AUSTRALIAN PYTHONS (PART 4)

(GENUS *"Morelia"* AND *"Python carinatus"*, FOLLOWED BY DISCUSSIONS ON THE TAXONOMY AND EVOLUTION OF AUSTRALASIAN PYTHONS)

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Introduction

For various reasons I have saved this group of snakes till last in my discussion of Australian pythons. The main reason being that this group is in a state of flux taxonomically and the longer I delayed writing about this group the more information that may clear up the picture may come to light. Unfortunately over the last twelve months the situation appears to have become more confused rather than clear cut.

"Python carinatus" a recently described species from the Kimberly region of Western Australia will be dealt with as an extreme form of the *Python (=Morelia) spilotes* group, although it is definitely a species in its own right. I will save my discussion of *"Python carinatus"* till the end of my discussion of the Carpet and Diamond snakes species complex, for reasons of convenience.

The generic name *Morelia* shall not be used in this article except for the introduction of this group of snakes (so as to distinguish them from other *Python*), and when used in my discussion of the evolution and taxonomy of Australasian pythons.

Cogger (1975 and 1979) regards all Carpet snakes and the Diamond Python as being of the same species. Although the consensus of opinion is now not so sure of this (Gow 1981), all this group of snakes do show similarities in form, biology and captive habits. For this reason I shall discuss features common to all forms of the Carpet snake and the Diamond Python, and then outline unique features of each regional form (sub-species or species depending upon one's opinion).

Genus *Morelia* (Modified from Krefft 1869 and Cogger 1979)

Morelia is a genus found in Australia and southern New Guinea. Characterised by the presence of teeth on the maxilla, pits present in some labial scales, and smooth scales (thereby excluding *"Python carinatus"*). This group is distinguished from the genus *Python* by the small irregular broken shields covering the head, and is distinguished from *Chondropython* by having, generally, double rowed subcaudals, (*Chondropython*'s subcaudals are generally single). Like all pythons these snakes are oviparous (egg-layers).

Description of all Carpet snakes and the Diamond snake excluding *"Python carinatus"*.

These are large heavily built snakes with broad distinctive heads. All forms tend to have distinctive colours and patterns, and variation in each form is great. Hybridization occurs naturally in the three eastern forms although to date it is not known in the three western forms. A Diamond Snake, Western New South Wales Carpet Snake, South-East Queensland Carpet Snake (typical form), Northern Queensland (Atherton Tableland Form) Carpet Snake, Northern Territory "Banded" Carpet Snake are shown.
(see photos). Dorsally these snakes range through yellows, browns, reds, oranges and black, with varying striped and mottled patterns consisting of various combinations of the preceding colours. Generally these snakes are lighter in colour ventrally, particularly around the fore part of the body where they are usually white, cream or yellow. These snakes are coloured so as to afford maximum protection by camouflage in the wild (Waite 1929).

Average maximum lengths vary regionally but as an average would be about two metres (Cogger 1979, Hoser unpublished data). Specimens in excess of four metres in length are known, though fairly rare. Adults only a metre long are known (Worrell 1951). The scalation is smooth with 40-65 mid body rows, 225-310 ventrals, usually a single anal, and 60-95 usually divided subcaudals.

Juveniles are sometimes laterally compressed, particularly in specimens from the north of the Northern Territory where lateral compression in young is the rule. Lateral compression in adults is much rarer. Anal spurs which are used in mating are of the same size at least in specimens from New Guinea (McDowall 1975), and of the three eastern Australian forms (Hoser unpublished data). Further, there appears to be no sexual dimorphism in either body size or relative tail length in all forms of these snakes. To accurately sex one of these snakes one must use a probe.

Habits.

In all forms there is a sex ratio of 5-10 males to every female. This includes the Diamond Python, contrary to the statement by Chris Banks in an article in ASRA Journal Vol.1 No.2 in 1980.

This group of snakes is widely distributed in Australia (see map; fig 1). This distribution map differs markedly from that given in all previously published popular literature including Cogger 1975 and 1979, Worrell 1970. Cogger's third edition of Reptiles and Amphibians of Australia which is currently in preparation will contain a distribution map similar to that provided in fig 1, (assuming no new data comes to light). Fig 1 was drawn from the best currently available information including that provided by Gow 1981, Hoser 1981, Kinghorn 1956, McCoy 1885, McDowall 1975, Smith 1981, Worrell 1970.

Two, possibly three forms of the Carpet Python are geographically isolated from every other form of Carpet Snake or the Diamond Snake. Eastern Australian forms (including the Diamond Snake) are not reproductively isolated from one another, with hybrid or intergrade forms occurring wherever the ranges of those forms meet, (See Fig 1). All forms of the Carpet Snake and the Diamond Snake are usually common where they occur.

