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A review of the systematics and taxonomy of Pythonidae: an ancient serpent lineage

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Here we review research over the past quarter century regarding the systematics and taxonomy of an ancient, popular and economically valuable group of snakes referred to as pythons (Serpentes, Pythonidae). All recent phylogenetic studies recognize the pythons as monophyletic; however, the phylogenetic relationships at supraspecific levels are conflicting, and many of the relationships recovered are paraphyletic. We identify several taxonomic changes as necessary to clarify supraspecific relationships and which resolve the issue of paraphyly recovered in several studies. Overall, our review of the phylogenetic systematics of pythons points to considerable incongruence among recovered relationships. Instances of paraphyly emerge, low node support is detected, and terminal taxa are unstable across phylogenetic hypotheses. We thus recognize that pythonid gene trees have been unable, for various reasons, to reveal the true species tree. This occurrence is not unexpected and can arise from incomplete taxon sampling, long-branch attraction and repulsion, homoplasy, ancestral polymorphism, and, more notably, the anomaly zone. These phenomena ultimately yield incomplete lineage sorting, or the failure of lineages to coalesce over evolutionary time. We discuss future directions to resolve these troubling issues. Without resolution, adaptive hypotheses about pythons will be limited, including hypotheses of geographic origin. Analyses that recover the clade *Python* as sister to the Indo-Australian clade are interpreted to support a Laurasian origin of Pythonidae. In contrast, a Gondwanan origin is supported when the Indo-Australian clade is recovered as basal to the *Python* clade. We describe the morphology of two recently proposed genera. Finally, we designate and describe the neotype for *Morelia azurea* and offer a list of the currently accepted python species and their taxonomy.

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ADDITIONAL KEYWORDS: ancestral polymorphism – anomaly zone – homoplasy – incongruence – long-branch attraction – morphology – mtDNA – nDNA – neotype of *Morelia azurea* – phylogenetics – python.

INTRODUCTION

Pythons (Pythonidae) are an ancient Old World snake lineage composed of both diminutive and giant constricting species (Henderson & Powell, 2007; Reynolds, Niemiller & Revell, 2014; Reptile Database: http://www.reptile-database.org/). All taxa are restricted to the tropics and subtropics of the Eastern Hemisphere, primarily sub-Saharan Africa, Asia below 30 degrees N latitude, Indonesia, Philippines, Papua New Guinea, and Australia (Barker & Barker, 2003). Two species are restricted to the Northern Hemisphere (*Python regius* and *P. molurus*), while all remaining

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species (n = 42) occupy equatorial or subequatorial regions.

The first description of a python (*Coluber molurus*) was included in Linnaeus (1758). By 1850, 13 species, including the largest species in the genus *Python*, were identified. In the second half of the 19th century, 12 new species were described and are still recognized today. In the 20th century, 15 taxa were described that remain recognized, ten of which are considered species and five as subspecies (Wallach, Williams & Boundy, 2014)). From 2000 to 2013, 12 new taxa were described and named, three of which show minor morphological variation and are considered as subspecies. Currently, Pythonidae is comprised of 44 species of which four have recognized subspecies (Table 1). Based on this trend it seems likely that more species will be discovered and named as remote regions are explored more thoroughly, especially in Southeast Asia.

All recent phylogenetic studies recognize the pythons as monophyletic (Lawson, Slowinski & Burbrink, 2004; Noonan & Chippindale, 2006; Grazziotin *et al*., 2007; Pyron, Burbrink & Wiens, 2013; Reynolds *et al*., 2014). Morphological studies include those of Underwood & Stimson (1990), Kluge (1993), and Rawlings *et al*. (2008). Phylogenetic studies based on molecular characters include Slowinski & Lawson (2002), Wilcox *et al*. (2002), Lawson *et al*. (2004), Noonan & Chippindale (2006), Grazziotin *et al*. (2007), Vidal, Delmas & Hedges (2007), Pyron *et al*. (2013), and Reynolds *et al*. (2014).

Descriptions of the phylogenetic relationships of pythons at supraspecific levels are conflicting, and many of the derived relationships resulted in paraphyly. Our purpose here is to compare the phylogenetic relationships hypothesized in modern systematic studies, identify and evaluate conflicts and congruences among the analyses in order to create a current and correct list of the species in the Pythonidae. For the purpose of comparison, we provide the phylogenetic relationships of taxa hypothesized in multiple studies and illustrated by a variety of trees.

The phylogeny of pythons is of particular historical interest as evidence in the question of their geographic origin. Some phylogenetic studies of pythons have uncovered two basic divisions, a clade that includes the species in the genus *Python*, and a sister clade comprised of all other species, referred to as the Indo-Australian clade (Rawlings *et al*., 2008). Analyses that place the *Python* clade as the sister species to the Indo-Australian clade are interpreted to support a Laurasian origin of the Pythonidae. A Gondwanan origin is supported, however, when the lineages in the Indo-Australian clade are hypothesized to be basal to the clade composed of *Python* (Kluge, 1993).

During the 20th century, there were several prominent publications in which the supraspecific taxonomy of various python species was changed. The assignment of various species to genera was originally accomplished on the basis of overall similarity (Stull, 1935; Stimson, 1969; McDowell, 1975; Cogger, Cameron & Cogger, 1983), but evolutionary methods of analysis (sensu Hennig, 1966) were eventually employed, beginning with Underwood & Stimson (1990) and Kluge (1993).

A REVIEW OF THE PHYLOGENETIC STUDIES OF PYTHONIDAE

McDowell's (1975) systematic research on pythons remains one of the most detailed morphological studies of this group of snakes. His phenetic analysis had taxonomic implications for all members of Pythonidae, his concentration on the pythons of New Guinea notwithstanding. With the exception of the Australian genus *Aspidites*, McDowell described the genera of pythons as 'weakly defined', stating '. . . a good case could be made for referring to all species as *Python* (Daudin, 1803)'. McDowell also was first to recognize that the genus *Python* could be partitioned into two groups, which he identified as the *reticulatus* group and the *molurus* group. He noted that species of the *reticulatus* group shared features with *Liasis*, which at that time included *amethistina*, *boeleni*, *boa*, *albertisii*, *papuanus*, and *childreni*. McDowell removed *amethistina* and *boeleni* from *Liasis* and *spilota* from *Morelia*, referring all to *Python* because of their affinities to the *reticulatus* group. McDowell also included *timoriensis* in the *reticulatus* clade.

Underwood (1976) compared phenetic and phyletic analyses of the Boidae. Today, however, species included in Underwood's analysis are currently classified as members of Pythonidae, Loxocemidae, Bolyeriidae, Xenopeltidae, Calabariidae, Tropidophiidae, and Boidae (Pyron *et al*., 2013). Nine species of pythons were included in Underwood's analysis but no taxonomic changes were recommended. He hypothesized a Laurasian origin of pythons.

The first phylogenetic analysis of Pythonidae, using outgroup methods and character states, was undertaken by Underwood & Stimson (1990). Their analysis was based on 38 morphological characters using 18 python species. The authors used a 'common ancestor' as an outgroup, coding as primitive the most common character states primarily within *Loxocemus* and *Xenopeltis*, but they also considered the conditions of *Cylindrophis*, *Uropeltis, Anomalepis*, and *Anilius*. Based on their study, Underwood and Stimson concluded that the pythons represent a monophyletic group of Laurasian origin. They also recommended that pythons not classified as either *Python* or *Aspidites* be assigned to the genus *Morelia*.

In our opinion, the phylogenetic analysis of Kluge (1993; Fig. 1) seems to have had the greatest impact

Table 1. List of currently recognized Python species and associated nomenclatural changes. Forty four species of Python are currently recognized, and numerous molecular and morphological phylogenetic inquiries have influenced their taxonomic nomenclature. Individuals marked with an asterisk (*) were not included in analyses. With the exception of the Reynolds *et al*. manuscript, taxonomic sampling was less than 60% coverage, and thus numerous gaps in phylogenetically valuable data exist. This table illustrates the taxonomic changes that would be required if strict nomenclatural rules were followed based on the analyses of these studies

