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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

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ABSTRACT.—**This study is the first comprehensive systematic study on the python genus *Leiopython* Hubrecht 1879 native to New Guinea. The taxonomic arrangement recently made is critically reviewed, and proper descriptions for taxa herein recognized as valid are provided. Twenty external morphological characters were recorded from 90 preserved specimens from throughout most of the distribution of the genus. Thirteen characters were used with principal coordinate analysis to test the diversity of populations from different distributions. Additional evidence for some species was obtained by maximum parsimony and maximum likelihood analysis of mitochondrial DNA sequences (cytochrome *b* gene) taken from GenBank. Besides three conventional taxa, two new species from the mainland, and one new island species were recognized in accordance with the evolutionary species concept. Additionally, a new locality record is provided.**

The island of New Guinea is known for its extremely diverse flora and fauna and for its high level of species endemism (e.g., McDowell, 1984; Heads, 2002; Kraus and Allison, 2002; Austin, 2006). This megadiversity may result from a variety of climates (McApline et al., 1983; Prentice and Hope, 2007) and habitats (Austin, 2006) such as tropical savannahs, mixed lowland forests, rain forests, montane forests, and even alpine vegetation at higher altitude. The herpetofauna of New Guinea currently consists of 109 snake species (Allison, 2007), including several endemic python species (Rawlings et al., 2004; Allison, 2007). However, some areas are difficult to access, and it is likely that many species remain undiscovered (e.g., Austin, 2006). Just recently, O'Shea et al. (2004) reported the occurrence of *Antaresia maculosa* in the Western Province, previously unknown from New Guinea.

The genus *Leiopython* (Serpentes: Pythonidae) represents medium-sized, unpatterned, terrestrial, and nocturnal snakes (Barker and Barker, 1994; O'Shea, 1996; Kend, 1997) that are widely distributed throughout tropical and subtropical New Guinea and closely associated with various wetland habitats. Several populations occur on offshore islands (McDowell, 1975; Barker and Barker, 1994; O'Shea, 1996), such as Salawati Island (terra typical of *Leiopython gracilis* Hubrecht, 1879), Biak Island (Brongersma, 1956), and the remote Mussau Island of the Bismarck Archipelago (McDowell, 1975). Various authors (e.g., McDowell, 1975; Cogger et al., 1983; Barker and Barker, 1994; O'Shea, 1996) have mentioned the occurrence of *Leiopython* on the northern Torres Strait Islands of Australia. A detailed description of such specimens can be found in Barker and Barker (1994), stating that populations would occur on the islands of Dauan, Saibai, and ''possibly Boigu.'' Nevertheless, reports of the occurrence on the mainland of Australia around Pascoe River, Cape York Peninsula (Ehmann, 1992) remain unconfirmed (Barker and Barker, 1994), as does the occurrence on Aru Island, mentioned by Hoser (2000). Some authors assumed that, in the former case, specimens may have been confused with *Liasis fuscus* Peters (Kend, 1997; O'Shea, 2007). However, the occurrence of *Leiopython* on Normanby Island (McDowell, 1975; McDiarmid et al., 1999) appears dubious because McDowell (1975) had erroneously assigned Bara Bara to the Normanby Island, rather than to the mainland of Papua New Guinea (PNG) at the Milne Bay Province as stated by Boulenger (1898) and Koopman (1982).

Although specimens of the genus *Leiopython* Hubrecht 1879 are well represented in natural history museum collections around the world, this genus remains taxonomically rather understudied. Even though the genus was considered monotypic until recently, two distinct populations, separated by the Central Mountain Range, were recognized in the international pet trade for over the last 30 years (McDowell, 1975; Parker, 1982; Barker and Barker, 1994; O'Shea, 1996), called the ''golden'' or ''northern race'' and the ''black'' or ''southern race.'' Nevertheless, published locality data of specimens and distributional ranges were always assigned to

Leiopython albertisii in the literature (e.g., Parker, 1982; McDowell, 1984; Barker and Barker, 1994; A. Allison, Reptiles and amphibians of the trans-Fly region, New Guinea, report submitted to World Wildlife Fund, South Pacific Program, WWF PNG Madang Office, Madang, Papua New Guinea, available at http://www.wwfpacific.org.fj/publications/png/Transfly_reptiles_report.pdf [February 2008], unpubl. data. 2006).

Taxonomic History.—Hubrecht (1879), obviously unaware of the prior description of *Liasis albertisii* by Peters and Doria 1878, described a new species based on a single specimen from Salawati Island. He introduced it to his new genus *Leiopython*, an intermediate genus between *Liasis* Gray 1842 and *Nardoa* Gray 1842 (generic name was preoccupied for a starfish, *Nardoa* Gray 1840) as *Leiopython gracilis*, characterized by a pitted rostral and the presence of pits in the supralabials. However, Boulenger (1893) did not follow Hubrecht's proposal and synonymized *Leiopython* with *Liasis*. Later, Stull (1935) placed the taxon *albertisii* as a subspecies of *Liasis fuscus* Peters 1873 and, although she had not provided reasoning for her action, Stull's proposal was widely followed by subsequent workers (e.g., Loveridge, 1948; De Haas, 1950; Brongersma, 1953, 1956). Nevertheless, after examining the skulls of the two taxa, Worrell (1961) reassigned specific level to *albertisii*. The ambiguous taxonomic status of the type species of *Liasis* (Gray had not designated a type species for *Liasis*) prompted Cogger et al. (1983) to synonymize *Liasis* with *Bothrochilus* Fitzinger 1843 (for discussion, see Stimson and McDowell, 1986). Later, Underwood and Stimson (1990) conducted a phylogenetic study and synonymized *Bothrochilus* and *Liasis* with *Morelia* Gray 1842. Kluge (1993) contradicted this study in parts, examining 121 external and internal morphological and behavioral characters in a phylogenetic study, finding evidence for the distinction of the taxon *albertisii* from other python species and, therefore, resurrected the oldest available synonym *Leiopython* Hubrecht. More recently, Hoser (2000) introduced two new subspecies and one species to the genus, but subsequent workers did not follow this taxonomic arrangement because of inadequate descriptions and the lack of evidence for the taxa described (see Wüster et al., 2001; Williams et al., 2006). Besides the weakly defined diagnoses and erroneous authorship (i.e., assigning *Leiopython albertisii* to Gray 1842 instead of Peters and Doria 1878), emendation of the subspecific names is required (Wüster et al., 2001) because of erroneous latinization (*barkeri* and *bennetti* were both named after sets of two persons). A recent study on the phylogeny of pythonid snakes (Rawlings et al., 2008) identified *Leiopython* Hubrecht and *Bothrochilus* Fitzinger as sister species. Rawlings et al. (2008) suggest their placement into a single genus, namely *Bothrochilus* Fitzinger, as the oldest available synonym. However, this placement will require further study.

Aim of the Study.—In this paper, I critically evaluate the current taxonomic arrangement and provide detailed descriptions of the taxa recognized as valid. I also provide new morphological and ecological data on the genus that may serve for future research. The examination of a larger number of specimens from throughout the distribution of the genus makes this the first comprehensive systematic study of the genus. It is hypothesized that the genus forms a species complex comprising several species under the evolutionary species concept (ESC; sensu Frost and Kluge, 1994). The hypothesis of species diversity was tested using principal coordinate analysis of morphological characters. Additionally, the analysis of available mitochondrial DNA (cytochrome b) sequences provides evidence for the separation of the so-called northern and southern races.

Materials and Methods

Museum Abbreviations.—Museum abbreviations used in this paper are those of Leviton et al. (1985) with the following additions of International Commission on Zoological Nomenclature (ICZN); School of Biological Sciences, Bangor University, Wales, UK (UWB); ''Vida Preciosa'' International, Boerne, Texas, USA (VPI); and Southeastern Louisiana University, Hammond, Louisiana, USA (SELU).

Specimens Examined.—A total of 90 preserved specimens from natural history museum collections was examined (Appendix 1). Additionally, data was obtained from literature sources (Peters and Doria, 1878; Hubrecht, 1879; Brongersma, 1953, 1956; McDowell, 1975; Underwood and Stimson, 1990; Kluge, 1993). Furthermore, curatorial staff members of natural history museums provided scale counts along with pictures of some specimens (see Acknowledgments). The numbers of available specimens from some localities (Salawati, Biak, Mussau and Emirau Islands, Enga Province, PNG, the upper Fly-River region of the Western Province, PNG, and Merauke, Indonesia) were small, and specimens from other localities (e.g., Torres Strait Islands, Australia and southwestern Papua) were unavailable for this study. Data and pictures from one specimen (road kill) from the Milne Bay Province, near Alotau, were provided by anonymous.

TABLE 1. Overview of morphological characters used for the multivariate morphometric analysis.

Character	Acronym	Character states	As characterized by
Number of dorsal midbody rows	DMB	Meristic	Underwood and Stimson (1990) Character 37; Kluge (1993) Character 98
Number of ventrals	VEN	Meristic	Underwood and Stimson (1990) Character 34; following Dowling (1951)
Number of subcaudals	SCA	Meristic	Underwood and Stimson (1990) Character 35 (in part); Kluge (1993) Character 96
Number of supralabials	SPL	Meristic	Underwood and Stimson (1990) Character 7–9; Kluge (1993) Characters 88–90 (in part)
Number of infralabials	INL	Meristic	
Number of postoculars	POC	Meristic	Underwood and Stimson (1990) Character 11; Kluge (1993) Character 77
Number of supralabials entering the eye	SLE	Meristic	Kluge (1993) Character 90
Presence of suboculars	SOC	0 = absent; 1 = present	Kluge (1993) Character 79
Number of loreals	LOR	Meristic	Kluge (1993) Character 87
Number of prefrontals	PFR	Meristic	Kluge (1993) character 84 and 85
Number of parietal scale pairs	PAR	Meristic	Underwood and Stimson (1990) Character 4; Kluge (1993) Character 76 (in part)
Parietal scales that border the frontal in contact at the median line	PML	0 = no; 1 = yes	Underwood and Stimson (1990) Character 5, included in Kluge's mutlistate Character 76
Whitish spot on the postoculars	SPT	0 = absent; 1 = present	Whitish markings on the postoculars and sometimes on the supraocular as well.

Morphological Characters.—Twenty external morphological characters were recorded based on characters found taxonomically important by previous workers (e.g., McDowell, 1975; Underwood and Stimson, 1990; Kluge, 1993). Species-specific characters such as the whitish markings on the postoculars were used as well. The definition of head scales follows Underwood and Stimson (1990) and Kluge (1993; Table 1). Loreal scales were defined as the scales between the nasal scales and the preoculars. Interparietals separate the parietal scales at the median line or lay between the anterior and posterior pair of parietal scales. Anterior temporals are scales that directly follow the postoculars and are in between the supralabials and the parietal scales. Posterior temporals directly followed the anterior ones (also see O'Shea, 1996; Fig. 1). Ventral scale counts were in accordance with Dowling (1951). The whitish markings on the postoculars are either present or absent. Based on my own observations in juveniles and adults, these markings develop within the first year of age, depending on the growth of the specimens.

Previous workers (e.g., Brongersma, 1956; McDowell, 1975; Shine and Slip, 1990) did not find sexual dimorphism in size in this species. In fact, Brongersma (1956) reported distinctly larger anal spurs in males, but this seems to be only an insignificant trend (Shine and Slip, 1990). Therefore, males and females were analyzed jointly.

Basic Statistics.—The morphological characters of each population (with $N > 7$) were tested for outliers using Grubbs's test (with 95% significance). Specimens that showed outliers in one or more characters were marked accordingly. Statistically significant differences in meristic characters between populations were tested with Kruskal-Wallis (KW)-test and with chi-square (χ^2)-test for binary coded characters. KyPlot 2.0 beta 15 (Yoshioka, 2002) was used for the basic statistics. Means are given ± 1 SD.

