	2	3/4	0/1	1	3/4	1/2	7	4	1	N	7	8	6	5/6	2/3	N	2	6	8/9	2/3	1/2	3	1/2
106.	0	5	5/6	1/3	2	4	4	3	2	1	2	0	1/2	5	3/4	2/3	1	0	1/2	4	1/2	5	3	4	
107.	N	2	2	0	N	2	1	2	0	2	2	N	0	2	2	2	2	N	0	0	0	2	2	0	1/2
108.	[0]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]
109.	[0]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]
110.	[0]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]
111.	0	[1]	[1]	0	[1]	[1]	?	[1]	[0]	[1]	1	0	[0]	1	1	[1]	1	0	[0]	[0]	[0]	[1]	1	[0]	[1]
112.	1	1	1	0	?	1	?	1	1	1	1	1	2	?	1	?	?	1	0	2	2	1	1	?	0
113.	[0]	0	0	1	?	0	?	0	1	0	0	0	0	?	0	?	?	0	1	0	0	0	0	?	0
114.	[0]	?	0	1	?	0	?	1/2	2	1	1	1	?	?	1	?	?	1	2	2	2	2	1	?	2
115.	0	3	?	1	?	1	?	1	2	2	1	2	?	?	3	?	?	2	2	1	1	2	1	?	0
116.	[0]	1	0	1	?	1	?	0	1	1	0	0	1	?	1	?	?	0	1	0	0	0	0	?	0
117.	0	1	1	1	?	1	?	1	1	1	1	1	?	?	1	?	?	1	1	1	?	1	1	?	1
118.	[0]	0	1	0	?	1	?	1	0	1	0	1	?	?	1	?	?	0	0	0	0	0	0	?	0
119.	[0]	1	1	1	?	1	?	1	1	1	1	1	1	?	1	?	?	1	1	1	1	1	1	?	1
120.	[0]	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1
121.	0	1	2	1	0	1	1	0	1	1	0	1	2	2	2	2	0	1	1	2	2	2	0	1	1

Table 32. Character metrics. The actual number of steps (s), and consistency (c) and retention (r) indices for each character (Table 31) used to construct the phylogenetic hypothesis illustrated in Figure 21 (Kluge & Farris, 1969; Farris, 1989; Kluge, 1989a). See Methods and Materials section for further explanation. All multistate characters (Table 31) are assumed to be additive, and their binary factors are treated separately.

Characters									Characters										
	1a	1b	2	3	4	5	6	7		71a	71b	72	73a	73b	74a	74b	74c		
s	1	4	1	4	2	4	1	1	s	1	2	1	1	3	2	3	5		
c	1.0	.25	1.0	.25	.50	.25	1.0	1.0	c	1.0	.50	1.0	1.0	.33	.50	.33	.20		
r	1.0	.50	1.0	.40	.75	.62	1.0	1.0	r	1.0	.00	1.0	1.0	.60	.00	.75	.60		
	8	9a	9b	10	11a	11b	12a	12b		74d	74e	74f	75a	75b	75c	76a	76b		
s	2	4	2	3	3	3	4	6	s	4	4	3	4	3	1	5	5		
c	.50	.25	.50	.33	.33	.33	.25	.16	c	.25	.25	.33	.25	.33	1.0	.20	.20		
r	.66	.62	.00	.60	.50	.33	.00	.50	r	.40	.25	.00	.62	.00	1.0	.42	.55		
	12c	12d	13	14	15	16a	16b	17		76c	77a	77b	77c	78	79	80	81a		
s	2	1	1	2	1	3	1	2	s	4	3	4	3	3	1	3	2		
c	.50	1.0	1.0	.50	1.0	.33	1.0	.50	c	.25	.33	.25	.33	.33	1.0	.33	.50		
r	.75	1.0	1.0	.90	1.0	.66	1.0	.75	r	.25	.00	.50	.33	.60	1.0	.50	.75		
