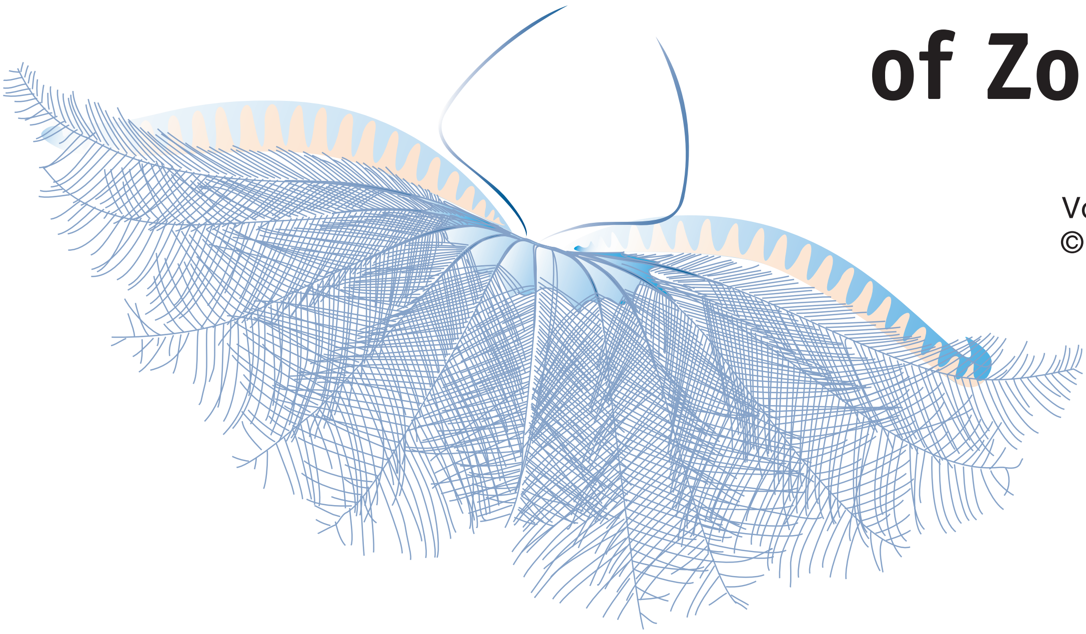
CSIRO PUBLISHING

Australian Journal of Zoology



Volume 48 2000

A journal for the publication of the results of
original scientific research in all branches of zoology,
except the taxonomy of invertebrates

www.publish.csiro.au/journals/ajz

All enquiries and manuscripts should be directed to
Australian Journal of Zoology
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood Telephone: 61 3 9662 7622
Vic. 3066 Facsimile: 61 3 9662 7611
Australia Email: david.morton@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO and
the Australian Academy of Science

CSIRO AUSTRALIA

Academy of Science

© CSIRO 2000 *Australian Journal of Zoology*, 2000, **48**, 357–367

Morphology of the brown tree snake, *Boiga irregularis*, with a comparison of native and extralimital populations

Joan Whittier[AB], *Conrad Macrokanis*[A] *and Robert T. Mason*[C]

[A]Department of Anatomical Sciences and Centre for Conservation Biology, University of Queensland, St Lucia, Qld 4072, Australia.
[B]To whom correspondence should be addressed. Email: j.whittier@mailbox.uq.edu.au
[C]Department of Zoology, Oregon State University, Corvallis, OR 97331, USA.

Abstract

We conducted an analysis of the morphology of specimens of the brown tree snake, *Boiga irregularis*, from the native range of eastern and northern Australia, Papua New Guinea and the Solomon Islands. First, a cluster analysis was conducted to determine natural groupings in the data; however, no groupings based on morphological characters were found. Then the importance of additional factors such as geographical groupings and coloration was analysed in a nonparametric analysis of variance. Significant differences were found in the mean rankings of key characters such as dorsal mid-body, ventral and subcaudal scale counts. However, the amount of variation and the degree of overlap among populations and groupings precluded separating animals on the basis of these features. Our data support the recognition of a single species with two subspecies based on colour variation. We also compared the morphology of a sample of brown tree snakes from an extralimital population on Guam to that of this species in the areas of the native range. Our data supported suggestions of alliances of the Guam population with northern Papuan populations. However, the Guam population of the brown tree snake was found to be less variable than were localised natural populations. Morphologically, the Guam population is distinctive, suggesting that it has undergone significant morphological change since its introduction.