Construction of OTUs.—Thirteen operational taxonomic units (OTU's) were constructed a priori based on distribution (e.g., geographically isolated or disjunctive populations); currently accepted knowledge of the genus (recognition of two color races in common usage as stated earlier) and abiotic data (temperatures, humidity and annual rainfall) were obtained from McAlpine et al. (1983). Additionally, the ''UNKNOWN'' OTU consists of two specimens that were included in the analysis without adequate locality data (BMNH 1892.3.15.1–2 labeled only ''New Guinea'') to test their species affiliation. Another OTU contained a single specimen from Bulolo, Morobe Province, PNG (Table 2). Three preserved specimens from the pet trade (ZFMK 20331–20332, SFM 72616) although with inadequate locality data (only labeled ''Irian Jaya'') were included in the analysis as ''NORTH1'' OTU.

Morphometric Analysis.—Principal coordinate analysis (PCoA; Gower, 1966) was performed

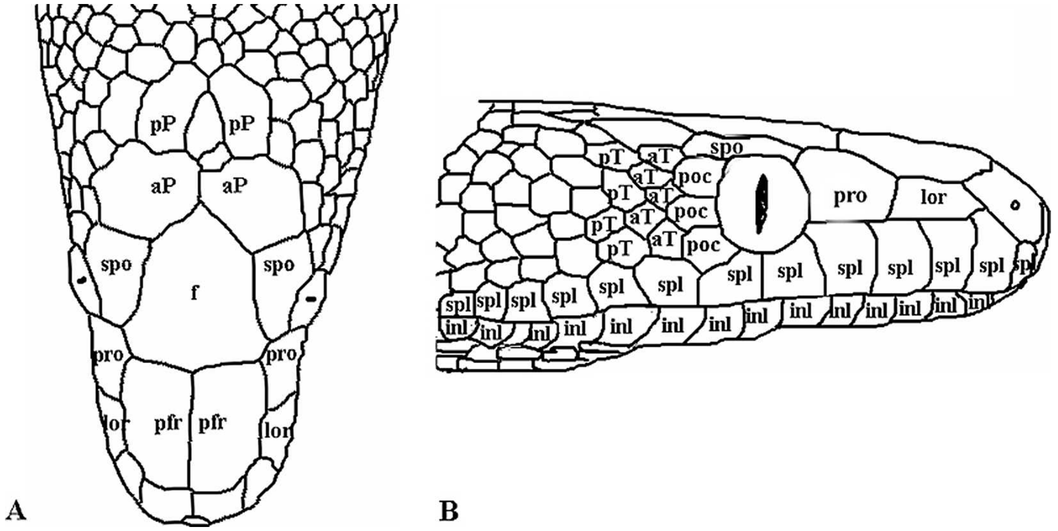

FIG. 1. Simplified illustration of the head scalation in *Leiopython* (RMNH R-4796, holotype of *Leiopython gracilis* Hubrecht) A: dorsal surface B: right lateral view. aP - anterior parietal, aT - anterior temporal, f - frontal, lor - loreal, inl - infralabial, pfr - prefrontal, poc - postocular, pro - preocular, pT - posterior temporal, spl - supralabial, spo - supraocular.

with MVSP 3.13p (Kovach, 1999), using the Gower General Similarity Coefficient for mixed data sets. Data were Log-e transformed before analysis. PCoA has an advantage over PCA because it computes the distances between OTU's rather than the correlation between characters. Therefore, all characters found statistically significant among populations were used. Furthermore, PCoA does not assume normal distribution of the data and, therefore, is applicable for mixed data sets (Gower, 1966).

Molecular Data.—Three sequences of mtDNA (cytochrome *b* gene) were obtained from the NCBI GenBank. Additionally, two sequences, one from a specimen from Madang, and a second from a specimen from the Milne Bay Province near Alotau, were provided (Appendix 2). Two of the GenBank sequences (U69835–U69836), submitted by Campbell (1997) were provided without proper locality data and, therefore, were backtracked to the LSUMZ (B. N. Campbell, pers. comm.). D. Dittmann from the LSUMZ provided locality data from the

TABLE 2. Operational taxonomic units (OTU's) used for the morphometric analysis. The last column (*N*) shows the sample size of each OTU. Additionally, two specimens (BMNH 1892.3.15.1–2) were included to the analysis without adequate locality to test their affiliation.

Id	Acronym of OTUs	Localities	*N*
1	NORTH1	Papua (Salawati Island, Sorong, Manokwari, Fak Fak)	13
2	NORTH2	Sepik and Madang Provinces, Eastern Jayapura and north coast of PNG	10
3	ENGA	Enga Province, Wabag, Sau River Region	2
4	WAU	Morobe Province, Wau, Highlands	5
5	BULOLO	Morobe Province, Bulolo, Highlands	1
6	KARIM	Simbu Province, Karimui, Bomai Tive Plateau	13
7	SOUTH1	Central Province, (Port Moresby Sogeri), Milne Bay Province, PNG, (Alotau), Oro Province (Popondetta)	18
8	SOUTH2	Western Province, trans-Fly river region	4
9	HUONP	Morobe Province: Huon Peninsula, Lae, Finschhafen, Madang Province: Ramu River (near Dumpu)	15
10	BIAK	Biak Island	2
11	MUSS	Mussau Island	2
12	EMIR	Emirau Island	3
13	UNKNOWN	Two specimens with uncertain locality data: BMNH 1892.3.15.1–2, unknown locality	2
	Total		90

tissue sample database of these two samples (pers. comm.). The locality data of the sequence U69836 was found erroneous (stating that *Leiopython* would occur at New Britain) and, therefore, was verified and corrected to the locality of Madang by H. G. Cogger (pers. comm.). One sequence (AF241406), used as the outgroup in Harvey et al. (2000), is assumed to be from a specimen from Merauke, Indonesia (D. G. Barker, pers. comm.). Two cytochrome *b* gene GenBank sequences (AF241399 and AF241404) from *Morelia amethistina* were used as outgroups (Appendix 2).

Phylogenetic Analysis.—Sequences were initially aligned by eye and by the built-in alignment algorithm (ClustalW) in MEGA 3.1 (Kumar et al., 2004). Because of variation in sequence length (642–1,114 base pairs), only the first 642 base pairs (bp) were used, and sites containing gaps were excluded. Phylogenetic analysis of the remaining 624 sites was conducted using maximum parsimony (MP) and maximum likelihood (ML) methods as implemented in PAUP* 4.0b10 for Windows (D. L. Swofford, Sinauer Associates, Sunderland, MA, unpubl. data, 2002). Trees were rooted using *Morelia amethistina* sequences as the outgroup (Appendix 2). In the MP analysis, data were treated as equally weighted, and phylogenetic inference was performed by exhaustive search. Additionally, 2,000 bootstrap replicates were performed using heuristic search with tree bisection-reconnection (TBR) branch swapping and random stepwise addition. ML was performed using these parameters as well along with the substitution model (HKY85 + G) estimated by Modeltest 3.7 (Posada and Crandall, 1998). This model revealed 47 distinct data patterns. A genetic distance matrix was computed using the substitution model estimated by Modeltest.

RESULTS

General Patterns of Parietal Scales.—The examination of specimens from throughout the distribution uncovered specific patterns in the scale arrangement of the parietal region (Fig. 2). In specimens from the northern part of New Guinea, including the populations from the Bismarck Archipelago, Biak, and Salawati Islands, two pairs of parietals are present, whereas only one pair was recognized in specimens from the southern parts of New Guinea and from the Huon Peninsula. This is in agreement with McDowell's (1975) findings, and O'Shea (1996: fig. 12) identified two pairs of parietals in a specimen from Siar, Madang Province, PNG. In northern species, the anterior pair is most often (93%, $N = 30$) in contact at the median line followed by a second pair of large scales often separated from the median line by one or more small interparietals (Fig. 2A). Specimens from the southern part show a large pair of parietals followed by two smaller scales separated from the median line by an elongate scale that gets wider posteriorly (96%, $N = 22$). This pattern (Fig. 2B) was found in all southern specimens from Alotau on the east coast of PNG to Merauke in the Papua Province. Specimens from the Huon Peninsula (93%, $N = 15$), as well as two specimens from the Enga Province (100%, $N = 2$), showed a large pair of parietal scales followed by small, irregular scales (Fig. 2C). Specimens from Karimui and the Tive Plateau both in the Simbu Province at an elevation of 1,000–1,500 m have two pairs of parietal scales with the posterior ones being slender and elongate (83%, $N = 12$), often separated at the median line by an elongate interparietal scale (Fig. 2D). Further information and schemata of the parietal structures can be found at http://www.leiopython.de.

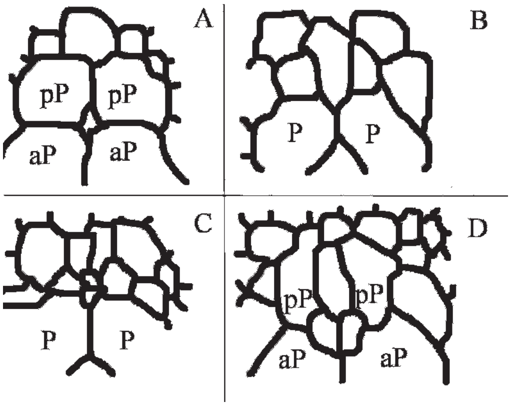

FIG. 2. Simplified general patterns of the parietal region. A: two pairs of parietals with the anterior ones (aP) in contact at the median line and the posterior ones (pP) in either contact at the median line or separated by one or more small interparietals ("*albertisii* type"). B: one pair of large parietal scales followed by two small scales separated at the median line by an elongate scale that gets wider posteriory ("*hoserae* type"). C: one pair of large parietal scales followed by small, irregular scales ("*huonensis* type"). D: two pairs of parietal scales, the anterior ones large, the posterior ones slender and elongate often separated at the median line by an elongate interparietal about the length of the posterior parietal scales. Small interparietals are often present in the center of the anterior and posterior parietals ("*fredparkeri* type").

Morphological Analysis.—Some characters (number of anterior and posterior temporals, parietal scales in contact with the postoculars) were excluded from the analysis because of little variation within the genus or because of random

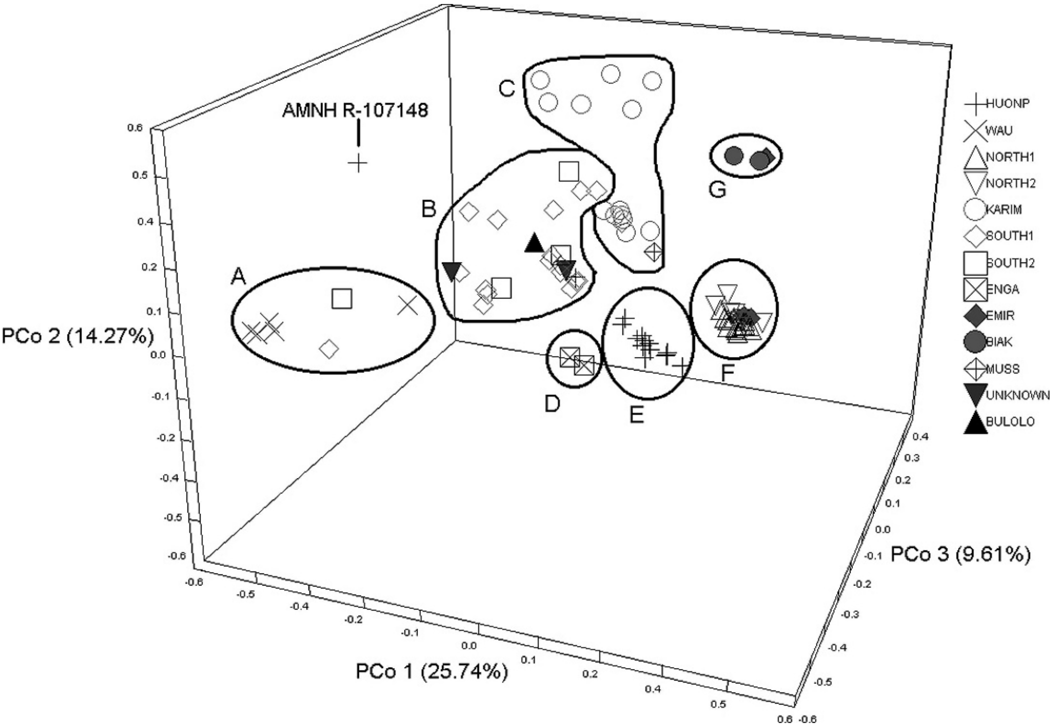

FIG. 3. Scatter plot of the PCoA. The three axes comprised 49.63% of the total variance. See text for abbreviations.

distribution throughout different populations. Head and body color were excluded from the analysis, because of possible fading of colors during prolonged storage in preservative. Nevertheless, color pattern was considered in live specimens. The patterns of the parietal region as described above may be helpful to identify species but were not included in the morphometric analysis.