These snakes are found in all habitats (Krefft 1869), ranging through deserts, savannahs, woodlands, montane and other forests that may even have snow in winter, rainforests and island habitats. In arid regions these snakes are often confined to areas adjacent to water (Banks 1974), such as hills and river valleys. All forms are largely arboreal (Waite 1929, Cogger 1979), commonly found sheltering in trees and cliffs. To date none have ever been recorded inhabiting termite mounds. All forms tend to be diurnal in cool weather and nocturnal in warm weather.

Diets in the wild consist of any suitable vertebrate although it is a well known fact that juveniles tend to eat a higher proportion of ectotherms whilst adults eat mainly endotherms (mammals and birds). These prey items are caught both by ambush and active stalking, and are then killed in the "normal constricting manner". Diamond and Carpet snakes are known to eat prey killed by other animals both in the wild state and in captivity (Hoser in press). The common liking by large specimens for pet birds often leads to them entering bird cages, eating the birds and then being unable to escape because the bulges in their bodies will not fit through the bird cage wire. Unfortunately ignorance usually prevails and these snakes are usually killed when discovered in such circumstances. The labial "heat pits" can detect the presence of an object only 0.026°C warmer than its surroundings (J.W.[initials] Year Unknown).

Large specimens are almost immune from attack by predators, juveniles could be preyed upon by birds, foxes, dingoes, monitors, etc. Parasites such as ticks and tapeworms commonly infest these snakes (Krefft 1869), although the harm these would cause to the snakes in the wild is hard to judge.

The breeding biology of all forms is well known and apparently virtually identical for each form. All forms of the Carpet Snake and the Diamond Snake have been bred in captivity at least twice (Hoser, Snake Breeding Survey Data 1981). Their breeding cycle typically involves autumn to spring mating, and laying and incubating eggs (maternally) in the summer (northern Australian wet season). Many specimens however tend to lay eggs outside of the above mentioned breeding season (Ross 1978, Hoser, Snake Breeding Survey Data 1981). Eggs laid outside of the typical breeding season are often simply the result of a female holding eggs inside her body which should have been laid earlier but have been held due to adverse conditions. An example of this was seen in a Diamond Python (nearly 3m) which held mature (ready to lay) eggs inside her body through late summer, autumn, and half of winter and laid the eggs in July (mid winter in Australia). "Off season breedings" also commonly result from snakes kept in captivity with temperature conditions not in alignment with those in the snakes'

natural habitat. In Australia and many parts of North America many herpetologists keep their reptiles heated in winter but not in summer thereby "reversing the seasons". Incubation periods range from 37 to 102 days depending upon the origin of the snake that laid the eggs (and its mate), and the temperature at which incubation occurs.

Clutches range in size from 5 (Hose unpublished data) to 47 (Martin 1973) eggs. These were for a Diamond Python and a Rockhampton (Old) Carpet Python respectively. Gow (1981) records a centralian Carpet Snake (*"Python bredli"*) producing a clutch of 43 eggs. 12 to 30 eggs per clutch appears to be the norm however (Hoser, Snake Breeding Survey Data 1981, Martin 1973). One readily sees a high degree in clutch size variability for this group of snakes.

All Carpet and Diamond Pythons coil around their eggs when incubating in the wild. They also raise their body temperatures by rapid muscular contractions when incubating their eggs and thus also raise the temperature of the eggs simultaneously. By coiling around their eggs (in a ball) pythons conserve heat by exposing only about 30 to 50% of their body (and egg) surface (Cogger and Holmes 1961).

In the literature are records of aggregation in Carpet and Diamond Pythons at all times of the year for generally uncertain purposes, (Covacevich and Limpus 1973, Hoser 1980, Webber 1978). The largest single one site, aggregation recorded was by Diamond Pythons (Webber 1978), and although the number was not specified it exceeded 10.

In captivity

Nine out of ten specimens of any form of Carpet or Diamond Snake are very docile. Many refuse to bite even when highly provoked. These are the most commonly kept pythons in Australia. Unfortunately few survive in captivity for very long because most people who obtain them don't know how to look after them properly, (J.W. [initials] year unknown). Queensland Carpet Snakes are among the most commonly sold and cheapest Australian snakes in the United States of America, Britain and Europe, where they usually cost £100-200 sterling (1980 prices).

Housing of these snakes is typical of that for most large pythons. That is provide a clean dry cage with fresh water in a container, perching and hiding spots. Ground cover may be leaves, rocks, etc. or newspaper. These snakes are prone to scale rot and body blisters if their cages are too moist, and "dry rot" (scale rot) if their cages are too dry. These scale ailments are commonly linked to nutritional deficiencies. These snakes are highly prone to mouthrot (canker), pneumonia and mites, all of which can kill these snakes.

