

***Agra*, arboreal beetles of Neotropical forests: *pusilla* group and *piranha* group systematics and notes on their ways of life (Coleoptera, Carabidae, Lebiini, Agrina)**

Terry L. Erwin

Hyper-diversity Group, Department of Entomology, MRC-187, National Museum of Natural History, Smithsonian Institution, Washington, P.O. Box 37012, DC 20013-7012, USA

urn:lsid:zoobank.org:author:A7923396-E5AB-4C31-842A-12B8D8C0F315

Corresponding author: Terry L. Erwin (erwint@si.edu)

Academic editor: *Achille Casale* | Received 29 September 2010 | Accepted 11 October 2010 | Published 4 November 2010

urn:lsid:zoobank.org:pub:176306EB-6342-4E75-AD76-C4A82040A002

Citation: Erwin TL (2010) *Agra*, arboreal beetles of Neotropical forests: *pusilla* group and *piranha* group systematics and notes on their ways of life (Coleoptera, Carabidae, Lebiini, Agrina). ZooKeys 66: 1–28. doi: 10.3897/zookeys.66.606

Abstract

Revisions of two new species groups of the genus *Agra* Fabricius are presented with the following species described as new: *pusilla* group - *Agra cruciaria* **sp. n.** (Brazil), *Agra grace* **sp. n.** (Ecuador, Perú), *Agra max* **sp. n.** (Brazil), *Agra minasianus* **sp. n.** (Brazil),

Agra notpusilla **sp. n.** (Brazil), *Agra pseudopusilla* **sp. n.** (Brazil); *piranha* group - *Agra ce* **sp. n.** (Perú), *Agra risseri* **sp. n.** (Bolivia, Brazil), *Agra maia* **sp. n.** (Bolivia), *Agra piranha* **sp. n.** (Ecuador); *Agra tiputini* **sp. n.** (Ecuador). Species of these two groups have adults that are the smallest in the entire genus, although this does not indicate they are closely related based on other attributes. All species are Amazonian in distribution.

Keywords

Neotropics, Bolivia, Brazil, Ecuador, Perú, rainforest canopy

Introduction

The purpose of this 17th contribution in my series of papers with diagnoses of new taxa and redescriptions of known taxa in the beetle genus *Agra* Fabricius, 1801 (Carabidae) is to present a revision of the species in the *pusilla* and *piranha* groups. For the previous papers, see Erwin (1978, 1982a, 1982b, 1983, 1984, 1986, 1991, 1993, 1996, 1998, 2000a, 2000b, 2000c, 2002), Erwin and Pogue (1988), and Arndt et al. (2001). New species descriptions provided here will not be the end of the story. New species of this incredibly speciose and diverse genus continue to be discovered each year throughout the Neotropics and subtropical México /Texas and northern Argentina.

These beetles belong to the Tribe Lebiini, Subtribe Agrina, of which the genus *Agra* Fabricius is by far the largest lineage in number of species. Subtribe Agrina consists of those species formerly included in the Subtribe Calleidina (cf. Lorenz 1998, 2005). More than 2000 neotropical/subtropical species of *Agra* are known from museum collections; however, only some 592 of these have been described since Fabricius erected the genus in 1801, plus three species described in the very late 1700's by Olivier and Fabricius, but originally placed in the Linnaean genus *Carabus*. The sister group was hypothesized to be an African/Madagascan group near *Callidiola* Jeannel 1949, however Casale (1998) argues against that. His analysis suggested that *Agra* is more closely aligned with Physoderina, as the adelphotaxon. Certainly, the female stylocomere 2 fits that hypothesis in a general way and the male median lobe is not *Calleida* or *Callidiola* like. However, there is little in the overall “gestalt” that might lead one to conclude these lineages are at all related. It is time for comparative DNA analysis, I suggest, to determine where these higher lebiine lineages fall out on an updated classificatory scheme. Unfortunately, in the fine contribution of Ober and Maddison (2008), the Physoderina were not included, even though they saw possible monophyly amongst Calleidina (sensu Casale 1998), Agrina, Metallicina etc. This will mean that specimens of the *pusilla* group need to be in the DNA mix of samples because of their clearly, based on structural attributes, less derived features amongst all the other species groups of this very diverse genus. And, members of Physoderina will need to be in the mix, as well.

The *pusilla* group contains what appear to be the least derived lineage of *Agra* and obtaining DNA from them will be crucial in locating the sister lineage – an additional reason for this present revision is making the species and their localities more broadly available, so that fresh specimens can be appropriately acquired and identified. The *piranha* group apparently is more derived than the *pusilla* group, but both groups are composed in part of little blue beetles and I thought it better to treat them together for purposes of easier identification and classification.

Likely, adult *Agra* are predaceous on other arthropods; one specimen of another species group dissected had fragments of termites in its gut contents. Adults also have been observed drinking exudates from young new shoots and young leaves on a variety of tree species, as well as feeding on pollen (Arndt et al. 2001). Adults are active on tree surfaces in the canopy and along forest edges at night, as well as in suspended dry leaves

in the understory; in addition, at least one species group is often found on savannah grasses. Adult tarsi are adapted for running on the surfaces of leaves with pads similar to those found in adult Chrysomelidae and Cerambycidae. Adults rest under these leaves “concealed” with legs and antennae tucked close to the body, the beetle aligned perfectly with the midrib of the leaf; in the case of grass-dwelling species they align with the culms. *Agra* adults are nocturnal and commonly fly to lights at night and into Malaise traps, however, none are known so far from ground level flight-intercept traps. These beetles have a potent defensive secretion from paired glands in their abdomen that, in field tests, bats definitely do not like (Erwin 1978). And, males of many species of this genus have special ventral patches of setae or pubescence that suggest they may waft pheromones to attract females. If correct, these chemicals have not been explored for their composition or possible uses. Known larvae are thought to occur normally under bark of standing trees, probably in burrows of other insects, and are thought to be predatory (Arndt et al. 2001). A few larvae have been obtained by rearing from eggs of known females and with insecticidal fogging techniques before dawn (Arndt et al. 2001), the latter indicating the larvae may wander on the tree surfaces at night.

Specimens and methods

Methods and species concepts follow those previously described (Erwin and Kavanaugh 1981; Kavanaugh and Erwin 1991). The species validation and diagnosis format follows as closely as possible that suggested in Erwin and Johnson (2000) and as used in Erwin (2000a, 2004). Measurements of length (ABL, SBL) and width (TW) follow those of Ball (1972) and Kavanaugh (1979): ABL (apparent body length), measured from apex of labrum to apex of longer elytron; SBL (standardized body length), equals the sum of the lengths of the head (measured from apex of clypeus to a point on midline at level of the posterior edge of compound eyes), pronotum (measured from apical to basal margin along midline), and elytron length (measured from apex of scutellum to apex of the longer elytron); and TW, (total width), measured across both elytra at their widest point.

Included in this study are a total of 22 specimens from the National Museum of Natural History, Washington, DC (NMNH); H. Perrin, J. Menier, Muséum National d’Histoire Naturelle, Paris (MNHN); A. Kuska, Institut Zoologique, Warsaw, Poland (WAR); S. Fragoso, M. Monné, Brazil National Collection, Museu Nacional, Rio de Janeiro, Brazil (BNCRio); M. Baccis, British Museum (Natural History), London, England (BMNH); O.V. Ferreira and J. Jurberg, Oswaldo Cruz Institute, Rio de Janeiro, Brazil, (ZIKAN); R. Woodruff, Florida Department of Agriculture, Gainesville (FSCA). Note that the curators named were on duty at the time of the loan; many of these have since retired.

The habitus images of the adult beetles portray most of the character states referred to in the keys provided. Illustrations of male genitalia are standard for descriptive taxonomy of carabid beetles. The habitus images of the adults were made with a Visionary

Digital™ high resolution imaging system. Figure captions include an ADP number, which is a unique identification number for the specimen that was illustrated or imaged and links the specimen and associated illustrations and/or image to additional information in electronic databases at the NMNH. All scale lines are 0.5mm.

Geographical data are presented for species based on all known specimens available at the time of manuscript preparation. Georeferences have been determined from locality information provided on specimen labels; only those exact Georeferences that are provided on the label are placed in quotes, otherwise I have estimated the Georeferences as closely as possible from places, mileage, etc. listed on the label and searched with Google Earth Pro. Latitude and longitude are reported in decimal degrees. Distribution maps are provided for the species (Figs 10, 11). Here, English vernacular names are proposed, as common names are becoming increasingly needed in conservation and/or agricultural and forestry applications.

The species list below, as well as arrangement of descriptions that follows is ordered alphabetically.

Accounts of taxa

Genus *Agra* Fabricius, 1801

Elegant Canopy Beetles

Agra Fabricius, 1801:224. Type-species: *Agra aenea* Fabricius 1801:224, named first among three species described by Fabricius. Designated by Erwin (1982a).

Agridia Chaudoir, 1861:109. Type-species: *Agridia platyscelis* Chaudoir (1861:109), named first among two species described by Chaudoir. Designated by Erwin (1982a).

Diagnostic combination. During evolution toward a canopy domain and away from a likely under canopy sister group, *Agra* adults acquired numerous generic-level autapotypic features as follows: head elongate with prognathate mandibles, securiform labial ultimate palpomeres (Erwin 1982a), extended cranium, and constricted neck; prothorax elongate and tubular, plural sutures effaced; tarsomeres (Erwin 1982a) dilated with setiferous pads beneath, claws explanate and pectinate; elytron with latero-basal sinus and latero-apical callus, apex medially and laterally toothed or somewhat produced, apical margin truncate, sinuate, or medially lobed; and male venter variously adorned with setal or pubescent patches; female reproductive system adapted to egg-laying deep in substrate (telescopic) (Erwin 2002) with (usually) stout, apically-armed with ensiform setae, stylomere 2. Defense system very large (Erwin 1982a). Size. ABL=6.0mm to 29.0mm; TW=1.5mm to 6.0mm.

Note. For descriptions of species groups previously recognized, refer to Erwin (1996, 1998, 2002).

The *pusilla* species-group

Members of the *pusilla* group are the smallest of the genus *Agra* and in part, of a beautiful blue color and matte luster with highly contrasting bicolored femora.

Diagnosis: Femur bicolored. Back of head rounded and sparsely punctate. Adult males with extensive ventral tarsomere pads on both front and middle legs. Prothorax markedly punctate. Elytral interneurs of uni- and/or biseriate rows of cribriform punctures. Aedeagus with narrow spatulate apex. Female stylomere 2 short and arcuate, glabrous, and apically armed with two ensiform setae, as in Fig. 7.

Note: The known composite range of the *pusilla* group extends from Amazonian Ecuador and Perú across southeastern Brazil and into the Mata Atlântica.

Included Species

<i>Agra cruciaria</i> Erwin, sp. n.	Brazil
<i>Agra grace</i> Erwin, sp. n.	Ecuador, Perú
<i>Agra max</i> Erwin, sp. n.	Brazil
<i>Agra minasianus</i> Erwin, sp. n.	Brazil
<i>Agra notpusilla</i> Erwin, sp. n.	Brazil
<i>Agra perforata</i> Liebke, 1938	Brazil
<i>Agra pseudopusilla</i> Erwin, sp. n.	Brazil
<i>Agra pusilla</i> Chaudoir, 1847	Brazil

Key to the species of the *pusilla* group of *Agra* Fabricius, 1801

1	Elytra bright metallic blue.....	2
1'	Elytra dull matte smoky black or smoky black-blue, not bright.....	3
2(1)	Elytral interneurs each with a single row of cribriform punctures.....	
	<i>Agra grace</i> sp. n.
2'	Elytral interneurs each with double rows of cribriform punctures at least in part in apical half.....	<i>Agra max</i> sp. n.
3(1')	Antennal scape unicolorous testaceous, or testaceous with slight dorso-apical infuscation.....	4
3'	Antennal scape bicolored, ventrally testaceous, dorsally infuscated.....	6
4(3)	Head posteriorly and pronotum with surface brassy.....	<i>A. cruciaria</i> sp. n.
4'	Head and pronotum matte smoky black, shiny or not.....	5
5(4')	Elytra constricted at apical third, side margin moderately arcuate, apex moderately lobed medially.....	<i>A. notpusilla</i> sp. n.
5'	Elytra not constricted at apical third, side margin straight, apex markedly lobed medially.....	<i>A. pusilla</i> Chaudoir
6(3')	Elytral apex shallowly lobed medially, lobe rounded.....	<i>A. pseudopusilla</i> sp. n.
6'	Elytral apex moderately lobed medially, lobe obtusely dentate.....	7

- 7(6') Frons laterad, anterior to eye markedly rugose; larger species (ABL = 8.2 mm) ***A. perforata* Liebke**
 7' Frons laterad, anterior to eye, unicarinate and smooth, smaller species (ABL = 7.2 mm) ***A. minasianus* sp. n.**

***Agra cruciaria* Erwin, sp. n.**

urn:lsid:zoobank.org:act:7906629D-6846-4348-A3CD-B7A3031C7AE9

Figs 3, 10

Holotype: Brazil: Rio de Janeiro, Rio de Janeiro, Corcovado, 585m, 22.9517°S, 43.2116°W, 5 May 1958 (C.A. Campos Seabra & M. Alvarenga)(NMNH: ADP 070044, male).

Derivation of specific epithet. The epithet “*cruciaria*” is a Latin adjective meaning “of/pertaining to the cross/torture” and is based upon the large cross on Corcovado flooded each night with high powered lights that attract insects by the millions and is the type locality of this species.

Proposed English vernacular name. Cross Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and medium sized for the *pusilla* group. Adults with black integument; head behind eyes and prothorax with slight brassy reflections. Frons laterad unicarinate and rugose. Occiput with sparse punctures, some punctures with short setae.

Elytra with moderately lobed apex.

Description. (Fig. 3). *Size:* Small, ABL = 6.4 – 7.7 mm, SBL = 5.75 – 6.48 mm, TW = 1.74 – 1.8 mm. *Color:* Head black with brassy reflection posteriorly, pronotum with brassy reflections; antennae blackish blue with scape testaceous and with slight metallic blue reflections, mouthparts piceous, and legs and tarsi blackish blue, with mostly testaceous femur. *Luster:* Head, pronotum and legs shiny metallic, elytra matte smoky-blue. *Head:* Labrum moderately elongate and truncate apically, barely emarginate medially. Frons medially raised and smooth, laterally depressed and unicarinate and rugose. Gena with hind angles broadly rounded to constricted neck in males. Genae and occiput moderately densely and coarsely some punctures setiferous.

Prothorax: Slightly broader medially, flared basally; surface with dense punctures, many setiferous; lateral elongate callous with single row of setiferous punctures along middle. *Pterothorax:* Elytron markedly convex, intervals slightly costate, interneurons of rows of somewhat irregularly shaped punctures that are double in some places, apex slightly oblique and moderately lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex slightly produced, narrowly pointed. Metasternum sparsely setiferous in male. *Legs:* Normal in male. *Abdomen:* Abdominal sterna III to VII of male moderately and bilaterally setiferous; sternum VII of male barely emarginated, corners rounded. *Male genitalia:* Phallus (Fig. 3) elongate and narrow with ostium elongate, nearly half the length of the phallus, apex a narrowly lobate expansion of distal end, this slipper-shaped

in lateral aspect. Parameres small, left twice the size of the right, both broadly rounded. *Female ovipositor*: Female unknown.

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; larvae of this genus are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. cruciaria* occur at midland altitudes in the Mata Atlântica. Adults are active in May, the rainy season.

Other specimens examined. **Brazil**: Minas Gerais, (MNHNP: ADP 060040, male paratype).

Geographic distribution. (Fig. 10). This species is currently known from the type locality and an unknown location in the State of Minas Gerais.

Notes. Right antenna glued to card of holotype not of this specimen.

***Agra grace* Erwin, sp. n.**

urn:lsid:zoobank.org:act:2B0E0A90-4A13-404A-9047-8D61E61E7419

Figs 1, 4, 10

Holotype: Perú: Madre de Dios, Pakitza, Tachigali Trail /47, 324m, “11.9352°S, 71.3039°W,” 6 October 1991 (T.L. Erwin & M.G. Pogue)(NMNH: BIOLAT 012952, female).

Derivation of specific epithet. The epithet “*grace*” is an eponym, based on the given name of the Peruvian Ornithologist, Grace Servat, who has shared the bird-infested Amazon and Andes with me for many years, including two of the known localities of this species, including the type locality.

Proposed English vernacular name. Grace’s Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and small sized for the *pusilla* group. Adults with blue integument; head behind eyes and prothorax with metallic reflections. Frons laterad unicarinate and very finely rugose. Occiput not punctate, some fine rugae present. Elytra with moderately lobed apex in female, more so in male. Hind coxae of male multisetiferous.

Description. (Figs 1, 4). *Size*: Very small, ABL = 5.71 – 6.1 mm, SBL = 4.77 – 6.67 mm, TW = 1.44 – 1.66 mm. *Color*: Head and pronotum bright blue, body metallic blue; antennae and mouthparts piceous, scape and antennomeres 2 and 3 with slight metallic blue reflections. *Luster*: Shiny metallic, elytra somewhat matte. *Head*: (Fig. 1) Labrum moderately elongate and truncate apically. Frons medially raised and smooth, laterally depressed, unicarinate, not rugose. Gena slightly tapered with broadly rounded corners to constricted neck in both sexes. Occiput not punctate, some fine rugae present. *Prothorax*: Slightly broader medially, flared basally; surface with dense coarse punctures, some setiferous; lateral elongate callous with single row of punc-



Figure 1. *Agra grace* Erwin, sp. n., dorsal aspect (BIOLAT 012952).

tures, along middle. *Pterothorax*: Elytron (Fig. 1) markedly convex, intervals slightly costate, interneurs of rows of somewhat laterally ovate punctures, apex truncate, barely oblique, apical dentation asymmetric, lateral tooth broad, obtuse, sutural apex not produced. Metasternum sparsely setiferous in both sexes. *Legs*: Normal. *Abdomen*: Abdominal sterna III to VII of both sexes moderately and bilaterally setiferous; sternum VII of both sexes barely emarginate, corners rounded. *Male genitalia*: Phallus (Fig. 4)

elongate and narrow with ostium not elongate, extended to about 1/3 the length of phallus, apex a small rounded lobe. Parameres small, left twice the size of the right, both broadly rounded. *Female ovipositor*: Stylomere 2 as in *A. notpusilla* (Fig. 7).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. grace* occur at lowland altitudes in the Amazon Basin. Adults are active in September — October, the transition season between dry and wet seasons. The holotype was fogged from a medium-sized tree with lianas and suspended dead leaves; the area fogged was from 2 meters up to 15 meters in the tree. The Ecuadorian paratype was fogged from a mixed canopy consisting of the trees *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr., *Protium* cf. *nodulosum*, and *Eschweilera* cf. *coriacea*. The Peruvian paratype was fogged from a species of the tree genus *Pouteria*.

Other specimens examined. Ecuador: Orellana, 1 km S Onkone Gare Camp, Entomology Transect, 216m, “0.6569°S, 76.4527°W,” 7 October 1994 (T.L. Erwin, et al.)(NMNH: ADP 087438, male paratype). **Perú:** Madre de Dios, Pakitza, 324m, “11.9352°S, 71.3039°W,” 9 September 1988 (T.L. Erwin & B.D. Farrell)(NMNH: BIOLAT 008430, male paratype).

Geographic distribution. (Fig. 10). This species is currently known from Perú and Ecuador.

Notes. Males are smaller than females.

Agra max Erwin, sp. n.

urn:lsid:zoobank.org:act:20642068-3310-4BCC-B9A8-69D9FBEABB41

Fig. 10

Holotype: Brazil: Santa Catarina, Nova Teutonia, 823m, 27.047°S, 52.394°W, 4 February 1938 (F. Plaumann)(WAR: ADP 004374, female).

Derivation of specific epithet. The epithet “*max*” is an eponym, based on the given name of Max Liebke, an early pioneer in the taxonomy of the genus *Agra*.

Proposed English vernacular name. Max’s Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and frons laterally unicarinate and rugose; occiput finely punctate; all elytral interneurs in apical half with double rows of cribriform punctures.

Description. *Size:* Small, ABL = 7.0 mm, SBL = 5.95 mm, TW = 1.5 mm. *Color:* Head and pronotum black with bluish reflections, venter metallic blue, elytra matte blue, antennae and mouthparts piceous with slightly bluish reflections, scape rufous with shiny infuscated apex. *Luster:* Shiny metallic, elytra matte metallic. *Head:* Labrum moderately elongate and truncate apically. Frons medially raised and smooth, laterally depressed,

slightly rugose. Gena slightly markedly rounded to constricted neck in female. Genae and occiput with sparse coarse punctures, some setiferous.

Prothorax: Short, slightly broader medially, flared basally; surface with dense and coarse punctures, some setiferous; lateral elongate callous with single row of setiferous puncture along middle. *Pterothorax*: Elytron markedly convex, intervals slightly costate, interneurs of rows of somewhat laterally ovate punctures, doubled in some places, apex moderately oblique and lobed, apical dentation asymmetric, lateral tooth small, broad, obtuse, sutural apex not produced. Metasternum sparsely setiferous in females. *Legs*: Normal in female. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of female barely emarginate, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. notpusilla* (Fig. 7).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. max* occur at midland altitudes in the Mata Atlântica. Adults are active in February, the dry season.

Other specimens examined. None.

Geographic distribution. (Fig. 10). This species is currently known only from the type locality.

***Agra minasianus* Erwin, sp. n.**

urn:lsid:zoobank.org:act:B3072B22-36A7-415D-A2B6-E6FE05270DC0

Fig. 10

Holotype: Brazil: Minas Gerais, (Laferte)(MNHNP: ADP 060090, female).

Derivation of specific epithet. The epithet “*minasianus*” is a Latinized adjective meaning “derived from, or pertaining to” Minas Gerais, a State in Brazil, and the type area.

Proposed English vernacular name. Minas Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and scape and legs bicolored, frons laterad, anterior to eye, unicarinate and smooth, prothorax moderately setiferous both laterally and ventrally, and elytra barely constricted at apical third, side margin slightly arcuate, apex moderately lobed medially, lobe obtusely dentate, smaller species.

Description. *Size*: Very small, ABL = 7.2 mm, SBL = 6.24 mm, TW = 1.5 mm. *Color*: Head and prothorax black, legs and scape bicolored; flagellar antennomeres and mouthparts piceous. *Luster*: Matte. *Head*: Labrum moderately elongate and truncate apically, anterior margin slightly emarginate medially. Frons laterad, anterior to eye, uni-

carinate and smooth. Gena rounded to constricted neck in females. Genae and occiput with sparse coarse punctures, some setiferous.

Prothorax: Slightly broader at basal third, constricted near base and flared basally; surface densely punctate, laterally and ventrally setiferous, pronotum apparently with six lateral setae as in other species of the group, but not present on holotype. *Pterothorax*: Elytron markedly convex, intervals not costate, interneurs of rows of somewhat laterally ovate punctures, some in doubles, apex lobate, lobe well developed obtuse projection, apical dentation asymmetric, lateral and sutural apices slightly produced, each obtuse. Metasternum sparsely setiferous in female. *Legs*: Normal. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of female barely emarginate, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. notpusilla* (Fig. 7).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. The single specimen of *A. minasianus* has no associated data on its labels.

Other specimens examined. None.

Geographic distribution. (Fig. 10). This species is currently known from Minas Gerais, Brazil.

Agra notpusilla Erwin, sp. n.

urn:lsid:zoobank.org:act:988FCC3E-1A4F-439D-833C-66B524B7269F

Figs 7, 10

Holotype: Brazil: (MNHP: ADP 058647, male).

Derivation of specific epithet. The epithet “*pusilla*” is a Latin adjective meaning very little, small, pretty. Although this species resembles *A. pusilla* it is “not” that species.

Proposed English vernacular name. Brazilian Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and frons laterally multicarinate; elytra with interneurs composed of double rows (in part) of coarse irregularly shaped punctures, apex moderately lobed medially.