In the scatter plot (Fig. 3) of the PCoA, the first axis (PCo 1) summarized 25.7% (eigenvalue = 6.311), the second axis explained 14.3% (eigenvalue = 3.499), and the third axis (PCo 3) explained 9.6% (eigenvalue = 2.357) of the total variance. The scatter plot revealed the existence of seven clusters. Besides the ''WAU'' OTU, cluster A, which represented the taxon *bennettorum*, also included two specimens from the ''SOUTH'' OTU's, one from Port Moresby (MCZ R-145941, ''SOUTH1'') and another one from Oslobip (MCZ R-129393, ''SOUTH2'') because of their aberrant morphology from other specimens of the ''SOUTH'' OTU's. Both specimens showed two pairs of loreals and prefrontals (see subsection Variation in *Leiopython hoserae*). Cluster B comprised four OTU's, of which the two ''SOUTH'' OTU's corresponded to the taxon *hoserae*. The considerable overlap of the ''UNKNOWN'' OTU with the ''SOUTH'' OTU's suggested an affiliation of these specimens to this taxon. However, the ''BULOLO'' OTU was also found within this cluster, but it is difficult to draw conclusions on the taxonomic placement of this population based on only one specimen. The third cluster (C) primarily contained the ''KARIM'' OTU. However, the analysis was not able to separate two specimens, from Kokoda (MCZ R-84333, ''SOUTH1'') and another from Mussau Island (ZMUC R-5445, ''MUSS'') from this OTU in morphometric space. Nevertheless, the Karimui population was assumed geographically isolated from other populations, and, along with diagnosable differences in morphology, it is herein regarded as a new species *Leiopython fredparkeri* sp. nov. The two specimens from the Enga Province (''ENGA'' OTU) formed a tight cluster (D) in morphometric space but were morphologically indistinguishable from specimens from the Huon Peninsula (''HUONP'' OTU), represented by the neighboring cluster (E) and, therefore, were not recognized taxonomically. One specimen (AMNH R-107148) from the ''HUONP'' OTU was detected as an outlier (Grubbs-test, 95% significance; $N = 15$, PG = 2.372) in several morphological characters (see also McDowell, 1975) and was specially marked in the ordination plot. The cluster F comprised four

OTUs (''NORTH1,'' ''NORTH2,'' ''MUSS,'' and ''EMIR'') with the ''NORTH1'' and ''NORTH2'' OTUs corresponding to the conventional taxon *albertisii*. These four OTUs formed a tight cluster with considerable overlap, indicating few morphological differences between the populations represented by the OTUs. Therefore, specimens from Mussau (''MUSS'' OTU) and Emirau (''EMIR'' OTU) islands are herein considered conspecific with *albertisii*, but further research is needed to determine the actual taxonomic status of these island populations. Nevertheless, specimens from Biak Island (''BIAK'' OTU) were found distinct from *albertisii* forming a separate cluster (G) and are herein regarded as a separate species *Leiopython biakensis* sp. nov.

Clinal Variation.—Clinal variation was found in scalation patterns in the two widespread species *Leiopython albertisii* and *Leiopython hoserae*. In *Leiopython albertisii*, ventral scale counts increase from east to west as reported previously by McDowell (1975). Furthermore, the number of subcaudal scales and maximum midbody scale rows were highest in the west at Salawati Island and in the latter case were lowest in the east at Emirau Island. In *Leiopython hoserae*, the number of subcaudal scales was higher in specimens of the Western Province than they were in specimens found in the east, at the Central and Milne Bay Provinces. No significant variation was observed in other characters.

Polymorphism.—Polymorphism was not detected in populations of *Leiopython albertisii*. However, polymorphic patterns were observed in head scalation in populations of *Leiopython hoserae* from the Central and the Western Provinces. Variation within populations was found in the number of infra- and supralabials, the number of supralabials entering the eye, and in the number of postoculars, but little variation was found in other morphological characters (Table 3).

Phylogenetic Analysis.—Of the 624 bp, 525 were constant; 31 sites were parsimony uninformative, and 68 were parsimony informative. The most parsimonious tree (Fig. 4A) was obtained by exhaustive search (tree length [TL] = 117; consistency index [CI] = 0.940; homoplasy index [HI] = 0.060; retention index [RI] = 0.921; rescaled consistency [RC] index = 0.965). Modeltest estimated HKY85+G (base frequencies: A = 0.3108, C = 0.3315, G = 0.1149, T = 0.2428; Ti/Tv ratio = 8.7913; shape parameter = 0.0139) as the most adequate substitution model for the ML analysis. Seventy-four distinct data patterns were found under this model. The best ML tree (Fig. 4B) was evaluated (of 945 trees) by exhaustive search (TL = 119, likelihood-ln L 1404.64980, CI = 0.924, RI = 0.898, RC = 0.830, HI = 0.076, G-fit = −65.750). The genetic distance was about 0.6% within species, whereas

TABLE 3. Scale comparison and basic statistics of the taxa of the genus *Leiopython* (BMNH 1892.3.15.1–2 were excluded, see text). Character acronyms as given in Table 1. Numbers in parentheses represent mean values and ± is SD. The following exceptions must be considered: [1] without MVZ 74917, [2] without MVZ 40848, [3] without ZMUC R-5445, [4] except MVZ 40847, [5] except AMNH R-107148, [6] except BMNH 1922.11.24.29, and [7] except CAS 103384 and 135211.

Character	*albertisii*	*bennettorum*	*hoserae*	*fredparkeri* sp. nov.	*huonensis* sp. nov.	*biakensis* sp. nov.
Sample size	30	5	22	13	15	2
DMB	43–51 [1] (47.1) ± 2.53	49–54 (51.6) ± 2.30	45–52 (48.1) ± 1.50	47–51 (49.1) ±1.04	43–55 (48.3) ± 2.99	45–47 (46) ± 1.41
VEN	262–283 [1] (274.5) ± 4.83	263–274 (268.4) ± 4.45	264–278 (272.6) ± 4.30	266–277 (270.5) ± 3.15	258–282 (268.2) ± 6.12	270–272 (271) ± 1.41
SCA	65–79 [1] (71.5) ± 2.85	62–70 (66.0) ± 3.39	64–77 (68.7) ± 3.33	63–76 (69.8) ± 3.35	65–78 (70.6) ± 3.94	65–70 (67.5) ± 3.54
SPL	12–13 (12.9) ± 0.28	13	12–14 (13.1) ± 0.37	12–14 (13.0) ± 0.32	12–13 (12.7) ± 0.45	11–12 (11.8) ± 0.35
IFL	15–17 [1, 2] (15.9) ± 0.38	16–18 (17.0) ± 0.35	15–18 (16.6) ± 0.66	16–18 (17.2) ± 0.59	15–17 (16.1) ± 0.59	14–16 (15.3) ± 1.1
POC	2–4 (3.0) ± 0.25	3–4 (3.5) ± 0.35	2–4 (3.0) ± 0.35	2–4 (3.1) ± 0.45	3–4 (3.2) ± 0.24	3
SLE	2–3 (3.0) ± 0.18	3	2–3 (2.8) ± 0.37	2–3 (2.7) ± 0.43	2–3 (2.9) ± 0.26	2
SOC	0 [4]	0	0–1 (0.2) ± 0.36	0–1 (0.5) ± 0.52	0 [5]	0
LOR	1	2–3 (2.3) ± 0.45	1–2 (1.1) ± 0.35	1–2 (1.1) ± 0.13	1 [5]	1
PFR	1	2	1–2 (1.1) ± 0.35	1	1 [5]	1
PAR	2 [7]	1	1–2 (1.0) ± 0.21	2	1	2
PML	yes (93%)	no (100%)	yes (96%)	yes (85%)	yes (93%)	yes (100%)
SPT	present [3]	absent	absent	absent	present [5, 6]	present

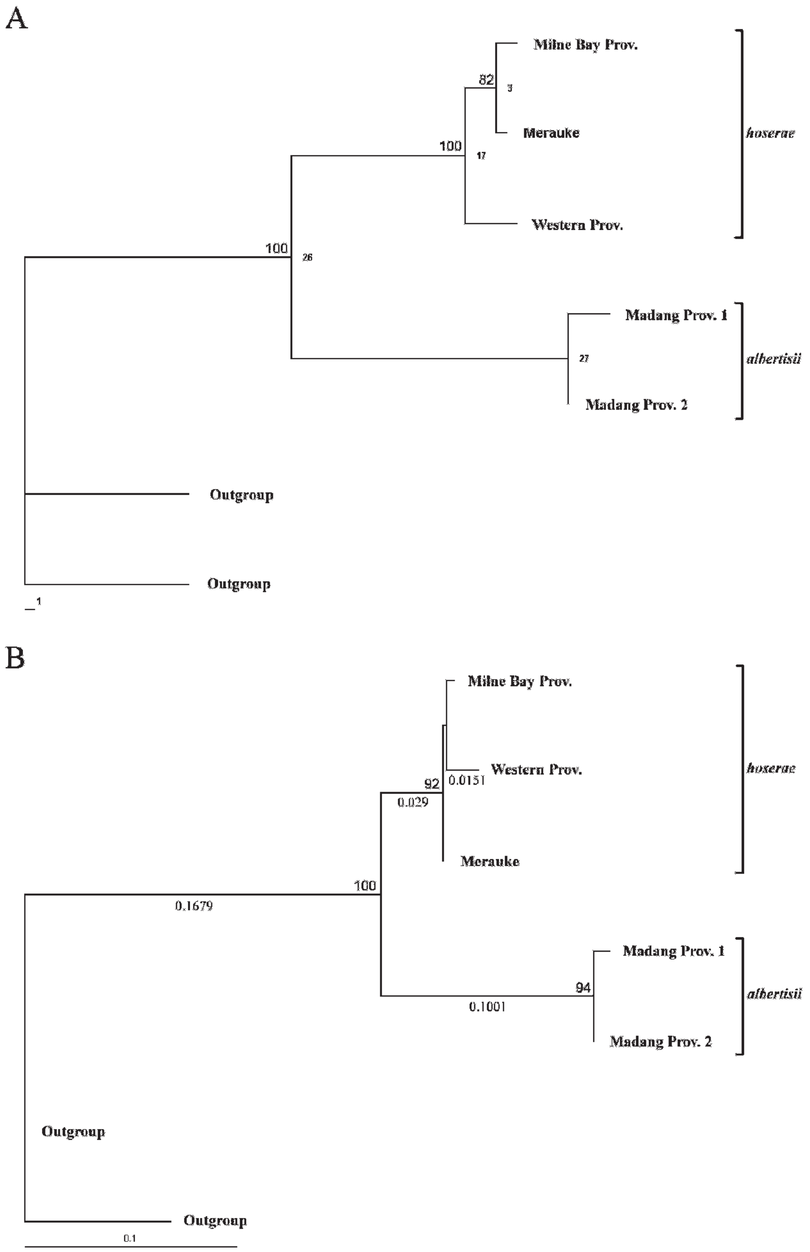

FIG. 4. Phylograms of the maximum parsimony (MP) (A) and the maximum likelihood (ML) tree (B). Numbers above the branches represent bootstrap proportions. Bootstrap proportions less 50% are not shown. Numbers to the right of the internal nodes in the MP tree, and below the branches in the ML tree represent branch lengths. The ML tree differs from the MP tree only by the arrangement of the Merauke and Western Province samples within the branch representing *Leiopython hoserae*.

the distance between the species was between 8.7 and 9.3%.

