Records of the Australian Museum (1993) Supplement 19. ISBN 0 7310 1164 3

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 amethistina*, *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 Subsaharan 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; basipterygoid process has a distinct and flattened distal facet for the pterygoid; Meckelian cartilage is extended forward beyond the dentary onto the skin of the symphysial 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