Carpet Snakes (all forms) and the Diamond Snake are virtually always good feeders, readily accepting live and dead food, often on their first day in captivity if offered.

Many people in Australia keep pet Carpet and Diamond Snakes in their bedrooms or living rooms giving them a free run of any part of the room. The disadvantages of this form of keeping large pythons are obvious. For example the snakes may knock things off shelves, they are sometimes very difficult to locate and their excrement may cause undue hardship.

As stated earlier all forms of the Carpet Snake and the Diamond Snake have been bred in captivity. Breeding may be accomplished with or without separation of the sexes prior to anticipated matings although the former is probably the best means to achieve a successful mating. The relative shortage of females means that should a breeder be offered a choice of males or females they should take the females first. Many breeders only have success in breeding Diamond and Carpet Snakes every second year only.

Although eggs are usually maternally incubated when laid and if left alone (in a suitable cage) the eggs would probably hatch, I would suggest artificial incubation. This gives one total control of the eggs and hence a greater chance of successful hatching. Incubation should be at 32-33°C with a high humidity (greater than 80%). There is a case where a female Carpet Python (form uncertain) laid 32 eggs (of which 4 hatched) where the female had laid the eggs shortly after being captured, and was then sent with her eggs by rail over a distance of 1120 kms (Ross 1978). One should always remember that Python eggs are already partially developed when laid.

Descriptions of the main forms (Sub-species) of Carpet Python and the Diamond Snake.

My opinion is that there are six regional forms of the Carpet/Diamond Snake. They are:

1) The Diamond Python (*Python [=Morelia] spilotes spilotes*) restricted to south eastern coastal Australia (see Fig 1). Dorsally Diamond Pythons are typically Jet black with small white or yellow spots in a pattern.

2) The inland New South Wales and Victoria Carpet Snake. This snake has not been given any subspecific or specific name although one is imminent. These snakes are typically patterned in light grey and brown patterned blotches dorsally. They hybridise with "Coastal Queensland Carpet Snakes" in the south west of that state.

3) The "Typical Coastal Queensland Carpet Snake" which occurs in north east N.S.W. most of Queensland (except for the extreme far west of that state) and includes the unusual Atherton tableland colour phases. Queensland Carpet Pythons vary greatly in colour, even in the one area. For example in the Townsville district there are no less than four distinct colour phases (excluding intermediates), and all interbreed. This pattern is true for much of Queensland. This is probably not the snake sub-species described as *Morelia spilotes variegata* as the type locality for that sub-

species is Port Essington (Northern Territory). Hence this snake's sub-specific name is in doubt. Queensland Carpet Snakes are typically yellow and brown in colour although yellow and black is common in northern specimens. North Queensland specimens commonly have very dark heads. Some specimens in northern N.S.W. are a brownish orange in colour with scattered small orange blotches only. Colour patterns probably vary more in this race of Carpet Snake than in any other race of Carpet Snake. These snakes may have horizontal or lateral bands, blotches, or more commonly a mixture of these.

4) The north Northern Territory form with well marked dorsal bands, is the type sub-species *Python spilotes variegata*, and thus will retain this name. The sub-species *Python spilotes macropsilia* has its status in doubt and quite possibly is invalid. It is not the Northern Territory race of the Carpet Snake as stated by Banks (1979) and Kinghorn (1956). Dr. H.G. Cogger (pers. comm.) believes that the snake described is quite possibly a Carpet Snake from North Queensland, in which case it may be a valid sub-species. The north Northern Territory Carpet Snake has brown to black and yellow to orange bands dorsally which may be broken on the sides.

5) *Python (spilotes) bredli*, the Centralian Carpet Snake was described by Gow in 1981 as a new species *"Python bredli"*. This is a large race of Carpet Snake. Dorsally *"Python bredli"* is reddish to dark brown with numerous irregular pale fawn to yellow, dark edged blotches, stripes and bars (Gow 1981).

6) *Python spilotes imbricatus*, the large race from the south west of Australia was described in 1981 by Laurie A. Smith of the west Australian museum. *Python spilotes imbricatus* is highly variable in colour. Dorsally it is brownish with numerous irregular pale fawn blotches or transverse bars edged with one or two rows of black scales (Smith 1981). Live specimens give the overall impression of being greenish black.

These descriptions have been kept short due to space limitations. For further information consult the references given.

"Python carinatus"

This is the celebrated Rough Scaled Carpet Snake, known from only one (now dead) specimen. Effectively nothing is known about this newly described species. Information on the type specimen provided by Smith (1981) is provided below.