SPECIES ACCOUNTS

Leiopython albertisii Peters and Doria 1878

Synonymy.—Liasis alberitisii Peters and Doria, 1878

Leiopython gracilis Hubrecht, 1879
Liasis albertisii Boulenger, 1893
Liasis fuscus albertisii Stull, 1935

Liasis fuscus albertisi Capocaccia, 1961
Liasis fuscus albertisii Stimson, 1969
Liasis albertisii Switak, 1973
Liasis albertisii McDowell, 1975
Bothrochilus albertisii Cogger, Cameron, and Cogger, 1983
Lisalia albertisii Wells and Wellington, 1984
Morelia albertisii Underwood and Stimson, 1990
Leiopython albertisii Kluge, 1993
Leiopython albertisii McDiarmid et al., 1999
Leiopython albertisii albertisii Hoser, 2000

Syntypes.—Two specimens from Papua collected at Kapoar [= Fak Fak regency], Onin peninsula (MSNG 29990) by Mr. L. M. D'Albertis on April 1872 and at Andai (near Dorei) [=Manokwari regency], Birds Head Peninsula (MSNG 29989) collected during June 1875 by Beccari. The present state of disposition of the syntypes is unknown (see also McDowell, 1975).

Diagnosis.—*Leiopython albertisii* is distinguishable from *Leiopython hoserae*, *Leiopython bennettorum*, and *Leiopython huonensis* sp. nov. by the presence of two pairs of parietals. A pair of large scales often separated from the median line by one or more small interparietal follows the anterior pair (Fig. 2A). It further differs from the former two species and from *Leiopython fredparkeri* sp. nov. by the presence of whitish postocular spots, and can easily be distinguished from *Leiopython bennettorum* in the number of loreals and prefrontals (Table 3), the average number of postoculars (KW-test: $\chi^2_1 = 14.22$, $P < 0.001$), dorsal midbody rows (KW-test: $\chi^2_1 = 7.98$, $P < 0.01$), ventrals (KW-test: $\chi^2_1 = 5.59$, $P < 0.05$), and subcaudal scales (KW-test: $\chi^2_1 = 8.54$, $P < 0.01$). *Leiopython albertisii* further differs from *Leiopython hoserae* and from *Leiopython fredparkeri* in lighter dorsal color and in having a yellowish flank (Parker, 1982; Barker and Barker, 1994; O'Shea, 1996, 2007), smaller average body size in hatchlings and adults, and additionally from *Leiopython hoserae* by molecular evidence (see Fig. 4). *Leiopython albertisii* can be distinguished from *Leiopython biakensis* sp. nov. by higher average subcaudal (71.5 ± 2.85; range = 65–79, $N = 30$ vs. 67.5 ± 3.54; range = 65–70, $N = 2$), and supralabial scale counts (12.9 ± 0.28; range = 12–13, $N = 30$ vs. 11.8 ± 0.35; range = 11–12, $N = 2$) along with a higher number of supralabials entering the eye (3.0 ± 0.18; range = 2–3, $N = 30$ vs. 2, $N = 2$).

Description.—Medium-sized unpatterned python; elongate head and snout; rostral with two to three diagonal pits; nasals with diagonal slitlike pits; one pair of internasals; 12–13 supralabials, first and second or first to third pitted and fifth to seventh entering the orbit, lateral depression dorsally on fifth and sometimes also on the sixth supralabial; 16–17 infralabials, seventh to 12th pitted and in a skin fold; single loreal and preocular scale; usually three postoculars; four to five anterior and posterior temporals; one pair of elongate prefrontals, two to three times longer than the internasals; bell-shaped frontal; two pairs of parietals (see also Peters and Doria, 1878: pl. III, fig 2), anterior ones in median contact but most often not in contact with the uppermost postoculars, posterior parietals sometimes separated by one or more interparietals at median line. Scales are smooth and arranged in 43–51 longitudinal dorsal rows; 262–283 ventrals; anal entire; 65–79 subcaudals mostly paired.

Color in Life.—The color of the dorsum is yellowish or reddish-brown to purplish-brown with an iridescence gleam, fading to lighter yellowish laterally, and white ventrally. Specimens from the Sorong peninsula are often lighter yellowish in color dorsally (D. G. Barker, pers. comm.). Specimens from the Fak Fak and Manokwari regencies, as well as from the Madang Province are more brownish-violet dorsally fading to brownish-yellow laterally and white ventrally. The dorsal surface of the head is shiny black with iridescence gleam. Supra- and infralabials are white with black vertical markings on anterior edge of supralabials, reaching into infralabials. Chin is white. Whitish markings on postoculars (sometimes on supraoculars, too) were found in all but one specimen (ZMUC R-5445, Mussau Island). This species also shows physiological color change by turning lighter at night and darker brownish-violet within a period of 20 min during the day (pers. obs.). Pictures of this species in the wild can be found in O'Shea (1996, 2007).

Color in Preservative.—Specimens in preservative show only little fading in body color, but ventral scales sometimes have turned yellowish. The dorsal surface of the head is black and the chin is white or off-white.

Variation.—In general, only little variation in morphological characters occurs in *Leiopython albertisii* throughout its distribution. Minor differences in the presence/absence and in the number of interparietals were recognized. Additionally, as already stated by McDowell (1975), ventral counts of specimens from the western part of Papua (Birds Head [including Salawati Island] and the Onin Peninsulas) exceeded those found in specimens from eastern Jayapura (near the border to PNG) and from PNG significantly (KW-test: $\chi^2_1 = 14.80$, $P < 0.001$). Nevertheless, no significant variation was found in other characters, but two specimens from the Sorong peninsula (pictures only) were morphologically aberrant from *Leiopython albertisii*. UTA R-36312 had a second pair of small posterior prefrontals and a third pair of

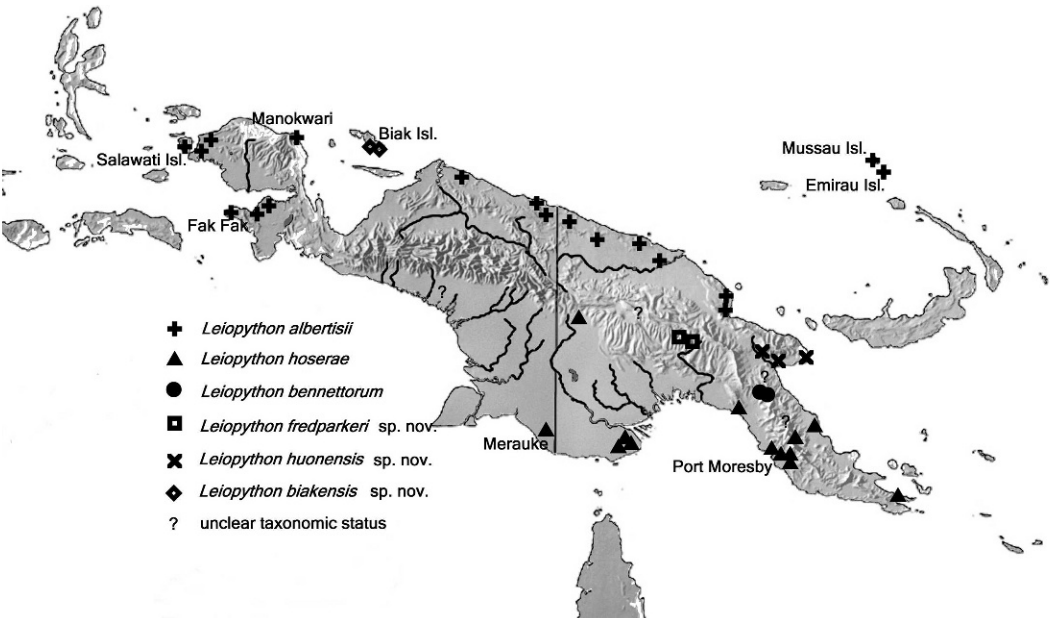

FIG. 5. Distribution map of specimens examined. The line in the center of the island separates Papua New Guinea (east) from Indonesian Papua (west). The question marks indicate populations of unclear taxonomic status. See text for details.

parietals bordering the first and second pairs laterally on one side and the loreal and preocular on the other side. In UTA R-44692, posterior parietals were fused, and enlarged temporals bordered the anterior and posterior parietals laterally.

Ontogeny.—Ontogenetic color change was observed in *Leiopython albertisii*, but not in *Leiopython hoserae*. Hatchlings are uniformly very dark grayish-black in color, including the ventral and subcaudal scales. The whitish spots are absent in juveniles but develop with age and growth. The dorsal color turns into a brownish-violet, and ventral and subcaudal scales turn white in semiadult specimens (pers. obs.). The yellowish color ventrolaterally develops at last.

Distribution.—*Leiopython albertisii* is a widespread species ranging from Sorong (including Salawati Island) and the Fak Fak regency on the Onin Peninsula to Madang at the east coast of PNG (Fig. 5). However, it remains unclear whether the distribution is disjunctive at the southeastern part of the Manokwari regency and along the north coast of the Yapen-Waropen and Nabire regencies. Nevertheless, specimens were collected at the Jayapura regency (Toem, Doromena, Joka and around the Lake Santiani), the Sanduan (former West Sepik) and East Sepik Provinces (on the foot of the Torricelli Mountains, Aitape, Mt. Somoro and Lumi, Wewak, Marienberg) and at the Madang Province (Siar, Madang, and Alexishafen), although no specimens were sighted in the Kau Wildlife area, a lowland rain-forest area near Madang (Austin, 2006). In the Morobe Province, this species is replaced by *Leiopython huonensis* sp. nov. at the southern Huon Peninsula and by *Leiopython bennettorum* at Wau.