Description. (Fig. 7). *Size*: Very small, ABL = 7.74 mm, SBL = 6.58 mm, TW = 1.88 mm. *Color*: Piceous, antennae and legs bicolored, scape and basal 5/6th of femur testaceous; antennal flagellum and mouthparts piceous. *Luster*: Head and abdomen shiny, elytral disc somewhat matte. *Head*: Labrum moderately elongate and truncate apically, slightly emarginate medially. Frons medially raised and smooth, laterally depressed, multicarinate. Gena rounded in female to constricted neck. Genae and with occiput sparse and moderately coarse punctures, some of which likely setiferous in undamaged specimens (no setae present in holotype), and with two larger punctures. *Prothorax*: Slightly

broad in basal third, constricted, and flared basally; surface densely punctate, laterally and ventrally setiferous. *Pterothorax*: Elytron markedly convex, intervals not costate, interneurons of double rows (in part) of somewhat irregularly shaped punctures, apex truncate, moderately lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex slightly produced, rounded. Metasternum sparsely setiferous in both females. *Legs*: Legs normal. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of females barely emarginate, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 (Fig. 7).

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. notpusilla* have no recorded information.

Other specimens examined. None.

Geographic distribution. (Fig. 10). This species is currently known from Brazil.

Agra perforata Liebke, 1938

Fig. 10

Agra perforata Liebke 1938:60

Holotype: Brazil: Rio de Janeiro, Rio de Janeiro, 585m, 22.9517°S, 43.2116°W (WAR: ADP 060035, female).

Derivation of specific epithet. The epithet “*perforata*” is a Latin adjective referring to the cribriform punctures of the elytral interneurons.

Proposed English vernacular name. Perforated Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and frons laterally multicarinate; occiput coarsely punctate; all elytral interneurons throughout with double rows of cribriform punctures.

Description. *Size*: Small, ABL = 8.22 mm, SBL = 6.58 mm, TW = 1.88 mm. *Color*: All black with mostly testaceous femur. *Luster*: Head slightly shiny, pronotum and elytra matte black. *Head*: Labrum moderately elongate and rounded apically. Frons medially raised and smooth, laterally depressed, moderately rugose. Gena markedly rounded to constricted neck in female. Genae and occiput with sparse and coarse punctures, some setiferous. *Prothorax*: Short, slightly broader medially, flared basally; surface with dense and coarse punctures, some setiferous; lateral elongate callous with single row of setiferous punctures along middle. *Pterothorax*: Elytron markedly convex, intervals slightly costate, interneurons of double rows of somewhat irregularly shaped punctures, apex moderately oblique and lobed, apical dentation asymmetric, lateral tooth small, broad, obtuse, sutural apex not produced. Metasternum sparsely setiferous in females. *Legs*: Normal in female. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of female barely emarginate.

ate, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. notpusilla* (Fig. 7).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. perforata* occur at midland altitudes in the Mata Atlântica.

Other specimens examined. None.

Geographic distribution. (Fig. 10). This species is currently known only from the type locality.

Notes. Additional character state information can be found in Liebke, 1938:60.

Agra pseudopusilla Erwin, sp. n.

urn:lsid:zoobank.org:act:B39D7377-B0B7-43D8-AE76-0F3F0EF58ABB

Figs 5, 10

Holotype: Brazil: (Comte G. de Mnischez)(MNHNP: ADP 060088, female).

Derivation of specific epithet. The epithet “*pseudopusilla*” refers to the similarity between adults of this species and those of *A. pusilla*, treated below.

Proposed English vernacular name. Mnischez’s Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and frons laterally multicarinate; occiput coarsely bi-punctate, with several smaller punctures; elytral interneurs with mostly uni-serial rows of cribriform punctures, doubled apico-laterally.

Description. (Fig. 5). *Size*: Small, ABL = 6.57 – 8.63 mm, SBL = 5.67 – 7.15 mm, TW = 1.34 – 2.08 mm. *Color*: Head and pronotum black, elytra smoky black, legs bi-colored, antennae and mouthparts piceous, scape with testaceous venter, piceous dorsum. *Luster*: Shiny forebody, matte elytra. *Head*: Labrum moderately elongate and truncate apically, anterior corners rounded. Frons medially raised and smooth, laterally depressed, multicarinate. Gena slightly tapered with broadly rounded corners to constricted neck in both male. Occiput coarsely bi-punctate, with several smaller punctures. *Prothorax*: Slightly broader medially, flared basally; surface with dense and coarse punctures, some setiferous; lateral elongate callous with single row of setigerous punctures along middle. *Pterothorax*: Elytron markedly convex, intervals slightly costate, interneurs of rows of somewhat laterally ovate punctures, doubled in some places, apex oblique, slightly lobed at middle, apical dentation asymmetric, lateral tooth short, acute, sutural apex not produced. Metasternum sparsely setiferous in males. *Legs*: Normal. *Abdomen*: Abdominal sterna III to VII of male moderately and bilaterally setiferous; sternum VII of males barely emarginate, corners rounded. *Male genitalia*: Phallus (Fig. 5) elongate and narrow with ostium not elongate, extended to about 1/2 the length of phallus, apex a small rounded

lobe. Parameres small, left twice the size of the right, both moderately rounded. *Female ovipositor*: Female unknown

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. pseudo-pusilla* are labeled Brazil without further information.

Other specimens examined. Brazil: (Ehrenreiche)(BNCRio: ADP 070045, male paratype).

Geographic distribution. (Fig. 10). This species is currently known only from Brazil, without specific location.

Agra pusilla Chaudoir, 1847

Figs 6, 10

Agra pusilla Chaudoir 1847:110.

Holotype: Brazil: (MNHNP: ADP 060087, male).

Derivation of specific epithet. The epithet “*pusilla*” is a Latin adjective meaning very little, small, pretty.

Proposed English vernacular name. Small Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and frons laterally unicarinate and rugose; elytra with interneurs composed of a single row of coarse irregularly shaped punctures, apex markedly lobed medially.

Description. (Fig. 6). *Size*: Very small, ABL = 6.28 – 6.45 mm, SBL = 5.27 – 5.37 mm, TW = 1.32 – 1.46 mm. *Color*: Piceous, antennae and legs bicolored, scape and basal 5/6th of femur testaceous; antennal flagellum and mouthparts piceous. *Luster*: Shiny, elytral disc somewhat matte. *Head*: Labrum moderately elongate and rounded apically, slightly emarginate medially. Frons medially raised and smooth, laterally depressed, unicarinate, and shallowly rugose. Gena slightly tapered-rounded in both sexes to constricted neck. Genae and occiput moderately finely punctate and wrinkled, and with two larger punctures each of which is setiferous. *Prothorax*: Slightly broader medially, flared basally; surface with densely punctures, some setiferous; lateral elongate callous with single row of setiferous punctures along middle. *Pterothorax*: Elytron markedly convex, intervals not costate, interneurs of rows of single somewhat irregularly shaped punctures, apex truncate, markedly lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex slightly produced, rounded. Metasternum sparsely setiferous in both sexes. *Legs*: Legs normal. *Abdomen*: Abdominal sterna III to

VII of male moderately and bilaterally setiferous; sternum VII of males barely emarginate, corners rounded. *Male genitalia*: Phallus (Fig. 6) with ostium elongate, about half the length of the phallus, apex a small rounded lobe with basal corners. Parameres small, left twice the size of the right, both moderately rounded. *Female ovipositor*: Stylomere 2 as in *A. notpusilla* (Fig. 7).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. pusilla* occur at lowland altitudes in the Mata Atlântica. Adults are active in October, the rainy season.

Other specimens examined. Brazil: Espírito Santo, nr. Itapemirim, Rio Itapemirim, 3m, 21.005°S, 40.834°W, 15 October 1906 (J.F. Zikan) (ZIKAN: ADP 070043, male).

Geographic distribution. (Fig. 10). This species is currently known from eastern Brazil.

Notes. Because of the severe deforestation over the last 100 years in the area where this species was found, it is likely it is now extinct or at least with a much smaller range.

The *piranha* species-group

Members of this group are of very small size for the genus and range in color from midnight metallic blue to smoky-black with a somewhat matte luster. Male adults have a much reduced version of the expansive ventral tarsomere pads found in all other species in the genus. Femur unicolored. Occiput and prothorax markedly punctuate. Elytral interneurs of uniseriate rows of cribriform punctures. Aedeagus with typical arrowhead shape. Female stylomere 2 short and arcuate, setiferous, and armed with two ensiform setae. Female stylomere as in Fig. 9.

Notes: The known composite range of the *piranha* group extends from Amazonian Ecuador to Bolivia across into south-central Brazil (Goiás).

Included Species

<i>Agra ce</i> Erwin, sp. n.	Perú
<i>Agra risseri</i> Erwin, sp. n.	Bolivia, Brazil
<i>Agra maia</i> Erwin, sp. n.	Bolivia
<i>Agra piranha</i> Erwin, sp. n.	Ecuador
<i>Agra tiputini</i> Erwin, sp. n.	Ecuador

Key to the species of the *piranha* group of *Agra* Fabricius, 1801

- 1 Prothorax markedly setiferous both laterally and ventrally, pronotum with 3 long setae on each side **2**
- 1' Prothorax not setiferous laterally, pronotum with 4 long setae on each side **4**
- 2(1) Head very broad across occiput, wider than pronotum at its widest ***A. risseri* sp. n.**
- 2' Head not broad across occiput, narrower than pronotum at its widest **3**
- 3(2') Elytra constricted at apical third, side margin markedly arcuate ***A. maia* sp. n.**
- 3' Elytra barely constricted at apical third, side margin slightly arcuate ***A. ce* sp. n.**
- 4(1') Elytra constricted at apical third, side margin markedly arcuate; head markedly narrowed basally ***A. tiputini* sp. n.**
- 4' Elytra barely constricted at apical third, side margin slightly arcuate; head slightly tapered yet broad basally ***A. piranha* sp. n.**

***Agra ce* Erwin, sp. n.**

urn:lsid:zoobank.org:act:6A25E44D-7927-4FD0-9FD2-9B37E12458D7

Fig. 11

Holotype: Perú: Madre de Dios, 30 air km SW Puerto Maldonado, 205m, “12.8368°S, 69.2933°W,” 10 September 1984 (T.L. Erwin, et al.)(NMNH: ADP 093837, female).

Derivation of specific epithet. The epithet “*ce*” is a combination of pronounceable letters that when joined with the last three letters of the genus name, *Agra*, spells “grace,” for the Peruvian Ornithologist, Grace Servat, who has shared the lowland Amazon and the high Andes with me for many years, including the known localities of this species.

Proposed English vernacular name. Graceful Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and elytra and prothorax metallic blue, legs unicolored, frons laterad slightly rugose, prothorax markedly setiferous both laterally and ventrally, and elytra barely constricted at apical third, side margin slightly arcuate.

Description. *Size:* Small, ABL = 8.04 – 9.21 mm, SBL = 7.09 – 8.07 mm, TW = 2.36 – 2.78 mm. *Color:* Head black with bluish reflection posteriorly, body and legs metallic blue; antennae and mouthparts piceous, scape with slight metallic blue reflections. *Luster:* Shiny metallic. *Head:* Labrum moderately elongate and rounded apically. Frons medially raised and smooth, laterally depressed and rugose. Gena almost squared to constricted neck in females. Genae and occiput moderately densely punctate, each puncture setiferous. *Prothorax:* Slightly broader medially, flared basally; surface with dense and coarse setiferous punctures; lateral elongate callous with single row of setiferous punctures along middle. *Pterothorax:* Elytron markedly convex, inter-

vals moderately costate, interneurs of rows of somewhat laterally ovate punctures, apex truncate, barely lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex slightly produced, narrowly pointed. Metasternum sparsely setiferous in female. *Legs*: Normal in female. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of female barely emarginated, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. piranha* (Fig. 9).

Dispersal potential. These beetles are macropterous and are capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; larvae of this genus are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. ce* occur at lowland altitudes in the Amazon Basin. Adults are active in September, the late dry season. The holotype was collected in an Erwin Plot at the type locality; the forest of this plot is designated as a Swamp Forest with internal drainage (Erwin 1985) and is dominated by the palm *Mauritia flexuosa* L. and the hardwood tree *Lueheopsis hoehnei* Burret. The holotype was fogged from the later named species. The paratype was attracted to MV light.

Other specimens examined. **Perú**: Madre de Dios, Pakitza, Trocha Uno /14, 324m, “11.9352°S, 71.3039°W,” 8 September 1989 (R.A. Faitoute, et al.)(NMNH: BIOLAT 017465, female paratype).

Geographic distribution. (Fig. 11). This species is currently known only from two localities in southeastern Perú.

Agra maia Erwin, sp. n.

urn:lsid:zoobank.org:act:4CBBDF28-0E25-4818-A2DA-72D2CE6B3697

Fig. 11

Holotype: Bolivia: Santa Cruz, 4–6 km SSE Buena Vista, Hotel Flora & Fauna, 400–500m, “17.479°S, 63.631°W,” 1–10 November 2002 (S.W. Lingafelter)(NMNH: ADP 116043, female).

Derivation of specific epithet. The epithet “*maia*” is a Latinized genitive eponym, based on the given name of Maia Samuel, Executive Producer of the Smithsonian Spotlight program, *The Bug House*, in recognition of the hours of dedication she put into developing the program.

Proposed English vernacular name. Maia’s Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and prothorax brassy black, legs unicolored, frons laterad unicarinate, smooth, prothorax markedly setiferous both laterally and ventrally, and elytra markedly constricted at apical third, side margin markedly arcuate.

Description. *Size*: Small, ABL = 8.57 mm, SBL = 7.25 mm, TW = 2.2 mm. *Color*: Head black with faint bluish reflection posteriorly, pronotum brassy black legs and venter black, elytra metallic blue; antennae and mouthparts piceous. *Luster*: Shiny, prono-

tum brassy and elytra shiny metallic. *Head*: Labrum moderately elongate and moderately rounded apically. Frons medially raised and smooth, laterally depressed and smooth. Gena almost squared to constricted neck in females. Genae and occiput with moderately dense disc each side with four long setae, punctures, most setiferous. *Prothorax*: Slightly broader medially, flared basally; surface densely punctuate, disc each side with four long setae; lateral elongate callous with single row of setiferous punctures along middle. *Pterothorax*: Elytron moderately convex, broadly flared at apical third, intervals moderately costate, interneurons of rows of somewhat laterally ovate punctures, apex truncate, barely lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex slightly produced, narrowly pointed. Metasternum sparsely setiferous in female. *Legs*: Normal in female. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of female barely emarginated, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. piranha* (Fig. 9).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. maia* occur at lowland altitudes in the Amazon Basin. Adults are active in November, the rainy season.

Other specimens examined. None.

Geographic distribution. (Fig. 11). This species is currently known only from the type locality.

Agra piranha Erwin, sp. n.

urn:lsid:zoobank.org:act:0B2DB88C-89F6-485D-B2FB-C2B54813D0DC

Figs 8, 9, 11

Holotype: Ecuador: Orellana, 1 km S Onkone Gare Camp, Entomology Transect, 216m, “0.6569°S, 76.4527°W,” 2 July 1995 (T.L. Erwin, et al.)(NMNH: ADP 087440, male).

Derivation of specific epithet. The epithet “*piranha*” or *piraña*, is a translation of the Huaorani word, Onkone Gare, the name of the camp near which the holotype was discovered.

Proposed English vernacular name. *Piraña Elegant Canopy Beetle*.

Diagnosis. With the attributes of the genus and species-group as described above and brassy pronotum, legs unicolored, frons laterad unicarinate, smooth, prothorax not setiferous laterally, and elytra barely constricted at apical third, side margin slightly arcuate, apex truncate, barely lobed medially.

Description. (Fig. 8, 9). *Size*: Very small, ABL = 7.18 – 7.29 mm, SBL = 5.98 – 6.13 mm, TW = 1.76 – 1.86 mm. *Color*: Head black with bluish reflection posteriorly,

body and legs with metallic blue reflections, elytra metallic cobalt blue; antennae and mouthparts piceous, scape with slight metallic blue reflections. *Luster*: Shiny metallic, elytra matte. *Head*: Labrum moderately elongate and rounded at corners, slightly emarginate medially. Frons medially raised and smooth, laterally depressed and uni-carinate. Gena slightly tapered, hind angle obtuse to constricted neck in both sexes. Genae and occiput with moderately dense and coarse punctures, some setiferous. *Prothorax*: Slightly broader medially, flared basally; surface densely punctuate, disc each side with three long setae; lateral elongate callous with single row of non-setiferous punctures along middle. *Pterothorax*: Elytron markedly convex, intervals moderately costate, interneurs of rows of somewhat laterally ovate punctures, apex truncate, barely lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex not produced, rounded. Metasternum sparsely setiferous in both sexes. *Legs*: Middle tibia of male with dense brush of short setae on medial margin. *Abdomen*: Abdominal sterna III, IV, and V of both sexes sparsely setiferous bilaterally; sternum VII of both sexes very slightly emarginate. *Male genitalia*: Phallus (Fig. 8) elongate, narrow, with moderately broad arrow-shaped apex; ostium elongate. Parameres small, left twice the size of the right, both broadly rounded. *Female ovipositor*: Stylocere 2 (Fig. 9).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults are found in the canopy of terre firme rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. piranha* occur at lowland altitudes in the Amazon Basin. Adults are active in July and October, in both the rainy and transition seasons. The holotype was fogged from the hardwood *Eschweilera* cf. *laevicarpa* in the family Lecythidaceae. The paratype was fogged from a mixed canopy consisting of the palms *Iriartea deltoidea* Ruiz. & Pav. and *Wettinia maynensis* Spruce, and the hardwood *Macrolobium* cf. *ischnocalx*, plus an unidentified species of Apocynaceae.

Other specimens examined. Ecuador: Rio Tiputini, Erwin Transect, 232m, “0.63173°S, 76.14420°W,” 23 October 1998 (T.L. Erwin, et al.)(NMNH: ADP 117227, female paratype).

Geographic distribution. (Fig. 11). This species is currently known from the Ecuadorian Amazon Basin.

***Agra risseri* Erwin, sp. n.**

urn:lsid:zoobank.org:act:358EFA50-1C15-4476-946C-0E35E74FB47C

Figs 2, 11

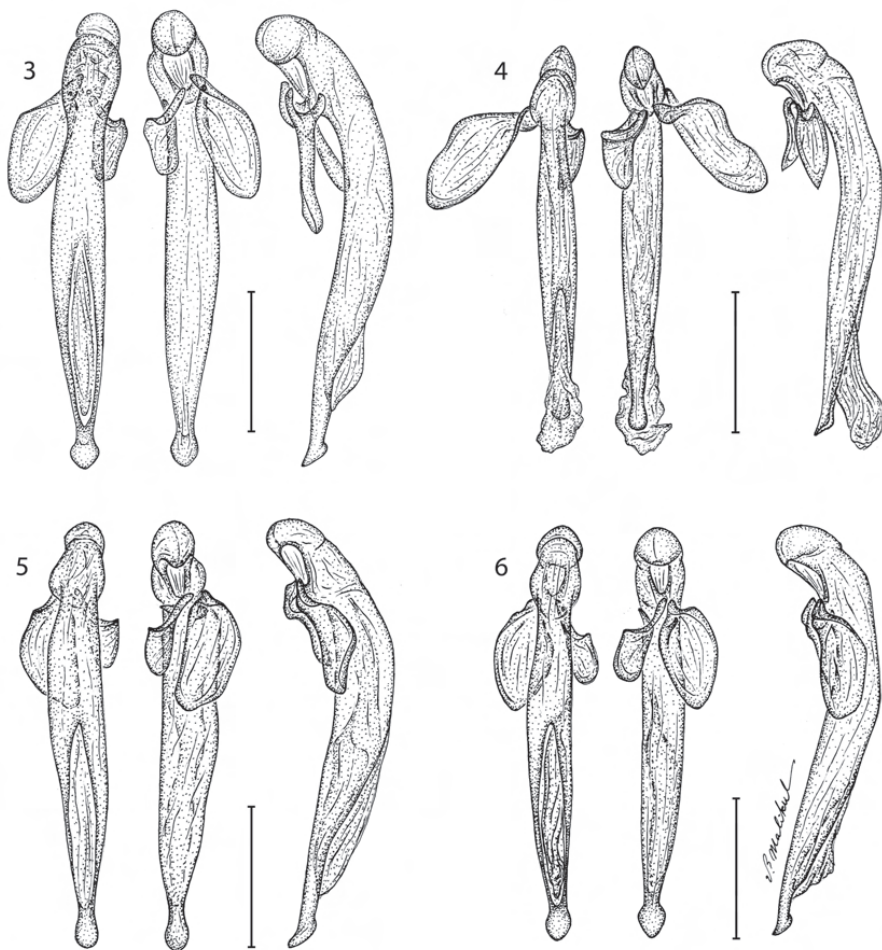
Holotype: Bolivia: Santa Cruz, 4–6 km SSE Buena Vista, Hotel Flora & Fauna, 383m, “17.479°S, 63.631°W,” 27–29 October 2000 (J.E. Wappes & R. Morris)(FSCA: ADP 115786, female).



Figure 2. *Agra risseri* Erwin, sp. n., dorsal aspect (ADP 115786).

Derivation of specific epithet. The epithet “*risseri*” is a Latinized genitive eponym, based on the surname of Dr. Paul G. Risser, outgoing Chairman of the National Board of the Smithsonian’s National Museum of Natural History, in honoring his long and invaluable service to the Smithsonian Institution.

Proposed English vernacular name. Risser’s Elegant Canopy Beetle.



Figures 3–6. **3** *Agra cruciaria* Erwin, sp. n., male genitalia (dorsal, ventral, left lateral aspects) (ADP 070044) **4** *Agra grace* Erwin, sp. n., male genitalia (dorsal, ventral, left lateral aspects) (ADP 087638) **5** *Agra pseudopusilla* Erwin, sp. n., male genitalia (dorsal, ventral, left lateral aspects) (ADP 070045) **6** *Agra pusilla* Chaudoir, male genitalia (dorsal, ventral, left lateral aspects) (ADP 060087).

Diagnosis. With the attributes of the genus and species-group as described above and legs unicolorous, head very broad across occiput, wider than pronotum at its widest, frons laterad unicarinate, smooth, prothorax markedly setiferous both laterally and ventrally, and elytra slightly constricted at apical third, side margin barely arcuate.