Genus	Species	Common name	Kluge (1993)	Lawson *et al*. (2004)	Rawlings *et al*. (2008)	Pyron *et al*. (2013)	Reynolds *et al*. (2014)
Antaresia	*childreni*	Children's Python	*Antaresia childreni*	*Morelia childreni*	*Antaresia childreni*	*Antaresia childreni*	*Chondropython childreni*
Antaresia	*maculosa*	Spotted Python	*Antaresia maculosa*	*Morelia maculosa*	*Antaresia maculosa*	*Antaresia maculosa*	*Chondropython maculosus*
Antaresia	*perthensis*	Pygmy Python	*Antaresia perthensis*	*	*Antaresia perthensis*	*Antaresia perthensis*	*Chondropython perthensis*
Antaresia	*stimsoni*	Large-blotched Python	*Antaresia stimsoni*	*	*Antaresia stimsoni*	*Antaresia stimsoni*	*Chondropython stimsoni*
Apodora	*papuana*	Papuan Python	*Apodora papuana*	*Liasis papuanus*	*Lisalia papuana*	*Liasis papuanus*	*Lisalia papuanus*
Aspidites	*melanocephalus*	Black-headed Python	*Aspidites melanocephalus*	*	*Aspidites melanocephalus*	*Aspidites melanocephalus*	*Aspidites melanocephalus*
Aspidites	*ramsayi*	Woma	*Aspidites ramsayi*	*	*Aspidites ramsayi*	*Aspidites ramsayi*	*Aspidites ramsayi*
Bothrochilus	*boa*	Ringed Python	*Bothrochilus boa*	*	*Bothrochilus boa*	*Bothrochilus boa*	*Bothrochilus boa*
Leiopython	*albertisii*	Northern Whitelip Python	*Leiopython albertisii*	*Leiopython albertisii*	*Bothrochilus albertisii*	*Bothrochilus albertisii*	*Bothrochilus albertisii*
Leiopython	*biakensis*	Biak Whitelip Python	*	*	*	*	*
Leiopython	*fredparkeri*	Karimui Basin Whitelip Python	*	*	*	*	*
Leiopython	*huonensis*	Huon Peninsula Whitelip Python	*	*	*	*	*
Leiopython	*meridionalis*	Southern Whitelip Python	*	*	*	*	*Leiopython meridionalis*
Leiopython	*montanus*	Wau Whitelip Python	*	*	*	*	*
Liasis	*dunni*	Wetar Python	*	*	*	*	*
Liasis	*fuscus*	Water Python	*	*	*Liasis fuscus*	*Liasis fuscus*	*Liasis fuscus*
Liasis	*mackloti*	Freckled Python	*Liasis mackloti*	*Liasis mackloti*	*Liasis mackloti*	*Liasis mackloti*	*Liasis mackloti*
Liasis	*olivaceus*	Olive Python	*Liasis olivaceus*	*Liasis olivaceus*	*Lisalia olivacea*	*Liasis olivaceus*	*Lisalia olivaceus*
Liasis	*savuensis*	Savu Python	*	*	*	*	*Liasis savuensis*
Malayopython	*reticulatus*	Reticulated Python	*Python reticulatus*	*Python reticulatus*	*Broghammerus reticulatus*	*Broghammerus reticulatus*	*Malayopython reticulatus*
Malayopython	*timoriensis*	Lesser Sundas Python	*Python timoriensis*	*	*Broghammerus timoriensis*	*Broghammerus timoriensis*	*Malayopython timorensis*
Morelia	*azurea*	Northern Green Python	*	*	*Chondropython viridis (N)*	*	*
Morelia	*bredli*	Centralian Python	*	*	*Morelia bredli*	*Morelia bredli*	*Morelia bredli*
Morelia	*carinata*	Rough-scaled Python	*Morelia carinata*	*	*Chondropython carinata*	*Morelia carinata*	*Morelia carinata*
Morelia	*imbricata*	Southwestern Carpet Python	*	*	*	*	*
Morelia	*spilota*	Diamond Python	*Morelia spilota*	*Morelia spilota*	*Morelia spilota*	*Morelia spilota*	*Morelia spilota*
Morelia	*viridis*	Southern Green Python	*Morelia viridis*	*Morelia viridis*	*Chondropython viridis (S)*	*Morelia viridis*	*Chondropython viridis*
Simalia	*amethistina*	Amethystine Python	*Morelia amethistina*	*Simalia amethistina*	*Morelia amethistina*	*Simalia amethistina*	*Simalia amethistina*
Simalia	*boeleni*	Black Python	*Morelia boeleni*	*	*Genus novum boeleni*	*Simalia boeleni*	*Simalia boeleni*
Simalia	*clastolepis*	Southern Moluccan Python	*	*	*	*	*Simalia clastolepis*
Simalia	*kinghorni*	Scrub Python	*	*	*	*	*Simalia kinghorni*
Simalia	*nauta*	Tanimbar Python	*	*	*	*	*Simalia nauta*
Simalia	*oenpelliensis*	Oenpelli Python	*Morelia oenpelliensis*	*	*Morelia oenpelleniesis*	*Simalia oenpelleniesis*	*Nyctophylopython oenpelliensis*
Simalia	*tracyae*	Halmahera Python	*	*	*	*	*Simalia tracyae*
Python	*anchietae*	Escarpment Python	*Python anchiete*	*	*	*	*Python anchietae*
Python	*bivittatus*	Burmese Python	*	*	*	*	*Python bivittatus*
Python	*breitensteini*	Borneo Python	*	*	*	*Python curtus*	*
Python	*brongersmai*	Blood Python	*	*	*Python brongersmai*	*Python brongersmai*	*Python brongersmai*
Python	*curtus*	Sumatran Python	*Python curtus*	*	*	*	*Python curtus*
Python	*kyaiktiyo*	Mon Python	*	*	*	*	*
Python	*molurus*	Indian Python	*Python molurus*	*Python molurus*	*Python molurus*	*Python molurus*	*Python molurus*
Python	*natalensis*	Lesser African Python	*	*	*	*	*
Python	*regius*	Ball Python	*Python regius*	*Python regius*	*Python regius*	*Python regius*	*Python regius*
Python	*sebae*	African Python	*Python sebae*	*Python sebae*	*Python sebae*	*Python sebae*	*Python sebae*
Taxonomic Coverage (%)			0.55	0.30	0.59	0.59	0.77

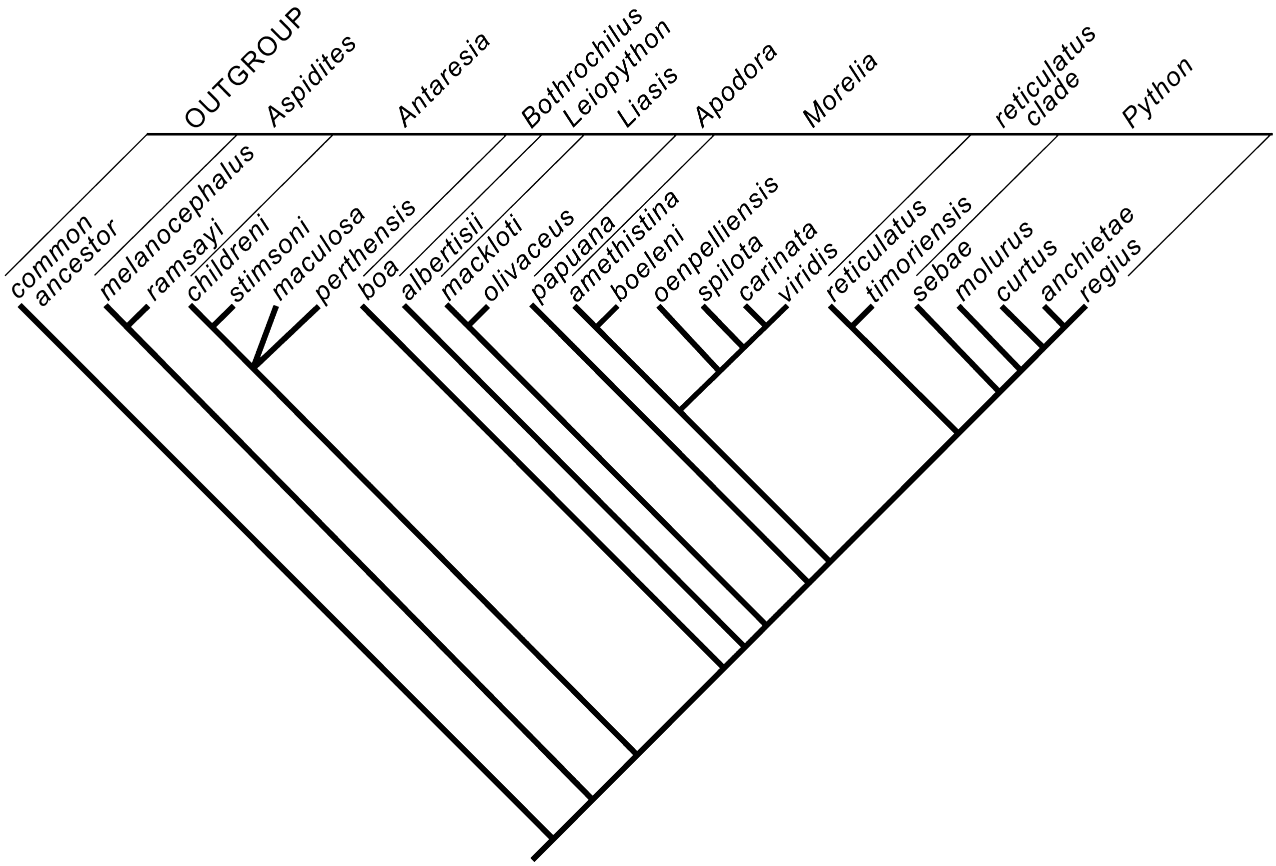

Figure 1. Kluge's (1993) phylogenetic hypothesis of the pythons based on 121 morphological, meristic, and behavioural characters.

and influence on the systematics and taxonomy of pythons. His analysis of 24 extant species of pythons was based on a data set of 121 morphological and behavioural characters. Kluge's first outgroup included what were then classified as the boines, erycines, tropidophiines, bolyeriines, and *Acrochordus*. Successively distant outgroups were *Loxocemus*, *Xenopeltis*, and anilioid snakes (*Anilius*, *Cylindrophis*, and uropeltines).

Kluge hypothesized that the most primitive species are characterized by small body size, small heads, no-or-few labial pits, and entire subcaudals, whereas the species with the most derived traits showed a trend to be larger, have increased head size, numerous labial pits with complex development and structure, and an extensive division of the scalation, particularly on the head. The python genus *Aspidites* emerged as the sister to all other pythons, and the python lineages with the most derived characters were the sister clades *Morelia* and *Python*. Kluge's systematic arrangement recognized three monotypic genera. The hypothesized relationships illustrated in Figure 1 required some taxonomic changes that were accepted as appropriate nomenclature. This analysis required that *Bothrochilus* (Schlegel, 1837) be restricted to *boa*, and *Leiopython* Hubrecht, 1879 was resurrected from synonymy for *albertisii*. In the 20 years prior to this study, these two species had been shuffled from *Morelia* to *Liasis* to *Bothrochilus*.