Emirau Island Population.—The occurrence of *Leiopython* at Emirau Island, St. Matthias group in the Bismarck Archipelago is first reported herein. This contradicts statements made by previous authors that the genus does not occur elsewhere in the Bismarck Archipelago than on Mussau Island (McDowell, 1975; O'Shea, 1996). Three specimens were collected in 1944 by the ornithologist C. G. Sibley and were stored at the MVZ (MVZ 40847–40849). The following brief description of the specimens may serve for future research. Specimens of this population are similar to *Leiopython albertisii* in general appearance (Fig. 6A, B). Scale counts are 13/13 (12/12 in MVZ 40847) supralabials, first and second pitted, fifth with lateral depression, fifth to seventh (fifth to sixth in MVZ 40847) entering the orbit; 15/15 infralabials (lower jaw absent in MVZ 40848), seventh to 11th pitted; single loreal and preocular; single supraocular; 3/3 postoculars; 4–5 anterior temporals; 4–5 posterior temporals; two pairs of parietals, both in median contact enclosing a small rhombic interparietal in the center; maximum dorsal scale rows 43–44, ventrals 273–275, anal entire, subcaudals 68–70,

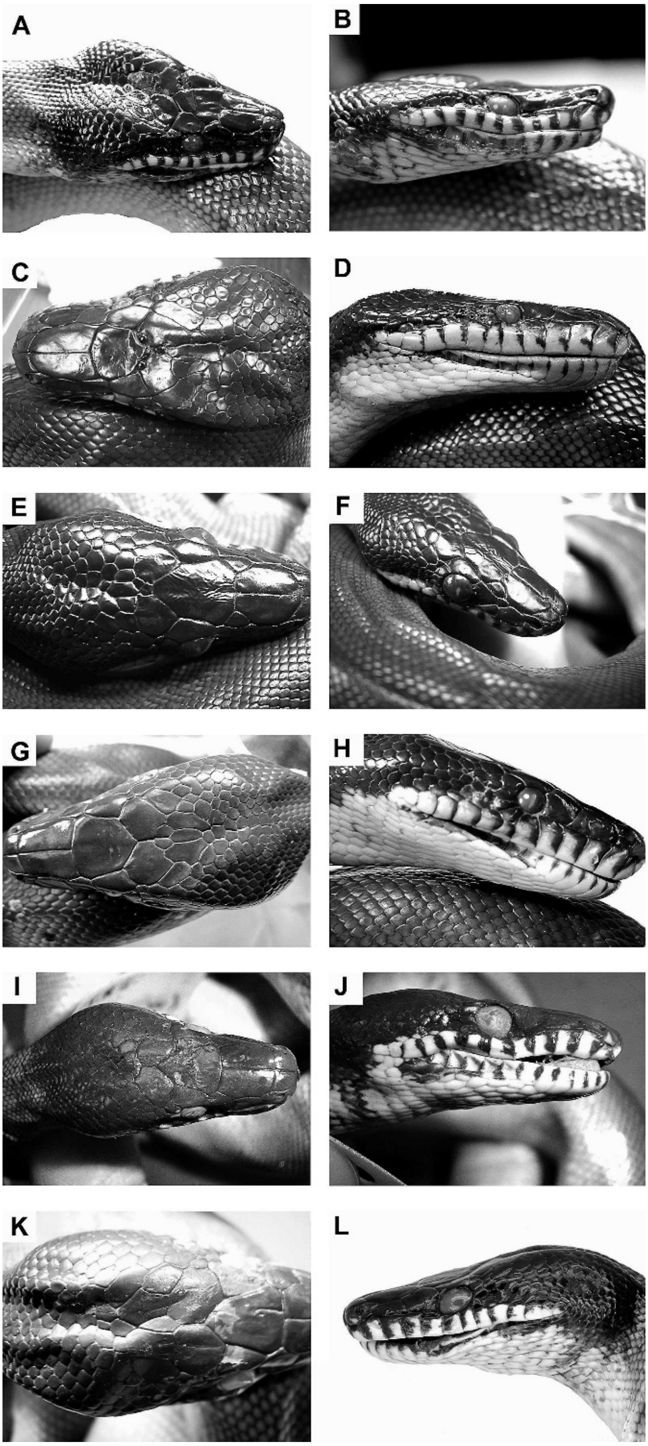

FIG. 6. Dorsolateral or dorsal (left) and lateral (right) views of the head of specimens. (A, B): *Leiopython albertisii* from Emirau Island, MVZ 40849, (C, D): holotype of *Leiopython hoserae* AMNH R-107150, (E, F): holotype of *Leiopython bennettorum* BPBM 5452, (G, H): holotype of *Leiopython fredparkeri* CAS 118906, (I, J): holotype of *Leiopython huonensis* AMNH R-95535, and (K, L): specimen of *Leiopython albertisii* from Mussau Island ZMUC R-5444.

mostly paired. The color of the dorsum is light reddish-brown fading to yellowish laterally and off-white ventrally in preservative. The dorsal surface of the head is black.

Leiopython hoserae Hoser 2000
Figure 6C, D

Holotype.—AMNH R-107150, a large male specimen from Wipim, Western Province, PNG, 2.41 m in length, collected by F. Parker in August 1969.

Paratype.—CAS 118910, an adult (sex unknown) specimen from the Laloki River/Brown River Road, Central District, PNG, collected by F. Parker on 29 August 1967.

Diagnosis.—*Leiopython hoserae* can be distinguished from *Leiopython fredparkeri*, *Leiopython albertisii*, and *Leiopython biakensis* by the presence of only one pair of parietals followed by a characteristic scale pattern of two small scales separated from the median line by an elongate scale that gets wider posteriorly (see Fig. 2B, 6C). It further differs from the former species in a lower average number of dorsal midbody rows (KW-test: $\chi^2{}_1 = 5.68$, $P < 0.05$), and from the latter two species by the absence of the whitish postocular spot. Furthermore, *Leiopython hoserae* exceeds *Leiopython albertisii* and *Leiopython biakensis* in adult and hatchling body size and is darker in color (Parker, 1982; Barker and Barker, 1994; O'Shea, 1996). Molecular evidence also supports the separation of *Leiopython hoserae* from *Leiopython albertisii* (genetic distance of up to 9.3%). It differs from *Leiopython bennettorum* in the number of loreals and prefrontals as well as in lower midbody scale row counts (KW-test: $\chi^2{}_1 = 8.92$, $P < 0.01$) and in the average number of postoculars (KW-test: $\chi^2{}_1 = 7.19$, $P < 0.01$). *Leiopython hoserae* can be distinguished from *Leiopython huonensis* by the absence of the whitish postocular spot, the characteristic scale arrangement in the parietal region (*Leiopython huonensis* has one pair of parietals followed by small, irregular scales) and in higher ventral scale counts (KW-test: $\chi^2{}_1 = 6.62$, $P < 0.05$). *Leiopython hoserae* also occurs in drier and hotter climate conditions than other taxa of the genus (detailed below).

Redescription of Holotype.—Supralabials 13/13, first two pitted, fifth to sixth entering the orbit and with a lateral depression; infralabials 18/18; loreals 1/1; preoculars 1/1; postoculars 3/3, without the whitish postocular spots; supraoculars 1/1; one pair of prefrontals; anterior parietals in median contact anteriorly, but do not meet uppermost postoculars, right parietal scale larger than the left; two scales behind the parietals, the left smaller than the right, both separated at the median line by an elongate scale; enlarged anterior temporals; midbody 50; ventrals 264; anal entire; subcaudals 73.

Description of Paratype.—CAS 118910: supralabials 13/13, first two pitted, fifth to seventh entering the orbit with a lateral depression at the fifth to sixth scute; infralabials 16/16, with 8–12/9–13 pitted and in a skin fold; loreals 1/1; preoculars 1/1; postoculars 3/3 without a whitish spot; supraoculars 1/1; one pair of prefrontals; one pair of parietals separated by two small interparietals at the median line, an elongate scale behind the posterior interparietal that gets wider posteriorly and is laterally bordered by two small scales posteriorly in contact with the parietals; parietals do not meet the uppermost postoculars, midbody scale rows 47; ventrals 277; anal entire; subcaudals 66.

Color in Life.—The body color of this species is blackish-blue dorsally fading to grayish ventrolaterally and white laterally. The dorsal surface of the head is shiny black and the chin is white. The whitish spot behind the eye is absent. Pictures of specimens in the wild can be found in Barker and Barker (1994), and in O'Shea (1996, 2007).

Color in Preservative.—The holotype's body color in life was, according to Parker (1982), very dark grey to black and iridescent. The dorsal surface of the head was shiny black. The preserved specimen today shows a brownish-violet head and body color, the head was only slightly darker than the body, rich brown color ventrolateral fading to yellowish ventrally. Similar color fading was also found in the paratype.

Variation.—Variation in morphological characters was found in several specimens. Three specimens (AMNH R-107150 from Wipim, USNM 213396 and USNM 213397 from Port Moresby) had only two supralabials entering the eye, but the latter two specimens with a small subocular scale on each side. Another two specimens (USNM 213398 and USNM 213399 from Laloki River, near Port Moresby) showed three supralabials entering the eye on one side, but only two on the other side with an additional small subocular. The number of postoculars was more variable than in *Leiopython albertisii*, so were the supralabial counts. Three specimens, one from Port Moresby (MCZ R-145941), and the other two from the Western Province, PNG from Abam (USNM 195754) and from Oslobip (MCZ R-129393) had a small triangular scale bordering the prefrontal, loreal, and preocular scales laterally on each side. These scales might be considered a second small loreal scale. USNM 195754 also showed four postoculars on the right side, whereas MCZ R-145941 and MCZ R-129393 had a small scale posteriory bordering the prefrontal scales at the median line and anteriorly bordering the frontal. Furthermore, MCZ R-145941 and MCZ R-129393 as well as one specimen from Sogeri (CAS 118939) showed aberrant morphology from *Leiopython hoserae* and could be confused with *Leiopython bennettorum* in having a second pair of prefrontals. Specimens from the Western Province ($N = 4$) showed significantly higher average subcaudal scale counts (KW-test: $\chi^2_1 = 6.46$, $P < 0.05$) than found in populations from the Central and Milne Bay Provinces (68.1 ± 2.76; range = 64–73, $N = 18$ vs. 73.3 ± 2.76; range = 70–77, $N = 4$). Furthermore, the average number of infralabials was higher in Western Province specimens than in the latter two populations (16.5 ± 0.58; range = 15–18, $N = 18$ vs. 17.1 ± 0.85; range = 16–18, $N = 4$). All PNG specimens of *Leiopython hoserae* had only one pair of parietals showing a characteristic arrangement, also seen in a captive bred specimen (parents both from the Gulf region) shown in Barker and Barker (1994:73) and in a specimen from Merauke (UTA R-195941, pictures only). A small triangular interparietal separated the parietal scales along the median line in three specimens from around the Brown River (near Port Moresby; MCZ R-150792, MCZ R-145941 and USNM 195609, but not in USNM 195611 from Boroko, Brown River). In two specimens, one from Kokoda (MCZ R-84333) and the other one from Garaina (AMNH R-101073) two pairs of parietals are present (for the latter see also McDowell, 1975). In the Kokoda specimen, the anterior parietal scales were also separated along the median line by three small interparietals. Furthermore, this specimen showed an unusual head color, perhaps caused by preservation. Moreover, this specimen also had several black markings on the genial scales of the throat, only seen in one other specimen examined from Popondetta (MCZ R-140775). A single specimen from Timika, southwest Papua (UMMZ 227653, pictures only), as well as a number of live specimens exported for pet trade from Indonesia (examined by the author) as the so-called black race White-Lipped Python showed two pairs of parietals, not seen in specimens of *Leiopython hoserae* from PNG and Merauke. The whitish spot found in *Leiopython albertisii* was absent in all specimens of *Leiopython hoserae* examined.

Distribution and Ecology.—*Leiopython hoserae* differs not only morphologically from *Leiopython albertisii* but is also geographically separated from the latter taxon by the Central Mountain Range, a known zoogeographic barrier (Austin, 2000; Whittier et al., 2000; Rawlings and Donnellan, 2003) that limits the distributional range of *Leiopython hoserae* to the south of the mountain range.