Description. (Fig. 2). *Size:* Small, ABL = 9.42 – 10.45 mm, SBL = 8.14 – 8.77 mm, TW = 2.4 – 3.08 mm. *Color:* Head, body, and appendages black, pronotum with brassy reflection elytra metallic blue. *Luster:* Shiny. *Head:* (Fig. 2) Labrum moderately elongate and slightly rounded at anterior corners. Frons medially raised and smooth, laterally depressed and unicarinate, smooth. Gena almost squared to constricted neck in

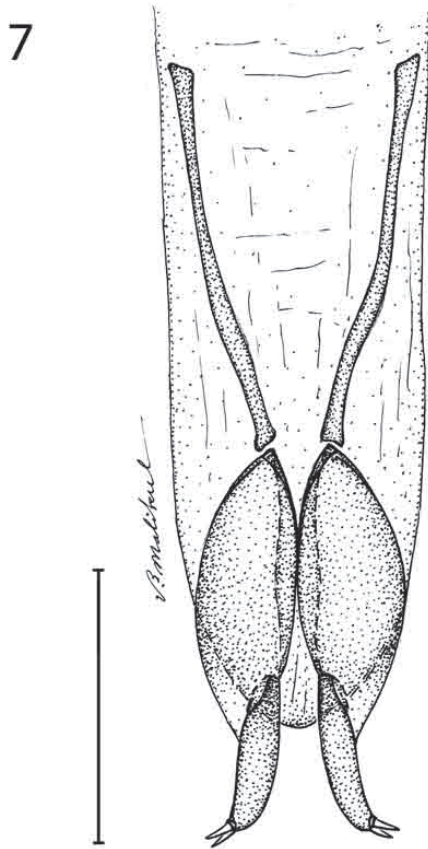
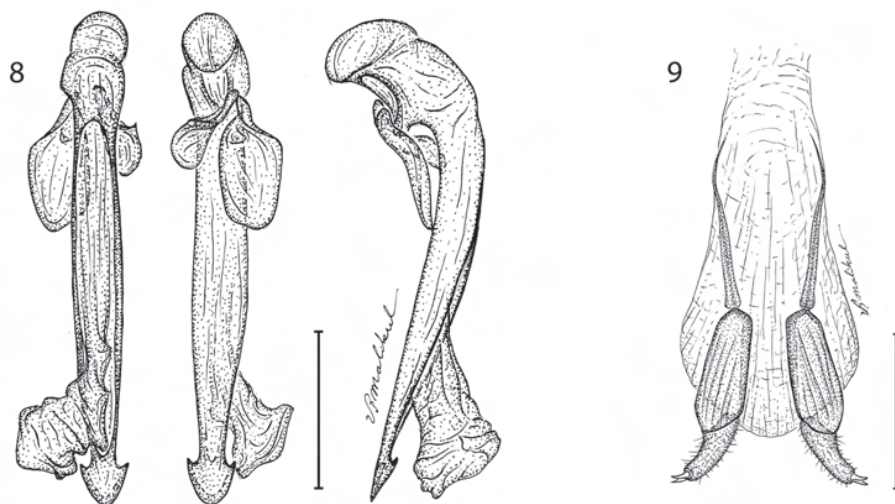


Figure 7. *Agra notpusilla* Erwin, sp. n., female stylomeres (dorsal aspect) (ADP 058647).

females. Genae and occiput with moderately dense punctures, most setiferous. *Prothorax*: Slightly broader medially, flared basally; surface with dense punctures, some setiferous; lateral elongate callous with single row of setiferous punctures along middle. *Pterothorax*: Elytron (Fig. 2) with discal area flat, intervals moderately costate, interneurs of rows of somewhat laterally ovate punctures, apex truncate, barely lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex slightly produced, narrowly pointed. Metasternum sparsely setiferous in female. *Legs*: Normal in female. *Abdomen*: Abdominal sterna III to VII of female moderately and bilaterally setiferous; sternum VII of female shallowly emarginate, corners rounded. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. piranha* (Fig. 9).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults of other *Agra* species are found in the canopy of rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees,



Figures 8–9. 8 *Agra piranha* Erwin, sp. n., male genitalia (dorsal, ventral, left lateral aspects) (ADP 087440) 9 *Agra piranha* Erwin, sp. n., female stylomeres (dorsal aspect) (ADP 117227).

however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. risseri* occur at lowland to midland altitudes in the Amazon Basin. Adults are active in October, the rainy season.

Other specimens examined. **Brazil:** Goiás, Jataí (Jatahy), 736m, 17.880°S, 51.720°W (BMNH: ADP 004375, female paratype).

Geographic distribution. (Fig. 11). This species is currently known from Bolivia and Brazil.

Agra tiputini Erwin, sp. n.

urn:lsid:zoobank.org:act:97A92342-25C2-461C-95F1-52FDDB63741B

Fig. 11

Holotype: **Ecuador:** **Ecuador:** Orellana, Tiputini Biodiversity Station, Rio Tiputini, Erwin Transect, 232m, “0.63173°S, 76.14420°W,” 23 October 1998 (T.L. Erwin, et al.) (NMNH: 117233, female).

Derivation of specific epithet. The epithet “*tiputini*” is the name of the Research Station and the river near which the holotype was collected.

Proposed English vernacular name. Tiputini Elegant Canopy Beetle.

Diagnosis. With the attributes of the genus and species-group as described above and pronotum brassy, legs unicolorous, lateral depression of frons unicarinate, smooth, gena and occiput with sparse and moderately small setigerous punctures plus two larger ones; elytra constricted at basal third, flared at apical third, side markedly arcuate, intervals not costate.

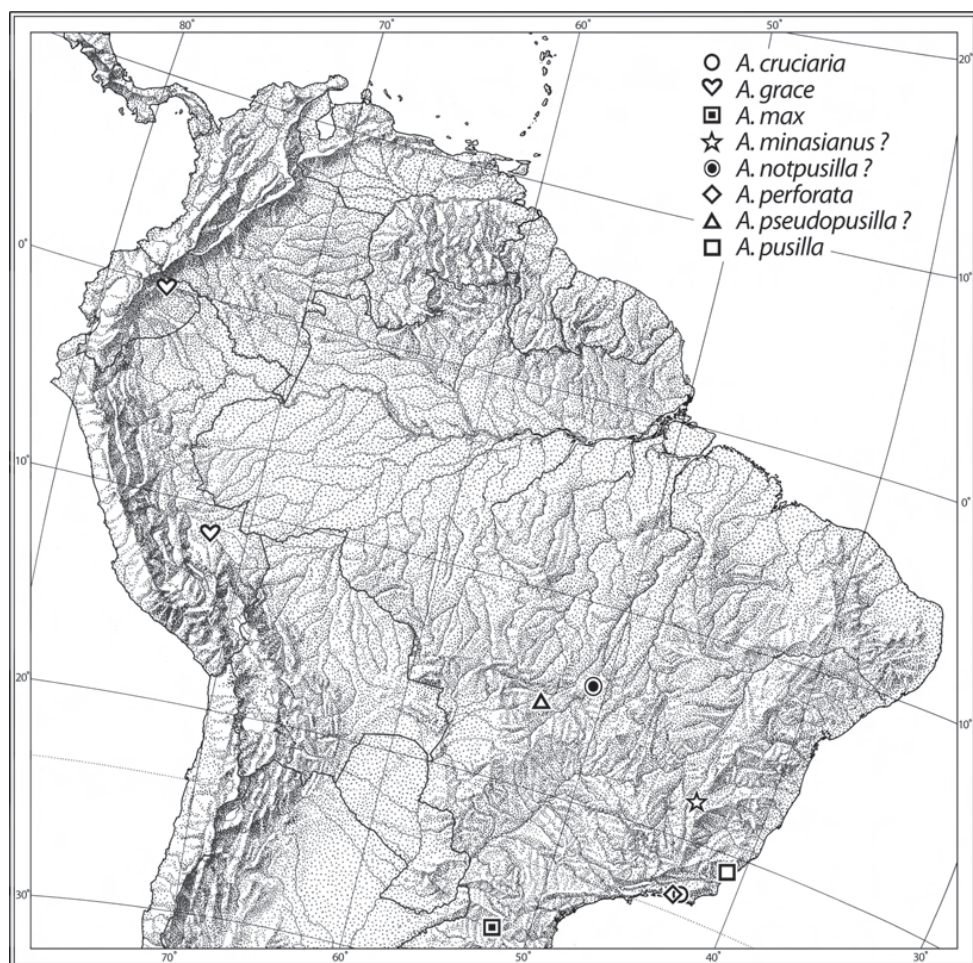


Figure 10. Distribution map of the species of the *pusilla* group. Names marked with a “?” do not have precise localities on the specimen label(s).

Description. *Size:* Small, ABL = 5.98 – 7.17 mm, SBL = 5.98 – 6.04 mm, TW = 2.04 mm. *Color:* Head black with bluish reflection posteriorly, body and legs with metallic blue reflections, elytra metallic cobalt blue; antennae and mouthparts piceous, scape with slight metallic blue reflections. *Luster:* Shiny metallic, elytra matte. *Head:* Labrum moderately elongate and rounded at corners, slightly emarginate medially. Frons medially raised and smooth, laterally depressed and smooth. Gena slightly tapered, hind angle obtuse to constricted neck in both female. Genae and occiput with sparse setiferous punctures, some coarsely so. *Prothorax:* Slightly broader medially, slightly flared basally; surface with dense punctures, disc each side with four long setae, with short setae both basally and apically; lateral elongate callous with single row of non-setiferous puncture along middle. *Pterothorax:* Elytron moderately convex, flared at apical third, intervals not costate, interneurs of rows of somewhat laterally ovate cribriform punctures, apex trun-

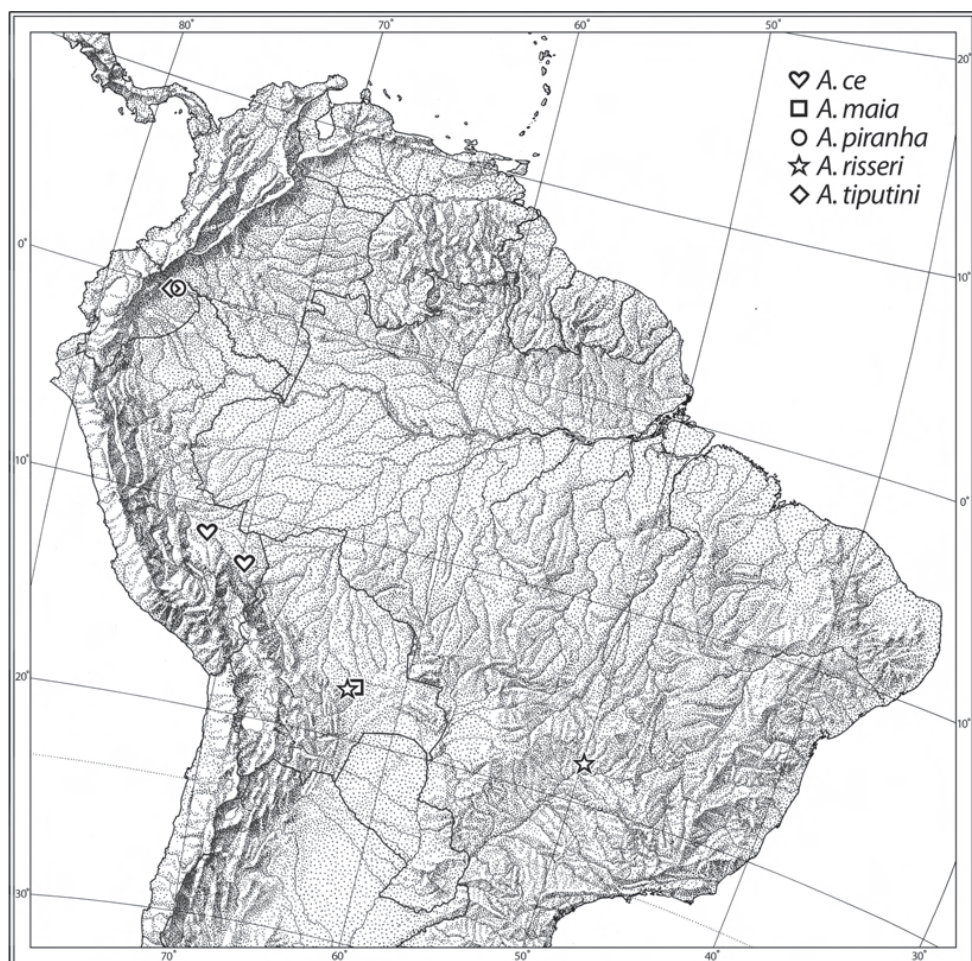


Figure 11. Distribution map of the species of the *piranha* group.

cate, barely lobate, apical dentation asymmetric, lateral tooth small, acute, sutural apex not produced, rounded. Metasternum sparsely setiferous in females. *Legs*: Legs normal. *Abdomen*: Abdominal sterna III, IV, and V of females sparsely setiferous bilaterally; sternum VII of female very slightly emarginate. *Male genitalia*: Unknown. *Female ovipositor*: Stylomere 2 as in *A. piranha* (Fig. 9).

Dispersal potential. These beetles are macropterous and are probably capable of flight; they are swift and agile runners.

Way of life. Adults are found in the canopy of terre firme rainforest trees; known larvae of this genus (Arndt et al. 2001) are found under the bark of these trees, however they must also roam on the surface, as they have been collected by insecticidal fogging techniques in the very early morning before first light. Members of *A. tiputini* occur at lowland altitudes in the Amazon Basin. Adults are active in February and October,

the dry season and the transition season. The holotype was fogged from a mixed canopy consisting of the crowns of the palms *Iriartea deltoidea* Ruiz. & Pav. and *Wettinia maynensis* Spruce, and the hardwood *Macrolobium* cf. *ischnocalyx*. The paratype was fogged from the hardwood family Myrtaceae. The February specimen is very teneral suggesting that the dry season triggers pupation and emergence.

Other specimens examined. Orellana, 1 km S Onkone Gare Camp, Entomology Transect, 216m, “0.6569°S, 76.4527°W,” 8 February 1995 (T.L. Erwin, et al.) (NMNH: ADP 087439, male paratype).

Geographic distribution. (Fig. 11). This species is currently known from Amazonian Ecuador.

Discussion

The relatively narrow tarsi, spatulate apex of the median lobe of the male genitalia, and very small size of its adults suggest that the *pusilla* species group represents the most basal lineage in the evolution of the hyper diverse genus *Agra*, given that more highly derived states of tarsal width, male genitalic form, and size are found in the *platyscelis*, *famula*, and *formicaria* species groups, as well as the *piranhna* group, treated herein? In the “Introduction” above, I suggested that fresh specimens should be collected to provide DNA that can be sequenced and analyzed concomitant with those of other adult *Agrina* genera from Africa to determine the adelphotaxon. Subsequent to such an analysis, a better understanding of the evolution of structural attributes among *Agra* lineages and species will be possible than it is at present.

Acknowledgements

In addition to the Museum curators and technicians noted above, I also extend a hearty thanks to Charyn Micheli (the Resumen, measures, and friendly review of the manuscript), Warren Steiner (dissections), Karie Darrow (images and plates), and Vichai Malikul (genitalic illustrations) all of the Department of Entomology at the Smithsonian Institution.

References

- Arndt E, Kimse S, Erwin, TL (2001) Arboreal beetles of Neotropical forests: *Agra* Fabricius, larval descriptions with notes on natural history and behaviour (Coleoptera, Carabidae, Lebiini, Agrina). The Coleopterists Bulletin 55(3): 297–311.
- Ball GE (1972) Classification of the species of the *Harpalus* subgenus *Glanodes* Casey (Carabidae, Coleoptera). The Coleopterists Bulletin 26: 179–204.

- Casale A (1998) Phylogeny and biogeography of Calleidina (Coleoptera: Carabidae: Lebiini): a preliminary survey. In: Ball GE, Casale A, Vigna-Taglianti A (Eds) Phylogeny and classification of Caraboidea. Atti Museo regionale di Scienze naturali, Torino, 381–428.
- Chaudoir M de (1847) Notes sur le genre *Agra* et description de plusieurs espèces nouvelles. Bulletin de la Société Impériale des naturalistes de Moscou 20: 87–113.
- Erwin TL (1978) Systematic, natural history, and zoogeographic notes on the Genus *Agra* Fabricius, with a description of a new species from Panamá (Coleoptera: Carabidae: Lebiini). The Coleopterists Bulletin 32(4): 261–268.
- Erwin TL (1982a) *Agra*, arboreal beetles of Neotropical forests: *erythropus* group systematics (Carabidae). Systematic Entomology 7: 39–71.
- Erwin TL (1982b) *Agra*, arboreal beetles of Neotropical forests: *platyscelis* group systematics (Carabidae). Systematic Entomology 7: 185–210.
- Erwin TL (1983) *Agra*, arboreal beetles of Neotropical forests: *famula* and *formicaria* groups systematics (Carabidae). Systematic Entomology 8: 263–292.
- Erwin TL (1984) *Agra*, arboreal beetles of Neotropical forests: *palmata* species-group systematics (Carabidae). Systematic Entomology 11: 293–316.
- Erwin TL (1985) Tambopata Reserved Zone, Madre de Dios, Perú: History and description of the reserve. Revista Peruana de Entomología 27: 1–8.
- Erwin TL (1986) *Agra*, arboreal beetles of Neotropical forests: *mixta*-group, *virgata*-group, and *ohausi*-group systematics (Carabidae). Systematic Entomology 11: 293–316.
- Erwin TL (1991) Natural history of the carabid beetles at the BIOLAT Rio Manu Biological Station, Pakitza, Perú. Revista Peruana de Entomología 33: 1–85.
- Erwin TL (1993) *Agra*, arboreal beetles of Neotropical forests: *rufoaenea* and *quararibea* group systematics (Carabidae). Revista peruana de Entomologia (1991) 34: 15–28.
- Erwin TL (1996) Arboreal Beetles of Neotropical Forests: *Agra* Fabricius, the *cayennensis* complex (Coleoptera: Carabidae: Lebiini: Calleidina). Annales Zoologici Fennici 33(1): 17–21.
- Erwin TL (1998) Evolution at the equator arboreal and alticolous beetles and their taxon pulses with descriptions of a new *Agra* subclade and its species (Coleoptera: Carabidae: Lebiini). In: Ball GE, Casale A, Vigna Taglianti A (Eds) Phylogeny and classification of Caraboidea (Coleoptera: Adephaga). Proceedings of a Symposium (28 August, 1996, Florence, Italy), XX International Congress of Entomology Museo Regionale Scienze Naturali - Torino, Atti. Torino, 491–510.
- Erwin TL (2000a) Arboreal beetles of Neotropical forests: *Agra* Fabricius, the Novaurora Complex (Coleoptera: Carabidae: Lebiini: Agrina). Smithsonian Contributions to Zoology No. 608: i-iv + 1–33.
- Erwin TL (2000b) Arboreal beetles of Neotropical Forests: *Agra* Fabricius, a taxonomic supplement for the *platyscelis* group with new species and distribution records (Coleoptera: Carabidae, Lebiini, Agrina). The Coleopterists Bulletin 54(1): 90–119.
- Erwin TL (2000c) Arboreal beetles of Neotropical Forests: Taxonomic supplement for the *Agra virgata* and *ohausi* groups with a new species and additional distribution records (Coleoptera: Carabidae). The Coleopterists Bulletin 54(2): 251–262.
- Erwin TL (2002) The Beetle Family Carabidae of Costa Rica: Twenty-nine new species of Costa Rican *Agra* Fabricius 1801 (Coleoptera: Carabidae, Lebiini, Agrina). Zootaxa 119: 1–68.

- Erwin TL (2004) The Beetle Family Carabidae of Costa Rica and Panamá: Descriptions of four new genera and six new species with notes on their way of life (Insecta: Coleoptera). *Zootaxa* 537: 1–18.
- Erwin TL, Johnson PJ (2000) Naming species, a new paradigm for crisis management in taxonomy: Rapid journal validation of scientific names enhanced with more complete descriptions on the internet. *The Coleopterists Bulletin* 54(3): 269–278.
- Erwin TL, Kavanaugh DH (1981) Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of Western North America (Coleoptera: Carabidae: Bembidiini). *Entomologica Scandinavica Supplement* 15: 33–72.
- Erwin TL, Pogue MG (1988) *Agra*, arboreal beetles of Neotropical forests: Biogeography and the forest refugium hypothesis (Carabidae). In: Heyer WR, Vanzolini PE (Eds) *Neotropical Distribution Patterns: Proceedings of a 1987 Workshop*. Proceedings of the Brazilian Academy of Sciences, 161–188.
- Fabricius C (1801) *Systema eleutheratorum: secundum ordines, genera, species adiecitis synonymymis, locis, observationibus, descriptionibus*. Tome 1, xxiv + 506pp; Tome 2, 687pp. Bibliopolii Academici Novi, Kiliae.
- Jeannel R (1949) Coléoptères Carabiques de la Region Malgache (Troisième Partie). *Faune de l'Empire Francais*, Paris, XI: 767–1146.
- Kavanaugh DH (1979) Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. *Proceedings of the California Academy of Sciences ser. 4*, 42: 87–133.
- Kavanaugh DH, Erwin TL (1991) The tribe Cicindini Bänninger (Coleoptera: Carabidae): Comparative morphology, natural history, and reclassification. *Proceedings of the Entomological Society of Washington* 93(2): 356–389.
- Liebke M (1938) Beschreibung neuer Arten der Gattung *Agra* F. Coleoptera Carabidae. *Proceedings of the Royal Entomological Society of London*, B, 7: 53–72.
- Lorenz W (1998) Systematic list of extant ground beetles of the world (Insecta, Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). W. Lorenz, Tutzing, Germany, iv + 502pp.
- Lorenz W (2005) Systematic list of extant ground beetles of the world (Insecta, Coleoptera "Geadephaga": Trachypachidae and Carabidae, incl. Paussinae, Cicindelinae, Rhysodinae). W. Lorenz, Tutzing, iv + 530 pp.
- Ober KA, Maddison DR (2008) Phylogenetic relationships of tribes within Harpalinae (Coleoptera: Carabidae) as inferred from 28S ribosomal DNA and the *wingless* gene. 32pp. *Journal of Insect Science* 8(63): 1536–2442.

Annotated checklist of the recent and extinct pythons (Serpentes, Pythonidae), with notes on nomenclature, taxonomy, and distribution

Wulf D. Schleip¹, Mark O'Shea^{2,3}

1 Fichtenweg 11, 53340 Meckenheim, Germany **2** Australian Venom Research Unit, Dept. Pharmacology, University of Melbourne, Vic., 3010, Australia **3** Reptile Department, West Midland Safari Park, Bewdley, Worcs., DY12 1LF, United Kingdom

Corresponding authors: Wulf D. Schleip (publication@leiopython.de), Mark O'Shea (mos@wmssp.co.uk)

Academic editor: Hans-Dieter Sues | Received 11 December 2009 | Accepted 22 September 2010 | Published 4 November 2010

Citation: Schleip WD, O'Shea M (2010) Annotated checklist of the recent and extinct pythons (Serpentes, Pythonidae), with notes on nomenclature, taxonomy, and distribution. *ZooKeys* 66: 29–79. doi: 10.3897/zookeys.66.367

Abstract

McDiarmid et al. (1999) published the first part of their planned taxonomic catalog of the snakes of the world. Since then, several new python taxa have been described in both the scientific literature and non-peer-reviewed publications. This checklist evaluates the nomenclatural status of the names and discusses the taxonomic status of the new taxa, and aims to continue the work of McDiarmid et al. (1999) for the family Pythonidae, covering the period 1999 to 2010. Numerous new taxa are listed, and where appropriate recent synonymies are included and annotations are made. A checklist and a taxonomic identification key of valid taxa are provided.

Keywords

snakes, ICZN, *Antaresia*, *Apodora*, *Aspidites*, *Bothrochilus*, *Broghammerus*, *Leiopython*, *Liasis*, *Morelia*, *Python*, taxa

Introduction

Pythons (family Pythonidae) represent a family of non-venomous basal snakes within the superfamily Pythonoidea Fitzinger, 1826 (*sensu* Vidal et al. 2007, Vidal and Hedges 2009). Although present in Europe during the Miocene, and probably since the late Eocene (Szyndlar and Rage 2003), pythons are now restricted to the warmer regions of

the Old World, ranging from Africa through South and Southeast Asia, Indo-Malaysia and New Guinea, to Australia (Kluge 1993, Scanlon 2001, Rawlings and Donnellan 2003, Rawlings et al. 2008). More than two thirds of the currently recognized extant species are found in the Australo-Papuan region (Kluge 1993, Scanlon 2001, Rawlings et al. 2008), where they have the greatest level of morphological and genetic diversity (Heds 2002, Rawlings and Donnellan 2003), and a high degree of endemism (Harvey et al. 2000, Rawlings et al. 2004). Whereas two Asian species (*P. molurus* and *P. bivittatus*) range north of the Tropic of Cancer, an African and at least seven Australian species extend their ranges south of the Tropic of Capricorn. Pythons occur in a variety of habitats, from desert and savanna, to subtropical and tropical rainforest (Kluge 1993) and into seasonally flooded grasslands and paddifields. Most species are terrestrial, some are arboreal (Kluge 1993) and a few are semi-aquatic. The 40 recognized extant species range in maximum adult length from 0.61 m to 10.0 m, and include the longest extant snake species.

Taxonomic changes since 1999

McDiarmid et al. (1999) has become a standard reference for snake taxonomists. Since then python systematics has received considerable attention as new phylogenetic and geographical evidence has become available. Aside from the descriptions of new genera, species, and subspecies (Table 1), the most noteworthy action was the split of the genus *Python* by Rawlings et al. (2008), placing two Asian taxa, *reticulatus* and *timo-riensis*, into *Broghammerus*.