The type specimen was collected at Mitchell River Falls, Western Australia (14°50'S, 125°42'E) (See Fig 1), on the 14th January 1973 by Laurie Smith and others.

It is readily distinguished from other *Python* (incl. *Morelia*) by its keeled dorsal scales. The type measured nearly 2 metres in length and physically appears very closely related to other Carpet Snakes. Its dorsal colour is brownish white with dark brown variegations and blotches. Ventrals are mainly off-white with

every second to fifth scale smugged brown. Its scalation is as follows: 298 ventrals, 45 mid body rows, single anal and 83 mainly divided subcaudals. Interestingly this species does not have a prehensile tail (one of McDowall's (1975) main criterion for diagnosing the genus *Python*). Cogger (Pers. comm.) and myself believe that Smith made a mistake placing this snake in the genus *Python*. The biology of this species in the wild or captivity is unknown.

REFERENCES: See after remarks on taxonomy and evolution of Australian Pythons.

SOME REMARKS ON THE TAXONOMY AND EVOLUTION OF AUSTRALASIAN PYTHONS.

TAXONOMY

The most significant recent article pertaining to the evolution and taxonomy of Australasian Pythons was published by McDowall in 1975. Other articles and the positive identification of three new species of snake since then (*Liasis perthensis*, *Python oenpelliensis*, *Python carinatus*), have led to a greater understanding of Australian Pythons and their inter-relationships.

McDowall's 80 page article is comprehensive but reveals how McDowall and most other herpetologists-cum taxonomists feel about meddling with taxonomy of pythons - highly cautious.

An important point of McDowall's article is that pythons can be grouped into three main groups: The Genera *Calabaria* (a West African group), *Aspidites* (an Australian group) and the rest which McDowall and myself believe a reasonable case could be made for placing entirely in the genus *Python*. Like McDowall, Cogger and others, I believe that a move to place such a large number of species in the genus *Python* would be undesirable from the point of view that inter-relationships within the group would be masked. From McDowall's and other articles the following picture may be drawn. The Pythons excluding *Calabaria* and *Aspidites* may be placed into well defined groups. They are the *Python molurus* group including the African species of *Python* as well as *Python molurus* and *Python curtus*, the *Python reticulatus* group including *P.reticulatus*, *P.timorensis*, *P.amethystinus*, *P.oenpelliensis*, *Python(=Morelia) spilotes*, *P.carinatus*, and *Chondropython viridis*, and the group of snakes McDowall groups into the genus *Liasis*, including *Liasis boa*, *Liasis childreni*, *Liasis perthensis*, *Liasis oliveaceous*, *Liasis fuscus(=mackloti)*, *Liasis papuanis*, *Liasis albertisi*. The taxonomic status of *Liasis boeleni* is in doubt, with it appearing to lie somewhere between the *Python reticulatus* group and the *Liasis* group. These groups can be further split. The *"reticulatus"* group is retained, though only consisting of *P.reticulatus*, *P.timorensis*, *P.amethystinus*, (and probably *P.oenpelliensis)*. The next division I call the *spilotes* group (which would thus have the generic name *Morelia*), consisting of *Morelia spilotes*, *Python (=Morelia) carinatus*, and *Chondropython (=Morelia) viridis*. The fourth group

(after the *molurus, reticulatus* and *spilotes* groups) for which McDowall suggests the generic name *"Lisalia"* is a group of snakes formerly in the genus *Liasis*, consisting of *Liasis olivaceous*, *Liasis papuanis*, and *Liasis mackloti (=fuscus)*. The next group includes *Liasis albertisi*, *Bothrochilus (=Liasis) boa*, *Liasis childreni* and *Liasis perthensis*. This group would retain the generic name *Liasis* as *Liasis childreni* is the type species of this genus (McDowall 1975). (On 31/12/81 Dr. Cogger informed me that he has reason to believe that the first snake described under the name *Liasis*, was in fact a snake of a previously described genus and species hence making the generic name *Liasis* invalid: this possibility won't be taken into consideration in this article). *Liasis (=Python) boeleni* appears to be intermediate between *Liasis albertsi*, *Python amethystinus* and *Morelia spilotes*, (superficially at least), and hence should be placed outside any group until further taxonomic studies reveal its closest affinities. (See Fig 2). Hence under this classification there are five Australasian python genera, 1) *Aspidites*, 2) *Python*, 3) *Morelia*, 4) *Liasis*, 5) *Lisalia*. *Chondropython* would be incorporated into the genus *Morelia*, because *Morelia* was described some 50 years (approx) earlier. The classification of Pythons just outlined is supported in the latestimmunological studies by Schwaner and Dessauer (1981), whose main significant conclusion is that the *molurus* and *reticulatus* groups are generically distinct.