In PNG, *Leiopython hoserae* is a common species around the Port Moresby/Sogeri area, where it replaces the more commonly found Papuan Carpet Python (*Morelia spilota variegata*) in the lowland (O'Shea, 1996). It is also found around Alotau (Milne Bay Province) and Popondetta (Oro Province). In the highlands of the Owen Stanley Range specimens were found at Garaina and Kokoda, but these specimens are somewhat aberrant from other specimens of this species (see remarks below). Although *Leiopython hoserae* was found in the Gulf Province at Malalaua (W. Wüster, pers. comm.), near the border to the Central Province, and at Omati (O'Shea, 1996), near to the border of the Western Province, this species seems to be absent from major parts of the Gulf Province (see also distribution maps in O'Shea, 1996). Heads (2001) gave a possible explanation for this disjunct distribution pattern assuming that this is because of sinking ocean floors in the Gulf Province. In the Western Province *Leiopython hoserae* is commonly found in the southern trans-Fly River region (Oriomo Plateau). Specimens were reported from Daru (mainland), Abam, Boze, Wipim, and Morehead. Northwards it was found at Emeti and at the upper Fly River region around Lake Murray, Kiunga, Ningerum, and Oslobip but is not a common species there (Parker, 1982). Barker and Barker (1994) gave a detailed description of specimens from the northern islands of the Torres Strait, politically belonging to Australia. In the Indonesian part of New Guinea, this species occurs around Merauke, but it remains unclear how far the distribution of *Leiopython hoserae* extends westward. However, specimens were collected at the coastal area of Timika but showed morphological differences to *Leiopython hoserae* from PNG. Nevertheless, because of inadequate sample size, specimens from the south coast of Papua are considered conspecific with *Leiopython hoserae*, but further research is needed to determine the actual status of these populations.

Leiopython hoserae is primarily found in drier areas, receiving lower annual rainfall than *Leiopython albertisii* (1,800–2,000 mm vs. > 2200 mm) and having a pronounced dry season with mean monthly rainfall of 100 mm or less (vs. > 100 mm for *Leiopython albertisii*, except the Wewak region) (McAlpine et al., 1983). Both the Port Moresby/Sogeri and the trans-Fly area are called the ''dry strips'' in PNG (Nix, 1982:56; Crisp et al., 2001: fig. 10), and according to Heads (2002), these areas show the highest diversity in snakes (for the trans-Fly region, also see A. Allison, Reptiles and amphibians of the trans-Fly region, New Guinea, report submitted to World Wildlife Fund, South Pacific Program, WWF PNG Madang Office, Madang, Papua New

Guinea, available at http://www.wwfpacific.org.fj/publications/png/Transfly_reptiles_report.pdf [February 2008], unpubl. data, 2006). *Leiopython hoserae* shares its distribution with many other snake species (e.g., *Morelia spilota variegata*, *Demansia vestigiata*, *Pseudechis papuanus*, and others) that do not occur north of the Central Mountain Range and are absent from much or all of Gulf Province (see also distribution maps in O'Shea, 1996).

The vegetation found throughout the drier parts of the distribution consists of dry evergreen forests, woodlands, and mixed or Eucalypt savannahs in the dry season that are frequently burning. During the wet season, these areas are only infrequently flooded for short periods (see McAlpine et al., 1983), at which the vegetation turns more into rain forests (Paijmans, 1976).

Remarks.—Hoser's (2000) introduction of *Leiopython hoserae* was heavily criticized by subsequent workers because of a lack of evidence (e.g., Wüster et al., 2001; Williams et al., 2006). The author had distinguished this taxon from *Leiopython albertisii* by body color and by larger average size only. These characters alone are somewhat problematic, at least in preserved specimens, because color fade may have taken place in specimens preserved for a long time, as shown above. Nonetheless, dorsal color was considered as a significant character in live specimens. Body size is subject to environmental factors and life-history traits (e.g., Forsman, 1991; Madsen and Shine, 2000; Wüster et al., 2001). Furthermore, Barker and Barker (1994) and O'Shea (1996) reported behavioral differences to *Leiopython albertisii*. The placement of specimens from the highlands of the Owen Stanley Range around Garaina and Kokoda into this species is ambiguous because of their morphological differences from all other specimens examined. Therefore, I recommend further collecting and research on specimens from the highlands of the Owen Stanley Range.

Leiopython bennettorum Hoser 2000
Figure 6E, F

Synonymy.—*Leiopython albertisii bennetti* Hoser 2000 (need of emendation)

Holotype.—BPBM 5452, a juvenile female specimen from near Wau, PNG collected by A. C. Ziegler on 13 June 1967.

Paratypes.—BPBM 3890, a male specimen from near Wau, PNG, collected by O. R. Wilkes on or around 1 May 1966 at an elevation of about 1,150 m. The snake is skinned out except for the head and tail.

Another specimen designated as paratype by Hoser (2000) from near Wau, originally labeled BPBM 5137 was donated to the AMNH (AMNH R-142857) in 1997 (C. Kishinami, pers. comm.). H. Clissold collected this specimen on 24 August 1963 at an elevation of about 1,066 m in a forest habitat. The snake is skinned out except for most of the skull.

Diagnosis.—*Leiopython bennettorum* is easily distinguishable from all other members of the genus *Leiopython* by higher loreal scale count and by a second pair of small lateral prefrontals (Fig. 6E, F). Furthermore, higher average midbody scale row and postocular scale counts separate this species from *Leiopython hoserae* (KW-test: $\chi^2_1 = 8.92$, $P < 0.01$ and $\chi^2_1 = 7.19$, $P < 0.05$), *Leiopython huonensis* (KW-test: $\chi^2_1 = 4.48$, $P < 0.05$ and $\chi^2_1 = 3.95$, $P < 0.05$), *Leiopython fredparkeri* (KW-test: $\chi^2_1 = 5.30$, $P < 0.05$ and $\chi^2_1 = 4.28$, $P < 0.05$), and *Leiopython albertisii* (KW-test: $\chi^2_1 = 7.98$, $P < 0.01$ and $\chi^2_1 = 14.22$, $P < 0.001$). It can also be distinguished from the latter two species in having only one pair of parietals and, additionally, differs from *Leiopython albertisii* and *Leiopython biakensis* by the absence of the whitish postocular spot (contra Hoser, 2000).

Redescription of Holotype.—Total length 635 mm, SVL 540 mm head length 21 mm; 13/13 supralabials, first and second pitted, fifth to seventh entering the orbit; 17/18 infralabials, 8–14/8–15 pitted in a skin fold; 3/3 loreals (a second smaller one dorsolaterally bordering the large loreal on one side, laterally bordering the prefrontal on the other side, the third loreal posteriorly bordering the first, dorsolaterally the second and anteriorly bordering the preocular); single preocular; single supraocular; 4/4 postoculars; 6/6 anterior temporals; 7/7 posterior temporals; one pair of parietals about two-thirds of the length of the elongate prefrontals, separated by two small rhombic interparietals at the median line; parietals not in contact with the postoculars. Whitish postocular spot is absent; stomach contains rat. According to the size and body color of this specimen, it can be assumed that it is only a few months old. Scales smooth with 274 ventrals, anal entire, and 68 subcaudals mostly paired.

Redescription of Paratypes.—BPBM 3890: head length 55 mm; 13/13 supralabials, first to third pitted, fifth to seventh entering the orbit; 17/17 infralabials, 8–14/8–14 pitted in a skin fold; 2/2 loreals; single preocular; single supraocular; 4/3 postoculars; 5/5 anterior temporals; 5/7 posterior temporals; 263 ventrals and 62 subcaudals.

AMNH R-142857 (former BPBM 5137): supralabials 14/13, first two pitted, fifth to seventh entering the orbit, with a lateral depression at the fifth scale; infralabials 16/16; loreals 2/3; preoculars 1/1; postoculars 3/4; supraoculars 1/1; one pair of parietals, not in median contact (presumably separated by interparietal, but damaged), left parietal meets uppermost postocular; elongate anterior temporals; dorsal midbody scales 54; ventrals 271; anal entire; subcaudals 68.

Color in Life.—Brownish-black dorsally with a violet gleam, fading to lighter reddish-brown laterally, although it appears darker than in *Leiopython albertisii* and to white ventrolaterally and ventrally. The dorsal surface of the head is slightly darker than the dorsum. The supra- and infralabials are white with the typical black markings on the anterior edge. The chin is white.

Color in Preservative.—The body is greyish-brown with a violet gleam fading to lighter yellowish-brown laterally. The ventrals are very light yellowish. The dorsal surface of the head is black, supra- and infralabials are white with the typical black marking on the anterior edge of the labial scales. The chin is white to off-white.

Variation.—A second pair of prefrontals and higher loreal scale count was found in all specimens examined as well as on a picture of a live specimen from Wau. Three specimens (BPBM 3277, 3890 and CAS 139590) had two pairs of loreal scales. In AMNH R-142857, a small elongate scale borders the posterior loreal and the anterior prefrontal laterally on the right side, whereas the posterior prefrontal scale on the left side is larger. In BPBM 5452 (holotype of *Leiopython bennettorum*), three loreal scales were present on each side. A larger anterior loreal scale and two posterior smaller scales border each other laterally.

Distribution and Ecology.—*Leiopython bennettorum* only occurs at Wau at an elevation between 1,050 and 1,400 m. The climate at Wau is dry and only moderately seasonal. Annual rainfall is between 1,500 and 2,000 mm and relative humidity falls to 60% at midafternoon throughout the year (McAlpine et al., 1983). McPhee (1988) stated that at Wau peak breeding season in rodents is earlier than found elsewhere in PNG. This report is interesting, as rodents are the main prey of *Leiopython* (McDowell, 1975; Shine and Slip, 1990; Barker and Barker, 1994). According to Shine and Madsen (1997), there is a causal connection between prey abundance and reproductive output of *Liasis fuscus* Peters 1873. This might lead to the assumption that *Leiopython bennettorum* has a shift in timing of reproduction, but this assumption is speculative and further research on the ecology of this species is needed.

Leiopython fredparkeri sp. nov.
Figure 6G, H

Holotype.—A large male (everted hemipenes) collected by F. Parker 7 July 1967 at Karimui, Chimbu District, CAS 118906.

Paratypes.—Two large males collected by F. Parker on 7 July 1967 at Karimui, Chimbu District, CAS 118905 and CAS 118907. The latter had an everted hemipenis.

Diagnosis.—*Leiopython fredparkeri* differs from *Leiopython albertisii* and *Leiopython biakensis* in the absence of the whitish postocular spot, and in higher infralabial counts (KW-test: $\chi^2_1 = 28.22$, $P < 0.001$ and $\chi^2_1 = 5.06$, $P < 0.05$). It further differs from the former species by lower ventral counts (KW-test: $\chi^2_1 = 7.58$, $P < 0.01$). This species is distinguishable from *Leiopython bennettorum* by loreal, prefrontal, and lower average postocular scale counts (KW-test: $\chi^2_1 = 4.28$, $P < 0.05$), from *Leiopython huonensis* by the absence of the whitish postocular spot, and from the latter species and *Leiopython hoserae* in having two pairs of parietals.

Description of Holotype.—Total length about 1,620 mm; 13/13 supralabials, first and second pitted, fifth and sixth entering the orbit, having a lateral depression; 17/17 infralabials with 8–13 pitted; single loreal and preocular; 3/3 postoculars; 1/1 subocular separating the seventh supralabial from the orbit; single pair of prefrontals; two pairs of parietals, anterior ones larger and in median contact, but do not meet the postoculars, posterior ones elongate and separated by an elongate interparietal at the median; two smaller interparietals bordering anterior parietals posteriorly and the elongate interparietal anteriorly; dorsal midbody scale rows 50; ventrals 266; single anal scale; subcaudals 65, mostly paired.

Description of the Paratypes.—CAS 118905: total length about 1,800 mm, head length about 70 mm; 13/12 supralabials, first and second pitted, 6–7/5–6 entering the orbit, having a lateral depression; 17/16 infralabials with 8–13/7–12 pitted; single loreal and preocular; 2/2 postoculars; 1/1 subocular separating the 8/7 supralabial from the orbit; single pair of prefrontals; two pairs of parietals, anterior ones larger and in median contact, but do not meet the postoculars, posterior ones elongate and separated by an elongate interparietal at the median; two smaller interparietals bordering anterior parietals posteriorly and the elongate interparietal anteriorly; maximum dorsal scale rows 49; ventrals 266; single anal scale; subcaudals 70, mostly paired.