One author, the amateur herpetologist Raymond T. Hoser of Victoria, Australia, has caused considerable confusion in python taxonomy over the last decade by describing numerous taxa (6 new genera and subgenera, 4 new species, and 19 new subspecies) in the non-peer-reviewed literature without providing adequate descriptions for his proposed new taxa (for discussions see Aplin 1999, 2002, Wüster et al. 2001, Williams et al. 2006, 2008, Schleich 2008). Hoser rarely included important taxonomic information or data on scale counts, numbers of specimen examined, statistics, or the results of DNA analysis. Moreover, Hoser designated several types without ever having apparently examined them. Although not mandatory, the International Code of Zoological Nomenclature (ICZN 1999), hereafter termed the “Code”, recommends that only specimens personally examined by the author should be designated as types (Recommendation 73B). Furthermore, Hoser himself (1996, 1997) considered failing to examine type specimens “sloppy taxonomy”. Another recommendation (Recommendation 73C), which states which data should be provided with the holotype, is often not followed by this author. In general, inadequate descriptions inevitably lead to problems in clearly assigning specimens to established taxa, and are expensive and time-consuming for subsequent workers who have to re-examine the type material in order to make taxonomic decisions, instead of being able to rely on adequate original descriptions.

Table 1. New and resurrected taxa from 1999 until 2010. Numbers in parentheses represent the number of taxa deemed unavailable.

Year	New genera	Resurrected genera	New species	Resurrected species	Elevated to species rank	New subspecies	Resurrected subspecies
1999	0	0	0	0	2	0	0
2000	2(1)	2	5	0	8	7	2
2001	0	0	0	0	3	0	0
2002	0	0	1	0	0	2	0
2003	0	(1)	1(2)	(1)	0	(3)	0
2004	2	4	2	1	0	9	0
2005	0	0	0	0	0	0	0
2006	0	0	0	0	0	0	0
2007	0	0	0	0	0	0	0
2008	0	0	3	0	3	0	0
2009	(2)	0	0	(2)	(1)1	(4)1	0
2010	0	0	0	0	0	0	0
Total*	4	6	12	1	17	19	2

* Total figures exclude those taxa considered unavailable.

In general, the professional herpetological community has rarely accepted Hoser's taxa (Wüster et al. 2001, Aplin 2002, Williams et al. 2006, 2008, Schleip 2008, Zaher et al. 2009) unless one of his numerous names turns out to be valid and a senior synonym based on more exacting scientific work carried out by professional researchers, as was the case with *Broghammerus*.

Approach and Scope

The primary objective of this taxonomic checklist is to provide an overview of the taxa in the family Pythonidae, and to establish their nomenclatural status under the provisions of the Code and their current taxonomical status based on published works and knowledge. It is, however, beyond the scope of this list to propose re-classifications or re-arrangements of genera that lack fully resolved phylogenetic relationships. Although this checklist can only be a snapshot in time, it is intended to continue the work of McDiarmid et al. (1999) for the family Pythonidae over the past decade and provide updates to the list compiled by Henderson and Powell (2007). For taxa described during the past decade type species (for generic names) or type specimens (for specific names) are provided along with their type localities. Recently designated neotypes are also provided. Where new distributional information is available, this is included with the relevant citation. However, in contrast to the work of McDiarmid et al. (1999) and Henderson and Powell (2007), this checklist also contains extinct taxa.

Taxa are hierarchically arranged by indentation, and are presented in alphabetical order at the level of genera, species, and subspecies, although, in the case of sub-

species, the nominate subspecies precedes other subspecies, which then are listed in alphabetical order. Annotations are made directly below the relevant taxon, unless otherwise stated. Synonyms before the year 1999, and remarks on valid taxa, unless new data are available, can be found in McDiarmid et al. (1999). A key to the extent genera, species and subspecies recognized within the family of Pythonidae is provided in Appendix 2.

Interpretation and application of the Code

The Code rules on issues regarding nomenclatural acts and works, and aims to “provide the maximum universality and continuity in the scientific names of animals compatible with the freedom of scientists to classify animals according to taxonomic judgments” (ICZN 1999). Due to its universality, the wording of the Code leaves considerable room for interpretation. For the assessment of the nomenclatural status of published names, and for the purpose of nomenclatural stability, the Code was here strictly applied to all names. In any case of ambiguous wording, the authors have consulted the glossary of the Code as suggested in the Code’s “Explanatory Note”, and as stated in article 89. In the checklist we use the abbreviation “APP” (application):

APP1. “Characters”: To be available a name must “be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon” (ICZN 1999: Art. 13.1.1). A description in the meaning of the Code is “a statement in words of taxonomic characters of a specimen or a taxon” (ICZN 1999: glossary entry for “description”), and a definition is “a statement in words that purports to give those characters which, in combination uniquely distinguish a taxon” (ICZN 1999: glossary entry for “definition”). The glossary defines the word taxon as a “taxonomic unit, whether named or not: i.e., a population, or group of populations of organisms which are usually inferred to be phylogenetically related and which have characters in common which differentiate (...) the unit (e.g., a geographic population, a genus, a family, an order) from other such units” (ICZN 1999: glossary entry for “taxon”). This latter statement clearly excludes distribution itself as a character to differentiate taxa and that complies with article 13.1.1, since it requires characters to differentiate a “geographic population” from other such units. Many taxonomists are likely to accept a geographic population, especially an insular population, only separated from other such populations by distribution, at subspecific rank. However, the Code does not distinguish between specific and subspecific rank in its requirements (Arts. 45.1, 45.2), and therefore subspecies must also be distinguishable by characters other than by their isolated locality or distribution.

APP2. “Generalized statements”: Generalized statements such as “separated by distribution” or “separated by analysis of DNA” or relative statements such as “usually (but

not always) has” do not constitute a character in the sense of article 13.1.1 (APP1). Analysis of DNA clearly describes a method although genomic differences are of diagnostic value, and distribution itself is not a character, as it is not intrinsic to any specimen within the taxon. Therefore, these are not attributes of an organism (see glossary for character). Moreover, strictly following the glossary definition of the word description, the Code would require that a taxon must be uniquely distinguished from other taxa and generalized statements do not imply uniqueness.

APP3. “Priority”: Article 23.3.5 requires the replacement of an unavailable name with the oldest available synonym (senior synonym).

APP4. “Incorrect subsequent spelling”: Article 33.3 states that “any subsequent spelling of a name different from the correct original spelling, other than a mandatory change or an emendation, is an “incorrect subsequent spelling”; it is not an available name and, like an incorrect original spelling (...), it does not enter into homonymy and cannot be used as a substitute name” (ICZN 1999). For species-group names article 11.9.3.2 states that they are “deemed to have been published in combination with the correct original spelling of the generic name, even if it was actually published in combination with an emendation or incorrect spelling of the generic name” (ICZN 1999). Therefore, incorrect subsequent spellings are corrected to the original spelling.

APP5. “*Nomen dubium*” (pl. *nomina dubia*): According to the glossary of the Code a *nomen dubium* is “a name of unknown or doubtful application” (ICZN 1999). This glossary definition leaves a wide scope for applying the term. A *nomen dubium* may be a lost type specimen or a type that lacks important diagnostic features so that a name cannot be applied to a specimen with clarity. Melville (1980, 1984) noted that considering a name as *nomen dubium* is a matter of taxonomic decision and not a nomenclatural one. Moreover, Mones (1989) revealed that this term was first used for a taxon which was accompanied by an insufficient description. He states that the term “(...) denotes ignorance, incapability to interpret the facts, insufficient diagnosis, or actual poorness of the type specimen” (Mones, 1989: 232). We agree with the above mentioned views and, hence, insufficient information on the holotype (Recommendations 72E, 73A, see Introduction) that obviously was randomly chosen from an online database of a natural history museum and was not examined by the author (Recommendation 73B) along with an insufficient diagnosis or definition of taxonomic characters (see Art. 13.1.1, Recommendation 13A) may make a name be considered a *nomen dubium*. However, the name remains available, and a subsequent revision or re-description of the taxon may establish its validity.

APP6. “*Nomen nudum*” (pl. *nomina nuda*): For generic names to be available, the Code requires “the fixation of a type species in the original publication” (ICZN 1999: Art. 13.3). All names must be “explicitly indicated as intentionally new” (ICZN 1999:

Art. 16.1). Generic names, as well as specific and subspecific names, to which no characters were provided that comply with article 13.1.1 (see APP1, APP2), are deemed a *nomen nudum*, and therefore considered unavailable.

APP7. “*Species inquirenda*” (pl. *species inquirendae*): This is “a Latin term meaning a species of doubtful identity requiring further investigation” (ICZN 1999: glossary entry).

APP8. “Unavailable name”: A name is regarded as unavailable under the provisions of the Code, if either the requirements for publication or the requirements for availability are not met. This seems to be the case for names published by Hoser in his self-published Australasian Journal of Herpetology. Although the journal’s website states that several hard copies were placed in libraries to comply with the Code, these authors were unable to locate hard copies from any major European or North American library, or obtain such from the publisher when first issued (also see Recommendations 8B–D). An order form for hard copies (<http://www.smuggled.com/AJHHCO1.htm>, accessed 17 May 2009) was added to the publisher’s website on 7 May 2009. The National Library of Australia (NLA), the only library that lists this journal in their catalog, also has no hard copy (enquiry # NLAref21927, 16 April 2009) and only the PDF of the second issue (Hoser 2009) of the journal as of 17 May 2009 (NLA copy request CDC-10117150, 9.V.2009 could not be processed). Articles 8.1.2 and 8.1.3 of the Code state that to be regarded as published works they “must be obtainable, when first issued (...)”, and “must have been produced in an edition containing simultaneously obtainable copies by a method that assures numerous identical and durable copies”. Neither requirements was fulfilled. Later (20 May 2009), a colleague requesting original printed hard copies directly from the publisher only receiving single-sided, black and white versions of the online papers, printed on a domestic laser printer and bound by a large staple on the upper left hand corner (V. Wallach, pers. comm.). On his website, the publisher states “both print (first print run) and online are identical including use of color”. Therefore, the hard copy received by our colleague was apparently “printed on demand”. Article 9.7 states that “copies obtained on demand of an unpublished work [Art. 8], even if previously deposited in a library or other archive” do not constitute published work. The publisher disseminates the articles via the internet as PDFs downloadable from the journal’s website, and appears to rely on the trust of subsequent workers, that paper copies do exist (e.g., Zaher et al. 2009). However, the dissemination of PDFs over the internet does not currently constitute “published works” (Art. 9.6). Since no hard copies of the relevant second issue (Hoser 2009) were obtainable when first issued, and requested hard copies were “printed on demand”, this work must be regarded as “not published” under the provisions of the Code (Arts. 8.1.2, 8.1.3, 8.6, 9.6, 9.7) and the names therein are deemed unavailable (also see Wallach et al. 2009). The names, however, are listed for the completeness of the list but are not part of the formal synonymy.

Abbreviations for Depositories of type material

AM	Australian Museum, Sydney, Australia
AMNH	American Museum of Natural History, New York, NY, USA
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CAS	California Academy of Sciences, San Francisco, California, USA
FMNH	Field Museum, Chicago, IL, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
NMV	Museum of Victoria, Melbourne, Australia
MNHN	Muséum national d'Histoire naturelle, Paris, France
QM	Queensland Museum, Brisbane, Queensland, Australia
RMNH	Naturalis, Leiden, The Netherlands
SAMA	South Australian Museum, Adelaide, South Australia, Australia
UTA	University of Texas at Austin, Austin, Texas, USA
WAM	Western Australian Museum, Perth, Western Australia, Australia
ZFMK	Zoologisches Forschungsinstitut und Museum Koenig, Bonn, Germany
ZMUC	Zoologisk Museum, Copenhagen, Denmark

Checklist of the Pythonidae

Genus *Antaresia* Wells and Wellington, 1984

Remarks: Cogger (2000) did not recognize this genus but placed the four species recognized therein without subspecies in the genus *Liasis* Gray.

childreni (Gray, 1842)

maculosa (Peters, 1873)

Synonyms:

Antaresia maculosa brentonoloughlini Hoser, 2004

Distribution: O'Shea et al. (2004) reported the first occurrence outside Australia, at Weam, Western Province, Papua New Guinea.

maculosa brentonoloughlini Hoser, 2004 [synonym of *A. maculosa*]

Holotype: AM R16772.

Type locality: 16 km east of Coen, Queensland, Australia.

Remarks: Hoser (2004) separated this taxon from the nominate subspecies "by its greater preponderance of light colouration relative to dark blotches on the dorsal surface" (Hoser 2004), stating that the nominate form would "have roughly half to half (50:50) dark versus light blotches" whereas the ra-

tio in this taxon “is generally at least 60% light colour to 40% or less darker blotches” (Hoser 2004), and by larger average size.

***perthensis* (Stull, 1932)**

***stimsoni* (LA Smith, 1985)**

***stimsoni stimsoni* (LA Smith, 1985)**

***stimsoni campbelli* Hoser, 2000** [synonym of *A. stimsoni orientalis*]

Holotype: AM R69087.

Type locality: Wilcannia, New South Wales, Australia.

Remarks: The holotype of this taxon is also the paratype of *A. s. orientalis* Smith, 1985. Hoser (2000) separated this taxon from “other subspecies” by distribution (APP1, APP2), and from “other *A. stimsoni*” by color. Hoser (2000) cited without acknowledgment a statement made by Ehmann (1992) and quoted by Kend (1997: 148) and added to the statement, “the snout has a less box-like anterior when compared with other *A. stimsoni*” (Hoser 2000). However, since he considered *A. stimsoni* a synonym of “*A. saxacola*” (see comments on *A. s. orientalis*) and *A. stimsoni stimsoni* a separate subspecies, it is not clear what he means by *A. stimsoni*. This taxon is placed in the synonymy of *A. stimsoni orientalis* until further research has assessed its validity. Subsequent workers (e.g., Sonnemann 2007) have not recognized this taxon.

***stimsoni orientalis* (LA Smith, 1985)**

Synonyms:

Antaresia stimsoni campbelli Hoser, 2000

Remarks: Hoser (2000) resurrected the name *A. saxacola* Wells and Wellington, 1985, but, contrary to Hoser’s (2000) claims that *A. stimsoni* Smith, 1985 (Hoser provided an incorrect date: Smith 1995) would be a subjective junior synonym of *A. saxacola orientalis* Smith, 1985 (see Shea and Sadlier 1999), the date of publication for Smith (1985) preceded Wells and Wellington (1985) as stated by Wells (2009), which makes *A. saxacola* a subjective junior synonym of *A. stimsoni*. Nevertheless, because Wells and Wellington did not provide a description for *A. saxacola*, the name was considered a *nomen nudum* by Underwood and Stimson (1990) and Shea and Sadlier (1999). We agree with these authors in considering “*saxacola*” a *nomen nudum* (APP6), and *orientalis* replaces it (APP3). *A. stimsoni orientalis* was not listed by Cogger (1992), Barker and Barker (1994), Cogger (2000) and Henderson and Powell (2007), but was recognized by others (e.g., Ehmann 1992, Kend 1997, Walls 1998, Torr 2000, Wilson and Swan 2008).

Genus *Apodora* Kluge, 1993

Remarks: Kluge (1993) established this monotypic genus for the species *papuana*, which until then was included in the genus *Liasis* Gray as *Liasis papuanus*. Because of the lack of clarity concerning the phylogenetic position of this taxon (*Liasis*, *Apodora* (*Morelia*, *Python*)) (see Kluge, 1993: fig. 28), Kluge (1993: 53) characterized it with the term “*sedis mutabilis*” (of changing phylogenetic position, *sensu* Wiley, 1981, convention 4). However, recent researchers found some of the anatomical and morphological characters used in previous phylogenetic studies unsuitable due to misidentification (e.g., Scanlon 2001) or homoplasy (e.g., Wilcox et al. 2002, for detailed discussion see Rawlings et al., 2008). Scanlon (2001) analyzed a modified version of the dataset used by Kluge (1993) and found the genus *Liasis* to be paraphyletic (see Scanlon 2001: fig. 26). Later Rawlings et al. (2004) placed *A. papuana* as the sister clade to all other species of *Liasis*, which supports the separation of *A. papuana* as proposed by Kluge (1993), but this position was not well supported by their data. More recently, Rawlings et al. (2008) indicated a relationship between *A. papuana* and *L. olivaceus* within the monophyletic genus *Liasis*, both taxa forming a sister clade to the *L. fuscus/mackloti* complex, but again this position was not well supported. Hence, in anticipation of more robust data, we retain the current placement of this genus.

papuana (Peters & Doria, 1878)

Synonyms:

Liasis papuanus Peters & Doria – Hoser, 2000, 2004

Apodora papuana (Peters & Doria) – Rawlings and Donnellan, 2003; Henderson and Powell, 2007; Rawlings et al., 2008

Genus *Aspidites* Peters, 1877

Remarks: Henderson and Powell (2007) and Swan (2007) did not list subspecies within *Aspidites*. *Aspidites* was considered most primitive within the Pythonidae (e.g., Stimson and Underwood 1990, Kluge 1993) due to a lack of thermoreceptive pits in the labial scales. However, current research (Westhoff and Collin 2008) has revealed that *Aspidites* possesses a single thermoreceptive pit within the rostralia.

melanocephalus (Krefft, 1864)

Synonyms:

Aspidites melanocephalus adelynsensis Hoser, 2000

Aspidites melanocephalus davieii Hoser, 2000

Aspidites melanocephalus rickjonesii Hoser, 2009 (unavailable name, APP8)

***melanocephalus adelynsensis* Hoser, 2000** [synonym of *A. melanocephalus*]

Holotype: WAM R51208 (see remarks).

Type locality: Wyndham, Western Australia.

Remarks: Hoser (2000) provided the same erroneous accession number for the holotype as was already provided by Smith (1985) in his original description; WAM R51208 is the number for a skink, *Eremiascincus isolepis* (fide Mecke et al. 2009) (Doughty, pers. comm.). Hoser (2000) separated this taxon from the nominate form by lower loreal, subocular, and parietal scale counts (see Barker and Barker 1994: 1–2). The same is stated to be diagnostic for *A. m. davieii*, which makes them indistinguishable from each other, as already noted by Aplin (2002: 55–56) who considered *A. m. adelynsensis* the senior synonym due to page priority. The name is placed in the synonymy of *A. melanocephalus* until further research can clarify its taxonomic position.

***melanocephalus davieii* Hoser, 2000** [junior synonym of *A. m. adelynsensis* and of *A. melanocephalus*]

Holotype: WAM R46170.

Type locality: Tom Price, Western Australia.

Remarks: Contrary to Aplin (2002: 56), we do not consider this name a *nomen nudum* because Hoser (2000) provided characters that purport to differentiate it from the nominate form. However, based on Hoser's (2000) description, this taxon is indistinguishable from *A. m. adelynsensis* (see comments above). The name is therefore considered a subjective junior synonym of *A. m. adelynsensis* and is placed into the synonymy of *A. melanocephalus*.

***melanocephalus rickjonesii* Hoser, 2009** [unavailable name (APP8)]

Holotype: WAM 46170.

Type locality: Tom Price, Western Australia.

Remarks: Hoser (2009) had designated the same holotype and paratypes as for *A. m. davieii*. The name is considered “not published” under the provisions of the Code (APP8) but would nevertheless be an objective junior synonym of *A. m. davieii*.

***ramsayi* (Macleay, 1882)**

Synonyms:

Aspidites ramsayi panoptes Hoser, 2000

Aspidites ramsayi richardjonesii Hoser, 2000

Aspidites ramsayi neildavieii Hoser, 2009 (unavailable name, APP8)

Aspidites ramsayi neildavieii Hoser, 2009 [unavailable name (APP8)]

Holotype: WAM 34070.

Type species: near Port Hedland, Western Australia.

Remarks: Designation of the same type as for *A. r. richardjonesi*. The name is considered “not published” under the provisions of the Code (APP8) but would nevertheless be an objective junior synonym of *A. r. richardjonesi*.

***ramsayi panoptes* Hoser, 2000** [synonym of *A. ramsayi*]

Synonyms:

Aspidites ramsayi richardjonesii – Hoser, 2000

Holotype: WAM R43459.

Type locality: Burracoppin, Western Australia.

Remarks: Distinguished from “the main race” by lower average ventral and subcaudal scale counts (citing Barker and Barker [1994: 5] in support of this claim), color darkening above the eye in adults, and “from all other Wommas by distribution” (Hoser 2000: 10) (APP1, APP2). Because of the vague description of this taxon, specimens cannot be unambiguously assigned to this taxon. The name is placed into the synonymy of *A. ramsayi*. For further comments see *A. r. richardjonesii*.

***ramsayi richardjonesii* Hoser, 2000** [junior synonym of *A. r. panoptes*]

Holotype: WAM R34070.

Type locality: near Port Hedland, Western Australia.

Remarks: Aplin (2002) considered this taxon a *nomen nudum*. We disagree because Hoser (2000) provided characters that purport to differentiate this taxon from the “main race”. Nevertheless, this taxon is indistinguishable from *A. r. panoptes*, as both taxa share the diagnostic characters and are only separated by “vast distance” (Hoser 2000) (APP1, APP2) (also see Wüster et al. 2001). Without further data, these taxa must be treated as synonyms, with *A. r. panoptes* having priority.

Genus *Aspidoboa* Sauvage, 1884 [synonym of *Python*]

Remarks: Hoser (2004) resurrected this genus to include the species of the *Python curtus* complex (*sensu* Keogh et al. 2001). As demonstrated by Rawlings et al. (2008) after exclusion of the taxa *reticulatus* and *timoriensis* (see *Broghammerus*), the genus *Python* forms a monophyletic grouping, including the taxon *brongersmai*. Since Keogh et al. (2001) demonstrated that *brongersmai* is the sister taxon to *curtus* and *breitensteini*, separating these three taxa from the genus *Python* would result in the non-monophyly of the genus. It is our opinion that the recognition of *Aspidoboa* at subgeneric rank only causes confusion and is unnecessary in a low-diversity genus as *Python*.

Genus *Australiasis* Wells & Wellington, 1984 [synonym of *Morelia*]**Synonyms:**

Austroliasis Hoser, 2000 (incorrect subsequent spelling, APP4)

Remarks: Hoser (2004) used the correct spelling rather than his earlier incorrect spelling of this taxon as “*Austroliasis*” (see below) but also included the species of the *amethistina*-complex (*sensu* Harvey et al. 2000) and furthermore added *timorensis* (APP4) Peters, 1877. Nevertheless, Hoser only listed this genus without comment or evidence for its resurrection.

amethystinus (Schneider, 1801) [synonym of *M. amethistina*]

amethystinus clarki (Barbour, 1914) [synonym of *M. amethistina*]

Synonyms:

Austroliasis amethystinus clarki (Barbour) – Hoser, 2000 (APP4)

Australiasis amethystina clarki (Barbour) – Hoser, 2004 (APP4)

Australiasis clarki (Barbour) – Hoser, 2009 (APP8, see introduction)

Remarks: Hoser (2000) resurrected this taxon from the synonymy of *M. amethistina* and placed it along with the nominal form *amethistina amethistina* and the taxon *timorensis* Peters, 1877 (APP4, incorrect subsequent spelling of *timoriensis* Peters, 1877) into the genus “*Austroliasis*”. This generic name constitutes an incorrect subsequent spelling (APP4) of the genus *Australiasis* Wells and Wellington 1984. Harvey et al. (2000) examined the holotype of *Liasis clarki* Barbour and found it to be “conspecific with *M. amethistina*, rather than *M. kinghorni*” (Harvey et al. 2000: 155) and documented that “at least some snakes from [the Torres Strait] islands are *M. amethistina* (e.g., the Murray Islands where the type *Liasis clarki* was collected)” (Harvey et al. 2000: 162). Until further studies have evaluated the taxonomic status of this population, this taxon is placed in the synonymy of *M. amethistina*. Henderson and Powell (2007) did not recognize this taxon.

duceboracensis (Günther, 1879) [synonym of *M. amethistina*]

Remarks: Hoser (2004) listed this taxon for the population referred to as *M. amethistina* from New Ireland, Bismarck Archipelago, Papua New Guinea (see remarks on *M. amethistina* and *M. clarki*) without justification. Until further research has been carried out into the status of pythons in the Bismarck Archipelago, this species is herein assigned to the synonymy of *M. amethistina*.