Kluge (1993) also placed *papuana* in a new genus *Apodora*. We agree with Kluge that this species is sufficiently distinct from the genus *Liasis* to warrant recognition as an independent lineage. *Apodora papuana* in life is starkly different from any of the other species in *Liasis*. Though there are general overall similarities between *Apodora papuana* and *Liasis olivaceus* (i.e. both are large brown elongated snakes with similarly high counts of ventral scales), perceivable similarities end there. We have extensive experience with living specimens of *Apodora*, and also with all taxa of *Liasis* (*fuscus*, *dunni*, *mackloti*, *savuensis*, *olivaceus*) excepting *L. olivaceus barroni*. We have observed that *A. papuana* has the remarkable ability to change the colour of its head, eyes, and body, each independent of the other; this is not observed (or reported) in *Liasis*. Furthermore, *Apodora* has a low neural spine on the

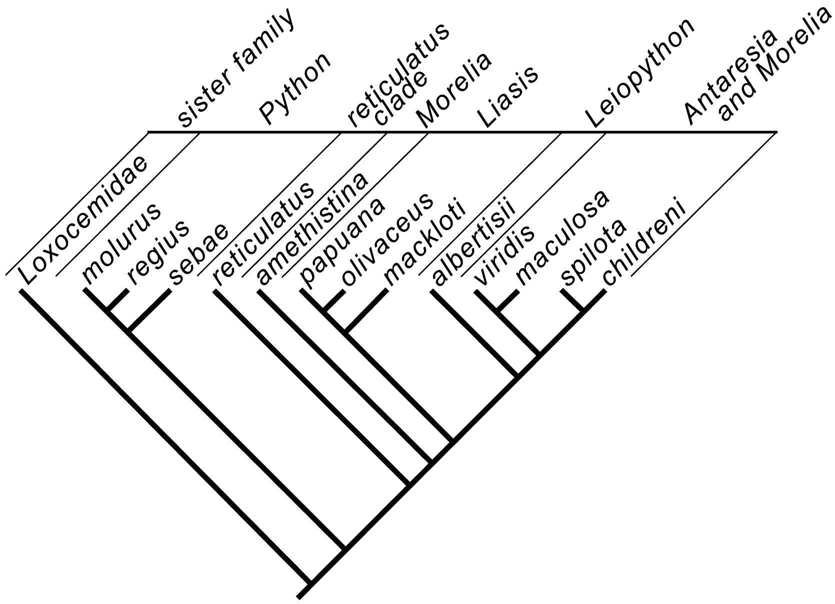

Figure 2. Lawson *et al.* 's (2004) phylogenetic hypothesis of the pythons based on sequence analysis of the mitochondrial cytochrome *b* region.

vertebrae of the neck and body relative to *Liasis*, a primitive condition (Scanlon & Mackness, 2002). *Apodora* has darkly pigmented skin, including the lining of the mouth and cloaca, and has an extremely long and deeply forked tongue. According to Parker (1982), *Apodora* appears to easily slough skin; this has not been observed by us and has not been reported in *Liasis*. *Apodora* has thermoreceptive pits in the rostral while *Liasis* species generally do not (individual specimens of *L. mackloti* may show shallow rostral pits, (Barker and Barker, pers. obs.; McDowell, 1975). When corrected for size (SVL), the eggs of *Apodora* are relatively larger than those of any of the four *Liasis* species with whose eggs which we have experience (Barker and Barker, unpubl. data). The phylogenetic analysis and conclusions of Rawlings, Barker & Donnellan (2004), based on mitochondrial DNA markers, strongly support the recognition of *Apodora* as the sister taxon to *Liasis*.

Kluge (1993) found that *Morelia* forms a clade that consists of the taxa (*boeleni* + *amethistina*) and (*spilota* + *viridis* + *oenpelliensis* + *carinata*). Kluge recommended that if future studies supported formal recognition of these sister clades, the (*boeleni* + *amethistina*) clade should be placed in the genus *Simalia* (Gray, 1849). The second clade would remain in the genus *Morelia*, as *spilota* is the type species of the genus. Kluge (1993) assigned *amethistina*, *spilota*, and *viridis* to the genus *Morelia*. He also illustrated a separation of the *reticulatus* clade from the clade comprised of the genus *Python*. However, the hypothesized placement of the *Python* clade and the *reticulatus* clade as derived sister clades (Fig. 1) allow the inclusion of *reticulatus* and *timoriensis* in the genus *Python* without paraphyly.

Lawson *et al*. (2004) included 13 species of pythons in their broad examination of phylogenetic relationships of alethinophidian snakes, relying on complete nucleotide sequences of the mitochondrial gene cytochrome *b*. The *molurus* group of *Python* (sensu McDowell, 1975) was used as the sister group to all other pythons (see Fig. 2). However, *reticulatus* is recovered as the sister group to all Indo-Australian python species; therefore, in this arrangement, the retention of *reticulatus* in *Python* renders that clade paraphyletic. In their Figure 1, '*Morelia*' *amethistina* is sister to a clade comprising *Liasis*, *Apodora*, *Antaresia*, *Leiopython*, plus other *Morelia*, which renders *Morelia* as paraphyletic. Interestingly, Lawson *et al*. (2004) recovered (*Morelia viridis* + *Antaresia maculosa*), and (*M. spilota* + *A. childreni*) as sister clades. These are highly unlikely relationships that appear in different variations in several subsequent analyses (see below).

Grazziotin *et al*. (2007) included pythons in their phylogenetic study of alethinophidian snakes (Fig. 3). This analysis is based solely on molecular characters. The dataset was comprised of the nucleotide sequences of four mitochondrial and five nuclear genes. The sample used in the study included 70 taxa, including all major higher squamate taxa. There is a unique relationship proposed by this analysis among the snakes in that the Pythonidae and the Boidae are hypothesized to be alethinophidians with the most

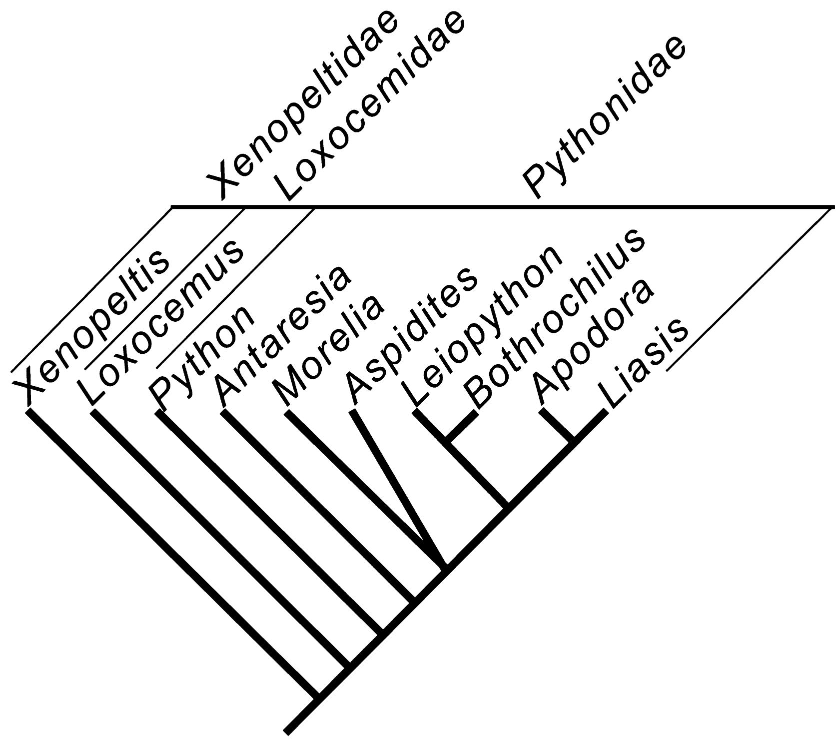

Figure 3. Grazziotin *et al.* 's (2007) phylogenetic hypothesis of the pythons based on a total evidence approach using sequence data from four mitochondrial DNA regions and five nuclear DNA loci.

derived characters. Within Pythonidae, the genus *Python* is hypothesized as the sister to all other pythons, which is consistent with all of the analyses based on molecular characters. However, the genus *Antaresia* is recovered as sister to all Indo-Australian pythons, which is a unique arrangement. In general, the relationships of the Indo-Australian pythons are not resolved. Based on this analysis, an argument could be made to place *Leiopython* in synonymy with *Bothrochilus*, and *Apodora* in synonymy with *Liasis*.

Grazziotin *et al*. (2007) '. . .suggest that some of the conflicting results obtained in molecular studies. . .can be interpreted as a problem of taxon sampling that produce spurious signals due to the relictual condition of the extant snake fauna. . .' They go on to say, 'A clearer picture of snake phylogeny would be possible only through a total evidence approach that includes morphology and fossil information.'

Rawlings *et al*. (2008) developed a phylogenetic hypothesis using a combined morphological and molecular (4 mtDNA regions and the structural features of the mitochondrial control region) data, re-analyzed Kluge's (1993) 121 character morphological data set, and compared their results with previous studies (see below). The central premise of this study concerns the geographic origin of Pythonidae. The phylogeny proposed by Kluge (1993) has *Aspidites* as sister to all other pythons and implies that the pythons arose in Gondwana. The phylogenies proposed by Underwood & Stimson (1990) and Lawson *et al*. (2004) have the genus *Python* as sister to all other pythons, which implies a Laurasian origin.

Three analyses were performed with combined molecular and morphological data for 26 python taxa and three outgroup taxa. These analyses – Maximum Parsimony, Bayesian, and a strict consensus – produced phylogenies that consistently show a paraphyletic arrangement in *Python*, with *Python* (*molurus* clade, sensu McDowell, 1975) recovered as sister to all other pythons, and the clade (*reticulatus* + *timoriensis*) recovered as sister to all Australo-Papuan species (see Fig. 4). In two of these phylogenies, *Morelia* is paraphyletic. In the two illustrated trees, *Apodora* is in a clade with *Liasis* with weak support; in a tree that is not illustrated but is equally parsimonious to the tree in their Figure 2A, *Apodora* is recovered as sister to *Liasis*. *Leiopython* and *Bothrochilus* are recovered as sister in all three trees. In one analysis, taxa of the *Morelia* clade (*viridis* N + *viridis* S + *carinata*) are sister to the *Antaresia* clade.