The formation and composition of the above genera is largely arbitrary. Whilst McDowall emphasises the closeness in relationships of the above pythons in his 80 page article he also says that the generic names currently applied to many pythons are the result of conformity to past ideas and not good taxonomic sense. For example, McDowell shows how snakes from three (so-called) genera *(Liasis boeleni, Morelia spilotes, Chondropython viridis)* are in fact very closely related. He does not however place them in a single named genus. Dean Metcalfe (a python taxonomist) and others support my viewpoints with regard to the splitting and lumping of Australian pythons into various genera. One should remember that a genus is an artificial tool only, used to show groups of "evolutionarily homogenous species".

That *Liasis childreni* and other closely related species form a distinct (somewhat aberrant group) is widely accepted (McDowall 1975, Metcalfe Pers. comm., Smith 1981) and their placement in the genus *Liasis* is generally recognised. Only are the status of *Liasis olivaceous*, *Liasis papuanis*, and *Liasis fuscus* disputed here, where I believe that the available name *Lisalia* is more suitable for this distinct group of snakes.

Finally *Morelia argus* is not a valid species name, even though it is widely used to describe the Carpet or Diamond Python erroneously, (Irvine 1976). The snake originally described in 1758 as *Coluber arges* and in 1766 corrected to *C.argus* by Linnaeus was based on a drawing of an African species by Seba (Irvine 1976). How can an Australian snake by described before Australia was discovered (by Cook in 1770)?

(This section has been kept brief due to space limitations)

EVOLUTION OF AUSTRALASIAN PYTHONS

Most of the world's living species of python are found in Australasia. McDowell (1975) points out the dramatic speciation of the Pythonidae in Australasia as compared to the rest of the world where relatively few species are found; and that was before the status or existence of *Liasis perthensis*, *Morelia (=Python) carinatus* and *Python oenpelliensis*, was confirmed.

Python reticulatus and *Python amethystinus* appear to be very closely related but in the wild at least do not interbreed (they are found together on Ceram and Ambon (McDowall 1975)). *Python timorensis* is apparently intermediate between the two species and hence it may be assumed that the three above species arose from the same stock in recent geological history, from the Australasian region. The two sub-species of *Python amethystinus*, *Python amethystinus amethystinus* (of New Guinea and adjacent islands) and *Python amethystinus kinghorni* (of Australia) obviously arose in very recent times as a result of the separation of Australia and New Guinea by Torres Strait. It is almost certain that *Python amethystinus* invaded Australia from New Guinea. The origins of *Python oenpelliensis* described by Gow in 1977 are uncertain.

Liasis olivaceous and *Liasis papuanis* are very similar species whose speciation has occurred in recent geological times again as a result of rising sea levels separating Australia and New Guinea. *Liasis mackloti (=fuscus)* is also in this group of pythons although its evolutionary relationship with other species is unclear. This group of snakes, whose original centre of distribution could be either Australia or New Guinea are sufficiently distinct in external morphology from other Australasian Pythons to warrant them being placed in a group of their own (Genus *Lisalia*), although the recent breeding of Water Python and Carpet Python, Scrub Python and Carpet Python (at the Royal Melbourne Zoo) indicates that the three genera (?) are only of recent origin (geologically speaking).

The drying up of the Australian continent, particularly over the last million years, has certainly led to a rapid speciation and sub-speciation in Australian Pythons. *Morelia spilotes* (all forms) has evolved primarily for the Australian climate (mainly dry), whilst *Morelia (=Chondropython) viridis* could be described as New Guinea's evolutionary counterpart to the Australian Carpet Snake. "Genetic conservatism" would probably have been the reason for the prevention of the evolution of a green "*Morelia*" in Australia where gene flow in and out of Rainforests was high due to a shortage of rainforest habitat. In New Guinea no such problem would have existed where virtually the whole island was closed forest. In recent geological times when sea levels permitted movement across Torres Strait *Morelia (=Chondropython) viridis* would have invaded Australia whilst *Morelia spilotes* would have invaded New Guinea. Neither species has been able to disperse widely in their newly invaded islands. Within Australia an evolutionary offshoot of the *Morelia spilotes* line gave rise to *Morelia (=Python) carinatus*. No doubt some of the isolated geographical races of *Morelia spilotes* will eventually give rise to new species in their own right,(e.g. *Morelia (=Python) spilotes imbricatus*).

Liasis (=Python) boeleni, according to McDowall represents an evolutionary intermediate between *Python amethystinus* and *Morelia spilotes*. The origins of *Liasis boeleni* are in doubt although presumably in the New Guinea area. Theoretically (if McDowall's conclusions are correct) it should be possible to interbreed in captive controlled conditions *Liasis boeleni* with *Morelia spilotes* or *Python amethystinus*. How *Liasis boeleni* is evolutionarily linked to other *"Liasis"* is not certain.