Introduction

The taxonomic status of the brown tree snake, *Boiga irregularis* Merrem, 1802, in its native Australasian range and in extralimital populations in Micronesia is unclear. Currently this opisthoglyphous colubrid snake is recognised as *B. irregularis* throughout Australia, Papua New Guinea, the Solomon Islands and eastern Indonesia (Cogger 1986; Wilson and Knowles 1988). However, others recognise the Australian brown tree snake as *B. fusca* Gray, 1842 and extra-Australian brown tree snakes as *B. irregularis* (Storr *et al.* 1986, pp. 52–55). Cogger (1986) suggests that the recognition of an endemic Australian species (*B. fusca*) may be warranted. Here, we compare *Boiga* Fitzinger, 1826, in Australia and in non-Australian portions of its range and in Guam to resolve these questions.

The extralimital population of brown tree snakes on Guam, which is invading other islands, is currently recognised as *B. irregularis* (Fritts 1988). This population has previously been allied with snakes of northern Papua New Guinea in the Manus Province (Admiralty Islands: Rodda *et al.* 1992). The purported designation of the source population was based on two factors: (1) mid-body scale counts and (2) historical records of cargo movement during World War II.

A number of studies have compared traditional morphological characters of snakes across geographic ranges to evaluate geographical variation and clines (Rossman 1979; Christman 1980; Thorpe 1985*a*, 1985*b*). Most of these studies have used multiple characters analysed in a parametric multivariate analysis of variance or cluster analysis. Congruence of characters, including morphological, physiological and genetic, has been examined and contrasted with known population groupings (Colless 1980; Thorpe 1986, 1989). In the present study we compile and analyse external morphological characters of *B. irregularis* with a cluster analysis

10.1071/ZO99025 0004-959X/00/040357

to examine any natural groupings. We then analyse the morphological characters with respect to geographic divisions (known population groupings are not yet available for this species) to test hypotheses about two different geographical groupings. We also compare the morphological characteristics of a sample of the extralimital Guam population to native populations based on our analysis. Differences in the variability of subpopulations from several regions in the native range and from Guam are evaluated.

Materials and Methods

Morphological examination

First we compiled information about the morphological characters on which previous descriptions of *B. irregularis* and related taxa were originally based (unpublished data, J. M.Whittier). From these historical observations we then generated hypotheses about the taxonomic relationships among the Australian, Papuan, and Solomon Island forms of this snake. Morphological features of 145 brown tree snakes collected from Australia, Papua New Guinea and the Solomon Islands, as well as 24 from Guam, were examined

Initially, a full assessment was conducted on a pilot group of animals. Snout–vent length (SVL) was measured to the nearest 0.5 cm; however, in coiled fixed specimens this measure is at best an estimate of SVL. A number of scale counts were conducted: (1) dorsal scales at the rostral end (at 20th ventral scale from head), middle, and caudal end (at 20th ventral scale from cloaca); (2) ventral scales, including the anal; (3) subcaudal scales, but only in specimens with unbroken tails; (4) preocular scales; (5) postocular scales; (6) right and left, upper and lower labial scales; and (7) primary, secondary, tertiary, and quaternary temporal scales. Several qualitative measures were made as well on the basis of morphological characters, including (1) the presence of a single or divided anal scale, (2) the presence of a single or divided subcaudal scales, (3) the degree of contact between the preocular scale and frontal scale (rated on a scale of 1 to 4, with 1 = no contact and 4 = broad contact), and (4) the shape of the four types of temporal scales. An estimate of the length of the palatine and maxillary teeth was also attempted but found to be too unreliable a feature on fixed specimens, and insufficient skeletal material was available. During a later part of the study, after specimens were collected from Guam, a measure of head length (to the nearest 0.1 mm) was also taken with vernier calipers. The measure of head length was then expressed as percentage of SVL.

After a preliminary analysis was conducted, the remaining animals were assessed only for morphological features that were found to vary across groups and that could be assessed reliably. These features included (1) mid-body dorsal, (2) ventral, and (3) subcaudal scale counts, (4) the degree of contact between the preocular and frontal scales, (5) right (selected to avoid redundancy) upper and lower labial scale counts, (6) head width, and (7) head length. The colour pattern of these snakes was recorded and snakes were assigned to one of three categories based on dorsal colour patterns: (1) patterned, (2) banded or (3) solid colour.