Four Maximum Parsimony analyses were then performed using morphological characters exclusively. Two analyses used Kluge's 121 character dataset, and two were made with modifications to the dataset. In

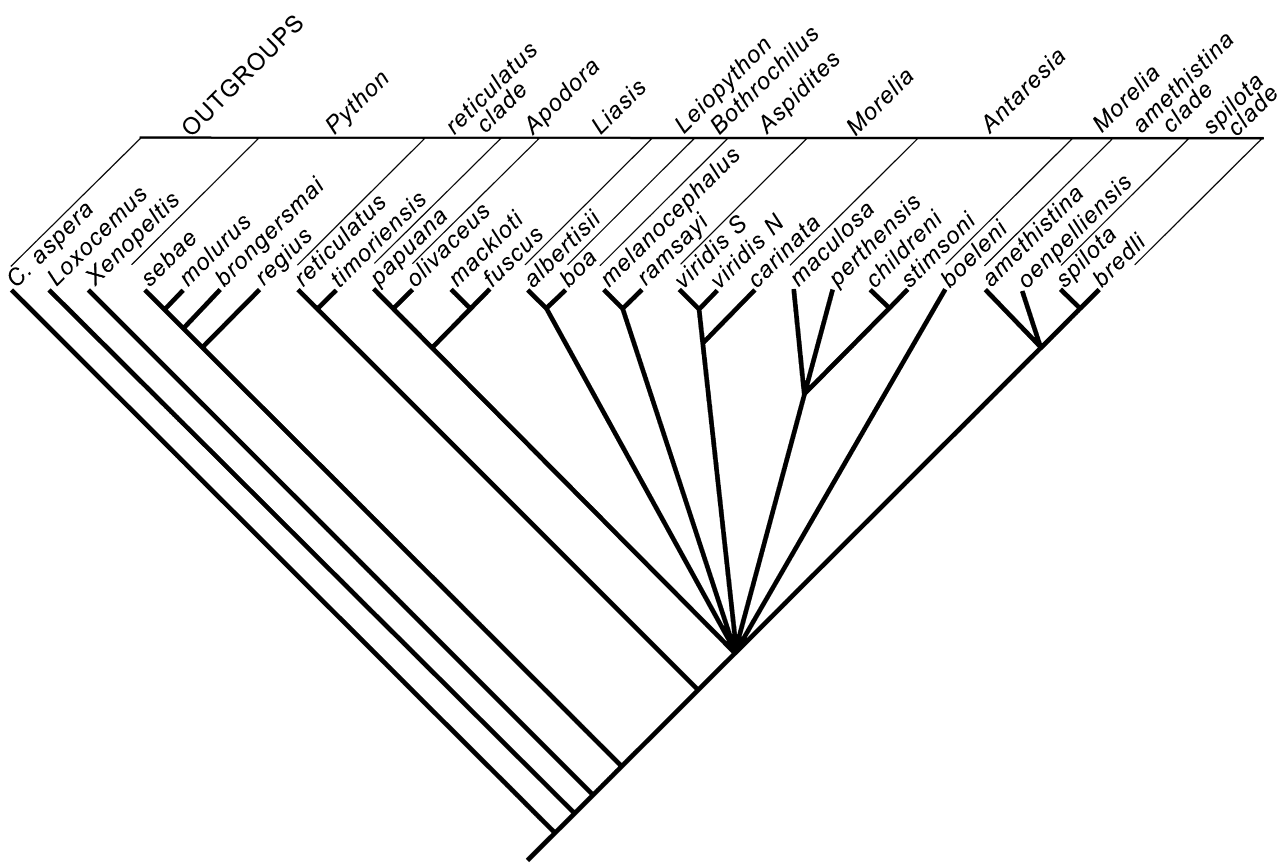

Figure 4. Rawlings *et al.* 's (2008) phylogenetic hypothesis of the pythons based on a combined analysis of morphological data and four mitochondrial DNA regions.

addition, two analyses used an expanded set of outgroups, and two incorporated a single 'common ancestor' outgroup, described by Rawlings *et al*. (2008) as "as per Kluge's analysis". We note that the single outgroup used was identified as boines, as defined in Kluge (1991). Kluge described the common ancestor as the common ancestral state of the characters of bolyeriines, tropidophiines, and rarely *Acrochordus*, but never the Caenophidia. The expanded outgroup in the two analyses includes anilioids, caenophidians, boines, and *Loxocemus* and *Xenopeltis*; this more closely follows the recent tree-of-life proposed by Pyron *et al*. (2013).

The rationale for modifications to the morphological dataset stemmed from 16 characters in the Kluge dataset that partition *Aspidites* from all other pythons, placing it sister to all other pythons in Kluge's hypothesized phylogeny (Fig. 1). Rawlings *et al*. (2008) and others re-evaluated those characters according to several criteria, including evaluating which characters are plesiomorphic and which, if any, are secondarily derived characters (e.g. reversals) resulting from the burrowing behaviour of *Aspidites*. Ultimately eight characters from the dataset were removed as they represented phylogenetically non-informative autapomorphies. We point out that Kluge stated specifically that he did not consider 'morphological specialization' (Marx & Raab, 1970) to determine the polarity of characters 'because that rule requires hypotheses of adaptive specialization which are difficult to evaluate critically'.

Re-analysis of the morphological data set (as above) consistently revealed *Aspidites* as sister to all other pythons, *Apodora* and *Leiopython* as monophyletic lineages, and *Morelia* as monophyletic with (*boeleni* + *amethistina*) as a subclade. *Python* is monophyletic, but in three analyses, (*reticulatus* + *timoriensis*) is positioned as a subclade. No species in the *spilota* clade of *Morelia* is recovered as sister to *Antaresia* in any of the analyses. The taxonomy of these four analyses follow Kluge (1993).

In sum, Rawlings *et al*. (2008) support the Laurasian origin of pythons, identify a paraphyletic division of *Python* that is hypothesized in all three analyses of combined morphological and molecular characters, and propose *Broghammerus* (*nomen dubium*) as a new genus for the (*reticulatus* + *timoriensis*) clade. They conclude by stating that the 'Relationships among the

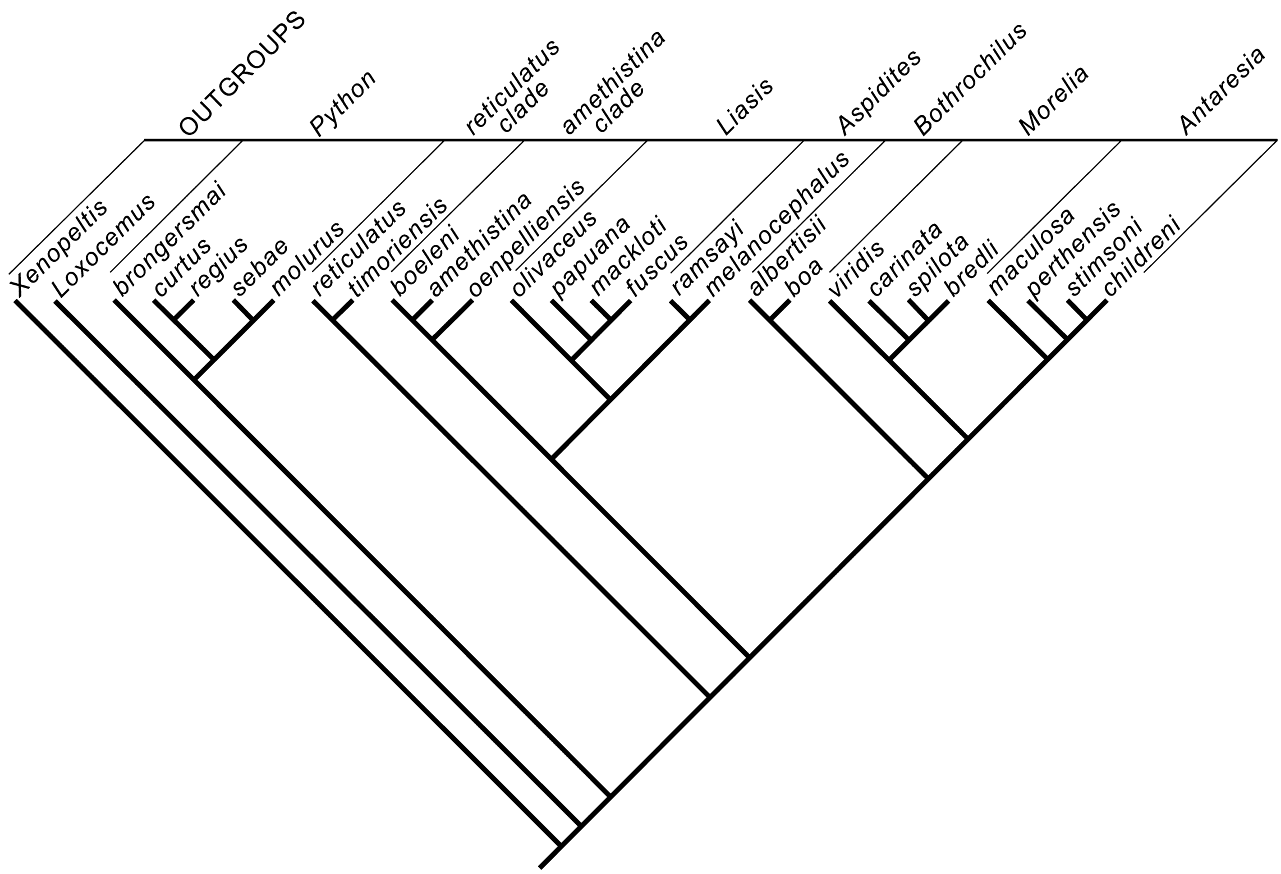

Figure 5. Pyron *et al.* 's (2013) phylogenetic hypothesis of the pythons based on a combined analysis of seven nuclear DNA loci and five mitochondrial DNA regions.

Australo-Papuan genera are sensitive to the methods of analysis and consequently are not well supported in either analysis where they show conflict.'

Pyron *et al*. (2013; Fig. 5) included a clade comprised of ((Pythonidae + Loxocemidae) Uropeltidae) as part of an enormous phylogenetic analysis of 4161 squamate species and based on up to 12 896 base pairs of sequence data per species (average = 2497 bp), including 12 genes, (seven nuclear loci and five mitochondrial). However, the exact number of base pairs on which is based the phylogeny of taxa in the Pythonidae is not made available, and in some instances may represent only partial genetic coverage. Pyron *et al*. (2013) recovered the genus *Python* as sister to all other python species, and the (*reticulatus* + *timoriensis*) clade was placed as sister to all Indo-Australian pythons. Otherwise, the relationships among the Indo-Australian pythons are largely unresolved. *Morelia* is rendered paraphyletic by inclusion of taxa of the *amethistina* clade. The species that comprise the *spilota* clade of *Morelia* seem correct, but the placement of *Morelia* and *Antaresia* as sister taxa requires that each lineage has undergone numerous reversals, which is unlikely. *Morelia oenpelliensis* is recovered as a member of the *amethistina* clade of *Morelia*. The species *papuana* is recovered as a member of the *Liasis* clade, but with weak bootstrap support. *Leiopython albertisii* and *Bothrochilus boa* are recovered as sisters and, as such, *Leiopython* would be placed in synonymy with *Bothrochilus*, following the recommendation of Rawlings *et al*. (2008). However, Pyron *et al*. (2013) comment that they do not find support to distinguish *Aspidites* from this arrangement of *Bothrochilus*, and we find that as problematic.