	18a	18b	19	20a	20b	21	22	23		81b	81c	82a	82b	83	84a	84b	85a		
s	3	2	1	2	2	1	3	1	s	2	3	3	3	3	5	1	5		
c	.33	.50	1.0	.50	.50	1.0	.33	1.0	c	.50	.33	.33	.33	.33	.20	1.0	.20		
r	.33	.50	1.0	.75	.75	1.0	.80	1.0	r	.80	.33	.66	.00	.00	.20	1.0	.42		
	24	25	26	27a	27b	28	29	30		85b	86a	86b	87a	87b	88	89	90a		
s	1	1	2	3	3	1	1	3	s	3	2	2	4	2	3	4	2		
c	1.0	1.0	.50	.33	.33	1.0	1.0	.33	c	.33	.50	.50	.25	.50	.33	.25	.50		
r	1.0	1.0	.00	.66	.33	1.0	1.0	.71	r	.33	.66	.00	.62	.87	.66	.66	.50		
	31	32	33	34	35a	35b	36	37		90b	91	92a	92b	93	94	95	96a		
s	4	3	1	3	2	3	2	2	s	2	2	0	2	1	3	1	4		
c	.25	.33	1.0	.33	.50	.33	.50	.50	c	.50	.50	1.0	.50	1.0	.33	1.0	.25		
r	.66	.60	1.0	.33	.75	.77	.80	.75	r	.00	.80	1.0	.00	1.0	.33	1.0	.40		
	38a	38b	39a	39b	40	41	42	43		96b	96c	97a	97b	97c	97d	97e	98		
s	1	2	3	1	2	2	4	3	s	3	3	4	4	3	1	2	4		
c	1.0	.50	.33	1.0	.50	.50	.25	.33	c	.33	.33	.25	.25	.33	1.0	.50	.25		
r	1.0	.66	.50	1.0	.50	.50	.57	.66	r	.66	.60	.40	.57	.71	1.0	.66	.50		
	44	45	46	47	48a	48b	49	50a		99	100	101	102a	102b	102c	102d	102e		
s	1	2	1	2	1	4	1	2	s	3	2	3	2	2	4	4	1		
c	1.0	.50	1.0	.50	1.0	.25	1.0	.50	c	.33	.50	.33	.50	.50	.25	.25	1.0		
r	1.0	.87	1.0	.80	1.0	.50	1.0	.00	r	.33	.88	.66	.66	.87	.72	.40	1.0		
	50b	51	52a	52b	53a	53b	54	55a		103	104	105a	105b	105c	105d	105e	105f		
s	3	2	1	2	1	2	1	2	s	2	2	2	3	4	4	3	1		
c	.33	.50	1.0	.50	1.0	.50	1.0	.50	c	.50	.50	.50	.33	.25	.25	.33	1.0		
r	.66	.87	1.0	.83	1.0	.83	1.0	.85	r	.00	.75	.50	.50	.40	.25	.00	1.0		
	55b	56a	56b	57a	57b	57c	57d	58a		106a	106b	106c	106d	106e	107a	107b	108		
s	1	2	3	4	4	3	2	1	s	1	3	4	3	3	1	2	1		
c	1.0	.50	.33	.25	.25	.33	.50	1.0	c	1.0	.33	.25	.33	.33	1.0	.50	1.0		
r	1.0	.50	.50	.25	.66	.50	.00	1.0	r	1.0	.50	.57	.66	.00	1.0	.85	1.0		
	58b	59a	59b	60	61	62	63	64a		109	110	111	112a	112b	113	114a	114b		
s	3	1	2	1	1	1	1	4	s	1	1	2	2	2	1	2	3		
c	.33	1.0	.50	1.0	1.0	1.0	1.0	.25	c	1.0	1.0	.50	.50	.50	1.0	.50	.33		
r	.50	1.0	.88	1.0	1.0	1.0	1.0	.25	r	1.0	1.0	.88	.50	.50	1.0	.50	.60		
	64b	64c	65	66	67	68	69	70		115a	115b	115c	116	117	118	119	120	121a	121b
s	5	2	1	5	3	1	2	3	s	2	6	2	4	1	4	1	1	2	6
c	.20	.50	1.0	.20	.33	1.0	.50	.33	c	.50	.16	.50	.25	1.0	.25	1.0	1.0	.50	.16
r	.42	.50	1.0	.50	.71	1.0	.00	.66	r	.00	.28	.00	.57	1.0	.40	1.0	1.0	.80	.28