Statistical analysis

Key characters were identified by a step-wise multiple regression to identify characters that explained significant variation across samples. Initially, a hierarchical cluster analysis of observations using standardised variables, Euclidean distance, and single-linkage protocols (Minitab Release 11 for Windows) was conducted to establish whether there were any natural groupings defined by the morphological data. In the cluster analysis the sample was restricted to 94 snakes because of missing data, particularly of subcaudal counts: the snakes' tails were often broken. Since no clusters were identified, thereafter a larger set of characters were analysed with respect to geographical location initially based on seven regions, including south-east Queensland, central Queensland, north-east Queensland, Northern Territory, Western Australia and Papua New Guinea and Solomon Islands and Guam (Fig. 1). We conducted a Kruskal–Wallis test, a non-parametric equivalent to analysis of variance, because most of the scalation counts and categories were not continuous variables (SOLO, BMDP Statistical Software, 1988). *Post hoc* comparisons were applied using z-tests after Daniel (1978, p. 214). Insufficient numbers of animals from the Indonesian archipelago were obtained so this region was excluded from the analysis. A second analysis based on geographic groupings was conducted using three regional populations: (1) north of the Papua New Guinea Highlands, (2) eastern Australia and south of the Papua New Guinea Highlands, and (3) Northern Territory and Western Australia. These groupings are suggested by natural groupings of other populations in these regions. We also analysed the morphological data on the basis of the three colour morphs: (1) solid, (2) patterned and (3) banded coloration. All native populations were similarly compared with a sample of snakes collected on Guam.

Intrapopulation variability was analysed by comparing variation (squared standard deviation) in morphological features (*F* test: Snedecor and Cochran 1980, pp. 98–99). Four disjunct local subpopulations

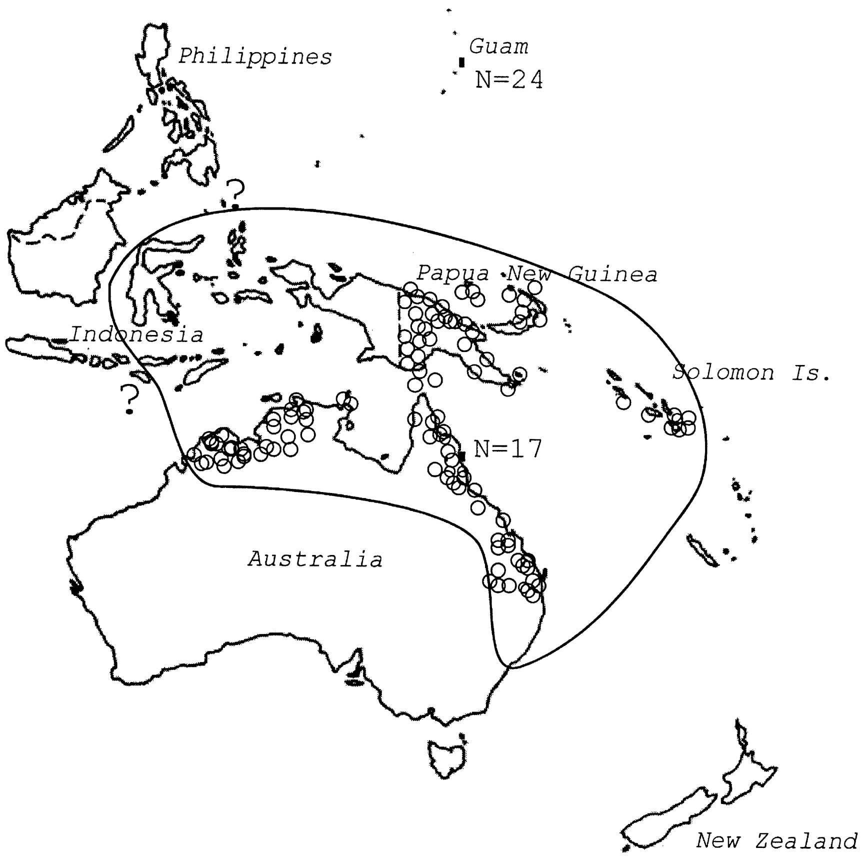


Fig. 1. Range map and sampling localities of *Boiga irregularis* in Indonesia, Australia, Papua New Guinea, the Solomon Islands and Guam.

of the brown tree snake were compared: (1) south-eastern Queensland (27°02′–28°10′S, 152°22′–153°5′E), (2) Babinda, north Queensland (17°4′S, 146°0′E), (3) northern mainland Papua New Guinea (4°37′–8°4′S, 145°–148°24′E), and (4) Agana, Guam (13°5′N, 145°E). These areas were selected because a relatively large sample of specimens were available from the localities in the museum collections and our private collection. Because there was a high variance in subcaudal counts in snakes from the native range we conducted a two-sample *t*-test on a sample of sexed snakes from one local area (Babinda: n = 10 males and 6 females). This test was conducted to examine possible sex differences in the scale counts.

Results

Relation to regional geography

We selected the key features to compare snakes we examined from the native range and from Guam, including mid-dorsal, ventral, and subcaudal scale counts, the degree of contact between preocular and frontal scales, right upper and lower labial scale counts and, later, a ratio of head length to SVL length. A cluster analysis of these data uncovered no meaningful clustering. A final partition with two clusters included one with a single individual and one with 93 individuals. Similarly, a partitioning into six clusters included five clusters with single individuals and one with 89.