Reynolds *et al*. (2014) present a multi-locus species-level phylogeny of the boas and pythons analysing 7561 base pairs of mt- and nuclear DNA, across 33 of 44 pythonid species. This study hypothesized numerous relationships among both python species and genera that differ from the study of Pyron *et al*. (2013). Based on the results of this study, the authors recommended a revised python taxonomy consisting of eight genera and 40 species (Fig. 6). The genus *Python* was hypothesized as a monophyletic basal clade composed of *regius* as sister to (*brongersmai* + *curtus*) that itself is sister to ((*bivittatus* + *molurus*) + (*anchietae* + *sebae*)). The

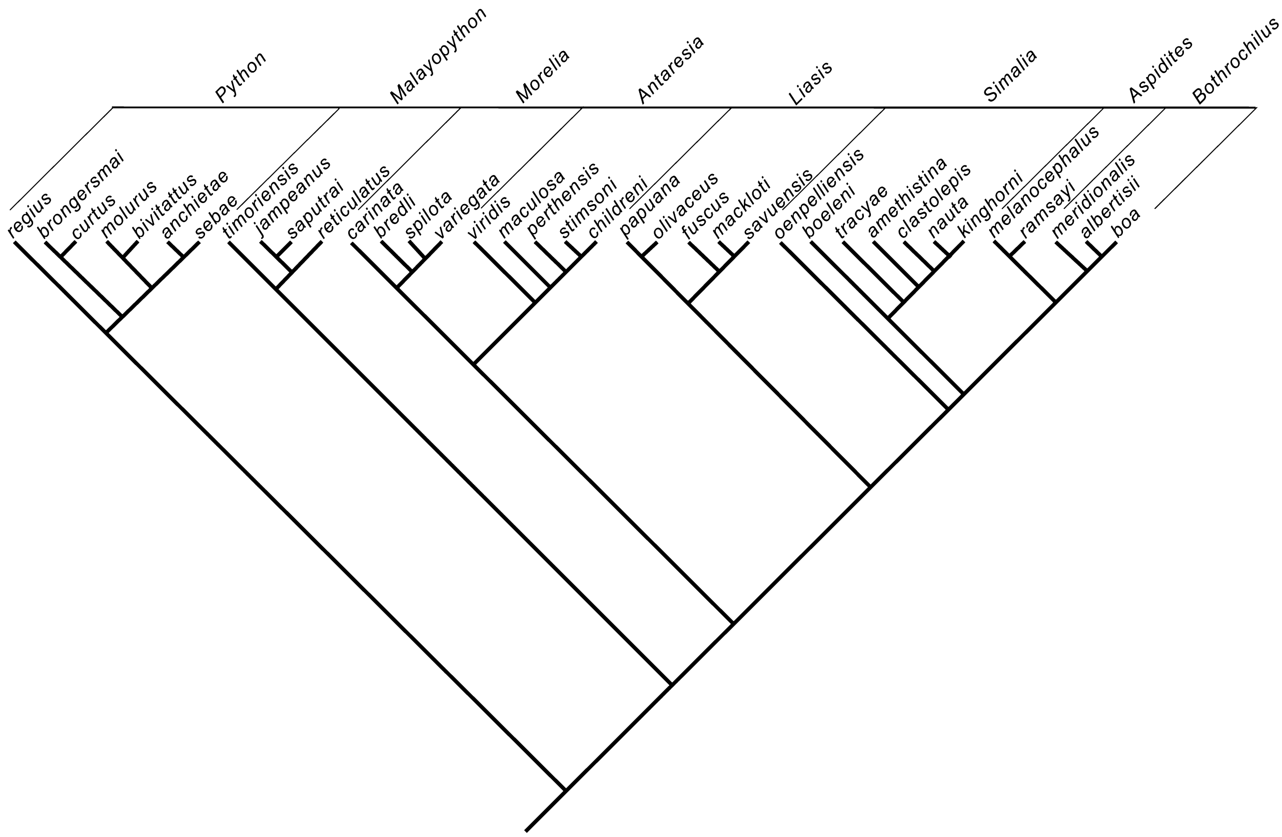

Figure 6. Reynolds *et al.* 's (2014) phylogenetic hypothesis of the pythons based on a combined analysis of eight nuclear DNA loci and three mitochondrial DNA regions.

(*reticulatus* + *timoriensis*) clade is placed in a new genus, *Malayopython* (Reynolds *et al.*, (2014), and is sister to the Indo-Australian genera. *Morelia* emerged in two clades: the *spilota* clade of *Morel*ia, recovered as sister to a clade comprised of (*Antaresia* + *Morelia viridis*), and the Australo-Papuan/Indonesian clade (*amethistina*, *boeleni, clastolepis, kinghorni*, *nauta, tracyae*, and *oenpelliensis*) recovered as sister to (*Aspidites* + *Leiopython* + *Bothrochilus*). Reynolds *et al.* (2014) rename the *amethistina* clade in the resurrected genus *Simalia* (Gray, 1849), thereby remedying the paraphyly noted in *Morelia* by many of the previous authors we have discussed. *Apodora* and *Liasis* were recovered as paraphyletic, and it was recommended that *Apodora* be subsumed by *Liasis*, thereby eliminating the problem of paraphyly. In addition, a close relationship was recovered among *Aspidites, Leiopython, and Bothrochilus*, and the authors support the recommendations of Rawlings *et al*. (2008; as above) which maintains *Aspidites* composed of (*ramsayi* + *melanocephalus*), and *Bothrochilus*, composed of (*hoserae* [*nomen dubium* corrected to *L. meridionalis* (Schleip, 2014)] + (*boa* + *albertisii*)).

In reviewing the phylogenetic systematics of pythons, we note considerable incongruence among the recovered trees (phylogenetic hypotheses). Instances of paraphyly emerge, low node support is detected on numerous occasions, and terminal taxa are unstable across the phylogenetic hypotheses. Ultimately, we recognize that pythonid gene trees struggle to reveal the true species tree. Such an occurrence is unsurprising and can arise from myriad sources with manifold effects (Hoelzer & Melnick, 1994). Specifically, incomplete taxon sampling (Pollock *et al.*, 2002; Zwickl & Hillis, 2002; Weins, 2003), long-branch attraction (Weins & Hollingsworth, 2000; Anderson & Swofford, 2004; Bergsten, 2005), long-branch repulsion (Siddall, 1998; Siddall & Whiting, 1999; Swofford *et al*., 2001), homoplasy (Kallersjo, Albert & Farris, 1999; Broughton, Stanley & Durrett, 2000; O'hUigin *et al.*, 2002), ancestral polymorphism (Weins, 1999; O'hUigin *et al.*, 2002), and, more notably, the anomaly zone (Degnan & Rosenberg, 2006) can yield incongruent phylogenetic hypotheses. These phenomena ultimately yield incomplete lineage sorting, or the failure of lineages to coalesce over evolutionary time (Maddison & Knowles, 2006; Carstens & Knowles, 2007).

A consequence of these processes acting or imposed on phylogenies is incongruence among recovered phylogenies. The pythons present a clear case of phylogenetic instability resulting from one or more of the above issues. Historically, the recommendations for dealing with incomplete lineage sorting tended to include increased taxonomic sampling (Pollock *et al.*, 2002) and combined analysis of multi-locus datasets (Maddison & Knowles, 2006; Heled & Drummond, 2009). Yet, as demonstrated above, increased taxonomic sampling and a multi-locus approach to the pythonids still yielded incongruent gene trees, paraphyly, and other problems.

We point to fig. 21 of Pyron *et al*. (2013), depicting their multi-locus phylogenetic hypothesis of the pythons, as illustrative. A striking degree of speciation in short evolutionary time is hypothesized to have occurred in the evolutionary history of pythonids, as noted by the extremely shallow internal branches in the phylogenies recovered. The presence of such a scenario, termed the 'anomaly zone,' may be driving considerable incongruence among gene trees (Degnan & Rosenberg, 2006; Kubatko & Degnan, 2007; Liu & Edwards, 2009).

This is of particular concern with multi-locus DNA sequence datasets, which include most of the phylogenetic investigations of the pythons discussed above. Such incongruence is of practical concern when employing gene trees to estimate species trees and, ultimately, being informative to permit robust taxonomic decisions (Huang & Knowles, 2009). Indeed, the anomaly zone can impose its effects on phylogenies with as few as five taxa (Rosenberg & Tao, 2008). Discordance between traditional concatenated sequence trees and phylogenomic trees have been detected in two diverse, rapid snake radiations (Lamphrophiidae and Colubridae), and further reveal, as a consequence of anomaly zones, certain lineages to appear to possess weak phylogenetic signals. Thus uncovering the true species tree has been difficult, even in the genomic age (Pyron *et al*., 2013). Inherent in this discussion is the notion that the philosophical underpinnings of the anomaly zone impact practical applications, most notably by impinging on nomenclatural accuracy via phylogenetic uncertainty. Yet gene-tree incongruence does not preclude species delimitation or taxonomic considerations (Knowles & Carstens, 2007). By considering all information available in concert, we take a total evidence approach (Kluge, 1998) in diagnosing the phylogenetic systematics of the group we call pythons.