Finally we are left with the remainder of the genus *Liasis*. which was presumably split between Australia and New Guinea several million years ago. *Liasis childreni* and *Liasis perthensis* speciated in Australia, and *Liasis albertisi* and *Liasis (=Bothrochilus) boa* arose in New Guinea. *Liasis boa* which appears intermediate to *Liasis childreni* (and *L.perthensis*) and *Liasis albertsi* would not constitute a stock linking those species directly, although in the distant past all four species presumably had the same ancestor.

CONCLUSION

The opinions expressed in this article are largely my own and I would advise those interested in the subject covered to carry out their own investigations when making decisions as to the status of Australasian Pythons. Finally may I apologise to those readers I may have confused by the use of varying scientific names to describe the same snake species.

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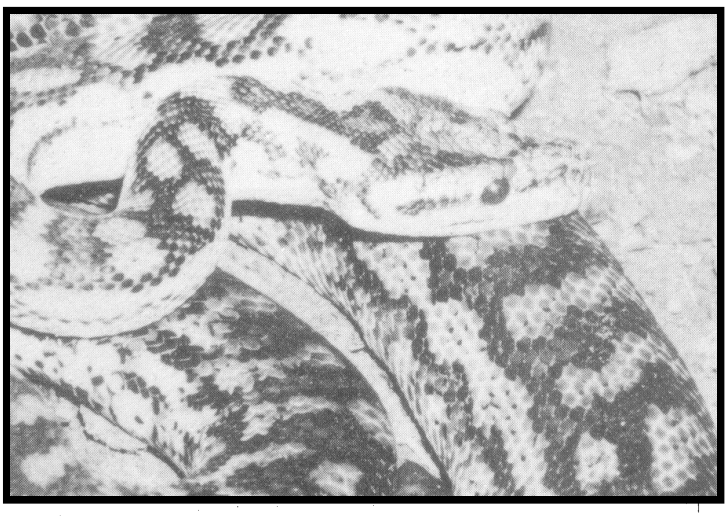
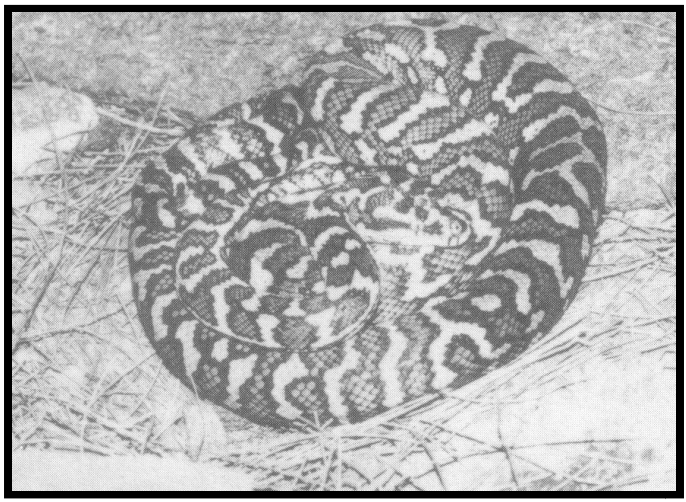
Photography by the Author

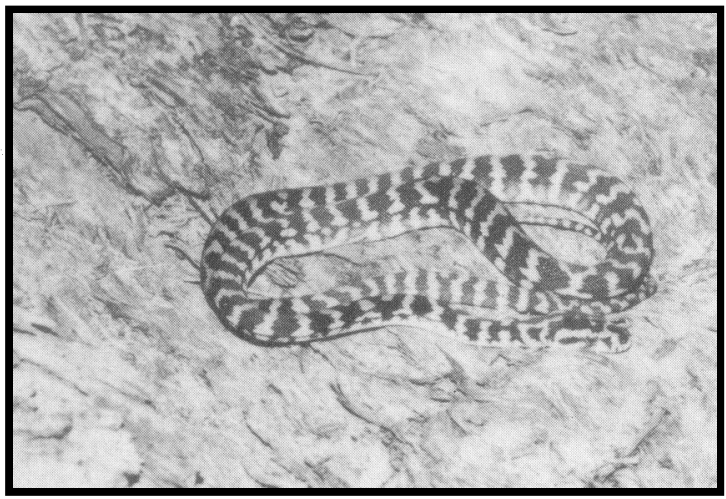
Murray Corridor (Western NSW) Form of Carpet Snake Adult Male 2 metre