We also analysed the data with respect to differences in seven geographic regions (Table 1). Five of these regions were in Australia, one in Papua New Guinea and the Solomon Islands, and

Table 1. Morphological characteristics of *Boiga irregularis* analysed by geographical division

Values are given as mean ± 1 s.d.; the range is shown in parentheses

Location	*n*	Mid-dorsal scale count	Ventral scale count	Subcaudal scale count	Preocular / frontal scales contact score	SVL (cm)	Head length / SVL (%)
South-eastern Queensland	13	19.4 ± 0.96 (18–21)	239.4 ± 7.8 (227–248)	96.8 ± 8.4 (85–112)	1.88 ± 1.35 (1–4)	94.8 ± 27.3 (44–130)	–
Central Queensland	10	19.1 ± 0.33 (19–20)	238.3 ± 10.9 (222–259)	97.2 ± 5.8 (90–110)	1.55 ± 1.01 (1–4)	78.6 ± 17.7 (43–103)	–
North-eastern Queensland	38	19.4 ± 1.23 (17–21)	250.9 ± 6.45 (239–267)	95.4 ± 7.8 (77–108)	1.57 ± 0.96 (1–4)	99.1 ± 23.8 (59–160)	3.07 ± 0.40 (2.20–4.00)
Papua New Guinea and Solomon Islands	50	20.8 ± 1.25 (19–25)	248.0 ± 9.68 (225–263)	108.9 ± 10.9 (79–127)	2.83 ± 1.42 (1–4)	110.9 ± 28.3 (28.7–150)	3.26 ± 0.81 (2.51–6.97)
Northern Territory	10	19.0 –	260.4 ± 8.92 (249–275)	98.8 ± 7.6 (90–116)	1.00 –	94.6 ± 17.5 (68.5–127)	2.58 ± 0.46 (2.00–3.16)
Western Australia	24	19.1 ± 0.41 (19–21)	277.5 ± 4.86 (269–286)	112.7 ± 4.6 (100–119)	1.75 ± 1.32 (1–4)	120.0 ± 31.4 (49.5–167)	2.60 ± 0.34 (2.14–3.31)
Guam	24	23.8 ± 1.02 (22–25)	253.3 ± 2.53 (250–259)	123.5 ± 2.3 (120–127)	2.83 ± 1.23 (1–4)	103.6 ± 24.3 (63–153)	3.30 ± 0.23 (2.50–3.91)

one in Guam. First we compared the characters among the animals from the native range, and then the characters of the extralimital population were contrasted with those in the native range.

Significant differences were found in dorsal mid-body, ventral and subcaudal scale counts among snakes grouped according to geographic region (t = 85.878, 92.974, 93.281, respectively; $P < 0.001$). However, the patterns of morphological variation differed for each character (Table 1). For example, mid-body dorsal scale counts of North Queensland snakes were significantly different only from snakes from Papua New Guinea and the Solomon Islands (Z = 3.5807, $P < 0.01$); they were not significantly different from snakes in the native range (south-east Queensland, central Queensland, Northern Territory and Western Australia). The snakes from Papua New Guinea and the Solomon Islands were significantly different from those of North Queensland (as above) and Western Australia (Z = 4.2353). When the sample of snakes from Guam was contrasted with the native snakes, we found that those from Guam were significantly different from those from North Queensland (Z = 7.147), Papua New Guinea and the Solomon Islands (Z = 4.3338), the Northern Territory (Z = 5.3106) and Western Australian (Z = 7.7011) with respect to the mid-dorsal scale counts.

Ventral scale counts had a different pattern of variation across the geographic range. South-east Queensland snakes differed significantly from snakes from North Queensland (Z = 3.1203, $P < 0.05$), the Northern Territory (Z = 4.4267), and Western Australia (Z = 7.6717), but were not significantly different from snakes from central Queensland or Papua New Guinea and the Solomon Islands ($Z < 3.09$). Central Queensland snakes differed significantly from those from the Northern Territory (Z = 3.7857) and Western Australia (Z = 6.25754) only while North Queensland snakes differed significantly from the snakes from south-east Queensland and Western Australia (Z = 6.2754) with respect to this character. When the snakes from Guam were contrasted with the native *B. irregularis*, we found that the Guam populations differed significantly in ventral count from the snakes from south-east Queensland (Z = 3.9802), Central Queensland (Z = 3.1931) and Western Australia (Z = 4.4488).