DISCUSSION

Here we reviewed the systematics and taxonomy of pythonid snakes. One main goal was to create a current inventory of the species in Pythonidae based on the most conservative and realistic interpretations of the various conflicts and congruences that exist among the analyses in the various studies. We underscore that since Kluge's work (1993), 10 genera have been used to identify what appear to be the natural pythonid lineages. Two of these genera, *Apodora* and *Bothrochilus* are currently monotypic. We revealed that there appears to be remarkable consistency in the groupings of species within these genera, with only one species assigned to another genus as the result of a re-interpretation of its phylogenetic relationship. *Simalia oenpelliensis* was placed in the *spilota* clade of *Morelia* by Kluge (1993), but is then classified in the *amethistina* clade of *Morelia* (Rawlings *et al*., 2008; Pyron *et al*., 2013). In order to resolve the obvious paraphyly in *Morelia* as then defined, the *amethistina* clade is recognized as *Simalia* by Reynolds *et al*. (2014).

The advent of analyses based solely on molecular characters that occurred after Kluge (1993) have all produced remarkably similar relationships to the python tree-of-life. Most analyses recover Loxocemidae and Xenopeltidae as basal to Pythonidae, with most arrangements placing the Loxocemidae as the sister clade to Pythonidae, with the Xenopeltidae as basal to (Loxocemidae + Pythonidae) (Wilcox *et al*., 2002; Lawson *et al*., 2004; Noonan & Chippindale, 2006; Vidal, Delmas & Hedges, 2007; Pyron *et al*., 2013; Reynolds *et al*., 2014). The basal position of the genus *Python* as the sister to all other python clades was suggested by McDowell (1975), recovered by Underwood & Stimson (1990) and confirmed by all molecular studies since Lawson *et al*. (2004).

The next branch on the tree is the sister relationship of *reticulatus* and *timoriensis*. The analysis of Kluge (1993) showed the close relationship between these two species. The later analyses of Rawlings *et al*. (2008), Pyron *et al*. (2013), and Reynolds *et al*. (2014) all strongly support this relationship. These studies recover this monophyletic clade as the sister taxon to all Indo-Australian python genera (by which we refer to *Apodora*, *Aspidites*, *Antaresia*, *Bothrochilus*, *Leiopython*, *Liasis*, *Morelia*, and *Simalia* [Rawlings *et al*., (2008) refers generally to this group as the 'Australo-Papuan group' while we have referred to it as the Indo-Australian group because of the inclusion of several Indonesian taxa, including *Simalia tracyae*, *S. clastolepis*, *S. nauta*, and *Liasis* species from the Lesser Sunda Archipelago, species which were not included in Rawlings *et al*., 2008]). Rawlings *et al*. (2008) identified (*reticulatus* + *timoriensis*) as a genus, but mistakenly assigned to it an unavailable name. Pyron *et al*. (2013) described the name as the result of 'taxonomic vandalism' (referring to the actions of the original author of the name and not Rawlings). No suitable synonym was available for the senior species *reticulatus*, and Reynolds *et al*. (2014) named this clade as *Malayopython*.

The relationships of the Indo-Australian genera and their placements on the tree-of-life have generated the primary contradictions and conflicts among the studies, and created uncertainty in the correct taxonomy for the species in the Pythonidae. In reviewing the analyses of Rawlings *et al*. (2008), Pyron *et al*. (2013) and Reynolds *et al*. (2014), there are numerous contradictions. Specifically, three genera are consistently presented in paraphyly. All three authors recommend that two of these genera, *Apodora* and *Leiopython*, be synonymized with their sister clades, respectively *Liasis* and *Bothrochilus*.

However, the *spilota* clade of *Morelia* was recovered in paraphyly with *Antaresia* in the analysis of Lawson *et al*. (2004), it shares a common ancestor with *Aspidites* in Grazziotin *et al*. (2007), and it is recovered in paraphyly with *Antaresia* in two different analyses of Rawlings *et al*. (2008) and as the sister clade of *Antaresia* in a third analysis. *Morelia* is placed in a paraphyletic relationship with *Antaresia* in Pyron *et al*. (2013). *Morelia* is not only placed in a paraphyletic relationship with *Antaresia* in Reynolds *et al*. (2014), but *Morelia viridis* is actually placed in *Antaresia*.

We assume that the authors of these studies did not call for *Antaresia* to be subsumed into *Morelia* because the species in these two genera contain species that are dramatically different both phenotypically and morphologically, and obviously not closely related. We also note that *Antaresia* and *Morelia* appear to have passed through an anomaly zone in their evolutionary history. Therein lies our primary justification for continuing to recognize *Apodora* and *Leiopython* as valid genera based on both molecular genetic and morphological data available to date.

We are familiar with living specimens of *Apodora papuana*, two species of *Leiopython*, *Bothrochilus boa*, all species of *Simalia* except *oenpelliensis*, and all species of *Antaresia*, *Aspidites*, *Liasis*, *Morelia*, *Malayopython* and *Python*. Over the past 25 years, we [DGB and TMB] have maintained and bred groups of most of these species, and have maintained small colonies of most of them for 10 years and longer. Within each of these genera, the species share a common general identity with their congeners. To recover *Apodora* as a member of *Liasis* or *Leiopython* as a member of *Bothrochilus* is incoherent when we inspect morphology. Similarly, recovering *Antaresia* as a member of *Morelia* is questionable for similar reasons. Molecular characters simply have yet to satisfactorily recover the relationships of the Indo-Australian pythons, given the issues we described above; until a true species tree can be revealed, it is not conservative to synonymize genera that are clearly separated by analyses using morphological characters. Again we note the python anomaly zone and cite the observation of Rawlings *et al*. (2008) that 'Relationships among the Australo-Papuan genera are sensitive to the method of analysis.' We anticipate the increasing accessibility and decreasing costs of modern genomics and proteomics will vastly increase resolution with respect to python phylogenetics. However, until these data are generated, analyzed, and interpreted, the wealth of already available data are certainly informative in a comprehensive phylogeny with taxonomic implications.

We have described a number of characters unique to *Apodora*. We note that not only did Kluge's (1993) morphological analysis recover *papuana* as a monotypic genus, so did the several re-analyses of Kluge's data with modifications done in Rawlings *et al*. (2008) continue to treat *Apodora* as a monotypic lineage. In that study, Maximum Parsimony analysis of combined molecular and morphological data produced two equally parsimonious trees; the one illustrated in the paper shows only weak bootstrap support for *papuana* as a member of *Liasis*, and the tree not illustrated recovered *papuana* as sister to *Liasis*.

Based on analyses of molecular characters, there is a stronger argument to place *Leiopython* in synonymy with *Bothrochilus* than to re-classify *Apodora*. However, the morphological analyses by Kluge (1993) and Rawlings *et al*. (2008) clearly show support for the partition of *Bothrochilus* and *Leiopython*. Schleip (2008, 2014) expanded *Leiopython* to include six species (genetic samples from four of these taxa are not available for study). It is our observation, based on decades of experience with *B. boa*, *L. albertisii* and *L. meridionalis*, and after looking at specimens and photographs of specimens of the other four *Leiopython* species described by Schleip (2008, 2014) that there is a common general appearance and numerous shared morphological characters (McDowell, 1975); Kluge, 1993) of all species of *Leiopython* that are not shared with *Bothrochilus boa*. Schleip (2014) continues to recognize *Leiopython*. We argue that it is conservative to continue recognition of *Leiopython*, perhaps as *sedis mutabilis*, until such time that a much larger sample of *Leiopython* becomes available for study, and when future analyses better sort out the relationships of the Indo-Australian python species.

There is a general trend in modern systematics to reexamine subspecies either to recognize them as species or place them in synonymy with their nominate species (Hey *et al*., 2003; Isaac, Mallet & Mace, 2004). At this time there are ten subspecies of pythons. Not counting the nominate races, they are divided among species as follows: *Liasis mackloti* (2); *Liasis olivaceus* (1); *Malayopython reticulatus* (2); *Morelia spilota* (4); *Python bivittatus* (1). Most of the phylogenetic relationships and taxonomic status of these subspecies have not been evaluated.

We herein elevate the two *L. mackloti* subspecies to the rank of species, and those are: *Liasis dunni* (Stull, 1932) and *Liasis savuensis* (Brongersma, 1956). We recommend these changes for the following reasons: Rawlings *et al*. (2004) and Carmichael (2007) both identified strong support for the monophyly of three lineages of *L. mackloti*, the population on Sawu (*savuensis*), the population on Wetar (*dunni*), and a population occurring on Roti, Semau, Timor and Babar (*mackloti*.). Carmichael *et al*. (2002) identified large differences in trailing and courtship behaviours among these three populations. These populations are restricted to islands and exist as disjunct and isolated. According to Carmichael (2007) these land-masses are separated by deep water, strong currents unfavourable for rafting, and have never been connected by dry land.

There is little reason to doubt that these three populations are descended from a most-recent common ancestor and are monophyletic. The three populations differ in characters of overall colour, eye colour, pattern, ontogenetic colour change, adult and neonate size, egg size, and reproductive behaviour (Stull, 1932; Brongersma, 1956; Barker & Barker, 1994; Carmichael, 2007; de Lang, 2011).

According to Frost & Hillis (1990), '. . . invoking a particular level of genetic distance or morphological divergence as a "species criterion" is neither appropriate nor fruitful'. We see these three populations as independent evolutionary entities that are not likely to reintegrate in the future. Each has a unique evolutionary history and independent trajectory. By every criterion of the evolutionary species concept, each of these three populations should be identified as a separate species. We have no doubt that other python subspecies are likely to be elevated to species rank. However, we are neither prepared nor able to do so at this time.

THE NEOTYPE FOR *Morelia azurea*

In our attempts to review the phylogeny of pythonid snakes and create a correct and current list of species, we note that there are several issues that require attention. One is that it necessary to denote a neotype for *Morelia azurea*. Rawlings & Donnellan (2003) revealed the existence of a cryptic species that is sister to *Morelia viridis*. The authors stated that the pattern of relationships found for mitochondrial and nuclear genes suggested the species *M. viridis* was actually two species, one present north of the central cordillera, referred to a 'viridis N,' and the other present in southern New Guinea and Australia, referred to as 'viridis S'. The authors found a genetic divergence of about 7% between two lineages. The type locality of *M. viridis* is the Aru Islands, and 'viridis S' then refers to *viridis*. The authors did not assign a name to 'viridis N'.