Atherton Tableland
(Old) Form of
Carpet Python
Adult Male
2 metre

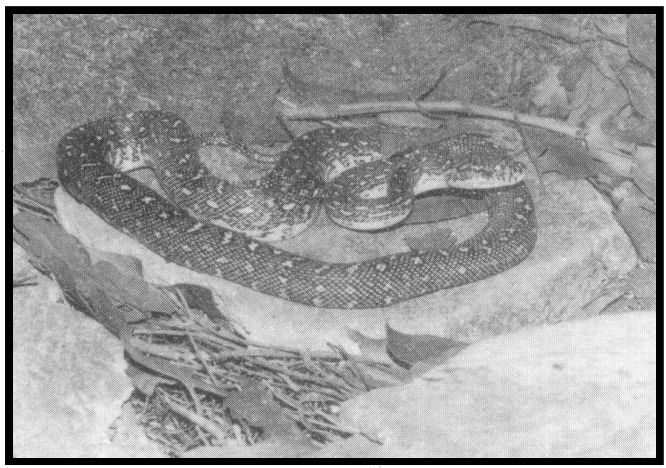


N.T. Form of
Carpet Python
(Juvenile) Male
.6 metre



Morelia
(=Python)
spilotes variegata
from Bundaberg Qld.
(Lat 24°52'
Long 152°25')
1 metre
(sub-adult male)

Morelia
(=Python)
s.spilotes
(The type species)
From Kenthurst
(in Sydney) N.S.W.
(Lat 33°38'
Long 150°57')
Male (sub-adult)
1 metre