CAS 118907: total length about 1,690 mm, head about 58 mm; 12/13 supralabials (12th and 13th fused on the left side), first to third pitted, fifth to seventh entering the orbit, having a lateral depression at fifth and sixth; 17/17 infralabials with 8–13/8–13 pitted; single loreal and preocular; 3/3 postoculars; two pairs of parietals, anterior ones larger and in median contact anteriorly, but posteriorly divided by a small triangular interparietal that meets an elongate interparietal anteriorly separating the posterior parietals at the median; maximum dorsal midbody scale rows 49; ventrals 266; single anal scale; subcaudals 61, mostly paired.

Color in Life.—Parker (1982) did not explicitly mention the coloration of live specimens from Karimui, but according to D. G. Barker (pers. comm.), these specimens are very dark in color.

Color in Preservative.—Body and head are rich brown or brownish with a violet gleam, the head was only slightly darker than the body. Body color fades to yellowish ventrolaterally and yellowish ventrally. Only one specimen from Karimui (AMNH R-98861) had a black dorsal surface of the head.

Variation.—In three specimens (AMNH R-98861, CAS 118908, and MCZ R-140801), the posterior parietal scales were fused at the median line. Additionally, two of these specimens (AMNH R-98861 and CAS 118908) also had enlarged temporals, laterally bordering both, the anterior and posterior parietal scales. Three specimens (23%, $N = 13$; CAS 118905, 118906 and 118909) had only two supralabials entering the eye, but with a subocular separating the eighth supralabial from the eye. Further three specimens MCZ R-130464, MCZ R-140802, and MCZ R-140804 with only two supralabials entering the eye on one side. A specimen from the Bomai Tive Plateau (MCZ R-130464) showed two loreal scales on one side, and one very large loreal on the other side. Additionally, a small scale laterally bordering the prefrontal and the two loreal scales were present.

Distribution and Ecology.—Little is known about the distributional extent of this species in the Simbu Province, and specimens were hitherto only collected from the Tive Plateau, Bomai, at an altitude of 1,100 m and from ''Karimui'' at an elevation up to 1,500 m. Although no precise data of the collecting locality are available, it may be assumed that this species was collected from the Karimui Basin. This Basin forms a plateau at an elevation between 1,000 and 1,500 m, surrounded by a ring of mountains, which isolates the more lowland fauna of the basin from others and is home of several endemic bird species (Diamond, 1967, 1972). The climate of this area is moderately seasonal (McAlpine et al., 1983) with mean annual rainfall of about 3,330 mm (Diamond, 1972). According to McAlpine et al. (1983), the mean maximum daily temperature at this elevation (1,000–1,500 m) is about 25°C. The habitat consists of evergreen forests, grasslands, and palm swamps.

Etymology.—This species is named in honor of the collector of these and many other specimens, the herpetologist Fred Parker, Townsville, Australia.

Remarks.—Besides separation from other species in morphometric space, this population is also geographically isolated. The morphological, geographical, and ecological factors seem to justify assigning species rank to this population, but this assignment should be subject to future studies on a genetic basis.

Leiopython huonensis sp. nov.

Figure 6I, J

Holotype.—An adult female from an area about 16 km west of Lae, collected by L. van Royen in 1964, AMNH R-95535. Labeled: ''Gift to H. M. van Deusen''; SVL 940 mm; tail 155 mm; head 37 mm.

Paratype.—A semiadult male collected by H. M. van Deusen and S. O. Grierson (7th Archibold Expedition) on 20 September 1964 at Finschhafen, Seboagisung cave on tunnel ceiling at an altitude of about 152 m, labeled: ''Bl[ack].H[ea]d[ed] Python Huon Peninsula Finschhafen ca. 152 m'' stored at the AMNH R-95532. SVL 666 mm; tail 110 mm; head 28 mm.

Diagnosis.—This species differs from *Leiopython albertisii*, *Leiopython biakensis*, and *Leiopython fredparkeri* in having only one pair of parietals followed by small, irregular scales (Fig. 2C, 6I). It can be distinguished from *Leiopython bennettorum* by the lower number of loreal and prefrontal scales as well as a lower average number of postoculars (KW-test: $\chi^2_1 = 3.95$, $P < 0.05$) and from *Leiopython hoserae* by the scale arrangement posterior to the parietal scales showing small, irregular scales. It also differs from *Leiopython albertisii* (KW-test: $\chi^2_1 = 10.31$, $P < 0.001$) and from *Leiopython hoserae* (KW-test: $\chi^2_1 = 5.35$, $P < 0.05$) by lower average ventral scale counts. Additionally, it can be distinguished from the latter taxon by the presence of the whitish postocular spot.

Description of the Holotype.—Supralabials 12/12, first two pitted, fifth to seventh entering the orbit with a lateral depression on the fifth scale; infralabials 16/16, with 7–13 pitted; loreals 1/1; postoculars 3/3 with whitish spot; supraoculars 1/1; one pair of prefrontals; one pair of parietals in median contact and meet uppermost postoculars; anterior temporals 5/4; posterior temporals 5/5; midbody scale rows 48; ventrals 269; anal entire; subcaudals 73.

Description of the Paratype.—AMNH R-95532: supralabials 12/12, first two pitted, fifth to seventh entering the orbit with a lateral depression at the fifth scale; infralabials 15/15, with 8–12 pitted; loreals 1/1; postoculars 3/3 with whitish spot; supraoculars 2/1 (left divided into two scales); one pair of prefrontals; one pair of parietals in median contact but do not meet uppermost postoculars; anterior temporals 4/4;

posterior temporals: 5/5; dorsal midbody scale rows 49; ventrals 282; anal entire; subcaudals 78.

Color in Preservative.—Specimens in preservation are light brownish dorsally only slightly fading in color ventrolaterally but yellowish ventrally. The dorsal surface of the head is black; the supra and infralabials are off-white with the typical black markings. The chin is off-white as well.

Distribution and Ecology.—*Leiopython huonensis* occurs at almost sea level around Finschhafen and Lae at the southern coast of the Huon Peninsula. One specimen (MCZ R-145252) was found east of the Ramu River at Dumpu in the Morobe Province. The Finesterre Mountains to the north and the Markham and Ramu Rivers to the west and southwest geographically separate this species from others, although, these rivers might not be insuperable barriers. Colgan et al. (1993) pointed out that the peninsula is a zoogeographic barrier in lowland mammals and Rawlins and Donnellan (2003) considered it as ''barrier to gene flow.'' As the Huon Peninsula originated from an oceanic island arc in late Pliocene (Zweifel, 1980; Norris and Musser, 2001), a high level of endemism could be expected in specimens. Nevertheless, McDowell (1984) did not find endemism in snakes at the Huon Peninsula.

McAlpine et al. (1983) stated that the Huon Peninsula area is highly seasonal showing a ''reverse'' seasonality in having a wet season between May and August, rather than between December and April, as found in most other parts of the country. Annual rainfall exceeds 4400 mm (McAlpine et al., 1983; Macfarlane, 1999). Recent studies (e.g., *Python reticulatus*: Shine et al., 1998, 1999; *Liasis fuscus*: Brown and Shine, 2002; Brown et al., 2002; Shine, 2003) have revealed that tropical snakes can reproduce seasonally. This is strictly true in captive held specimens of *Leiopython albertisii* and *Leiopython hoserae* in the northern hemisphere (pers. obs.). This evidence may lead to the conclusion that *Leiopython huonensis* is subject to a dramatic shift in timing of reproduction, because of prey availability and ''cost'' of reproduction (Shine, 2003) as found in *Liasis fuscus* Peters from Queensland and the Northern Territory (Shine and Slip, 1990), but this assumption is highly speculative and further studies are needed.

Etymology.—Named after the locality where this species is found, the Huon Peninsula at the east coast of PNG.

Remarks.—Specific rank was assigned to this population because of diagnosable morphological differences from other species, further because of different ecological and environmental conditions and an assumed allopatric distribution.

Leiopython biakensis sp. nov.

Holotype.—A large female specimen at the Museum of Natural History, Leiden, The Netherlands, RMNH 10193, collected at Biak, Schouten Islands, 1952–1953, donated by Fleet Air Arm Royal Netherlands Navy.

Paratype.—A large male specimen, RMNH 10194, collected at the Oregon Trail, Biak, Schouten Islands by Legion Quartermaster Talens, Royal Netherlands Navy; snout–vent length 1,550 mm, tail 220 mm.

Diagnosis.—This species differs from *Leiopython albertisii* in having only two labials entering the orbit (100%, $N = 2$) and in lower ventral scale counts (271 ± 1.41; range = 270–272, $N = 2$) than found in specimens from the western part of Papua (278 ± 2.49; range = 274–283, $N = 13$; KW-test: $\chi^2_1 = 4.99$, $P < 0.05$; see also Brongersma, 1956). However, ventral scales counts are in the range of specimens from PNG. It differs from *Leiopython fredparkeri* in the head scale arrangement, with this species having large and wide posterior parietals, whereas *Leiopython fredparkeri* shows two slender elongate posterior parietal scales (Fig. 2). It further differs from the latter species by the presence of whitish postocular spots, and additionally from *Leiopython huonensis* and *Leiopython hoserae* in having two pairs of parietals. It is also distinguishable from *Leiopython bennettorum* in the number of prefrontals and loreals.

Description of Holotype.—Total length 1,670 mm, tail 255 mm; supralabials 12/11, first to third pitted, fifth and sixth entering the orbit; infralabials 14/15 with 6–12/7–13 pitted; single loreal and 2/2 preoculars, the upper large, the lower very small triangular shield that is wedged between labials and the large preocular; single loreal and supraocular; two pairs of large parietals both in median contact, a small rhombic interparietal is wedged between anterior and posterior parietals (for parietal structure, see also Brongersma, 1956: fig. 1a), left posterior parietal divided into two scales (see Brongersma, 1956: fig. 1a); whitish spot behind the eye; maximum dorsal scale rows 45, ventrals 272, subcaudals 70 mostly paired (Brongersma, 1956).

Description of Paratype.—Single preocular on each side; 12 supralabials, only fifth and sixth entering the orbit, first to third pitted; infralabials 16/16, with seventh to 13th pitted; whitish spot behind the eye; midbody scale rows 47, ventrals 270, anal entire, subcaudals 65.

Color in Preservative.—The color of the dorsum is light purplish-brown fading to yellowish laterally and pale yellow ventrally. The color of the dorsal surface of the head is purplish-black.

Distribution.—This species is endemic to the island of Biak, Indonesia.

Etymology.—Named after the island where this species was found.

Remarks.—This allopatric population shows little, but diagnosable morphological, differences to other species. Brongersma (1956) assumed this population to form an incipient race. Because of the geographic distance to the mainland populations of *Leiopython albertisii*, it is unlikely that gene flow occurs among these populations. Hence, this population is considered reproductively isolated (sensu Wiens, 2004), and, in accordance with Frost and Hillis (1990) and based on the ESC (sensu Frost and Kluge, 1994), the assignment of specific rank to this population seems justified. Unfortunately, no adequate photograph was available from this species.

''*Leiopython albertisii barkeri*'' Hoser 2000
nomen nudum
Figure 6K, L

Holotype.—A semi adult female from Boliu, Mussau Island, St. Matthias group, Bismarck Archipelago collected by the Danish Noona Dan Expedition from 16 January to 18 February 1962. Stored at the ZMUC, collection number R-5444. Total length of the specimen was 1,020 mm (head length 50 mm; SVL 950 mm tail 170 mm).

Paratypes.—A semi adult male from Boliu, Mussau Island, St. Matthias group, Bismarck Archipelago collected by the Danish Noona Dan Expedition during 16 January and 18 February 1962. Stored at the ZMUC, collection number R-5445. Total length of the specimen was 910 mm (SVL 770 mm + tail 140 mm).