Subcaudal scale counts had a third pattern of variation across the geographical groupings. South-east Queensland and North Queensland snakes were significantly different from those from Papua New Guinea and the Solomon Islands (Z = 3.329 and 4.8928, respectively) and Western Australia (Z = 3.8372 and 5.1526). Central Queensland snakes were significantly different from Western Australian (Z = 3.3849) snakes. Subcaudal scale counts were not sexually dimorphic, as they are in some snakes (n = 16, t = 0.14, d.f. = 14, P = 0.89).

A key feature used by Boulenger (1896, pp. 59–81) to separate *Boiga fusca* and *B. irregularis*, the degree of contact between preocular and frontal scales, was found to be highly variable. There were significant differences among geographical samples with respect to this character (t = 38.218, $P < 0.001$). The mean score (Table 1) for the Papua New Guinea and Solomon Islands population was significantly greater than for the North Queensland (Z = 64.0214), Northern Territory (Z = 3.7076) and Western Australian (Z = 3.1814) samples. However, the variation was also greater, such that the range of this feature overlapped completely. A similar result was observed with respect to this character from the extralimital population on Guam. The Guam sample differed significantly from the North Queensland (Z = 3.5590) and Northern Territory (Z = 3.6047) snakes, but again, variation was high. In addition, this character was occasionally asymmetrical: individual animals were observed in all geographical samples with no contact and broad contact of the preocular and frontal scales on right and left sides of the head.

Significant differences in several morphological variables were found between the two regional groupings (the northern Highland Papua New Guinea versus the southern Highland Papua New Guinea and eastern Australian populations: Table 2). Mean mid-dorsal and subcaudal scale counts were significantly different (t = 55.388 and t = 14.936, $P < 0.001$), with the snakes from the northern Papuan region having significantly greater numbers of both scales. However, the range of these features overlapped significantly (Table 2), such that the features were not diagnostic of either grouping. Mean mid-dorsal and subcaudal scale counts of the snakes on Guam were significantly different from both the eastern Australian and southern

Table 2. Mean, variation and range of distinguishing morphological features of *Boiga irregularis* in Australia and Papua New Guinea and on Guam

Values are given as mean ± 1 s.d.; the range is shown in parentheses

Location	*n*	Mid-dorsal scale count	Ventral scale count	Subcaudal scale count	Preocular / frontal scales contact score	SVL (cm)	Head length / SVL (%)
Northern Territory and Western Australia	38	19.1 ± 0.35[A] (19–21)	272.2 ± 10.0[A] (249–286)	108.1 ± 8.6[B] (90–119)	1.53 ± 1.16[C] (1–4)	110.4 ± 30.5[B] (49.5–167)	2.58 ± 0.36[A] (2.00–3.31)
Eastern Australian and Southern Papua New Guinea	81	19.7 ± 1.2[C] (17–21)	248.0 ± 9.5 (222–267)	99.3 ± 10.0[C] (77–125)	1.88 ± 1.24[C] (1–4)	95.2 ± 24.4[C] (43–160)	3.09 ± 0.36[D] (2.22–4.00)
Northern Papua New Guinea	31	20.9 ± 1.4[B] (19–25)	246.0 ± 9.8 (225–259)	109.2 ± 11.9[B] (79–127)	2.89 ± 1.37[B] (1–4)	117.1 ± 26.8[B] (28.7–150)	3.39 ± 0.99 (2.51–6.97)
Guam	24	23.8 ± 1.0[D] (22–25)	253.3 ± 2.5[E] (250–259)	123.4 ± 2.3[D] (120–127)	2.83 ± 1.23[F] (1–4)	103.6 ± 24.4 (63–153)	3.30 ± 0.23[F] (2.50–3.91)

[A]Significantly different from eastern Australian and southern Papua New Guinea and northern Papua New Guinea forms.
[B]Significantly different from eastern Australian and southern Papua New Guinea forms.
[C]Significantly different from northern Papua New Guinea forms.
[D]Significantly different from all other forms.
[E]Significantly different from eastern Australian and southern Papua New Guinea and northern Papua New Guinea forms.
[F]Significantly different from eastern Australian and southern Papua New Guinea forms.

Papua New Guinean populations (Z = 7.4313) and the northern Papua New Guinean population (Z = 4.5110; Table 2). The range of the mid-dorsal and subcaudal scale counts of the Guam sample more closely resembled those of snakes from the northern Papuan region. In the case of mid-dorsal scales, the Guam snakes did not overlap with the southern Papuan and Australian forms; however, subcaudal counts for all three groups overlapped extensively.

Brown tree snakes on Guam differed from both natural populations in the mean number of ventral scales (Z = 2.892 for both comparisons), while the natural populations were not significantly different from one another with respect to this feature (Table 2). However, as with the other features of scalation, the number of ventral scales present overlapped extensively among the three populations (Table 2).