Genus *Austroliasis* Hoser, 2000 [incorrect subsequent spelling of *Australiasis* Wells and Wellington, 1984 (APP4)]

Remarks: Hoser (2000) intending to resurrect *Australiasis* Wells and Wellington, 1984 created an incorrect subsequent spelling. Under the rules of the ICZN, this name is not an available name (Art. 33.3, ICZN 1999). See *Australiasis*.

Genus *Bothrochilus* Fitzinger, 1843

Remarks: Rawlings et al. (2008) identified a sister-group relationship of this monotypic genus with *Leiopython*, which they also considered monotypic. They proposed synonymy of *Leiopython* with *Bothrochilus*, with the latter being the senior synonym. Also see comments on *Leiopython*.

boa Fitzinger, 1843

Genus *Broghammerus* Hoser, 2004 *fide* Rawlings et al. (2008)

Type species: *Python reticulatus* Schneider, 1801

Remarks: Subsequent workers did not recognize *Broghammerus* until a new analysis combining morphological and molecular evidence (Rawlings et al. 2008) led to a split of the genus *Python*. The latter authors expanded Hoser's original concept of the genus to include the taxon *timoriensis* Peters, since they demonstrated that this species is more closely related to *B. reticulatus* than species retained within the genus *Python* (or to *Austroliasis* [i.e., *Morelia*], the genus to which Hoser assigned *timoriensis*).

reticulatus (Schneider, 1801)

Neotype: ZFMK 32378. Type locality: Rengit, West Malaysia; designated by Auliya et al. (2002).

reticulatus reticulatus (Schneider, 1801)

Synonyms:

Python reticulatus reticulatus (Schneider) – Auliya et al., 2002

Broghammerus reticulatus dalegibbonsi Hoser, 2004

Broghammerus reticulatus euanedwardsi Hoser, 2004

Broghammerus reticulatus neilsonnemani Hoser, 2004

Broghammerus reticulatus patrickcouperi Hoser, 2004

Broghammerus reticulatus stuartbigmorei Hoser, 2004

Distribution: For records in western Thailand, see Pauwels et al. (2003). O'Shea and Lazell (2008) reported a specimen from Itbayat Island, Batanes Province, Philippines, the northeastern-most record for the taxon.

Remarks: Hoser (2004) describes the nominate form as "largish regional race with brownish head, much the same colour as the lighter dorsal body markings, although light-headed specimens are known and several colour variants and distinct colour mutations are also known".

reticulatus dalegibbonsi Hoser, 2004 [synonym of *B. r. reticulatus*]

Holotype: FMNH 142320.

Type locality: Ambon, Makulu (=Moluccas), Indonesia.

Remarks: Hoser (2004) asserts that size and color separate this subspecies from the nominate subspecies. The statement “generally smaller race” is as un-specific as the statement made for the size of the nominate form (see remarks there). Therefore, a differentiation of both based on size is nearly impossible. Hoser (2004) describes the color of this subspecies by stating “it rarely has a head lighter than the body as in some other variants of *Broghammerus*, such as those from Bali or parts of Thailand” (Hoser 2004). Based on this statement, this subspecies is indistinguishable from the nominate form (see remarks for *B. reticulatus*). No other characters are provided. Simply stating “best separated from all other *Broghammerus* by DNA analysis and/or accurate distribution information” does not constitute a statement of characters (APP1, APP2). The name is placed into the synonymy of the nominate form.

***reticulatus euanedwardsi* Hoser, 2004** [*nomen dubium*, synonym of *B. r. reticulatus*]

Holotype: FMNH 180232.

Type locality: Nakhom Ratchasima, Central Thailand.

Remarks: Hoser (2004) separated this subspecies from the nominate subspecies by size, stating that this would be “a large race”. However, the nominate form was also claimed to be “largish”, hence, the former statement cannot separate this taxon from the nominate form. No further characters are provided to separate this taxon from other subspecies. The name is herein treated as *nomen dubium* (APP5) and is assigned to the synonymy of the nominate form.

***reticulatus haydnmacphiei* Hoser, 2004** [synonym of *B. r. reticulatus*]

Holotype: FMNH 148968.

Type locality: Sarawak, Borneo, West Malaysia.

Remarks: In the original description, Hoser (2004) violated the Principle of Binominal Nomenclature (Arts. 5.2, 11.4.2) (*B. r. haydn macphiei*). In accordance with articles 11.9.5 and 32.5.2.2, the name was corrected to comply with this principle. The author separates this taxon from the nominate form (referred to as “normal *reticulatus*”) only by “larger average adult size” (Hoser 2004) (also see comments for *B. r. euanedwardsi*). Therefore, this taxon is indistinguishable from *B. r. euanedwardsi* or from *B. r. reticulatus* and is placed in the synonymy of the latter. Auliya et al. (2002) demonstrated that specimens from Bali, West Malaysia, Java, West Kalimantan, and Vietnam form a clade.

***reticulatus jampeanus* (Auliya et al., 2002)**

Holotype: ZFMK 73475.

Type locality: Tanahjampea Island, Indonesia.

Remarks: This subspecies was recognized by De Lang and Vogel (2006), and O'Shea (2007), but was overlooked by Henderson and Powell (2007)

(Henderson 2009, pers. comm.). However, the relevant paper was cited in the list of references by the latter authors.

***reticulatus neilsonnemani* Hoser, 2004** [synonym of *B. r. reticulatus*]

Holotype: FMNH 53272.

Type locality: Davao Province, Mindanao Island, Philippine Islands.

Remarks: In the diagnosis for this taxon, Hoser (2004) claimed that this taxon attains larger size and stated the same as for *B. r. dalegibbonsi* regarding the color (see remarks there). Since both are also true for the nominate form, and no further diagnostic characters are given, this taxon is placed in the synonymy of *B. r. reticulatus*.

***reticulatus patrickcouperi* Hoser, 2004** [synonym of *B. r. reticulatus*]

Holotype: MCZ R-25266.

Type locality: “Djamplong”, South Timor, Indonesia. The MCZ online collection database provides the following information on the locality: “Djamplong, S Timor Indoaustralia, Indonesia, Timor Timur?, Nusa Tenggara”.

Remarks: Hoser (2004) separated this subspecies from the nominate subspecies, referred to as “typical *reticulatus*”, by color, stating that this taxon is “usually a brightly coloured subspecies” (Hoser 2004). However, the author clearly stated that several color variants are known within the nominate form as well. Hoser did not provide other characters that would indicate whether the specimen is assignable to this taxon or the nominate form. The name is assigned to the synonymy of *B. r. reticulatus*.

***reticulatus saputrai* (Auliya et al., 2002)**

Holotype: ZFMK 73473.

Type locality: Selayar Island, Indonesia.

Remarks: Although this taxon was recognized by subsequent workers (e.g., De Lang and Vogel 2006, O’Shea 2007), it was overlooked by Henderson and Powell (2007) (Henderson 2009, pers. comm.). However, the latter authors cited the relevant work in the list of references.

***reticulatus stuartbigmorei* Hoser, 2004** [*nomen dubium*, synonym of *B. r. reticulatus*]

Holotype: MCZ R-8003.

Type locality: Buitenzore (believed a misspelling of Buitenzorg, the Dutch colonial name for Bogor), Java, Indonesia.

Remarks: Hoser (2004) provided characters to separate this taxon, but he attempts to distinguish this subspecies from the species “*Broghammerus reticulatus*”, which includes the subspecies itself. This taxon is indistinguishable from other subspecies based on the original description and is therefore treated as *nomen dubium* (APP5), and placed in the synonymy of the nominate form.

However, specimens from Bali, West Malaysia, Jaya, West Kalimantan, and Vietnam form a clade as demonstrated by Auliya et al. (2002).

***timoriensis* (Peters, 1876)**

Synonyms:

Austroliasis timorensis (Peters) – Hoser, 2000 (incorrect subsequent spelling of *Australiasis* Wells and Wellington and of *timoriensis* Peters, APP4)

Australiasis timorensis (Peters) – Hoser, 2004 (incorrect subsequent spelling of *timoriensis*, APP4)

Python timorensis (Peters) – Henderson and Powell, 2007 (incorrect subsequent spelling of *timoriensis*, APP4)

Broghammerus timoriensis (Peters) – Rawlings et al., 2008

Remarks: Doubts were casted in literature that this species occurs on Timor (e.g., Barker and Barker 1996, McDiarmid et al. 1999, O'Shea 2007) because no records other than the type specimen are known from Timor, and this reported occurrence is likely incorrect.

Genus *Chondropython* Meyer, 1874 [synonym of *Morelia*]

Remarks: Hoser (2000) resurrected this genus for *viridis*, and later added two new subspecies *viridis shireenae* Hoser, 2004 and *viridis adelynhoserae* Hoser 2009 (APP8). Rawlings et al. (2008) demonstrated that two lineages (“northern” and “southern” lineage) along with the taxon *M. carinata*, form a subclade within the clade that represented *Morelia*. Although *Chondropython* is the oldest available name for this subclade, we see no advantage in resurrecting taxa as subgenera in a low-diversity genus.

***azureus* (Meyer, 1874)**

Synonyms:

Chondropython viridis (Schlegel, 1872) – Hoser, 2000 (part)

Chondropython viridis viridis (Schlegel) – Hoser, 2004 (part)

Morelia viridis (Schlegel) – Henderson and Powell, 2007 (part)

Morelia azurea (Meyer, 1874) – this paper

Remarks: Resurrected from the synonymy of *M. viridis* by Hoser (2009). Rawlings and Donnellan (2003) revealed the existence of a sibling species pair within the green tree python. The authors found a genetic divergence of about 7% in mitochondrial DNA (cytochrome b gene) between the northern and southern lineages, separated by the Central Mountain Range that extends in an east-west direction through New Guinea (also see comments on *M. viridis*). Rawlings and Donnellan (2003) revealed the existence of two species, one from north of the central cordillera, the other from the south, including the Aru Island and Australian populations. Nevertheless, within the southern lineage the Australian material formed a well supported clade whereas material from Aru Island clustered with

that from Merauke and Timika. The authors state that “a determination of the species status of the northern and southern lineages awaits a more thorough assessment of divergence at nuclear genes based on wider geographic sampling than we could achieve herein with allozymes” (Rawlings and Donnellan 2003: 42). In 2008, Rawlings et al. (2008: 604) referred to the northern populations as the “unnamed sibling taxon of *M. viridis*”. However, it is not yet evident that only a single taxon occurs on Aru Island, and that the published type locality for *M. viridis* is correct. The name *azureus* Meyer 1874 would be available for the northern lineage, having its type locality on Biak Island, one of the localities from which specimens of “*M. viridis* N[orth]” were analyzed by Rawlings et al. (2008) and hence a strong candidate for the taxon name, based on priority. Since the types are presumed lost, we call for the designation of a neotype.

***viridis* Schlegel, 1872** [synonym of *M. viridis*]

***viridis adelynhoserae* Hoser, 2009** [unavailable name (APP8, see introduction)]

Holotype: AM R129716.

Type locality: Normanby Island, d’Entrecasteaux Archipelago, Milne Bay Province, Papua New Guinea.

Remarks: Rawlings and Donnellan (2003) revealed a genetic distance of about 3% in mitochondrial DNA (cytochrome b gene) between the Normanby Island specimen and all other specimens examined from the southern parts of New Guinea. However, this analysis was based on a single museum specimen from Normanby Island. Further research is needed to ascertain the taxonomic status of this population. However, this name is considered unavailable (APP8, also see introduction).

***viridis shireenae* Hoser, 2004** [synonym of *M. viridis*]

Holotype: NMV D51862.

Type locality: Cape York, Queensland, Australia.

Remarks: Hoser (2004) stated that the “white or other markings along the vertebra” are not diagnostic for this subspecies, but that “a very thin line or line of dots along the spine” is “generally a diagnostic trait for adults of this subspecies”, although the author further states, that he had seen specimens with and without such markings. Furthermore, he noticed that “vertebral markings decline with age”. With the latter comments, the author himself invalidated the utility of vertebral markings as a diagnostic character. In the absence of other characters, this taxon is apparently indistinguishable from the nominate form. Furthermore, as demonstrated by Rawlings and Donnellan (2003: 36), “all of the Australian haplotypes, which form a single lineage, are nested among the southern New Guinean haplotypes”. We therefore placed this taxon in the synonymy of *M. viridis* (see comments there).

Genus *Heleionomus* Gray, 1842 [synonym of *Python*]**Synonyms:**

Helionomus Gray, 1841 (*nomen nudum*) – Hoser, 2004 (*nomen nudum* APP6)

Remarks: The type species for *Heleionomus* Gray, 1842 is *H. variegatus* [= *Python natalensis*]. The resurrection of the genus *Heleionomus* for *Python sebae* and *P. natalensis* is unwarranted because the actual status of *natalensis* and *sebae* has not been fully resolved and, furthermore, separation from *Python* would compromise monophyly of the genus *Python*. Rawlings et al. (2008) showed a sister-group relationship between *sebae* and *molurus* and that the genus *Python* (after exclusion of *reticulatus* and *timo-riensis*) forms a monophyletic group. This genus is therefore assigned to the synonymy of *Python*.

Genus *Helionomus* Gray, 1842 [*nomen nudum* (APP6), incorrect subsequent spelling (APP4)]

Remarks: Hoser (2004) obviously intended to resurrect the genus *Heleionomus* Gray, 1842 but changed the name to “*Helionomus*”. This constitutes an incorrect subsequent spelling (Art. 33.3). However, the name *Helionomus* was already used by Gray (1841) listed in the index for Boidae, but no species was assigned to this name, and it is therefore considered a *nomen nudum*. Also see *Heleionomus*.

Genus *Jackypython* Hoser, 2009 [unavailable name (APP8)]

Type species: *Python carinatus* Smith, 1980

Remarks: Hoser (2009) introduced this name as a subgenus of *Morelia* Gray to include the single species *Morelia carinata*.

Genus *Katrinus* Hoser, 2000 [junior synonym of *Liasis*]

Type species: *Liasis fuscus* Peters, 1873

Remarks: Hoser (2000) established this genus for the separation of the water pythons (*L. fuscus* and *L. mackloti*) from the olive pythons (*L. olivaceus*), both currently referred to *Liasis*. He distinguished the two genera by the number of mid-body rows, stating that “*Liasis* usually has over 60” (Hoser 2000) (APP2). Barker and Barker (1994: 35) provided a range of 58–63 mid-body scale rows for *L. olivaceus barroni*. According to Rawlings et al. (2004, 2008), the taxa *fuscus* and *mackloti* are closely related to each other and since *L. mackloti* Duméril and Bibron is the name-bearing type of *Liasis* (by subsequent designation [see Stimson and McDowell (1986) and Opinion 1514, ICZN, 1988]) and because Gray (1849) had proposed the subgeneric name

Lisalia for *Liasis olivaceus* as well as *Simalia* (in part) for *Liasis mackloti*, the genus *Katrinus* must be considered a subjective junior synonym of *Simalia*, which itself is a synonym of *Liasis* Gray. See comments on the genus *Apodora*. Subsequent workers have not recognized *Katrinus* as a valid taxon.

***fuscus* (Peters, 1873) Hoser, 2000** [junior synonym of *Liasis fuscus*]

***fuscus cornwallisius* (Günther, 1879)** [junior synonym of *Liasis fuscus*]

Type locality: Dauan (as Cornwallis) Island, Torres Straits, Australia.

Remarks: *Katrinus cornwallisius* Günther, 1879 was resurrected from the synonymy of *L. fuscus* by Hoser (2000) for the Torres Strait islands and New Guinean populations. However, Rawlings et al. (2004) demonstrated that specimens from Queensland, the Torres Strait islands (Saibai), and New Guinea form a well-supported clade, which was considered the sister group to the clade comprising the Northern Territory and Indonesian populations. Since Queensland is the type locality of *L. fuscus* Peters, the resurrection of this name is unwarranted as it is a junior synonym to *L. fuscus*. The name *cornwallisius* is therefore placed into the synonymy of *L. fuscus*.

***fuscus jackyae* (Hoser, 2004)** [*nomen dubium*, synonym of *L. fuscus*]

Holotype: WAM R13882.

Type locality: Kalumburu, Western Australia.

Remarks: Hoser (2004) claimed that several diagnostic features separated this taxon from others, but discusses only one (APP2); he stated that “in *Katrinus fuscus fuscus* (from coastal Queensland) the upper lips are pale with a little brown peppering. However, in *K. fuscus jackyae* (from the NT and WA) the lips are usually darker with more dark brown peppering or even blotches” (Hoser 2004). He continued that this subspecies would intergrade with *K. f. cornwallisius* around the Gulf of Carpentaria. The name is herein considered a *nomen dubium* (APP5).

Genus *Leiopython* Hubrecht, 1879

Remarks: Recent studies revealed that *Bothrochilus* and *Leiopython* form a clade. Thus, since Rawlings et al. (2008) considered both genera monotypic, they proposed “the use of a single generic name (*Bothrochilus*) for this species pair” (Rawlings et al. 2008: 613). Later, Schleip (2008) demonstrated that this genus is not monotypic. Rawlings et al. (2008) had used material from *L. hosei* for their genetic analysis (GeneBank accession number U69835, Western Province, PNG at Mawatta). Until further molecular genetic data clarify the relationships of the taxa involved, and in deference to nomenclatural stability, we are reluctant to synonymize *Leiopython* with *Bothrochilus*.

albertisii* (Peters & Doria, 1878)*Synonym:**

Leiopython albertisii barkeri Hoser, 2000 (*nomen nudum*, APP6, see below)

Bothrochilus albertisii (Peters & Doria) – Rawlings et al., 2008

Leiopython albertisi barkerorum Hoser – Hoser, 2009 (unavailable name, APP8)

Distribution: Mulyadi (2007) reported the occurrence of *L. albertisii* from Lopintol (Waigeo) and Schleip (2008) from Emirau Island, St. Matthias Group, Bismarck Archipelago, New Ireland Province, Papua New Guinea.

Remarks: Henderson and Powell (2007) listed only *Leiopython albertisii* Peters & Doria, 1878. Hoser (2000) incorrectly ascribed *albertisii* to Gray 1842. The taxon was named in honor of Italian naturalist Luigi Maria D'Albertis, who made a name for himself in New Guinea. D'Albertis was only a few months old in 1842 and would, therefore, have been an unlikely recipient of Gray's dedication. Furthermore, Hoser repeatedly used an incorrect spelling for the species *albertisii* by omitting the terminal *-i* (APP4, article 33.4).

albertisii barkeri* Hoser, 2000 [*nomen nudum* (APP6)]*Synonyms:**

Leiopython albertisi barkerorum Hoser, 2009 (APP4, APP8, see introduction)

Remarks: Hoser (2000) differentiated this subspecies only by remote distribution (APP2). Other characters mentioned by Hoser (2000) were said to overlap with the nominate form. Wüster et al. (2001) and Schleip (2008) therefore considered the name a *nomen nudum*. Furthermore, since the name honours two persons, it should have been suffixed with *-orum*. In 2009 Hoser re-described this taxon with the name emended to *albertisi barkerorum*. However, the name is considered not published under the Code (APP8).

bennettorum* Hoser, 2000 (name emended by Wüster et al. 2001)*Synonyms:**

Leiopython albertisii bennetti Hoser, 2000

Leiopython bennettorum Hoser – Schleip, 2008 (name emended)

Holotype: BPBM 5452.

Type locality: near Wau, Morobe Province, Papua New Guinea.

Remarks: The original spelling *bennetti* (Hoser 2000) was emended (Wüster et al. 2001, Schleip 2008) because the taxon honours two persons (Art. 31.1.2, ICZN 1999) and should have been suffixed with *-orum*, a correction proposed by Wüster et al. (2001) and subsequently corrected by Schleip (2008).

***biakensis* Schleip, 2008**

Holotype: RMNH 10193.

Type locality: Biak Island.

***fredparkeri* Schleip, 2008**

Holotype: CAS 118906.

Type locality: Karimui, Simbu Province, Papua New Guinea.

***hoserae* Hoser, 2000**

Synonyms:

Leiopython albertisii (Peters & Doria) – Henderson and Powell, 2007

Leiopython hoserae Hoser – Schleip, 2008

Holotype: AMNH R-107150.

Type locality: Wipim, Western Province, Papua New Guinea.

***huonensis* Schleip, 2008**

Holotype: AMNH R-95535.

Type locality: Lae, Huon Peninsula, Morobe Province, Papua New Guinea.

Genus *Lenhoserus* Hoser, 2000 [synonym of *Morelia*]

Type species: *Python boeleni* Brongersma, 1953.

Remarks: Hoser (2000) established this monotypic genus for *Morelia boeleni* stating “while the Boelen’s Python (*boeleni*) has close affinities with the carpet pythons, there is no evidence before this author to suggest that the relationship is any closer than that between the Green (*viridis*) and carpets. Thus if *viridis* is entitled to be placed in a separate genus to the carpets, so too should be *boeleni*” (Hoser 2000: 21–22). Rawlings et al. (2008) supported monophyly of the genus *Morelia* including *M. boeleni*. *Lenhoserus* would therefore only be a subgenus within *Morelia*. Other authors have not adopted this name, and, in adherence to nomenclatural stability, we regard *Lenhoserus* as a subjective junior synonym of *Morelia* (see comments there).

Genus *Liasis* Gray, 1842

Synonyms:

Katrinus Hoser, 2000

Remarks: Scanlon and Mackness (2002) considered the gender of *Liasis* Gray feminine because Gray’s (1842) original use of the combination *Liasis olivacea* implied it to be feminine. However, Gray (1842) also used the masculine gender for *Liasis amethystinus* [= *Morelia amethystina* (Schneider)] within *Liasis*. Hence, Gray did not clearly indicate his intentions concerning the gender of *Liasis*. Despite this discordance in gender, the ICZN had used it plenary power (Art. 81.1, ICZN, 1999) to fix a type species for *Liasis* (Opinion 1514, ICZN 1988), and additionally (but perhaps not deliberately) fixed the gender as masculine. The name and gender also entered the List of Available Names in Zoology (also see Art. 80.6, 80.7, ICZN

1999). These authors therefore follow the predominant use of a masculine gender for *Liasis*.

***dubudingala* Scanlon & Mackness, 2002** [extinct species]

Synonyms:

?*Morelia* sp. – Archer and Wade 1976

Holotype: QMF 9132, mid-trunk vertebra.

Type locality: Main Quarry, Allingham Formation (early Pliocene), Bluff Downs Station, northeastern Queensland.

Remarks: Scanlon and Mackness (2002: 433) stated that “the limited number of characters identified here for pythonine vertebrae thus imply a position either within, or as a sister taxon to, *Liasis* (*sensu stricto*)”.

***fuscus* Peters, 1873**

Synonyms:

Katrinus fuscus (Peters) – Hoser, 2000

Liasis fuscus Peters – Rawlings et al., 2004; Henderson and Powell, 2007

Katrinus fuscus fuscus (Peters) – Hoser, 2000

Katrinus fuscus cornwallisius (Günther, 1879) – Hoser, 2000

Remarks: Kluge (1993) synonymized *Liasis fuscus* Peters, 1873 with *Liasis mackloti* Duméril and Bibron, 1844. However, Rawlings et al. (2004) demonstrated that specimens from Queensland (the type locality of this taxon), the Torres Strait islands (Saibai), and New Guinea form a well-supported clade, which is considered the sister group to the clade comprising the Northern Territory and Indonesian populations. Also see comments on *Katrinus*. Henderson and Powell (2007) did not recognize any subspecies within *L. fuscus*, a position followed herein. Some authors refer to this taxon as *L. mackloti* Duméril and Bibron (e.g., Hay 2007).

***mackloti* (Duméril & Bibron, 1844)**

Synonyms:

Katrinus mackloti (Duméril & Bibron, 1844) – Hoser, 2000

Liasis mackloti Duméril & Bibron – Rawlings et al., 2004; Henderson and Powell, 2007

Remarks: Hoser (2000) placed this species in his genus *Katrinus* (see comments there). The recognition of the subspecies *L. m. dunni* and *L. m. savuensis* is supported by Rawlings et al. (2004). Carmichael et al. (2007) provide additional evidence (different courtship behaviors and pheromone trailing) for this placement. See the latter citation for additional information on biogeography.