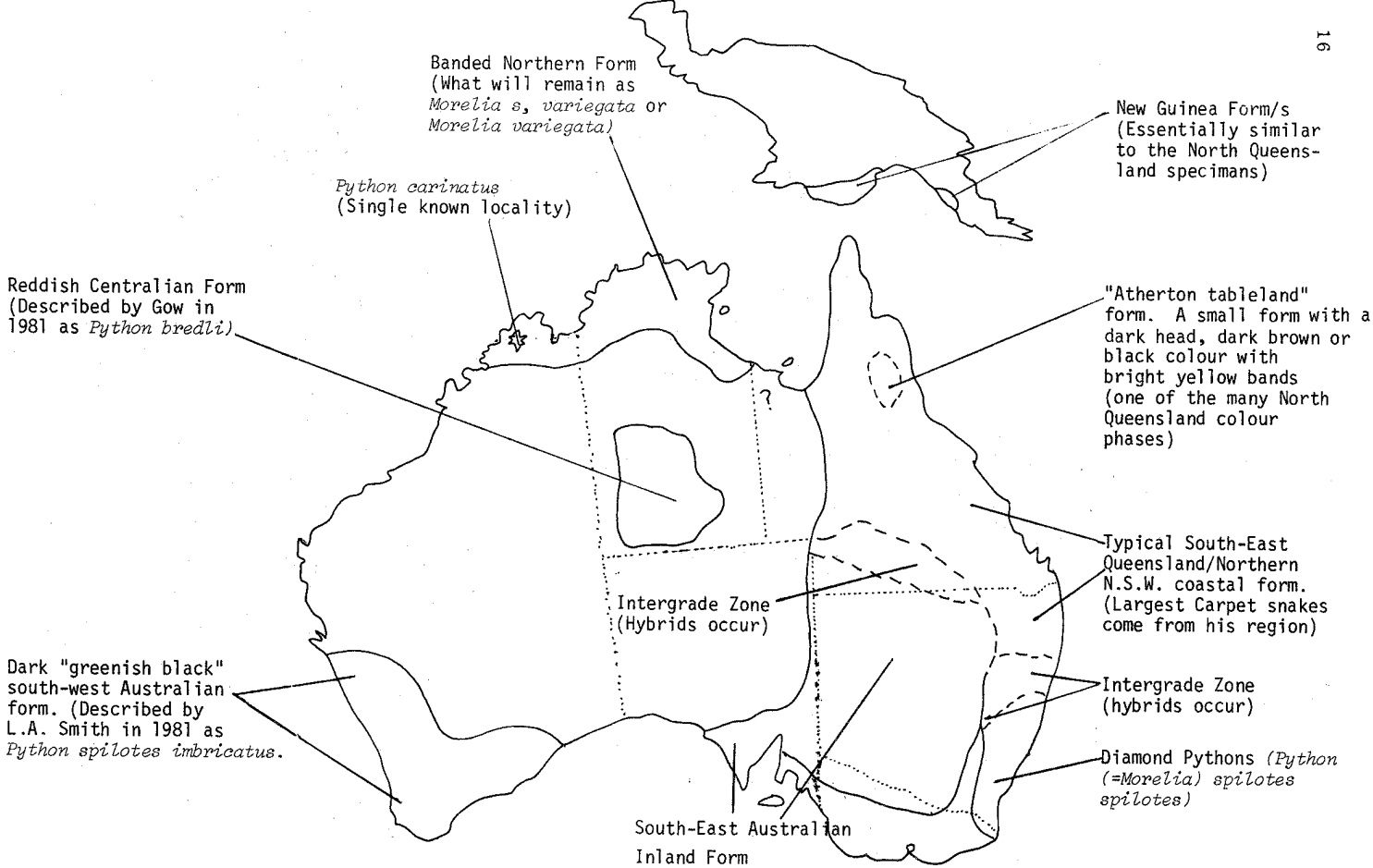


FIGURE 1. Detailed Distribution Map of the *Python(=Morelia) spilotes* group and *Python carinatus* according to the best available information.

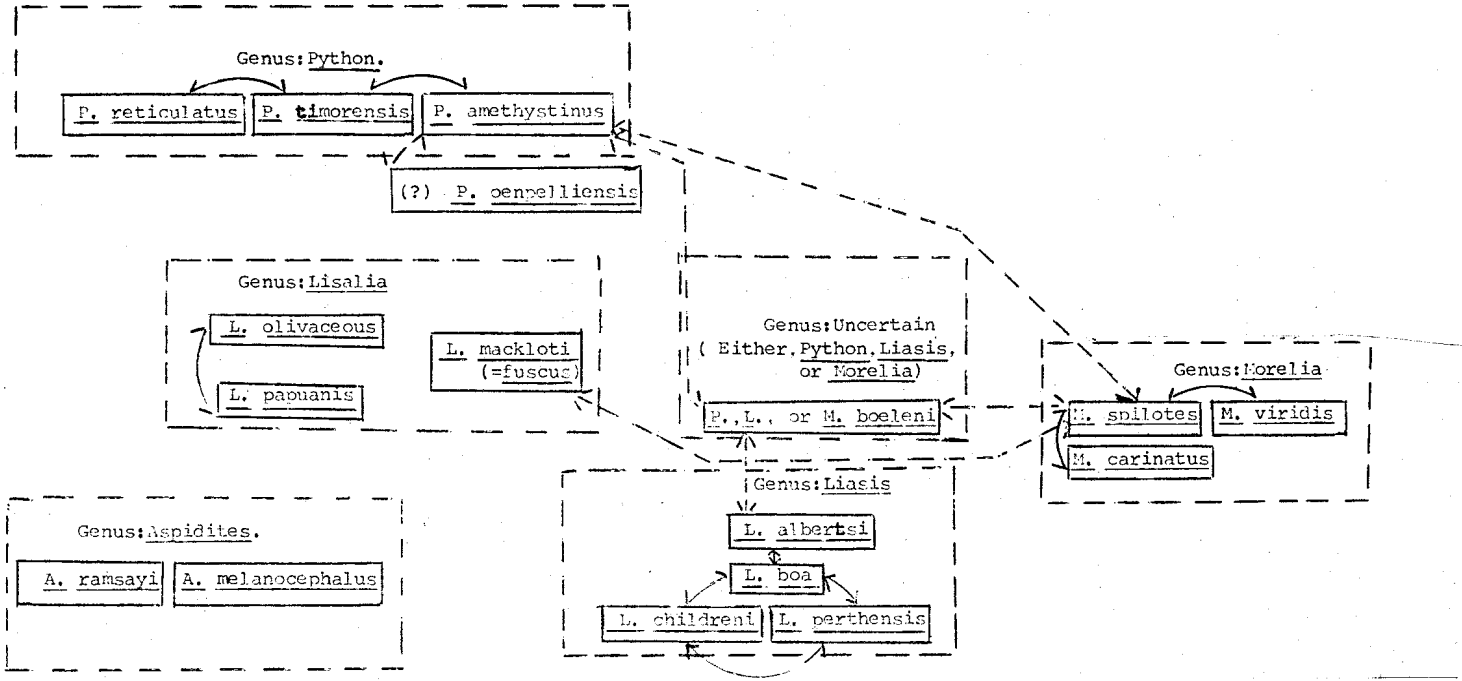


FIGURE 2. Simplified taxonomic relationships in Australasian Pythons (Hoser's System).
Notes for Fig.2. The positioning of a species in this diagram in relationship to another species reflects their "taxonomic closeness". Unbroken lines and arrows joining species indicates a strong possibility of relatively recent evolutionary divergence of the two species. Broken lines and arrows linking different species in different genera indicate possible links between different species and their respective genera. Each generic grouping is circled by a dotted line. (Hence: P.oenpelliensis and P., L., or M.boeleni are of uncertain taxonomic status, L.perthensis, M.viridis and P.reticulatus are evolutionarily, distant relatives.)