Relation to colour patterns

During this study we obtained additional information about the range of specific colour morphs of native *B. irregularis*. We found that the night tiger or banded forms occurred further east than has been recognised. We recorded banded forms from north-central and northern Queensland, with the Great Dividing Range apparently forming a dividing line in this area. Banded morphs have been reported from (1) Mt Surprise, in central northern Queensland, (2) Herberton, in north Queensland, and (3) Cape Melville, in coastal far north Queensland.

The analysis based on dorsal colour patterns of animals from the native range found significant differences in the preocular/frontal contact score (t = 7.659, P < 0.02; Z = 2.73, P = 0.05), the dorsal mid-body (t = 53.693, Z = 7.3225) and ventral (t = 45.241, Z = 6.4417) scale counts of banded specimens when compared with patterned or solid-coloured specimens. No significant differences were observed in upper or lower labial or subcaudal scale counts among these three groups (Figs 2, 3). Colour-banded snakes were also less variable in scale counts than were the other two colour morphs.

Overall, if the banded forms from Queensland, the Northern Territory and Western Australia are set aside as a separate subpopulation, there was a general trend of an increase in nearly all variables along a south to north direction (see Tables 1–3). This trend extends from south-eastern Australia, north through Papua New Guinea and includes the population on Guam.

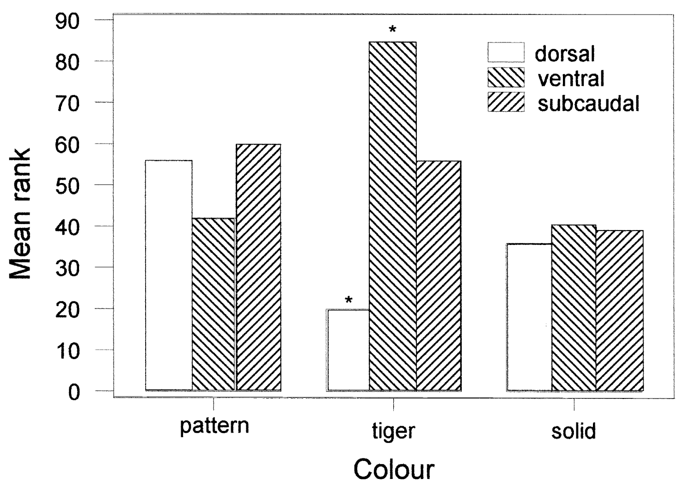


Fig. 2. Mean ranks of dorsal, ventral and subcaudal scale counts of three different colour morphs of *Boiga irregularis* from Australia and Papua New Guinea. The asterisks indicate significantly different mean ranks.

Table 3. Comparison of variation within selected subpopulations of *Boiga irregularis* collected from two locations in the native range and from Guam

Values are means, with variances shown in parentheses

Location	*n*	Mid-dorsal scale count	Ventral scale count	Subcaudal scale count	Preocular / frontal scales contact score	Head length / SVL (%)
South-eastern Queensland	11	19 (0.0)	238.0 (58.6)	98.7 (61.5)	1.75 (1.27)	–
Babinda, North Queensland	15	19.7 (1.7)	246.7 (22.9)	96.3 (50.1)	1.60 (0.69)	3.08 (0.025)
Northern mainland Papua New Guinea	15	20.5 (1.3)	248.5 (45.3)	110.4 (117.9)	3.12 (1.64)	3.11 (0.0014)
Guam	24	23.8 (1.04)	253.3 (6.41)	123.4 (5.50)	2.83 (1.51)	3.30 (0.0053)

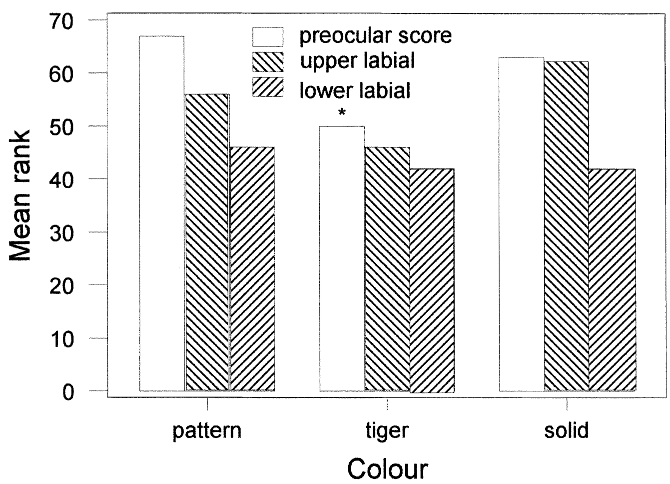


Fig. 3. Mean ranks of preocular–frontal contact scores, and right upper and lower labial scale counts, of three different colour morphs of *Boiga irregularis* from Australia and Papua New Guinea. The asterisk indicates a significantly different mean rank.