***mackloti mackloti* (Duméril & Bibron, 1844)**

Synonyms:

Katrinus mackloti mackloti (Duméril & Bibron) – Hoser, 2000

Liasis mackloti mackloti Duméril & Bibron – Rawlings et al., 2004; Henderson and Powell, 2007

***mackloti dunni* Stull, 1932**

Synonyms:

Katrinus mackloti dunni (Stull) – Hoser, 2000

Liasis mackloti dunni Stull – Rawlings et al., 2004; Henderson and Powell, 2007.

Remarks: Carmichael et al. (2007) note that sexual dimorphism is found among Macklot's pythons but it is different from *L. m. mackloti* and *L. m. savuensis*; in *L. m. dunni* males are larger than females and engage in male-male combat.

***mackloti savuensis* (Brongersma, 1956)**

Synonyms:

Katrinus savuensis (Brongersma) – Hoser, 2000

Liasis mackloti savuensis Brongersma – Rawlings et al., 2004; Henderson and Powell, 2007

Remarks: Referred to as *L. savuensis* by some authors (Hoser 2000, Vidal et al. 2007).

***olivaceus* Gray, 1842**

Synonyms:

Liasis olivacea Gray, 1842 – Gray, 1842

Morelia antiqua (Smith & Plane, 1985) – Kluge, 1993

Liasis olivacea Gray, 1842 – Scanlon and Mackness, 2002 (see remarks at *Liasis*)

Remarks: We accept the subspecies proposed by Smith (1981) and supported by molecular genetic evidence from Rawlings et al. (2004).

***olivaceus olivaceus* Gray, 1842**

***olivaceus barroni* LA Smith, 1981**

Genus *Montityphonoides* Smith & Plane, 1985 [subjective junior synonym of *Morelia*]

Type species: *Montityphonoides riversleighensis* Smith & Plane, 1985 [extinct species]

Remarks: Smith and Plane (1985: 194) stated that this genus "...shows strong relationship with species of *Morelia*". Also see *Morelia riversleighensis*.

Genus *Morelia* Gray, 1842

Synonyms:

Lenhoserus Hoser, 2000

Chondropython Meyer, 1874 – Hoser, 2000

Nyctophilopython Wells & Wellington, 1985 – Hoser, 2000

Montypythonoides Smith & Plane, 1985 – Scanlon, 2001

Australiasis Wells & Wellington, 1984 – Hoser, 2004

Remarks: Hoser (2000) proposed the splitting of this genus into several genera. He created a new genus, *Lenhoserus* Hoser (see comments there) (for *M. boeleni*), and resurrected *Australiasis* Wells & Wellington (for *M. amethistina* and *B. timoriensis*), but created an unavailable name (APP6) (“*Austroliasis*”) by incorrect subsequent spelling (APP4). Later, Hoser (2004) used the correct spelling *Australiasis* Wells & Wellington, added the species recognized by Harvey et al. (2000) and additionally resurrected the taxon *duceboracensis* Günther 1879 (see comments there). Furthermore, he resurrected *Chondropython* Meyer 1874 (for *M. viridis*) and *Nyctophilopython* Wells & Wellington (for *M. oenpelliensis*). However, phylogenetic studies (Rawlings et al. 2008) revealed that this taxonomic action is unwarranted. Although Rawlings et al.’s (2008) maximum parsimony analysis showed *Morelia* to be diphyletic (but monophyletic in Bayesian analysis), the separation of the *amethistina*-complex (*sensu* Harvey et al. 2000) and of *oenpelliensis* from the *breddlii spilota*-clade would in any case be unwarranted and would nullify the monophyly of this grouping. The resurrection of *Chondropython* would only be warranted at subgeneric rank with the inclusion of the two recognized lineages of the green tree python (*sensu* Rawlings and Donnellan, 2003) and of *M. carinata*. However, Rawlings and Donnellan (2003) and Rawlings et al. (2008) avoided such placement because the phylogeny was not fully resolved (see comments for *Chondropython azureus*). The placement of *M. boeleni* as a separate monotypic genus is also unwarranted. We do not see any value in dividing such a small genus, and in the interests of nomenclatural stability, we place *Australiasis*, *Lenhoserus*, *Chondropython*, and *Nyctophilopython* in the synonymy of *Morelia*.

amethistina (Schneider, 1801)

Synonyms:

Austroliasis amethistina (Schneider) – Hoser, 2000 (incorrect subsequent spelling, APP4)

Australiasis amethistina (Schneider) – Hoser, 2004

Australiasis amethystina clarki (Barbour, 1914) – Hoser, 2004

Australiasis duceboracensis (Günther 1879) – Hoser, 2004

Australiasis amethistina (Schneider) – Hoser, 2009 (APP8, see introduction)

Australiasis dipsadides (Ogilby, 1891) – Hoser, 2009 (APP8, see introduction)

Distribution: Kraus and Allison (2004) reported *M. amethistina* from Ferguson Island.

Remarks: Harvey et al. (2000) identified three races within the species, two from the mainland of New Guinea, separated by the Central Mountain Range

(also see remarks on *M. clarki*), and another race from New Ireland (see remarks on *M. duceboracensis*). This is consistent with other species found in this region (e.g., the two lineages of the green tree python (*sensu* Rawlings and Donnellan, 2003), and *L. albertisii*/*L. hoseae*). According to Harvey et al. (2000), the holotype of *A. amethistina* is lost. We call for the designation of a neotype.

***antiqua* (Smith & Plane, 1985)** [synonym of *Morelia riversleighensis*, extinct species]

Synonyms:

Morelia antiquus Smith & Plane, 1985 – Smith and Plane, 1985

Morelia antiqua – Scanlon, 1992 (*antiquus* amended for gender by Scanlon 1992)

Liasis olivacea Gray, 1842 – Kluge, 1993

Holotype: Commonwealth Paleontological Collection 25077 (not “20577”; see Scanlon 2001), right dentary.

Type locality: Camfield Beds, Blast Site, Bullock Creek, Northern Territory, Australia. Late middle Miocene (Scanlon 2001).

***riversleighensis* (Smith & Plane, 1985) – Scanlon, 2001**

Remarks: Smith and Plane (1985) documented significantly lesser curvature in the teeth of this taxon, to that found in species of the genera *Python* and *Morelia*, and because “...of the slight curvature of the dentary teeth...” (Smith and Plane 1985: 194) the authors considered this taxon more closely related to *Morelia* than to *Python*.

***azurea* (Meyer, 1874)**

Remarks: See Comments on *Chondropython azureus* and *Morelia viridis*.

***boeleni* (Brongersma, 1953)**

Synonyms:

Lenhoserus boeleni (Brongersma) – Hoser, 2000

Morelia boeleni (Brongersma) – Henderson and Powell, 2007; Flagle and Stoops, 2009

Remarks: Austin et al. (2009) found little genetic divergence within specimens across the species’ range. A single specimen out of 98 examined using the cytochrome b gene, from the eastern Morobe Province, PNG showed about 1.1% genetic divergence from specimens from West Papua. This demonstrates reduced genetic diversity within this taxon.

***bredli* (Gow, 1981)**

Remarks: Fyfe (2007) lists this species as subspecies *M. spilota bredli*.

***carinata* (Smith, 1981)**

clastolepis* Harvey et al., 2000*Synonyms:**

Australiasis clastolepis (Harvey et al.) – Hoser, 2004, 2009 (APP8, see introduction)

Morelia clastolepis Harvey et al. – Henderson and Powell, 2007

Holotype: UTA 44486.

Type locality: Ambon, Maluku (= Moluccas), Indonesia.

***kinghorni* Stull, 1933**

Distribution: For range extensions in Queensland see Augusteyn (2004) and Fearn and Trembath (2006).

***macburniei* Hoser, 2004 [synonym of *M. s. imbricata*]**

Holotype: SAMA R13994.

Type locality: St. Francis Island, South Australia.

Remarks: Hoser (2004) separated this taxon from its closest relative *M. s. imbricata* (see Schwaner et al. 1988) on the ground of “higher incidence of scale anomalies” to the ventral scales. It can be argued that anomalies do not make good diagnostic characters, and these anomalies were already described in detail by Schwaner et al. (1988). Hoser (2004) further claims that this taxon may be distinguished from *M. mippughae* “by having lanceolate-shaped dorsal scales as opposed to more rhomboidal-shaped dorsal scales” (also see comments on *M. mippughae*). According to Schwaner et al. (1988: 15), and in support of Smith (1981), “specimens of *imbricata* have distinctly elongated, lanceolate-shaped, posterior dorsal scales. *M. s. variegata* usually have the rhomboidal condition”. Furthermore, Schwaner et al. (1988) also reported that specimens from the St. Francis Island exhibited reduced ventral and subcaudal scale counts and a shorter tail than specimens from other populations. Hoser (2004) stated that this taxon is distinguishable from “all other *Morelia* by colouration and patterns” (Hoser 2004), but contradicted this statement when stating that this taxon is “highly variable in individual colouration and pattern”, and that “this species cannot be definitively separated from other *Morelia* on the basis of scalation alone as these properties (ventral counts and the like) may overlap with other *Morelia*” (Hoser 2004). Based on this description, it is unlikely that specimens can be correctly assigned to this species unless they were known to originate from the type locality. Schwaner et al. (1988: 14) and Pearson et al. (2002) assigned the St. Francis Island population to the subspecies *M. s. imbricata*. We concur with this and relegate this taxon to the synonymy of *M. s. imbricata*. Mense (2006), Henderson and Powell (2007), and Swan (2007) did not list this taxon.

***mippughae* Hoser, 2004 [*nomen dubium* (APP5)]**

Holotype: SAMA R14261.

Type locality: Iron Duchess, Middleback Ranges, South Australia.

Remarks: Hoser (2004) separated this taxon from its relative *M. macburniei* “by a lower incidence of scale anomalies” (Hoser 2004) of the ventral scales. This is meaningless because most populations will show few anomalies, hence, using the “normal state” as a character does not differentiate this taxon from others. Hoser (2004) continued that this taxon has “more rhomboidal-shaped dorsal scales as opposed to having lanceolate-shaped dorsal scales” (Hoser 2004), which is, according to Schwaner et al. (1988) also true for *M. s. variegata* (also see remarks on *M. macburniei*). It is further separated from its closest relative *M. s. metcalfei* by its color pattern and from all other *Morelia* by coloration and patterning. Hoser claimed that “a suite of characteristics” separate this taxon from its closest relatives *M. macburniei* and *M. metcalfei*, but failed to enumerate characters other than those cited above. Hence, the name cannot clearly be assigned to a specimen and this name is therefore considered a *nomen dubium* (APP5). Mense (2006), Henderson and Powell (2007), and Swan (2007) did not list this taxon.

***nauta* Harvey et al., 2000**

Synonyms:

Australiasis nauta (Harvey et al.) – Hoser, 2004, 2009 (APP8, see introduction)

Morelia nauta Harvey et al. – Henderson and Powell, 2007

Holotype: UTA 44482.

Type locality: Yamdena Island, Tanimbar Island Group, Maluku (=Moluccas), Indonesia.

***oenpelliensis* (Gow, 1977)**

Synonyms:

Nyctophilypython oenpelliensis (Gow) – Hoser, 2000

Morelia oenpelliensis Gow – Henderson and Powell, 2007

***riversleighensis* (Smith & Plane, 1985) [extinct species]**

Synonyms:

Montityphonoides riversleighensis – Smith and Plane 1985

Morelia spilota (Lacépède) – Kluge, 1993

Morelia antiqua Smith & Plane, 1985 – Scanlon, 2001

Morelia riversleighensis – Scanlon 2001

Holotype: QM F 12926 (=AR4058), incomplete right maxilla.

Type locality: Henk's Hollow Local Fauna, Tertiary System C, approximately 3.6 km southwest of Tedford's (1967) Site B, Riversleigh, northwestern Queensland, Australia. Late Oligocene - early middle Miocene (Scanlon 2001).

Remarks: Smith and Plane (1985) described the two extinct species *riversleighensis* and *antiquus* from Australia. Kluge (1993) synonymized *antiqua* (name amended for gender by Scanlon 1992) with *olivaceus* Gray due to the lack of auto-

pomorphies and great overall similarity and *riversleighensis* with *spilota* Lacépède. Scanlon (2001) synonymized *antiqua* with *riversleighensis*.

***spilota* (Lacépède, 1804)**

Synonyms:

Morelia riversleighensis (Smith & Plane, 1985) – Kluge, 1993 (part)

Remarks: Hoser (2000, 2004) listed several subspecies of *M. spilota* at specific rank, without comment. Since no new evidence is available, these authors continue to treat them all as subspecies. These authors also treat the taxon *M. harrisoni* described by Hoser (2000) as a subspecies of *M. spilota* (see comments there).

***spilota spilota* (Lacépède, 1804)**

***spilota cheynei* Wells & Wellington, 1984**

***spilota harrisoni* Hoser, 2000** [*subspecies inquirenda*, APP7]

Holotype: AMNH R-82433.

Type locality: Port Moresby, Central Province, Papua New Guinea.

Remarks: Hoser (2000: 24) described this taxon at specific rank but considered it “similar in most respects to the others in the genus *Morelia*” separating it from *M. s. cheynei*, *M. s. variegata*, and *M. s. mcdowellii* “by distribution” (APP1, APP2), and further stating that specimens of this taxon “tend to have a lower average ventral and subcaudal scale count than *Morelia cheynei*, *Morelia variegata* and *Morelia mcdowellii*, however the sample seen is too small to conclude if this trend is general” (Hoser 2000: 25). Hoser’s concept of this taxon comprises several populations throughout New Guinea. The author referred to Barker and Barker (1999) for further diagnostic characters. Barker and Barker identified several different and distinct populations from New Guinea, which Hoser (2000) placed within this catch-all taxon. For the “Port Moresby” population Barker and Barker (1999) stated that they “exhibit some characteristics of both *variegata* and *mcdowellii* (...). Most Port Moresby carpets have longitudinally expanded lateral pale blotches and bold facial stripes from the eye to the nasal scale, as do *mcdowellii* in northern Queensland. The patterns on the tops of the heads are similar to *variegata*”. For the “Irian Jaya” (now West Papuan or Papuan) population they stated that “[a]t 2 and 3 years of age, some are even as black and gold as *M. s. cheynei*”, but did not provide further information on the “Trans-fly” (PNG) or the “Northern New Guinea” populations. Hoser (2000: 25) finally stated that “*Morelia harrisoni* can best be definitively separated from the other species of *Morelia* by DNA analysis” (APP2). To the authors’s best knowledge, no such analysis has been carried out. Since the diagnostic characters provided by Hoser (2000) and by Barker and Barker (1999) overlap with those for other taxa of the *Morelia spilota* complex, this taxon is

likely to be confused with them. We consider this taxon a *subspecies inquirenda* (APP7). Henderson and Powell (2007) did not recognize this taxon. Mense (2006) discussed this taxon as a subspecies of *M. spilota*, and O'Shea (2007: 134) wrote: "Papuan Carpet Python *Morelia spilota* ssp. The status of all New Guinea Carpet Pythons is controversial (...). The New Guinea populations are fragmented and isolated, and their taxonomic status and relationships have yet to be determined with certainty". Until further research has established otherwise, these authors treat this taxon as a subspecies of *M. spilota*, as proposed by Mense (2006) and Flagle and Stoops (2009).

***spilota imbricata* LA Smith, 1981**

Synonyms:

Morelia macburniei Hoser, 2004

***spilota mcdowelli* Wells & Wellington, 1984**

***spilota metcalfei* Wells & Wellington, 1985**

***spilota variegata* Gray, 1842**

Remarks: Prior to Wells and Wellington (1984, 1985), this name comprised all the taxa now recognized at subspecific rank, excluding the nominate subspecies and *M. s. imbricata*, but including the New Guinean populations. Now *M. s. variegata* is taxonomically restricted to Northern Australia (Kend 1997, Mense 2006).

***tracyae* Harvey et al., 2000**

Synonyms:

Australiasis tracyae (Harvey et al.) – Hoser, 2004, 2009 (APP8, see introduction)

Morelia tracyae Harvey et al. – Henderson and Powell, 2007

Holotype: UTA 44473.

Type locality: Tobelo, Halmahera, Maluku (=Moluccas), Indonesia.

***viridis* (Schlegel, 1872)**

Synonyms:

Chondropython viridis (Schlegel) – Hoser, 2000 (part)

Chondropython viridis viridis (Schlegel) – Hoser, 2004 (part)

Chondropython viridis shireenae Hoser, 2004

Morelia viridis (Schlegel) – Henderson and Powell, 2007

Distribution: see Wilson and Heinsohn (2007)

Remarks: Rawlings and Donnellan (2003) found molecular evidence for cryptic diversity within *M. viridis*, resulting in two genetically distinct races. The type locality for *M. viridis* is Aru Island, which applies to the "southern lineage",

including Australian specimens (Rawlings and Donnellan 2003) (also see *Chondropython azureus*). However, Rawlings and Donnellan (2003: 42) noted that “(...) the east/west limits of the distribution of the two lineages may not necessarily be at the extreme ends of the central cordillera or the island”, and hence, there may be even more lineages present. Finally, due to the absence of molecular genetic data from the holotype, the type locality Aru Island cannot definitely be confirmed.

Genus *Python* Daudin, 1803

Synonyms:

Aspidoboa Sauvage, 1884 – Hoser, 2004

Helionomus Gray – Hoser 2004 (incorrect subsequent spelling, APP4)

Shireenhoserus Hoser, 2004 (junior synonym of *Enygrus* Wagler)

Distribution: Head (2005) reported remains of an indeterminate python from Miocene-age strata of the Siwalik Group of Pakistan. From the known distribution of extant species, this is likely to be a species of *Python*.

Remarks: Hoser (2004) split this genus into several genera, e.g., *Aspidoboa* Sauvage (for *breitensteini*, *brongersmai*, and *curtus*), *Broghammerus* Hoser (for *reticulatus*), and *Shireenhoserus* Hoser (for *anchietae* and *regius*). However, Hoser (2004) overlooked *Enygrus* Wagler, 1830 (also see McDowell 1979: 9–10, 28), which makes *Shireenhoserus* a subjective junior synonym of *Enygrus* Wagler. He further intended to resurrect *Heleionomus* Gray, 1842 (for *sebae* and *natalensis*) but spelt the name as “*Helionomus*”. This constitutes an incorrect subsequent spelling (APP4), although the name *Helionomus* was already listed in Gray 1841 but is considered a *nomen nudum* (see remarks for *Heleionomus*). Only *molurus* and *bivittatus* would have remained within *Python*. Evidence from genetic studies reveal that with the exception of *reticulatus* and *timoriensis*, which were placed into *Broghammerus* (see comments there) by Rawlings et al. (2008), no further splitting of the clade *Python* is indicated. Furthermore, the phylogenetic relationships of several species (e.g., *regius* and *anchietae*, *molurus* and *bivittatus*, and *sebae* and *natalensis*) have not been fully resolved (e.g., Douglas et al. 2010: fig. 4-6). Other groups (e.g. the *curtus*-group *sensu lato*) are currently under study.

anchietae Bocage, 1887

Synonyms:

Shireenhoserus anchietae (Bocage) – Hoser, 2004 (junior synonym of *Enygrus* Wagler).

Python anchietae Bocage – Henderson and Powell, 2007

bivittatus (Kuhl, 1820)

Distribution: See Greene et al. (2007), Snow et al. (2007), Pyron et al. (2008), and Barker and Barker (2009) for notes on introduced populations in Florida, USA. For distribution in Nepal, see O'Shea (1998), for distribution in Asia see

Pauwels et al. (2003), Barker and Barker (2008, 2010). Barker and Barker (2010) considered records of the occurrence of *bivittatus* in the Sichuan Province deviant due to complete isolation from the natural range of *bivittatus* and therefore excluded the province from the range of occurrence. Records from Sumatra and Borneo are believed to be incorrectly identified (Haile 1958, Groombridge and Luxmoore 1991).

Remarks: Jacobs et al. (2009) considered this taxon a valid species. Evidence for this placement was already provided by O'Shea (1998, 2007) and Barker and Barker (2008) who pointed out that isolated populations of *bivittatus* do exist within the distributional range of *molurus* along the southern Nepalese border and in north-east India as reported from Assam by O'Shea (2007). Jacobs et al. (2009) primarily referred to Barker and Barker (2008) when stating that the isolated populations appear to exist not only sympatrically but syntopically with *molurus* but maintain their own integrity by avoiding interbreeding. However, O'Shea (pers. obs.) has observed the species inhabiting different habitats. *P. molurus* appears to occur in dry sandy woodland whereas *bivittatus* prefers riverine forests and flooded grasslands. O'Shea had not observed the two species occurring sympatrically or syntopically. Jacobs et al. (2009: 12) stated that de Rooij (1917) had assumed the type locality of Kuhl's (1820) concept of *bivittatus*, which was based on unverified pictures by Seba, to be in Indochina rather than in the Sundaland and that the populations occurring between China and Java may be considered *P. molurus sondaica* (sic) Werner, 1899. Nevertheless, according to Jacobson et al (2009), Mertens (1930) fixed the type locality to Java without the designation of a neotype, which has led to nomenclatural problems. Mertens (1930) as well as Werner (1909, 1930) and Pope (1935) assumed that Schlegel (1837) rather than Kuhl (1820) had introduced the name *bivittatus*. According to Jacobs et al. (2009), Mertens (1930) was aware that Schlegel's (1837) composite concept of *P. bivittatus* included several python taxa, namely those from India (*P. molurus*) and from Africa (*P. sebae*), respectively.

***bivittatus bivittatus* (Kuhl, 1820)**

***bivittatus progschai* Jacobs et al., 2009** [*subspecies inquirenda*, APP7]

Holotype: ZFMK 87481, subadult male from SW-Sulawesi.

Type locality: Known only from the southwest of Sulawesi.

Remarks: Jacobs et al. (2009) separated this subspecies from the nominate form by its generally smaller size (up to 240 cm in TL), up to 50% smaller egg size, and the smaller size of the neonates as well as by slightly different patterning and scale counts.

***breitensteini* Steindachner, 1880**

Synonyms:

Python breitensteini Steindachner – Keogh et al., 2001

Aspidoboa breitensteini (Steindachner) – Hoser, 2004

Python breitensteini Steindachner – Henderson and Powell, 2007

Remarks: Elevated to specific rank by Keogh et al. (2001).

***brongersmai* Stull, 1938**

Synonyms:

Python brongersmai Stull – Keogh et al., 2001

Aspidoboa brongersmai (Stull) – Hoser, 2004

Python brongersmai Stull – Henderson and Powell, 2007

Remarks: Elevated to specific rank by Keogh et al. (2001).

***curtus* Schlegel, 1872**

Synonyms:

Python curtus Schlegel – Keogh et al., 2001

Aspidoboa curtus (Schlegel) – Hoser, 2004

Python curtus Schlegel – Henderson and Powell, 2007

Remarks: Elevated to specific rank by Keogh et al. (2001).

***euboicus* Römer, 1870** [extinct species, considered *nomen dubium* by Rage 1984]

Synonyms:

Python Euboicus Römer, 1870

Heteropython euboicus (Römer) – de Rochebrune, 1880

Heteropython euboicus (Römer) – Kuhn, 1939, 1963

Python euboicus Römer – Rage, 1984

Holotype: Fragment of the trunk portion of the vertebral column (25 vertebrae and ribs), left dentary. No accession number. According to Szyndlar (1991) the holotype is probably lost.

Type locality: Kimi (Euboea, Greece), early Miocene (MN ?3).

Remarks: See Szyndlar (1991) and Szyndlar and Rage (2003: 67–68) for further information.

***europaeus* Szyndlar & Rage, 2003** [extinct species]

Synonyms:

Python sp. – Rage 1982; Ivanov 2000, 2002

Python europaeus Szyndlar & Rage, 2003

Holotype: MNHN, VCO 29. One trunk vertebra.

Type locality: Vieux Collonges (=Mont Ceindre), France, early/middle Miocene (MN 4/5).

Remarks: See Szyndlar and Rage (2003: 68–72), and Rage and Bailon (2005: 427–428) for further information.