Schleip & O'Shea (2010) then identified 'viridis N' as *Chondropython azureus* (Meyer, 1874). They noted that *Chondropython* is now recognized as a junior synonym to *Morelia*; this then requires that *azureus* be corrected for gender to '*azurea*'. However, because the original type material for *azureus* on which Meyer based the name was lost in World War II, we here designate a neotype to bear the name.

Morelia azurea MEYER, 1874

The species *Chondropython azureus* was placed in synonymy with *Chondropython viridis* (Boulenger, 1893). The genus *Chondropython* was later placed in synonymy with *Morelia* (Kluge, 1993). The study of Rawlings & Donnellan (2003) identified a cryptic species of *viridis* that they labelled as '*viridis* N[orth]' on the basis of genetic divergence. Based on the accepted feminine gender of *Morelia*, it is necessary to correct the original *azureus* for gender to *azurea*. This species is correctly identified as *azurea*, as was done by Schleip & O'Shea (2010). *M. azurea* is the sister species to *M. viridis* (Rawlings & Donnellan, 2003).

According to Cogger, Cameron & Cogger (1983) and McDiarmid, Campbell & Touré (1999), the holotypic material for *azurea* consisted of three syntypes – a specimen labelled as holotype identified as ZMB 8832 and two specimens labelled as MTKD 638 and MTKD 639. However, these specimens were destroyed in World War II (Obst, 1977).

The type locality of *azurea* is '*Kordo auf Mysore*' [Biak] (Schüz, 1929). According to Barbour (1912), 'Kordo' is Korido, a village on the south shore of Supiori; Supiori and Biak are conjoined islands, today generally considered as one island, Biak.

The recognition and use of the name *azurea* and the loss of the original syntypes necessitates the designation of a neotype, as follows:

Neotype – Identified as UTA-R-61633, placed in the collection of the Amphibian and Reptile Diversity Research Center at the University of Texas Arlington; collected on Biak Island in 1990; died and preserved 1993.

Description – The neotype is an adult female. The total length is 121 cm; the tail is 17.8 cm in length. Supralabials number 15/15; with the 7^{th} and 8^{th} in contact with the orbit. The rostral has a pair of well developed thermoreceptive pits, and the anterior two supralabials on each side carry deep thermoreceptive pits, the third supralabial on each side carries a weakly defined pit (Fig. 7). Infralabials number 17/17; anterior infralabial pits are not apparent; infralabial pits begin in front of the anterior margin of the eye; the pits are in infralabials 8–12/9–13 (Fig. 8). Dorsal scales number 51/54/32; there are 244 ventrals and 99 + tip subcaudals.

DESCRIPTIONS AND DIAGNOSES OF *Simalia* AND *Malayopython*

Reynolds *et al*. (2014) added two genera to the Pythonidae. *Malayopython* is proposed as a

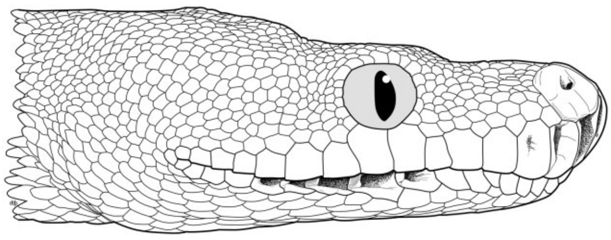

Figure 7. Lateral head illustration of the *Morelia azurea* neotype.

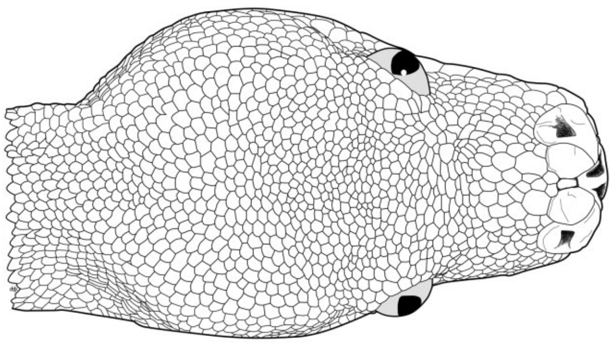

Figure 8. Dorsal head illustration of the *Morelia azurea* neotype.

replacement for the invalid name Rawlings *et al*. (2008) had given to the (*reticulatus* + *timoriensis*) clade. The second genus name, *Simalia*, had been entered into the literature in 1849, but placed in synonymy by Boulenger (1893); Reynolds applied the name to the *amethistina* clade that formerly was classified in *Morelia*. These additions were made obvious and necessary by the phylogeny of the pythons generated by Reynolds *et al*. (2014), supported by the studies of Pyron *et al*. (2013) and Rawlings *et al*. (2008). The existence of these two clades is inferred from and based on the phylogenetic analysis of genetic characters. Reynolds *et al*. (2014) offer a summary of taxonomic changes, but no diagnosis or morphological description is made, as here follows:

Simalia Gray, 1849

Morelia Gray, 1842, Zool. Misc. (2): 41–46 [43].

Simalia Gray, 1849, Cat. Spec. Snakes Collect. Brit. Mus., 125 pp. [84]. [Gray, (1849) created the name *Simalia* as a subgenus of *Liasis* to contain two species, *amethistina* and *mackloti*. Boulenger (1893: 81) considered *Simalia* as a synonym of *Python* and not *Liasis*, thereby restricting by implication the type species of *Simalia* to be *amethistina*, then classified by Boulenger as *Python amethystinus*.]

Type species – *Boa amethistina* Schneider, 1801

Definition – The genus including *Simalia amethistina* (Schneider, 1801) and all species formerly classified in the genus *Morelia* that share a more recent common ancestor with *amethistina* than with *spilota*.

Diagnosis – This is a genus of pythonid snakes of large size, with adult lengths of > 2 m to 5.5 m. This genus is shown to be a monophyletic clade separated from all other python clades on the basis of molecular characters as illustrated in Figure 6 (Pyron *et al*., 2013). Likewise, the morphological analysis illustrated in Figure 1 (Kluge, 1993) shows the split as internal to *Morelia*. *Simalia* shares a common ancestor with the clade of pythons comprised of *Morelia*, *Apodora*, *Liasis*, *Aspidites*, *Antaresia*, *Leiopython*, and *Bothrochilus*.

Simalia can be separated from *Apodora*, *Aspidites*, *Antaresia*, and *Liasis* by the presence and condition of the thermoreceptive pits on the supralabials and rostral. Species in *Simalia* have two large, deep thermoreceptive pits on the rostral scale and well developed thermoreceptive pits on 2–5 anterior supralabials; *Aspidites* and *Bothrochilus* have no thermoreceptive pits on the rostral and supralabials; *Antaresia* and *Liasis* typically have no pits in the rostral. *Apodora* has shallow pits on the rostral and anterior 2–3 supralabials. *Leiopython* varies in the condition of labial pits; most have a pitted rostral and the first 2–3 supralabials may have pits.

Simalia have subloreal scales, while Kluge (1993) did not observe subloreal scales in *Bothrochilus* or *Leiopython*; species in *Simalia* have > 4 loreal scales while *Bothrochilus* and *Leiopython* have 1–2. *Simalia* has a strongly prehensile tail, while the tail of *Aspidites*, *Antaresia*, *Leiopython*, and *Liasis* is weakly prehensile (McDowell, 1975).

Simalia can be distinguished from *Morelia* by the condition of the head scalation. Species in *Simalia* have large plate-like head scales identified as supraoculars, frontals, and one or more pairs of parietals. *Simalia oenpelliensis* varies from this formula, and has small parietals and irregular scalation posterior to large supraoculars that are in full contact with a large frontal.

The only large scales that might be considered 'plate-like' on the dorsal surface of the head of *Morelia* species are small internasals and anterior prefrontals on the front of the snout. *M. carinata* is one exception and it typically has a single round frontal centered between the eyes and surrounded by small scales, separated from contact with relatively large anterior supraoculars.

Etymology – Gray (1849) does not discuss the origin or meaning of 'Simalia'.

Included species – *amethistina* (Schneider, 1801), *boeleni* (Brongersma, 1953), *clastolepis* (Harvey *et al*., 2000), *kinghorni* (Stull, 1935), *nauta* (Harvey *et al*., 2000), *oenpelliensis* (Gow, 1977), and *tracyae* (Harvey *et al*., 2000).

Comment – in the analyses we have reviewed, *oenpelliensis* has been recovered as a member in both *Morelia* and *Simalia*. The species does appear to be intermediate between the two lineages in many morphological characters. The analysis of Pyron *et al*. (2013) places *oenpelliensis* in the *Simalia* clade, but this arrangement is not strongly supported with a bootstrap value of 76%. The phylogeny generated by the analysis of Reynolds *et al*. (2014) places *oenpelliensis* in a monotypic clade that is sister to (*Simalia* + *Leiopython* + *Bothrochilus*); this arrangement is not strongly supported. The authors then choose to include *oenpelliensis* in *Simalia* rather than place it in a separate genus, thereby placing it in paraphyly. At this time we choose to follow the placement of *oenpelliensis* in *Simalia* as hypothesized by the analyses of Pyron *et al*. (2013) and specifically assigned by Reynolds *et al*. (2014).

Malayopython Reynolds *et al*. (2014)

Python Daudin, 1803. Bull. Sci. Soc. Philomath. Paris (2)3: 187–188 [187].

Constrictor Wagler, 1830. Nat. Syst. Amph., 354 pp [168]. Type species not designated, later designated as '*Constrictor schneideri* Wagler' [= *Python reticulatus* (Schneider, 1801)] by Fitzinger, 1843, Syst. Rept., 106 pp. [24].

Type species – *Boa reticulata* Schneider, 1801

Definition – The genus including *Malayopython reticulatus* (Schneider, 1801) and all species formerly classified in the genus Python that share a more recent common ancestor with *reticulatus* than with *molurus*.