Analysis of variation in subpopulations

The Guam extralimital population was significantly less variable in ventral and subcaudal scale counts than were three local native populations (Table 3). The variation in head size, expressed as the ratio of head length to SVL, was also less variable in the Guam sample than in the samples from Babinda, North Queensland, and northern mainland Papua New Guinea.

Discussion

The results of our morphological assessment concur with the designation of Cogger *et al.* (1983) of a single species, *B. irregularis*, at least in Australia, Papua New Guinea, and the Solomon Islands in the native range. Within the native range we recommend that banded forms of *B. irregularis*, known as night tigers and banded cat snakes, be recognised as a subspecies, *B. irregularis ornata*, based on distinguishing morphology (Storr *et al.* 1986) and coloration. The remainder of the species, including unbanded patterned and solid-coloured brown tree snakes in eastern Australia, Papua New Guinea and the Solomon Islands, form a second subspecies, *B. irregularis irregularis* (Boulenger, 1896). On the basis of previously published scale counts, eastern Indonesian forms would be related to *B. i. irregularis.* Our study also confirms a related genetic assessment in that there is extensive overlap in morphological features, although some divergence of populations is supported (Rawlings 1995). Divergence of populations of *B. irregularis* and other reptilian species along a north–south division of Papua New Guinea suggests that the highlands of Papua New Guinea may serve as an isolating mechanism (Hall 1989; Rhodin 1993; Webb 1995).

Our data confirm that the Guam and Micronesian snakes are derived from the northern Papuan region (Rodda *et al.* 1992). However, the Guam extralimital population was significantly less variable than were the other populations of *B. i. irregularis.* Thus, the low degree of morphological variation in the Guam animals is significantly different from the high degree of variation observed in localised native brown tree snakes. This divergence may have resulted from genetic drift. Alternately, and perhaps linked with ecological release of the brown tree snake on Guam, morphological variation has been reduced in the extralimital population by selection pressures in the new environment.

Evidence of ecological release of the brown tree snake on Guam includes the larger maximum body size attained by the snakes on Guam, and the size of sexual maturity. Our data also show that snakes from Guam have a significantly larger number of mid-body scale rows and larger numbers of ventral and subcaudal scales than do the snakes from the source population of northern mainland Papua New Guinea. These increases in numbers of scales do not appear to be accompanied by a reduction in the size of the scales, and thus the increase in scalation number accommodates the larger body size and girth of the Guam forms of *B. i. irregularis*. These morphological differences permit Guam forms to feed on larger prey. We also would predict that females from the Guam population could accommodate larger clutches of eggs at a given size than could the snakes of Papua New Guinea. Female *B. i. irregularis* on Guam would also be expected to have a larger maximum clutch size than would those of the source population. These factors would increase the lifetime fecundity of the snake on Guam, and may have contributed to its ecological release there.

Acknowledgments

We thank P. Couper, J. Covacevich and G. Ingram of the Queensland Museum, L. Smith of the Western Australian Museum and R. Sadlier of the Australian Museum for access to specimens. We thank those who helped collect snakes, particularly K. Aland, B. James, J. S. Whittier and D. Moeller. We also thank S. Donnellan and L. Rawlings for comments on the manuscript, and L. Hall for the map sketch.

References

Boulenger, G. A. (1896). 'Catalogue of Snakes in the British Museum (Natural History). Vol. III.' (British Museum: London.) [1961 reprint by Wheldon and Wesley Ltd & Hafner Publishing Co.: New York.]

Christman, S. P. (1980). Patterns of geographic variation in Florida snakes. *Bulletin of the Florida State Museum in Biological Science* **25**, 157–256.

Cogger, H. (1986). 'Reptiles and Amphibians of Australia.' 4th Edn. (Reed Books: Sydney.)

Cogger, H., Cameron, E. E., and Cogger, H. M. (1983). 'Zoological Catalogue of Australia. Vol. 1 Amphibian and Reptilia.' (Australian Government Publishing Service: Canberra.)

Colless, D. H. (1980). Congruence between morphometric and allozyme data for *Menidia* species: a reappraisal. *Systematic Zoology* **29**, 288–299.

Daniel, W. (1978). 'Applied Nonparametric Statistics.' (Houghton Mifflin: Boston.)

Fritts, T. H. (1988). The brown tree snake (*Boiga irregularis*): a threat to Pacific Islands. Biological Report 88(31). U.S. Fish and Wildlife Service, September 1991.