***molurus* (Linnaeus, 1758)**

***molurus molurus* (Linnaeus, 1758)**

***molurus pimbura* (Deraniyagala, 1945)** [*subspecies inquirenda*, APP7]

Synonyms:

Python molurus molurus (Linnaeus) (part)

Python molurus molurus – Constable, 1949

Python molurus pimbura – Deraniyagala, 1955

Python molurus molurus – Stimson, 1969

Distribution: First reported from Nunavil (Thenmarachi), Jaffna Peninsula, Sri Lanka by Abyerami and Sivashanthini (2008).

Remarks: Hoser (2004) resurrected this taxon from the synonymy of *P. m. molurus* without providing reasons for this action. Deraniyagala (1945) separated the subspecies from *P. m. molurus* based on lower subcaudal scale counts and the irregular shape of the lateral markings. Dorsal midbody scale rows and ventral scale counts overlap those of the nominate subspecies. Constable (1949: 124) did not follow this placement and synonymized this taxon with the nominate subspecies, which was followed by Stimson (1969). A second paper by Deraniyagala (1955: 6) provided a more detailed description of the subspecies. Therein, he stated that this taxon is also separated from the nominate form “in generally possessing three preoculars instead of two” or four as stated by Wall (1921: 47) for some Indian populations of the nominate form. There appears to be a range in preocular scale counts across India, from three in the northeast, to four in the north-center, and two in northwest (O’Shea pers. obs.) but this data, from only a few specimens, requires further verification. Contrary to his findings in 1945, Deraniyagala (1955) reports this taxon to have “more subcaudals” than the nominate form, obviously a typographic error according to the scale count data provided therein. It seems likely that subsequent workers overlooked this latter work, since neither Stimson (1969) nor McDiarmid et al. (1999) or Henderson and Powell (2007) cited it. Several subsequent workers accepted the placement to the synonymy of the nominate form, but no further studies have been conducted on the *molurus*-complex. However, besides the lower subcaudal scale counts and the higher number of preoculars, the pink surface of the head may also constitute a morphological difference. Boulenger (1890, 1893) and MA Smith (1943) recorded two preoculars for *Python molurus*, while Wall (1921) records three preoculars for specimens from Ceylon. Since Sri Lanka is a known biodiversity hot spot with a high level of endemism, this allopatric population may represent a cryptic species. Because of the evidence provided by Deraniyagala (1955), these authors tentatively list this taxon as a valid subspecies and call for further research regarding its true status (APP7).

natalensis* A Smith, 1840*Synonyms:**

Python natalensis A Smith – Broadley, 1999

Helionomus natalensis (A Smith) – Hoser, 2004 (*nomen nudum*, also see remarks on *Python*)

Python natalensis A Smith – Henderson and Powell, 2007

Distribution: Notes on the distribution of this species can be found in Alexander (2007).

Remarks: McDiarmid et al. (1999) refer to A. Smith 1833. According to Branch and Bauer (2005), the name “*Python Natalensis*” already appeared in A. Smith (1833) as well as in A. Smith (1838) but without a description. The name appeared again in A. Smith (1840), but this time was accompanied by a plate. Gray (1842) also cites A. Smith (1840) as do Branch and Bauer (2005). Elevated to specific rank by Broadley (1999).

regius* (Shaw, 1802)*Synonyms:**

Shireenhoserus regia (Shaw) – Hoser, 2004 (junior synonym of *Enygrus* Wagler).

Python regius (Shaw) – Henderson and Powell, 2007

Remarks: For notes on the natural history and distribution of this species, see Barker and Barker (2006).

sardus* (Portis, 1901) [extinct species, *nomen dubium*]*Synonyms:**

Paleopython sardus – Portis, 1901

Paleryx sardus (Portis) – Kuhn, 1963

?*Python sardus* (Portis) – Rage, 1984

Holotype: Articulated palatine and anterior pterygoid fragment (not traced).

Type locality: Monte Albu (=Alba?)(Sardinia) Italy, middle Miocene (MN 6 or 7+8).

Remarks: Szyndlar and Rage (2003: 72–73) considered this name a *nomen dubium* as it is indistinguishable from other (extinct) *Python*.

sebae* (Gmelin, 1788)*Synonyms:**

Helionomus sebae (Gmelin) – Hoser, 2004 (*nomen nudum*, also see remarks on *Python*)

Python sebae (Gmelin) – Henderson and Powell, 2007

Remarks: Elevated to specific rank by Broadley (1999).

Genus *Rawlingspython* Hoser, 2009 [unavailable name (APP8)]

Type species: *Liasis perthensis* Stull, 1932

Remarks: Hoser (2009) introduced this name as a monotypic subgenus of *Antaresia* Wells and Wellington 1984.

Genus *Shireenhoserus* Hoser, 2004 [subjective junior synonym of *Python* and subjective junior synonym of *Enygrus* Wagler]

Type species: *Python anchietae* Bocage, 1887

Remarks: Hoser (2004) established this genus for the smaller African taxa *P. anchietae* and *P. regius*. Hoser (2004) overlooked the older name *Enygrus* Wagler, 1830 (see remarks under *Python*), relegating *Shireenhoserus* as a junior synonym. Moreover, after relocation of the two Asian taxa *reticulatus* and *timoriensis* the genus *Python* now forms a clade, including *P. regius*. The phylogenetic relationship between *P. regius* and *P. anchietae* has not yet been examined and separation would result in non-monophyly. Hence, the recognition of this genus is unwarranted and it is assigned to the synonymy of *Python*.

Discussion and Conclusion

In taxonomy, there have always been “lumpers” and “splitters”, but neither trend is helpful when taken to the extreme. “Splitters” could easily achieve monophyly by placing every single species in its own monotypic genus. Equally, lumping all taxa together into large unmanageable genera may obscure phylogenetic relationships and evolutionary diversity. Thus, a well-balanced “middle-ground” between “lumping” and “splitting” based on scientific evidence is the most desirable approach. In truth, Pythonidae is a relatively small family currently containing 40 extant species in nine genera, as defined here, yet it has been the subject of unprecedented attention by both professional and amateur taxonomists resulting in both papers that clarify and papers that confuse the phylogenetic relationships within the family. Whereas some subspecies may be recognized, erecting additional monotypic genera and creating subgenera within small genera is unwarranted and destabilizes taxonomy. Stable nomenclature, however, is most important for “unambiguous communication about biodiversity” and names must be clearly assignable to specimens to allow “unambiguous identifications” (Pyle and Michel 2008: 40). Since pythons are also highly desired by both the skin and pet trades an established and widely accepted taxonomy with associated nomenclature is essential if they are to be protected and conserved. Any unnecessary and unscientific deviations from a well-founded taxonomy can only serve to further threaten already vulnerable wild populations.

Acknowledgements

The authors are grateful to P. Doughty (WAM) for tracking down a type specimen accession number. We would like to thank L. MacKenzie of the Australian National Library and V. Wallach (MCZ) for providing important information on the status of the Australasian Journal of Herpetology, D.G. Barker (VPI), R.W. Henderson (Milwaukee Public Museum), G. Shea (University of Sydney) and two anonymous reviewers for valuable advice on the manuscript, and A.F. Stimson (BMNH, now retired) for reflecting on the status of *P. m. pimbura*.

References

- Abyerami S, Sivashanthini K (2008) Diversity of snakes from the Jaffna Peninsula, Sri Lanka. Pakistan Journal of Biological Sciences 11 (16): 1969–1978.
- Alexander GJ (2007) Thermal biology of the southern African Python (*Python natalensis*): Does temperature limit its distribution? In: Henderson RW, Powell R (Eds) Biology of the Boas and Pythons. Eagle Mountain Publishing, Utah, USA, 51–75.
- Aplin KP (1999) 'Amateur' taxonomy in Australian herpetology - help or hindrance? Monitor 10: 104–109.
- Aplin KP (2002) Genus *Aspidites* Peters 1876. In: Storr GM, Smith LA, Johnstone RE (Eds) Snakes of Western Australia. Revised edition. Western Australian Museum, Perth, Western Australia, 54–58.
- Archer M, Wade M (1976) Results of the Ray E. Lemley Expeditions, Part I. The Alligham Formation and a new Pliocene vertebrate fauna from northern Australia. Memoirs of the Queensland Museum 17: 379–397.
- Augusteyn J (2004) Southerly range extension for the Amethystine python *Morelia kinghorni* (Squamata: Boidae) in Queensland. Memoirs of the Queensland Museum 49(2): 602.
- Auliya M, Mausfeld P, Böhme W (2002) Review of the reticulated python (*Python reticulatus* Schneider, 1801) with the description of new subspecies from Indonesia. Naturwissenschaften 89: 201–213.
- Austin CC, Spataro M, Peterson S, Jordan J, McVay JD (2009) Conservation genetics of Boelen's python (*Morelia boeleni*) from New Guinea: reduced genetic diversity and divergence of captive and wild animals. Conservation Genetics 11 (3): 889–896.
- Barbour T (1914) On some Australasian reptiles. Proceedings of the Biological Society of Washington 27: 201–206.
- Barker DG, Barker TM (1994) Pythons of the World, Volume I, Australia. Advanced Vivarium Systems, Lakeside CA, USA, 171 pp.
- Barker DG, Barker TM (1995) The maintenance and reproduction of the Dwarf Python of Angola and Namibia. Vivarium 7 (1): 30–34.
- Barker DG, Barker TM (1996) The Lesser Sundas Python (*Python timoriensis*): Taxonomic history, distribution, husbandry, and captive reproduction. Advances in Herpetoculture, 103–108.

- Barker DG, Barker TM (1999) A tapestry of Carpet Pythons. Reptiles (US), May 1999: 48–71.
- Barker DG, Barker TM (2006) Pythons of the World, Vol. 2: Ball Pythons. The History, Natural History, Care and Breeding. VPI Library, Boerne, Texas, USA, 322 pp.
- Barker DG, Barker TM (2008) The distribution of the Burmese Python, *Python molurus bivittatus*. Bulletin of the Chicago Herpetological Society 43: 33–38.
- Barker DG, Barker TM (2009) On Burmese Pythons in the Everglades questions posed and answered on the issues of pythons in South Florida and in captivity. The Occasional Papers of Vida Preciosa International 1:2009, VPI Library, Boerne, Texas, USA, 1–17.
- Barker DG, Barker TM (2010) The distribution of the Burmese Python, *Python bivittatus*, in China. Bulletin of the Chicago Herpetological Society 45 (5): 86–88.
- Bocage JVB du (1887) Mélanges herpétologiques. IV. Reptiles du dernier voyage de MM. Capello et Ivens à travers l'Afrique. Jornal de Sciencias Mathematicas, Physicas e Naturaes, Academia Real das Sciencias de Lisboa, XI (44): 201–208.
- Boulenger GA (1890) Reptilia and Batrachia: The Fauna of British India, including Ceylon and Burma. Taylor and Francis, London, U.K., 564 pp.
- Boulenger GA (1893) Catalogue of the snakes in the British Museum (Natural History). Vol. I. British Museum (Natural History), London, U.K., 448 pp.
- Branch WR, Bauer AM (2005) The herpetological contributions of Sir Andrew Smith, with an introduction, concordance of names, and annotated bibliography. SSAR, Villanova, PA, iv+80 pp.
- Broadley DG (1999) The southern African Python, *Python natalensis* A. Smith 1840, is a valid species. African Herp News, Durban 29: 31–32.
- Brongersma LD (1953) Notes on New Guinean Reptiles and Amphibians. II. Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen, Amsterdam (C) 56: 317–325.
- Brongersma LD (1956) Notes of New Guinean reptiles and amphibians. IV. Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen (C) 59 (4): 447–453.
- Carmichael CK, Kreiser BR, Barker DG, Barker TM, Gillingham JC (2007) Geographic variation in pheromone trailing behaviors of the Indonesian Water Python (*Liasis mackloti*) of Indonesia's Lesser Sundas Archipelago. In: Henderson RW, Powell R (Eds) Biology of the Boas and Pythons. Eagle Mountain Publishing, Utah, USA, 227–240.
- Constable JD (1949) Reptiles from the Indian Peninsula in the Museum of Comparative Zoölogy. Bulletin of the Museum of Comparative Zoology, Harvard College 103 (2): 60–160.
- Cogger HG (1992) Reptiles and Amphibians of Australia. Fourth edition. Reed, Sydney, 775 pp.
- Cogger HG (2000) Reptiles and Amphibians of Australia. Sixth edition. New Holland, London, 808 pp.
- Daudin FM (1803) Histoire Naturelle, Générale et Particulière des Reptiles, Vol. 5. F. Dufart, Paris, 365 pp.
- De Lang R, Vogel G (2006) The Snakes of Sulawesi. In: Vences M, Köhler J, Ziegler T, Böhme W (Eds) Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica, Bonn (Germany), September–October 2005, Zoologisches Forschungsinstitut Museum Koenig, Bonn, 35–38.

- Deraniyagala PEP (1945) Some new races of the Python, Chrysopelea, Binocellate Cobra and Tith-Polonga inhabiting Ceylon and India. *Spolia Zeylanica*, 24: 103–113.
- Deraniyagala PEP (1955) *Python molurus*. In: A Colored Atlas of some vertebrates from Ceylon, Vol. 3, Serpentine Reptilia. Colombo, Sri Lanka, Government Press, xix+121 pp.
- Douglas ME, Douglas MR, Schuett GW, Beck DD, Sullivan BK (2010) Conservation phylogenetics of helodermatid lizards using multiple molecular markers and a supertree approach. *Molecular Phylogenetics and Evolution* 55: 153–167.
- Duméril AMC, Bibron G (1844) *Erpetologie Générale ou Histoire Naturelle Complete des Reptiles*. Vol.6. Libr. Encyclopédique Roret, Paris, 609 pp.
- Ehmann H (1992) *Encyclopedia of Australian Animals: Reptiles*. Angus and Robertson, Pymble, xv+495 pp.
- Fearn S, Trembath D (2006) Southern distribution limits and a translocated population of scrub python *Morelia kinghorni* (Serpentes: Pythonidae) in tropical Queensland. *Herpetofauna* 36 (2): 85–87.
- Flagle AR, Stoops ED (2009) Black Python *Morelia boeleni*. Frankfurt Contributions to Natural History No.26. Chimaira, Frankfurt am Main, 160 pp.
- Fitzinger LJ (1826) Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologischen Museum's zu Wien. Heubner Verlag, Wien, 66 pp.
- Fitzinger LJ (1843) *Systema reptilium, fasciculus primus Amblyglossae*. Braumüller und Seidel, Wien, 106 pp.
- Fyfe G (2007) Centralian Carpet Python. *Morelia spilota bredli* (Gow, 1981). In: Swan M (Ed) *Keeping and Breeding Australian Pythons*. Mike Swan Herp. Books, Lilydale, Victoria, Australia, 237–250.
- Gow GF (1977) A new species of *Python* from Amhem Land. *Australian Zoologist* 19: 133–139.
- Gow GF (1981) A new species of *Python* from central Australia. *Australian Journal of Herpetology* 1 (1): 29–34.
- Gray JE (1841) *Synopsis of the Contents of the British Museum*, 43. edition. Woodfall and Sons, London, 382 pp.
- Gray JE (1842) *Synopsis of the species of prehensile-tailed snakes, or Family Boidae*. The Zoological Miscellany 2: 41–46.
- Greene DU, Potts JM, Duquesnel JG, Snow RW (2007) *Python molurus bivittatus*. Distribution Note. *Herpetological Review* 38 (3): 335.
- Günther A (1879) Notice of a collection of reptiles from islands of Torres Straits. *Annals and Magazine of Natural History* 5 (3): 84–87.
- Haile NS (1958) The snakes of Borneo, with a key to the species. *Sarawak Museum Journal* 8: 743–771.
- Harvey MB, Barker DG, Ammerman LK, Chippindale PT (2000) Systematics of pythons of the *Morelia amethystina* Complex (Serpentes: Boidae) with the description of three new species. *Herpetological Monographs* 14: 139–185.

- Hay C (2007) Water Python *Liasis mackloti* (Duméril and Bibron, 1844). In: Swan M (Ed) Keeping and Breeding Australian Pythons. Mike Swan Herp Books, Lilydale, Victoria, Australia, 141–152.
- Head JJ (2005) Snakes of the Siwalik Group (Miocene of Pakistan): systematics and relationship to environmental change. *Palaeontologia Electronica* 8 (1): 81–33. http://palaeo-electronica.org/2005_1/head18/head18.pdf [accessed 08.IX.2010]
- Hedges M (2002) Regional patterns of biodiversity in New Guinea animals. *Journal of Biogeography* 29: 285–294.
- Henderson RW, Powell R (2007) The biology of boas and pythons: a retrospective look to the future. In: Henderson RW, Powell R (Eds) *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Utah, USA, 3–21.
- Hoser RT (1996) Australia – land of goannas and bureaucrats. *Reptilian Magazine* 4 (4): 7–21.
- Hoser RT (1997) Submission to the ICZN opposing the recently proposed resurrection of the scientific names *Varanus panoptes* in favor of the more widely accepted *Varanus gouldii* and *Varanus teriae* in favor of the earlier name *Varanus keithhorni*. Unpublished manuscript. <http://www.smuggled.com/iczn1.htm> [accessed 15.V.2009].
- Hoser RT (2000) A revision of the Australasian pythons. *Ophidia Review* 1 (1): 7–27. <http://www.smuggled.com/pytrsm1.pdf> [accessed 18.IV.2009].
- Hoser RT (2004) A reclassification of the Pythoninae including the description of two new genera, two new species and nine new subspecies. *Crocodilian – Journal of the Victorian Association of Amateur Herpetologists* 4 (3): 31–37 and 4 (4): 21–40.
- Hoser RT (2009) Creationism and contrived science: A review of recent python systematics papers and the resolution of issues of taxonomy and nomenclature. *Australasian Journal of Herpetology* 2: 1–34. <http://www.smuggled.com/AJHI2.pdf> [accessed 12.IV.2009].
- Hubrecht AAW (1879) Notes III. On a new genus and species of Pythonidae from Salawatti. *Notes from the Leyden Museum* 1: 14–15.
- Gmelin JF (1788) *Caroli a Linné Systema naturae per regna tria naturae : secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 13. edition, Tomus 1 Pars 3. GE Beer, Lipsiae, 1033–1516 pp [p.1118]. <http://www.biodiversitylibrary.org/item/83106> [accessed 02.VII.2010].
- Groombridge B, Luxmoore R (1991) *Pythons in South-East Asia. A review of distribution, status and trade in three selected species*. World Conservation Monitoring Centre, Cambridge, U.K., 127 pp.
- International Commission of Zoological Nomenclature (1988) Opinion 1514. *Liasis* Gray (Reptilia, Serpentes): *Liasis mackloti* Duméril and Bibron, 1844 designation as type species. *The Bulletin of Zoological Nomenclature* 45 (3): 244.
- International Commission on Zoological Nomenclature (1999) *International code of zoological nomenclature*. Fourth Edition. London: The International Trust for Zoological Nomenclature.
- Ivanov M (2000) Snakes of the lower/middle Miocene transition at Vieux Collonges (Rhône, France), with comments on the colonisation of western Europe by colubroids. *Geodiversitas* 22 (4): 559–588.

- Ivanov M (2002) The oldest known Miocene snake fauna from Central Europe: Merkur-North locality, Czech Republic. *Acta Palaeontologica Polonica* 47 (3): 513–534.
- Jacobs HJ, Auliya M, Böhme W (2009) Zur Taxonomie des Dunklen Tigerpythons, *Python molurus bivittatus* Kuhl, 1820, speziell der Population von Sulawesi. *Sauria* 31 (3): 5–16.
- Kend BA (1997) *Pythons of Australia*. Schuett GW, Schuett LW (Eds) Canyonlands Publishing, Provo, Utah, USA, 206 pp.
- Keogh JS, Barker DG, Shine R (2001) Heavily exploited but poorly known: systematics and biogeography of commercially harvested pythons (*Python curtus* group) in Southeast Asia. *Biological Journal of the Linnean Society* 73 (1): 113–129.
- Kluge AG (1993) *Aspidites* and the phylogeny of pythonine snakes. *Records of the Australian Museum Supplement* 19: 1–79.
- Kuhl H (1820) *Beiträge zur Zoologie und vergleichenden Anatomie. Erste Abtheilung. Beiträge zur Zoologie*, Frankfurt am Main, 151 pp.
- Kraus F, Allison A (2004) New Records for reptiles and amphibians from Milne Bay Province, Papua New Guinea. *Herpetological Review* 34 (4): 413–418.
- Kreff G (1864) Description of *Aspidiotes melanocephalus*, a new snake from Port Denison, N.E. Australia. *Annals and Magazine of Natural History* 3 (14): 225–226.
- Lacépède BGE (1804) Mémoire sur plusieurs animaux de la Nouvelle-Hollande dont la description n'a pas encore été publiée. *Annals du Museum National d'Histoire Naturelle*, Paris. 4: 184–211.
- Linnaeus C (1758) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Laurentii Salvii, Holmiæ, 10th Edition, 824 pp.
- Macleay W (1882) Description of two new species of snakes. *Proceeding of the Linnean Society, New South Wales, Sydney, Australia*, 6: 811–813.
- McDiarmid RW, Campbell JA, Touré TA (1999) *Snake species of the world: a taxonomic and geographic reference. Volume 1. The Herpetologist's League*, Washington, 511 pp.
- McDowell SB (1979) A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part III. Boinae and Acrochordoidea. *Journal of Herpetology* 13 (1): 1–92.
- Mecke S, Doughty P, Donnellan, SC (2009) A new species of *Eremiascincus* (Reptilia: Squamata: Scincidae) from the Great Sandy Desert and Pilbara Coast, Western Australia and re-assignment of eight species from *Glaphyromorphus* to *Eremiascincus*. *Zootaxa* 2246: 1–20.
- Melville RV (1980) *Nomina dubia* and Available Names. *Zeitschrift für Parasitenkunde* 62: 105–109.
- Melville RV (1984) Reply to Frenkel, Mehlhorn, and Heydorn on Protozoan *Nomina dubia*. *The Journal of Parasitology* 70 (5): 815.
- Mense M (2006) *Rautenpythons*. Natur und Tier Verlag. Münster, Germany, 208 pp.
- Mertens R (1930) Die Amphibien und Reptilien der Inseln Bali, Lombok, Sumbawa und Flores. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, Frankfurt am Main, 42 (3): 115–344.
- Meyer AB (1874) Eine Mitteilung von Hrn. Dr. Adolf Bernhard Meyer über die von ihm auf Neu-Guinea den Inseln Jobi, Mysore und Mafoor im Jahr 1873 gesammelten Amphibi-

- en. Monatsberichte der königlich preussischen Akademie der Wissenschaften zu Berlin, 128–140.
- Mones A (1989) *Nomen Dubium* vs. *Nomen Vanum*. Journal of Vertebrate Paleontology 9 (2): 232–234.
- Mulyadi AH (2007) Herpetofauna di pulau Waigeo. Museum Zoologicum Bogoriense Bidang Zoologi, Pusat Penelitian Biologi Lembaga Ilmu Pengetahuan Indonesia, 53 pp.
- O'Shea M (1998) Herpetological results of two short field excursions to the Royal Bardia region of western Nepal, including range extensions for Assamese/Indo-Chinese snake taxa. In: de Silva A (Ed) Biology and Conservation of the Amphibians, Reptiles and their Habitats in South Asia. Proceeding of the Conference on the Biology and Conservation of the Amphibians and Reptiles of South Asia, Sri Lanka, August 1996, 306–317.
- O'Shea M (2007) Boas and Pythons of the World. New Holland, London, 160 pp.
- O'Shea M, Lazell JD (2008) *Python reticulatus* (Reticulated Python) Philippines: Batanes Province: Itbayat Island. Herpetological Review 39 (4): 486.
- O'Shea M, Sprackland RG, Bigilale IH (2004) First Record for the Genus *Antaresia* (Squamata: Pythonidae) from Papua New Guinea. Herpetological Review 35 (3): 225–227.
- Pauwels OSG, David P, Chimsunchart C, Thirakhupt K (2003) Reptiles of Phetchaburi Province, Western Thailand: a list of species, with natural history notes, and a discussion on the biogeography at the Isthmus of Kra. The Natural History Journal of Chulalongkorn University 3 (1): 23–53.
- Pearson D, Shine R, How R (2002) Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). Biological Journal of the Linnean Society 77: 113–125.
- Peters WCH (1873) Über eine neue Schildkrötenart, *Cinosternon Effeldti* und einige andere mehr oder weniger bekannte Amphibien. Monatsbericht der königlich preussischen Akademie der Wissenschaften zu Berlin. October 1873: 607–609.
- Peters WCH (1876) Über die von S. M. S. Gazelle mitgebrachten Amphibien. Monatsbericht der königlich preussischen Akademie der Wissenschaften zu Berlin. August 1876: 528–535.
- Peters WCH (1877) Berichtigung (Errata and introduction of the replacement name *Aspidites* for *Aspidiotus*). Monatsbericht der königlich preussischen Akademie der Wissenschaften zu Berlin, Juli 1877: 914.
- Peters WCH, Doria G (1878) Catalogo dei retilli e dei batraci raccolti da O. Beccari, L. M. D'Alberts e A. A. Bruijn. nella sotto-regione Austro-Malese. Annali del Museo Civico de Storia Naturale di Genova ser. 1: 401–403, plate III, Fig. 2.
- Pope CH (1935) The Reptiles of China. American Museum of Natural History, New York, 604 pp.
- Portis A (1901) II *Paleopython sardus* PORT. Nuovo pythonide del Miocene medio della Sardegna. Bollettio della Società Geologica Italiana 20 (2): 247–253.
- Pyle RL, Michel E (2008) ZooBank: Developing a nomenclatural tool for unifying 250 years of biological information. Zootaxa 1950: 39–50.