Diagnosis – This is a genus of pythonid snakes of large size, with adult lengths of > 2 m to 8.5 m. This genus is shown to be a monophyletic clade separated from all other python clades on the basis of molecular characters (Lawson *et al*., 2004; Rawlings *et al*., 2008; Pyron *et al*., 2013). The genus *Malayopython* is shown to have unique structural modifications to the control region of the mitochondria not known in *Python*, but synapomorphic with the condition seen in *Simalia* and *Morelia* (Rawlings *et al*., 2008).

According to McDowell (1975) and Kluge (1993), snakes in this genus can be differentiated from *Python* (*sensu stricto*) by having anterior supralabial pits that are more shallow than the posterior infralabial pits (the converse being observed in *Python*). In *Malayopython* the posterior infralabial pits lie in a longitudinal channel defined ventrally by a longitudinal fold along the lower margins of the infralabials that carry the channel; in *Python* the pits on the posterior infralabials of several species (e.g. *regius* and *brongersmai*) also lie in a recessed channel, but this structure is not so deep or even along its length and the ventral margin is not so well defined as seen in *Malayopython*.

We observe that differences noted by McDowell (1975) in the condition of the anterior processes of the ectopterygoid are generally true, but not consistent. McDowell reported hemipenial differences between *M. reticulatus* and *P. molurus* regarding the shape of the flounces, but the condition and variation of this character in most species in those two groups is unknown.

Kluge (1993) noted the following distinguishing characters for *Malayopython*:

- In *Python* there is a low ridge on the ventral surface of the cultiform process of the parasphenoid, anterior to the basipterygoid processes and between the trabeculae cranii; in *Malayopython* (including *timoriensis*) there is a thin elevated ridge [character 58, page 25]. We have examined skulls of 3 *P. molurus*, 3 *P. regius*, 3 *P. breitensteini*, and 3 *M. reticulatus*, and we find this character to be consistent.
- *Malayopython* can be distinguished from *Simalia* and *Morelia* by having the suborbital portion of the maxilla without any lateral flare or bulge [character 15, page 16].
- *Malayopython* also can be distinguished from *Simalia*, *Morelia* and *Liasis* by having the dorsolateral margin of the suborbital region of the maxilla oriented nearly vertically while in *Simalia*, *Morelia* and *Liasis* it is oriented horizontally and projects laterally [character 16, page 16].
- The posterior margin of the mandibular foramen in the compound bone of *Simalia*, *Morelia* and *Liasis* lies posterior to the tooth-bearing portion of the dentary, while in *Malayopython* is located even with the posterior end of the tooth-bearing portion of the dentary [character 71, page 29].
- In *Malayopython*, the anterolateral margin of the horizontal portion of the nasal, opposite the anterior end of the prefrontal, is gradually curved anteriorly; in *Simalia* it is sharply directed medially [character 9, page 14].
- *Malayopython* has one supralabial scale entering the orbit, while *Simalia*, *Morelia* and *Liasis* have two or three. Most species in the genus *Python* have subocular scales (exceptions are *P. molurus*, *P. brongersmai*, and *P. kyaiktiyo*); *Malayopython* has no suboculars [character 90, page 34].
- *Malayopython* has 56 or more scale rows around the neck, more than species in *Simalia*, *Morelia* or *Liasis*, excepting *Simalia oenpelliensis* [character 97, page 37].
- Thermoreceptive pits are present on the second through fourth or fifth anterior infralabials in *Malayopython*, and absent in *Morelia* and *Liasis* [character 104, page 38].

The species in the genus *Simalia*, excepting *tracyae* and *oenpelliensis*, are either without a dorsal pattern or have a naturally occurring patternless morph; there are no populations of *Malayopython* in which the patternless morph is typical. Variations of ringed patterns are seen in some *Simalia*, including *tracyae*, *amethistina*, and *clastolepis*; ringed patterns are not known in *Malayopython*. Most *Simalia* undergo an ontogenetic change in colour and pattern as they mature; the juvenile coloration and pattern of *Malayopython* is not dramatically different from that of adults.

As noted by McDowell (1975) species in *Python* typically have a dark marking on the side of the head below the eye, in some the entire side of the head is dark; this is not necessarily diagnostic, there are individual exceptions. *Malayopython* rarely have any dark mark below the eye, and typically the side of the snout is similar in colour to the top of the snout.

Included species – *reticulatus* (Schneider, 1801), *timoriensis* (Peters, 1876).

CONCLUSIONS

Pythonidae is an ancient clade of serpents, and most data indicate its origin is Laurasian. Hence, the common ancestor to pythons likely evolved in a region far from the area of the greatest diversity today. Forged in the crucible of evolutionary time and geographic space, the relationships of some of the lineages of modern species and clades have become clouded and difficult to interpret. Indeed, if past studies are any prediction, future studies may call into question even those relationships that have been repeatedly confirmed in multiple analyses.

Species in nature are real entities, while all levels of classification above species are human constructs meant to answer questions of the history and evolution of the species. We would disagree with the opinion of McDowell (1975) that the pythons are weakly differentiated – species that vary from adults less than a metre in length to other species with large adults exceeding 7 m in length can scarcely be considered uniform. In some respects, the reality of the species of pythons has resulted in a relatively stable taxonomy. We include a list of the 44 species of pythons in an Appendix. Images of representative taxa are provided online as supplemental information. The validity of most of these species is unequivocal; many have been recognized for more than a century. Most of the species are easily observed to be distinct and divergent from the others. This also has made study of the phylogeny of Pythonidae attractive to researchers.

However, it is a reality and a problem that many python species are too large to fit in a gallon specimen jar, thus creating an extreme museum bias against pythons based on the cost and space needed to maintain collections of large snakes. Species long known to science, species that are or were common, are represented in museum collections by scant individuals. A few decades ago, it was a challenge for researchers to obtain sufficiently large sample sizes of most python species to be able to even begin to comprehend the variation within and among species – this problem continues to the present. Many python species are represented in museum collections by scant numbers of specimens, a problem that impedes robust taxonomic investigations. Studies based solely on molecular genetic characters, seemingly an alternative, have not satisfactorily resolved an acceptable phylogeny for all python species. We suggest that future researchers not lose sight of the importance of morphological characters in their studies.

A benefit to researchers has been the popularity of pythons in herpetoculture. This has supported an active trade in live specimens that in turn has provided a valuable source of specimens, tissues, and genetic samples for researchers that simply are not available for most other snake families. Today it would be relatively simple to obtain samples from multiple specimens of 35 or more of the 44 species of pythons. Thirty-eight species have been bred in captivity, and at least 30 species are currently maintained around the world in viable, self-sustaining captive populations. Among all families of snakes, this availability is unique in its comprehensiveness and it is a factor that contributes to the desirability of studying pythons.

We look forward to future systematic investigations of Pythonidae, and in particular into the relationships of the Indo-Australian python genera. It may be that investigations into the extended history of this ancient family will never produce one single accepted hypothesis of the origin and pedigree. But it seems a certainty that the Pythonidae will remain interesting and a challenge to systematists and taxonomists.

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APPENDIX

A list of the binomials of python species of the world with standard common names

Antaresia childreni Children's python (Supporting Information, Fig. S1)
Antaresia maculosa Spotted python
Antaresia perthensis Pygmy python
Antaresia stimsoni Large-blotched python
Apodora papuana Papuan python (Supporting Information, Fig. S2)
Aspidites melanocephalus Black-headed python (Supporting Information, Fig. S3)
Aspidites ramsayi Woma
Bothrochilus boa Ringed Python (Supporting Information, Fig. S4)
Leiopython albertisii Northern whitelip python (Supporting Information, Fig. S5)
Leiopython biakensis Biak whitelip python
Leiopython fredparkeri Karimui Basin whitelip python
Leiopython huonensis Huon Peninsula whitelip python
Leiopython meridionalis Southern whitelip python
Leiopython montanus Wau whitelip python
Liasis dunni Wetar python
Liasis fuscus Water python
Liasis mackloti Freckled python (Supporting Information, Fig. S6)
Liasis olivaceus Olive python
Liasis savuensis Savu python
Malayopython reticulatus Reticulated python (Supporting Information, Fig. S7)
Malayopython timoriensis Lesser Sundas python
Morelia azurea Northern green python
Morelia bredli Centralian python
Morelia carinata Rough-scaled python
Morelia imbricata Southwestern carpet python
Morelia spilota Diamond python (Supporting Information, Fig. S8)
Morelia viridis Southern green python
Simalia amethistina Amethystine python (Supporting Information, Fig. S9)
Simalia boeleni Black python
Simalia clastolepis Southern Moluccan python
Simalia kinghorni Scrub python
Simalia nauta Tanimbar python
Simalia oenpelliensis Oenpelli python
Simalia tracyae Halmahera python
Python anchietae Escarpment python
Python bivittatus Burmese python
Python breitensteini Borneo python
Python brongersmai Blood python
Python curtus Sumatran python
Python kyaiktiyo Mon python
Python molurus Indian python (Supporting Information, Fig. S10)
Python natalensis Lesser African python
Python regius Ball python
Python sebae African python

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Children's Python, *Antaresia childreni*, from Australia: Queensland: near Mount Isa.
Figure S2. Papuan Python, *Apodora Papuana*, from Indonesia: West Papua Province: Doberai Peninsula.
Figure S3. Black-headed Python, *Aspidites melanocephalus*, from Australia: Queensland: near Normanton.
Figure S4. Ringed Python, *Bothrochilus boa*, from Papua New Guinea: Bismarck Archipelago: New Britain: near Rabaul.

Figure S5. Northern Whitelip Python, *Leiopython albertisii*, from Indonesia: West Papua Province: Doberai Peninsula.
Figure S6. Freckled Python, *Liasis mackloti*, from Indonesia: Lesser Sunda Islands: Timor.
Figure S7. Reticulated Python, *Malayopython reticulatus*, from Indonesia: Greater Sunda Islands: Sumatra.
Figure S8. Diamond Python, *Morelia spilota*, from Australia: New South Wales, Gosford.
Figure S9. Amethystine Python, *Simalia amethistina*, from Indonesia: Southeast Papua Province: near Merauke.
Figure S10. Indian Python, *Python molurus*, from India: Sri Lanka.