Hall, P. M. (1989). Variation in geographical isolates of the New Guinea crocodile (*Crocodylus novaguineae* Schmidt) compared with the similar, allopatric Philippine crocodile (*C. mindorensis* Schmidt). *Copeia* **1989**, 71–80.

Rawlings, L. H. (1995). Phylogeography of the brown tree snake, *Boiga irregularis*, particularly relating to populations in Guam. B.Sc.(Honours) Thesis, University of Adelaide.

Rhodin, A. G. J. (1993). Range extension for *Emydura subglobosa* in Papua New Guinea. *Chelonian Conservation and Biology* **1**, 47–48.

Rodda, G. H., Fritts, T. H., and Conry, P. J. (1992). Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. *Pacific Science* **46**, 46–57.

Rossman, D. A. (1979). Morphological evidence for taxonomic partitioning of the *Thamnophis elegans* complex (Serpentes, Colubridae). *Occasional Papers of the Museum of Zoology at Los Angeles State University* **55**, 1–12.

Snedecor, G. W., and Cochran, W. G. (1980). 'Statistical Methods.' (Iowa State University Press: Ames, Iowa.)

SOLO (1988). 'BMDP Statistical Software. Version 2.0.' (Los Angeles, California.)

Storr, G. M., Smith, L. A., and Johnstone, R. E. (1986). 'Snakes of Western Australia.' (Western Australian Museum: Perth.)

Thorpe, R. S. (1985*a*). Character number and the multivariate analysis of variance of simple patterns of geographical variation: categorised or "stepped clinal" variation. *Systematic Zoology* **34**, 127–139.

Thorpe, R. S. (1985*b*). Clines: character number and the multivariate analysis of simple patterns of geographical variation. *Biological Journal of the Linnean Society* **26**, 201–214.

Thorpe, R. S. (1986). Evolution and character congruence of some western Indian Ocean *Phelsuma*: numerical analysis of biochemistry, shape and scalation. *Journal of Zoology (London)* **208**, 429–441.

Thorpe, R. S. (1989). Geographical variation: multivariate analysis of six character systems in snakes in relation to character number. *Copeia* **1989**, 63–70.

Webb, R. G. (1995). Redescription and neotype designation of *Pelochelys bibroni* from southern New Guinea (Testudines : Trionychidae). *Chelonian Conservation* **1**, 301–310.

Wilson, S., and Knowles, D. (1988). 'Australia's Reptiles. A Photographic Reference to the Terrestrial Reptiles of Australia.' (Collins: Sydney.)

Appendix. Material examined

Queensland Museum: J#: 1281, 1429, 3128, 3129, 4096, 4188, 4382, 4596, 6432, 6749, 6969, 7064, 7065, 7739, 7860, 7874, 8454, 8648, 8704, 10213, 10221, 10574, 11269, 13128,.13512, 17702, 20460, 21774, 21785, 21787, 22412, 22413, 23219, 23774, 24415, 25439, 25673, 25766, 27709, 28065, 28426, 28763, 32249, 32250, 32963, 33747, 35037, 35038, 37043, 37045, 40209, 40949, 43426, 47312, 50410, 62493, 62494, 67842, 70319, 70320, 70321, 70322, 70323, 70324, 70325, 70326, 70327, 70328, 70329, 70330, 70331, 70332, 70333, 70334, 70335.

Australian Museum: R#: 28706, 40347, 40712, 86923, 93217, 115329, 115330, 115331, 115344, 115357, 120876, 121187, 121440, 122368, 122369, 122370, 122371, 122372, 122373, 122375, 122889, 124360, 124365, 124799, 124816, 125268, 125243, 127469, 129052, 129582, 130423, 130424, 134944, 134990, 135312, 135580, 136278, 136299, 136300, 137231, 137234, 142882.

Western Australian Museum: 10478, 11989, 13847, 22924, 23784, 24715, 26220, 28124, 28125, 29138, 29686, 31147, 31398, 43029, 43164, 47048, 47588, 47651, 47672, 50456, 50457, 50458, 50522, 50543, 50973, 55422, 56131, 57357, 58254, 60173, 62445, 68344, 86925, 86926, 106268, 117663.

Joan Whittier's private collection: 31, 57, 58, 59, 60, 61, 62, 63, 86, Gu-01, Gu-02, Gu-03, Gu-04, Gu-05, Gu-06, Gu–07, Gu-08, Gu-09, Gu-10, Gu-11, Gu-12, Gu-13, Gu-14, Gu-15, Gu–16, Gu-17, Gu-18, Gu-19, Gu-20, Gu-21, Gu-22.

Manuscript received 1 April 1999; accepted 20 June 2000