- Pyron RA, Burbrink FT, Guirer TJ (2008) Claims of potential expansion throughout the US by invasive python species are contradicted by ecological niche models. PLoS ONE 13 (8): e2931. doi:10.1371/journal.pone.0002931.
- Rage J-C (1982) Amphibia and Squamata. In: The lower Miocene Fauna of Al-Sarra (Eastern province, Saudi Arabia). Thomas H, Sen S, Khan M, Battail B, Ligabue G (Eds) Atlatl Journal of Saudi Arabian Archaeology 5 (3): 109–136.
- Rage J-C (1984) Serpentes. Handbuch der Paläoherpetologie, Part 11. Wellenhofer P (Ed) Gustav Fischer Verlag, Stuttgart-New York, 80 pp.
- Rage J-C, Bailon S (2005) Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, Southwestern France). Geodiversitas 27 (3): 413–441.
- Rawlings LH, Donnellan SC (2003) Phylogeographic analysis of the green python, *Morelia viridis*, reveals cryptic diversity. Molecular Phylogenetics and Evolution 27 (1): 36–44.
- Rawlings LH, Barker DG, Donnellan SC (2004) Phylogenetic relationships of the Australo-Papuan *Liasis* pythons (Reptilia: Macrostromata), based on mitochondrial DNA. Australian Journal of Zoology 52 (2): 215–227.
- Rawlings LH, Rabosky DL, Donnellan SC, Hutchinson MN (2008) Python phylogenetics: inference from morphology and mitochondrial DNA. Biological Journal of the Linnean Society 93: 603–619.
- Rochebrune de AT (1880) Révision des ophidiens fossiles du Muséum d'Histoire naturelle. Nouvelles Archives du Muséum d'Histoire naturelle 3: 271–296.
- Römer F (1870) Über *Python Euboicus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. Zeitschrift der Deutschen Geologischen Gesellschaft 22 (13): 582–590.
- Roos N de (1917) The reptiles of the Indo-Australian archipelago. II. Ophidia. Brill, Leiden, 334 pp.
- Scanlon JD (1992) A new large Madtsoiid snake from the Miocene of the Northern Territory. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 9 (1): 49–60.
- Scanlon JD (2001) *Montypythonoides*: the Miocene snake *Morelia riversleighensis* (Smith and Plane, 1985) and the geographical origin of pythons. Memoirs of the Association of Australasian Palaeontologists 25: 1–35.
- Scanlon JD, Mackness BS (2002) A new giant python from the Pliocene Bluff Downs Local Fauna of northeastern Queensland. Alcheringa 25: 425–437.
- Schlegel H (1837) Essai sur la physionomie des serpens. Partie Générale. Schonekat, Amsterdam, 251 pp.
- Schlegel H (1872) De Dientium Van het Koninklijk Zoologische Genootschap „Natura Artis Magistra“ te Amsterdam zoologisch geschetst door Prof. H. Schlegel, met historische herinneringen van PH Witkamp. Amsterdam, 64 pp.
- Schleip WD (2008) Revision of the Genus *Leiopython* Hubrecht 1879 (Serpentes: Pythonidae) with the redescription of taxa recently described by Hoser (2000) and the description of new species. Journal of Herpetology 42 (4): 645–667.
- Schneider JG (1801) Historiae Amphibiorum naturalis et literariae. Fasciculus secundus continens Crocodilos, Scincos, Chamaesauras, Boas. Pseudoboas, Elapes, Angues. Amphisbaenas et Caecilias. Frommani, Jena, 374 pp.

- Shaw G (1802) General Zoology or Systematic Natural History. Vol. 3, part 2. Kearsley G, Thomas Davison, London, 313–615.
- Shea GM, Sadler RA (1999) A catalogue of the non-fossil amphibian and reptile type specimens in the collection of the Australian Museum: types currently, previously and purportedly present. Technical Reports of the Australian Museum 15: 1–91.
- Smith LA (1981a) A revision of the *Liasis olivaceus* species-group (Serpentes: Boidae). Records of the Western Australian Museum 9 (2): 227–233.
- Smith LA (1981b) A revision of the Python genera *Aspidites* and *Python* (Serpentes: Boidae) in Western Australia. Records of the Western Australian Museum 9 (2): 211–226.
- Smith LA (1985) A revision of the *Liasis childreni* species-group (Serpentes: Boidae). Records of the Western Australian Museum 12 (3): 257–276.
- Smith MA (1943) The Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese subregion. Reptilia and Amphibia. Vol.III Serpentes. Taylor and Francis, London, xii+583 pp.
- Smith MJ, Plane M (1985) Pythonine snakes (Boidae) from the Miocene of Australia. Bureau of Mineral Resources, Geology and Geophysics, Journal of Australian Geology & Geophysics 9: 191–195.
- Snow RW, Krysko KL, Enge KM, Oberhofer L, Warren-Bradley A, Wilkins L (2007) Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida. In: Henderson RW, Powell R (Eds) Biology of the Boas and Pythons. Eagle Mountain Publishing, Utah, USA, 417–438.
- Sonnemann N (2007) Stimson's Python. *Antaresia stimsoni* (Smith, 1985). In: Swan M (Ed) Keeping and Breeding Australian Pythons. Mike Swan Herp. Books, Lilydale, Victoria, Australia, 98–110.
- Steindachner F (1880) Über eine neue Pythonart (*Python Breitensteini*) aus Borneo. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien, 82: 267–280.
- Stimson AF (1969) Liste der rezenten Amphibien und Reptilien. Boidae (Boinae + Bolyeriinae + Loxoceminae + Pythoninae). Das Tierreich 89: 1–49.
- Stimson AF, McDowell SB (1986) *Liasis* Gray, 1842 (Reptilia, Serpentes): proposed designation of *Liasis mackloti* Dumeril and Bibron 1844 as type species Z.N.(S)2439. Bulletin of Zoological Nomenclature 43: 330–334.
- Stull OG (1932) Five new subspecies of the family Boidae. Occasional Papers of the Boston Society of Natural History 8: 25–29.
- Stull OG (1933) Two new subspecies of the family Boidae. Occasional Papers Museum of Zoology, University of Michigan (267): 1–4.
- Swan M (Ed) (2007) Keeping and Breeding Australian Pythons. Mike Swan Herp Books, Lilydale, Victoria, Australia, 336 pp.
- Szyndlar Z (1991) A Review of Neogene and Quarternary Snakes of Central and Eastern Europe. Part 1: Scolecophidia, Boidae, Colubrinae. Estudios geologica 47: 103–126.
- Szyndlar Z, Rage J-C (2003) Non-erycine Booidea from the Oligocene and Miocene of Europe. Institute of Systematics and Evolution of Animals. Polish Academy of Sciences, Poland, 109 pp.

- Tedford RH (1967) Fossil mammals from the Tertiary Carl Creek Limestone, northerwestern Queensland. Bureau of Mineral Resources, Australia Bulletin 92: 217–236.
- Torr G (2000) *Pythons of Australia: A Natural History*. University of New South Wales Press, Sydney, New South Wales, Australia, 103 pp.
- Underwood G, Stimson AF (1990) A classification of pythons (Serpentes, Pythoninae). *Journal of Zoology*, London 221: 565–603.
- Vidal N, Delmes A-S, Hedges SB (2007) The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes. In: Henderson RW, Powell R (Eds) *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Utah, USA, 27–33.
- Vidal N, Hedges SB (2009) The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *Comptes Rendus Biologies* 332: 129–139.
- Wagler JG (1830) *Natürliches System der Amphibien, mit vorangehender Classification der Säugetiere und Vögel. Ein Beitrag zur vergleichenden Zoologie*. 1.0. Cotta, München, Stuttgart, und Tübingen, 354 pp.
- Wall F (1921) *Ophidia Taprobanica or the Snakes of Ceylon*. HR Cottle, Colombo, xxiii+581 pp.
- Wallach V, Wüster W, Broadley DG (2009) In praise of subgenera: taxonomic status of cobras of the genus *Naja* Laurenti (Serpentes: Elapidae). *Zootaxa* 2236: 26–36.
- Walls JG (1998) *The Living Pythons: A complete guide to the pythons of the world*. T.F.H. Publications, Neptune City, New York, USA, 256 pp.
- Wells RW, Wellington CR (1984) A synopsis of the Class Reptilia in Australia. *Australian Journal of Herpetology* 1 (3–4): 73–129.
- Wells RW, Wellington CR (1985) A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology Supplement Series* 1: 1–61.
- Wells RW (2009) some taxonomic and nomenclatural considerations on the Class Reptilia in Australia. A review of the genera *Eulamprus* and *Glaphyromorphus* (Scincidae), including the description of new genera and species. *Australian Biodiversity Record* 2009 (3): 1–96.
- Werner F (1899) Allerlei aus dem Kriechtierleben im Käfig. II. *Zoologischer Garten, Frankfurt am Main*, 40: 12–24.
- Werner F (1909) Neue oder seltnere Reptilien aus dem Musée Royal d'Histoire naturelle de Belgique in Brüssel. *Zoologisches Jahrbuch, Abteilung Systematik*, 28: 263–279.
- Werner F (1930) Boidenstudien im Wiener Naturhistorischen Museum. IV. *Python molurus* Gray und *bivittatus* Schlegel. *Zoologischer Anzeiger, Leipzig*, 87: 205–206.
- Westhoff G, Collin SP (2008) A new type of infrared sensitive organ in the python *Aspidites* sp., Presentation at the 6th World Congress of Herpetology.
- Wilcox TP, Zwickl DJ, Heath TA, Hillis DM (2002) Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution* 25: 361–371.
- Williams D, Wüster W, Fry BG (2006) The good, the bad and the ugly: Australian snake taxonomists and a history of the taxonomy of Australia's venomous snakes. *Toxicon* 48: 919–930.
- Williams DJ, O'Shea M, Daguerre RL, Pook CE, Wüster W, Hayden CJ, McVay JD, Paiva O, Matainaho T-L, Winkel KD, Austin CC (2008) Origin of the eastern brownsnake, *Pseudonaja textilis* (Duméril, Bibron and Duméril) (Serpentes: Elapidae: Hydrophiinae) in

- New Guinea: evidence of multiple dispersals from Australia, and comments on the status of *Pseudonaja textilis pughii* Hoser 2003. Zootaxa 1703: 47–61.
- Wilson D, Heinsohn R (2007) Geographic range, population structure and conservation status of the green python (*Morelia viridis*), a popular snake in the captive pet trade. Australian Journal of Zoology 55: 147–154.
- Wilson S, Swan G (2008) A Complete Guide to Reptiles of Australia. Second edition. New Holland, Sydney, 512 pp.
- Wüster W, Bush B, Keogh JS, O'Shea M, Shine R (2001) Taxonomic contributions in the “amateur” literature: Comments on recent descriptions of new genera and species by Raymond Hoser. Litteratura Serpentina 21: 67–79.
- Zaher H, Grazziotin FG, Cadle JE, Murphy RW, de Moura-Leiter JC, Bonatto SL (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American xenodontines: a revised classification and descriptions of new taxa. Papéis Avulsos de Zoologia 49 (11): 115–153.

Appendix I

A list of valid taxa of pythons recognized in this study. Doubtful names (*nomina dubia*) are not included.

Antaresia Wells & Wellington, 1984

Antaresia childreni (Gray, 1842)

Antaresia maculosa (Peters, 1873)

Antaresia perthensis (Stull, 1932)

Antaresia stimsoni (LA Smith, 1985)

Antaresia stimsoni stimsoni (LA Smith, 1985)

Antaresia stimsoni orientalis (LA Smith, 1985)

Apodora Kluge, 1993

Apodora papuana (Peters & Doria, 1878)

Aspidites Peters, 1877

Aspidites melanocephalus (Krefft, 1864)

Aspidites ramsayi (Macleay, 1882)

Bothrochilus Fitzinger, 1843

Bothrochilus boa Fitzinger, 1843

Broghammerus Hoser, 2004 *fide* Rawlings et al., 2008

Broghammerus reticulatus (Schneider, 1801)

Broghammerus reticulatus reticulatus (Schneider, 1801)

Broghammerus reticulatus jampeanus (Auliya et al., 2002)

Broghammerus reticulatus saputrai (Auliya et al., 2002)

Broghammerus timoriensis (Peters, 1876)

Leiopython Hubrecht, 1879

Leiopython albertisii (Peters & Doria, 1878)

Leiopython bennettorum Hoser, 2000

Leiopython biakensis Schleip, 2008

Leiopython fredparkeri Schleip, 2008

Leiopython hoseae Hoser, 2000

Leiopython huonensis Schleip, 2008

Liasis Gray, 1842

Liasis dubudingala Scanlon & Mackness, 2002 [extinct species]

Liasis fuscus Peters, 1873

Liasis mackloti (Duméril & Bibron, 1844)

Liasis mackloti mackloti (Duméril & Bibron, 1844)

Liasis mackloti dunni Stull, 1932

Liasis mackloti savuensis (Brongersma, 1956)

Liasis olivaceus Gray, 1842

Liasis olivaceus olivaceus Gray, 1842

Liasis olivaceus barroni LA Smith, 1981

Morelia Gray, 1842

Morelia azurea (Meyer, 1874)

Morelia amethistina (Schneider, 1801)

Morelia boeleni (Brongersma, 1953)

Morelia bredli (Gow, 1981)

Morelia carinata (LA Smith, 1981)

Morelia clastolepis Harvey et al., 2000

Morelia kinghorni Stull, 1933

Morelia nauta Harvey et al., 2000

Morelia oenpelliensis (Gow, 1977)

Morelia riversleighensis (Smith & Plane, 1985) [extinct species]

Morelia spilota (Lacépède, 1804)

Morelia spilota spilota (Lacépède, 1804)

Morelia spilota cheynei Wells & Wellington, 1984

Morelia spilota harrisoni Hoser, 2000

Morelia spilota imbricata LA Smith, 1981

Morelia spilota mcdowelli Wells & Wellington, 1984

Morelia spilota metcalfei Wells & Wellington, 1984

Morelia spilota variegata Gray, 1842

Morelia tracyae Harvey et al., 2000

Morelia viridis (Schlegel, 1872)

Python Daudin, 1803

Python anchietae Bocage, 1887

Python bivittatus (Kuhl, 1820)

Python bivittatus bivittatus (Kuhl, 1820)

Python bivittatus progschai Jacobs et al., 2009

Python breitensteini Steindachner, 1880

Python brongersmai Stull, 1938

Python curtus Schlegel, 1872

Python europaeus Szyndlar & Rage, 2003 [extinct species]

Python molurus (Linnaeus, 1758)

Python molurus molurus (Linnaeus, 1758)

Python molurus pimbura Deraniyagala, 1945

Python natalensis A Smith, 1840

Python regius (Shaw, 1802)

Python sebae (Gmelin, 1788)

Appendix 2

A. Key to the genera of the Pythonidae

1. Visible sensory pits absent..... *Aspidites*
- Visible sensory pits present 2
2. Rostral unpitted..... 3
- Rostral pitted 6
3. No visible black pigmentation between the scales 4
- Black pigmentation visible between the scales *Apodora*
4. Number of loreals fewer than 3..... 5
- Number of loreals more than 3 *Antaresia*
5. Head color not black, head distinct from neck, two pairs of prefrontals.....
- Head color black, head barely distinct from neck, one pair of prefrontals
- *Bothrochilus*
6. Body unpatterned..... *Leiopython*
- Body patterned 7
7. Lateroposterior margin of nasal exposed, plane of ventral position of postorbital is directed anterolaterally, neck is markedly narrower than the head in adults..... *Morelia*
- Lateroposterior margin of nasal is covered by prefrontal, plane ventral position of postorbital is directed anteriorly, neck is slightly narrower than the head in adults 8
8. Well defined square or triangular supralabial pits, infralabials less well developed and not set in a groove *Python*
- Less well defined diagonal supralabial pits, infralabials placed in a longitudinal groove and ventrally in a fold *Broghammerus*

B. Key to the species and subspecies of the genera of Pythonidae

Antaresia

1. Body color pale yellowish-brown to dark purplish-brown 2
- Head and neck color yellowish to reddish-brown 3
2. Midbody scale rows 35 or fewer, ventrals fewer than 250, 34–45 subcaudals
- Midbody scale rows 35 or more, ventrals more than 250, 38–57 subcaudals ..
- *perthensis*
- *childreni*
3. Dorsal pattern of ragged-edged dark blotches *maculosa*
- Dorsal pattern of smooth-edged blotches 4
4. Ventrals 260–302..... *stimsoni stimsoni*
- Ventrals 243–284..... *stimsoni orientalis*

Aspidites

1. Head and neck color glossy black, numerous dark brown crossbands, ventrals more than 310 ***melanocephalus***
- Head and neck color yellowish to reddish-brown, black markings above the eyes, ventrals fewer than 305..... ***ramsayi***

Apodora

Black skin pigmentation visible between head scales, rostral and (at least) second supralabial with shallow pits, prefrontals small or absent, ventrals 358–374, 83–88 subdaudals, low number of teeth on the maxilla***papuanus***

Bothrochilus

Uniform brownish-black head barely distinct from the head, orange color body ring pattern that fades with age, lack of rostral and supralabial pits, low number of dentary teeth***boa***

Broghammerus

1. Iris color olive-golden, midbody scale rows fewer than 64, ventrals fewer than 290 ***timoriensis***
- Iris color bright yellow to golden-orange, midbody scale rows 64 or more, ventrals more than 290 **2**
2. Ventrals more than 330..... ***reticulatus saputrai***
- Ventrals fewer than 330 **3**
3. Ventrals fewer than 304 ***reticulatus jampeanus***
- Ventral more than 304..... ***reticulatus reticulatus***

Leiopython

1. Dorsal color dark gray or blackish-blue fading to white on the flanks ***boserae***
- Dorsal color yellow to brownish-violet fading to yellowish on the flanks..... **2**
2. One pair of enlarged parietals ***huonensis***
- Two pairs of enlarged parietals **3**
3. Whitish postocular spot absent ***fredparkeri***
- Whitish postocular spot present **4**
4. Two prefrontals, two or more loreals present..... ***bennettorum***
- One prefrontal, one loreal present..... **5**
5. Subocular absent, three labials enter the orbit ***albertisii***
- Subocular present, only two labials enter the orbit..... ***biakensis***

Liasis

1. Body unpatterned **2**
- Body patterned **4**
2. Midbody scale rows fewer than 50, ventrals fewer than 300..... ***fuscus***
- Midbody scale rows more than 50, ventrals more than 300..... **3**

- 3. Midbody scale rows 61–72, 355–377 ventrals *olivaceus olivaceus*
- Midbody scale rows 58–63, 374–411 ventrals *olivaceus barroni*
- 4. Eyes pale or white *mackloti savuensis*
- Eyes silvery or dark 5
- 5. Chin and infralabials yellowish of color, brownish ground color, females larger than male..... *mackloti mackloti*
- Chin and infralabials of white color, grayish to reddish-brown ground color, males larger than females *mackloti dunni*

Morelia

- 1. Dorsal scales rough or keeled, large round frontal scale *carinata*
- Dorsal scales smooth, frontal of different shape partly fragmented 2
- 2. Two or more enlarged well-defined pairs of parietals 11
- Small granular or fragmented head scales 3
- 3. Body ground color shiny green with unpatterned head..... *azurea, viridis*
(Note: *M. azurea* is a cryptic species, only distinguishable by genetic markers)
- Body ground color pale cream; red or brown with head pattern..... 4
- 4. Loreal scales fewer than 28..... 5
- Loreal scales more than 28 *bredli*
- 5. Body pattern of speckled appearance *spilota spilota*
- Body pattern of pale and dark elements 6
- 6. Lack of partial structure in the posterior margin of the nasal scale..... 7
- Presence of partial structure in the posterior margin of the nasal scale..... 8
- 7. Nostril not in contact with the internasals *spilota imbricata*
- Nostril in contact with the internasals..... *spilota metcalfei*
- 8. Dorsal color dark 9
- Dorsal color pale cream with diagonal pale bars and lighter pattern, head pattern smudgy appearance..... *spilota mcdowellii*
- 9. Body ground color dark brown or blackish *spilota cheynei*
- Body ground color shade of brown or reddish-brown 10
- 10. Body pattern consists of 60–70 pale rings *spilota variegata*
- Body pattern with pale rings but connected by two lateral pale lines..... *spilota harrisoni*
- 11. Ventrals fewer than 400, subcaudals fewer than 125, infralabials fewer than 22, parietal scales not fragmented 12
- Ventrals more than 400, subcaudals more than 155, infralabials more than 22, parietal scales fragmented..... *oenpelliensis*
- 12. Overall glossy blackish head and body color with white or yellowish bars in the labials..... *boeleni*
- Overall head and body color variable 13
- 13. Neck bar pattern absent 14
- Neck bar pattern present..... 16
- 14. Postocular stripe absent..... 15

- Postocular stripe present *nauta*
- 15. Suboculars absent, single supraocular..... *kinghorni*
- Suboculars present, 2–3 supraoculars..... *clastolepis*
- 16. Iris color golden, 0–2 interparietals..... *amethistina*
- Iris color red, 2–3 interparietals *tracyae*

Python

- 1. Small or fragmented head scales 2
- Large, well-developed head scales 4
- 2. Midbody scale rows fewer than 75, subcaudal scale counts fewer than 50 ... 3
- Midbody scale rows more than 75, subcaudal scale counts more than 60
..... *natalensis*
- 3. Ventral scale counts fewer than 210, subcaudals fewer than 38 *regius*
- Ventral scale counts more than 250, subcaudals more than 46 *anchietae*
- 4. Ventral scale counts fewer than 200 5
- Ventral scale counts more than 200..... 7
- 5. Ventral scale counts fewer than 167 6
- Ventral scale counts more than 167..... *brongersmai*
- 6. Anterior pair of parietals not in contact or are only weakly contacting *curtus*
- Anterior pair of parietals in broad contact at the medial structure
..... *breitensteini*
- 7. Dorsal midbody scale rows fewer than 75 8
- Dorsal midbody scale rows more than 75..... *sebae*
- 8. Suboculars absent 9
- Suboculars present, separating the supralabials from the orbit..... 10
- 9. Two preoculars present, subcaudals 66–70 *molurus molurus*
- Three preoculars present, subcaudals 57–65 *molurus pimbura*
(Additional diagnostic information: longitudinal pink marking above the eyes, fewer dark blotches that also invade the ventral scutes)
- 10. Pale centered saddles, pale-centered brown blotches..... *bivittatus bivittatus*
(Additional diagnostic information: attains larger size up to 5m in length)
- Prevalent saddles with pale margins, increased incidence of ocellic blotches (more *molurus*-like) *bivittatus progschai*
(Additional diagnostic information: does not exceed 2.5 m in total length)