Redescription of the Holotype.—Supralabials 13/13, first two pitted, fifth to seventh entering the orbit with lateral depression at the fifth scale; infralabials 15/16, with 7–12 pitted; loreals 1/1; supraoculars 1/1; postoculars 3/4; one pair of prefrontals; preoculars 1/1 (+ a very small lower one), two pairs of parietals, anterior ones in medial contact but do not meet uppermost postoculars; 3 interparietals; anterior temporals 5/5; posterior temporals: 4/3; 44 midbody scale rows, 267 ventrals, 72 subcaudals.

Redescription of the Paratypes.—Supralabials 13/13, first two pitted, fifth to seventh entering the orbit with lateral depression at the fifth scale; infralabials 16/16, with seventh to 12th pitted; loreals 1/1; supraoculars 1/1; postoculars 3/4; one pair of prefrontals; preoculars 1/2 (a second very small lower one), two pairs of parietals (contra McDowell, 1975), anterior ones in medial contact but do not meet uppermost postoculars; single interparietal; anterior temporals 5/5; posterior temporals: 5/4; 45 dorsal midbody rows, 171 ventrals, 73 subcaudals; small pale spot on each preocular and on right uppermost postocular (contra McDowell, 1975), but not as clearly as found in New Guinea specimens of *Leiopython albertisii*; large spurs on the left and right side of the cloacae.

Color in Preservative.—Body color is brownish-violet fading to yellowish ventrolaterally and to off-white ventrally. The dorsal surface of the head is black, the supra- and infralabials are white with the typical black marking, and the chin is off-white.

Distribution.—According to Hoser (2000), this species is endemic to Mussau Island, St. Matthias Group, Bismarck Archipelago, PNG.

Remarks.—The original description ''*Leiopython albertisii barkeri*'' does not meet the requirements of the code (article 13.1.1; ICZN, 2000). Hoser (2000) did not specify characters that are able to differentiate this taxon from others. In addition, the name would have required emendation because of naming it after two persons (see also Wüster et al., 2001). Hoser (2000) states that this taxon is distinguishable from *Leiopython albertisii* by allopatry, by analysis of mitochondrial DNA, and by lower ventral counts, although in the range of *Leiopython albertisii*. Yet, Hoser (2000) had failed to provide evidence for these statements. ''Analysis of mitochondrial DNA'' (Hoser, 2000:19) is not a character as stipulated by article 13.1.1 of the International Code of Zoological Nomenclature (ICZN, 2000), but simply the proposed use of a method. Nowhere does Hoser (2000) provide evidence of mtDNA differentiation of the Mussau population. Allopatric distribution itself may separate the Mussau Island population geographically, but it is highly questionable if this alone is able to distinguish a taxon from another, regardless of the underlying species concept. Nonetheless, multivariate morphometric analysis was not able to separate this population from *Leiopython albertisii* in morphometric space (see Fig. 3), and therefore, it is considered conspecific with this taxon. Moreover, because of the inadequate diagnosis, the name is considered unavailable and is regarded as nomen nudum. The description and pictures are herein provided pro forma for future work on the genus.

Discussion

The results of this study support the hypothesis that the genus *Leiopython* comprises several taxa. Apart from the taxon *albertisii*, morphological analysis uncovered another two new species from the mainland (*Leiopython huonensis* sp. nov. and *Leiopython fredparkeri* sp. nov.) and one new island species (*Leiopython biakensis* sp.

nov.) from Biak Island. The recently recognized species *Leiopython hoserae* and *Leiopython bennettorum* (Hoser, 2000) could be verified. Additional evidence from molecular data also supports the separation of *Leiopython hoserae* from *Leiopython albertisii*, and with a genetic distance of about 10% between both species, both are clearly distinct from each other. However, specimens found in the Enga Province appear to be morphologically similar to *Leiopython huonensis* sp. nov., although of remote distribution (Fig. 5), but this population is herein not recognized taxonomically, because of the small sample size and inadequate data. The two island populations from the Mussau and Emirau islands were morphologically indistinguishable from *Leiopython albertisii* and, therefore, are considered conspecific with this species. Yet, their actual taxonomic status remains unclear. According to De Boer and Duffels (1996), the Bismarck Archipelago, which comprises these two islands, originated from the same island arc as central New Guinea and the Huon peninsula. Therefore, and because of the distance to the mainland of PNG, it can be assumed that these populations are either part of a relict fauna (McDowell, 1975) that have not diverged morphologically from the mainland populations (sibling species) or were introduced by humans. Future studies on a genetic basis might clear this ambiguity.

Besides morphological differentiation, the species recognized are geographically isolated from each other by either geographical barriers (e.g., mountain ranges and rivers) or altitude. Therefore, the taxonomic arrangement presented is in accordance with the ESC (sensu Frost and Kluge, 1994) in that these populations are diagnosable allopatric populations and, hence, are considered separate lineages. According to Wiens (2004), allopatric populations do not necessarily need to have undergone speciation mechanisms other than geographical isolation itself. Wiens (2004) argues that strict allopatry can be considered reproductive isolation because of a lack of gene flow among populations. However, it would be impractical to consider populations as separate lineages without evidence for their differentiation in some way (Frost and Hillis, 1990; Frost and Kluge, 1994; Wiens, 2004). Finally, I agree with Frost and Hillis (1990) for the given reasons, that diagnosable allopatric populations should be considered as species rather than as subspecies.

The two species *Leiopython hoserae* and *Leiopython fredparkeri* sp. nov. exceed other species of the genus in average body size (McDowell, 1975; Parker, 1982; Barker and Barker, 1994; O'Shea, 1996) and egg-size in clutches (Parker, 1982; Barker and Barker, 1994).

This study has shown that the genus *Leiopython* is more complex than previously assumed, but little is known about the biology and ecology of White-Lipped Pythons. Further collecting is necessary to determine the distributional extent of *Leiopython albertisii* in the Yapen-Waropen and Nabire regencies, Papua and of *Leiopython hoserae* at the southern coast of Papua, westwards to the Fak Fak regency. As indicated in this study, future research on a genetic basis might reveal the existence of even more species.

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Appendix 1

Material Examined.—Specimens are organized in OTU's as included given in Table 2. Only photographs were available from specimens marked with *. Photographs and scale counts and measurements provided by curatorial staff were available for specimens marked with **.

NORTH1, (*N* = 13): Salawati Island: ANSP 25095, RMNH 4796 (holotype *Leiopython gracilis* Hubrecht 1879, also see Brongersma, 1953); Sorong: ANSP 26096, RMNH 9653 (mainland, see also Brongersma 1953); Fak Fak: RMNH 9654 1–3 (three specimens, see also Brongersma 1953); Manokwari: RMNH 9655 1–2 (two specimens, see also Brongersma 1953), MSNG 29990* (syntype *Leiopython albertisii*, Peters and Doria 1878: fig 2a); without exact locality data (from pet trade) ZFMK 20331–20332, SFM 72616.

NORTH2, (*N* = 10): Eastern Jayapura: Joka: BPBM 2305 and RMNH 10192 (Lake Sentani, female); Sanduan (former West Sepik) Province: Mt. Somoro AMNH R-1000006 (7 miles east of Lumi, 2400–4650 ft, head and half of body), Aitape: MCZ R-48614; East Sepik Province: Miliom: AMNH R-100005; Wewak: AMNH R-75027, R-75028; Madang Province: Errima: BMNH 1922.11.24.30 (Astrolabe Bay); Ramu River Delta: BMNH 1926.5.31.4 (female); Madang: AMNH R-107149.

ENGA, (*N* = 2): Wabag: CAS 103384 (listed as «Southern Highlands District»), CAS 135211 (Jimi Region, Sau River, 50 miles northwest of Banz) listed as ''Western Highlands District''), 2,500 ft.

WAU, (*N* = 5): AMNH R-142857 (skin, former BPBM 5137), BPBM 3277, 3890 Wau, (vicinity of) Big Wau Creek, 1,150 m; 5452 Wau (Bishop Museum Field Station), 1,250 m; CAS 139590.

BULOLO, (*N* = 1): MVZ 74917**.

KARIM: (*N* = 13), Simbu Province, PNG; Karimui: AMNH R-98861 (also see McDowell, 1975), CAS 118905–118909; MCZ R-115582, MCZ R-123872, MCZ R-140801–R140804 (labeled as *Liasis fuscus*, Karimui, 3500 ft); Bomai Tive Plateau: MCZ R-130464.

SOUTH1, (*N* = 18): Central Province, PNG: Boroko: USNM 195611 (19 miles north of Brown River Road, near ford); USNM 195609 (Brown River Road, at ford approximately 2 miles south of Brown River); Madew: BMNH 1908.10.14.6 (St. Joseph River, Brit. New Guinea); Port Moresby: MCZ R-145941*, MCZ R-150792*, USNM 213396–213397 (Mc Donald's Corner); near Port Moresby: AMNH R-103636 (Hiknumu Plantation, 3 miles north 22 m east of Port Moresby, 520 m), CAS 118910 (Laloki River); Kokoda (highlands of the Owen Stanley Range): MCZ R-84333; Middletown: MCZ R-59091; USNM 213398–213399 (Nazareth Mission, on road to, adjacent to Laloki River); Sogeri: CAS 118939, MCZ R-149696*; Milne Bay Province, Alotau: road-kill specimen** (without collection number); Popondetta: MCZ R140775 (head and tail only); Other material: BMNH 97.12.10.108 (labeled ''British New Guinea'').

SOUTH2, (*N* = 4): Western Province: Abam: USNM 195754; Boze: BMNH 1986.1174 (Binaturi River, Southern Trans-Fly region); Wipim: AMNH R-107150 (holotype of *Leiopython hoserae* Hoser 2000); Oslobip: MCZ R-129393.

HUONP, (*N* = 15): Lae: AMNH R-66756, R-95534–R-95535, R-103869, R-107148, R-115056–R-115057, MCZ R-145942–R-145944; Finschhafen: AMNH R-99532–R-99533, USNM 118950 (south of Langemak Bay, inland about 1 mile from a point on the shore midway between Nasing Alater on Bugaim River and Kawalansam on Buka Creek); Tigrain: BMNH 1922.11.24.29 (Adler River, Huon Gulf); Ramu River (near Dampu): MCZ R-145252.

BIAK, (*N* = 2): RMNH 10193 (female) –10194 (Oregon Trail, male, head damaged, see also Brongersma 1956).

MUSS, (*N* = 2): R5444–R5445 (also see McDowell, 1975).

EMIR, (*N* = 3): MVZ 40847–40849**.

UNKNOWN, (*N* = 2): BMNH 97.12.10.108 (labeled ''British New Guinea'').

APPENDIX 2. Mitochondrial DNA sequences used in this study. Lengths of base pairs (bp) are provided and references are given in the Literature Cited section. Locality data were not given in the GenBank records but were backtracked to the tissue samples in museum collections and verified by the authorities given in the references.

Name/Locality	GenBank accession number	Length (bp)	Locality	Reference
Merauke	AF241406	715	Assumed from Merauke, Irian Jaya (D. G. Barker, pers. comm.)	Harvey et al. (2000)
Western Province	U69835	1114	Western Prov., PNG, Mawatta; Alpha-Helix Expedition 1969, tissue LSUMZ 10505	Campbell, B.N. (Thesis, 1997)
Milne Bay Province	EU179542	831	Gurney, Milne Bay Province, PNG	this study
Madang 1	U69836	642	Madang (not West New Britain Prov., Rabaul, PNG). Alpha- Helix Expedition 1969. Maiwara at Man Road, tissue LSUMZ 10626	Campbell, B.N. (Thesis, 1997), backtracked by Donna Dittmann, locality data corrected by H. Cogger.
Madang 2	EU183230	836	Madang Province, PNG	this study
Outgroup	AF241399	715	*Morelia amethistina*	Harvey et al. (2000)
Outgroup	AF241404	715	*Morelia amethistina*	Harvey et al. (2000)