

JCU ePrints

This file is part of the following reference:

Heatwole, Harold (2010) *Distribution and geographic variation of sea kraits in the *Laticauda colubrina* complex (Serpentes, Elapidae, Laticaudinae)*. PhD thesis, James Cook University.

Access to this file is available from:

<http://eprints.jcu.edu.au/19027>

**Distribution and Geographic Variation of Sea Kraits in the
Laticauda colubrina Complex (Serpentes, Elapidae,
Laticaudinae)**

Dissertation submitted by
Harold Heatwole B.A. (Bot.), M.S. (Zool.), Ph.D (Zool.), Ph.D (Bot.),
D.Sc
28 April 2010

For the degree of Doctor of Philosophy
Earth and Environmental Sciences
James Cook University
Townsville, Australia

STATEMENT OF SOURCES

DECLARATION

I declare that this dissertation is my own work and has not been submitted in any form for another degree or diploma at any other university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references if given.

Harold Heatwole
28 April 2010

ELECTRONIC COPY

I, the undersigned and author of this work, declare that the electronic copy of this dissertation provided to James Cook University is an accurate copy, within the limits of available technology, of the printed dissertation submitted to that same university.

Harold Heatwole
28 April 2010

STATEMENT OF ACCESS

I, the undersigned, author of this work, understand that James Cook University will make this thesis available for use within the University Library and, via the Australian Digital Theses network, for use elsewhere.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act but I do not wish to place any further restriction on access to this work.

Harold Heatwole

28 April 2010

Name

Signature

Date

TREATMENT OF ANIMALS

The animals used for the preparation of this thesis were mostly preserved specimens collected from the 16th century to the present. Most were collected before institutions or governments required approval for methods of handling animals and hence permit numbers, licence numbers, or approval numbers are not relevant. More recent specimens collected by various museums (see Statement of the Contributions of Others) were covered by the institutional permits and approvals of those organizations. Some tissue samples were collected during the time the present work was conducted but the research on those samples are not included in this thesis.

The only animals not covered elsewhere were the live ones that were captured in the field, briefly examined, and then released unharmed.

STATEMENT OF THE CONTRIBUTIONS MADE BY OTHERS

My supervisor, Prof. Helene Marsh, and my committee members, Dr. Carden Wallace and Dr. Jon Luly played an important role in my professional development through consultation, useful suggestions, providing literature, and helping me crystalise my ideas regarding the biogeography of sea kraits. Harold Cogger and Elizabeth Cameron from the Australian Museum had already recorded scale counts and made notes on colour pattern on some specimens in the Australian Museum, especially from Vanuatu, Fiji and Tonga. Rather than repeat those counts, I took advantage of their generous offer to use their data and merged their dataset with mine. Bryan Gill examined several waif specimens in the Auckland Museum and provided me with the data. Various persons advised on statistical procedures and/or computer methods. Stephen Busack, North Carolina State Museum of Natural Science, made available his statistical package for conducting Principal Components and Canonical Discriminant analyses and assisted in executing the analysis. Brian Wiegmann, Department of Entomology, North Carolina State University, advised in selecting a program for the phenotypically based trees and assisted in executing the analysis. John Monahan of the Statistics Department and Kenneth Pollock of the Biology Department of North Carolina State University, advised on various iterations of multivariate analysis. The final method used was one suggested by Monahan and he assisted in the analysis. Alana Grech, Earth and Environmental Sciences, James Cook University, generously made available her expertise in GIS to generate the environmental datasets and maps used in assessing temperature and rainfall as influences on sea kraits' distributions. The hierarchical analysis was designed and developed by the author alone.

Funding:

The research on which this thesis was based took place over a long period of time and was successively funded by the following institutions, in chronological order:

- National Science Foundation (USA)
- Alpha Helix program of Scripps Oceanographic Institution, La Jolla California
- Internal Research Funds of the University of New England, Armidale, NSW
- Japanese Ministry of Science, Education and Culture
- Centre d'Etudes Nucleaires, Giff sur Yvette, France
- North Carolina Agricultural Foundation, North Carolina State University, Raleigh, NC, USA
- Tropical Environment Studies and Geography, James Cook University, Townsville, Queensland
- Earth and Environmental Sciences, James Cook University, Townsville, Queensland

Access to Specimens:

The curators and staffs of 49 institutions and private collections provided access to specimens under their care. Those institutions and personnel are individually listed in Appendix 3.1.

PUBLICATIONS ARISING FROM THIS DISSERTATION AND THE CONTRIBUTIONS MADE BY CO-AUTHORS

Two scientific papers arising from this dissertation have already been published.

Heatwole, H., S. Busack and H. Cogger. 2005. Geographic variation in sea kraits of the *Laticauda colubrina* complex (Serpentes: Elapidae: Hydrophiinae; Laticaudini). *Herpetological Monographs* 19: 1-136.

This paper contains material taken directly from a draft of the dissertation and consequently figures and large portions of the text of these two documents are identical. Much of the tabular material incorporated into the text of the published paper, however, has been relegated to appendices in the dissertation.

The role of Dr. Busack in this paper was that the Discriminant Function Analysis was performed on his computer using his software for that program; he also advised on its application to the present data.

Dr. Cogger had made some scale counts on snakes in the Australian Museum from some of the eastern islands and he allowed his data to be combined with mine from those localities for my morphological analyses.

I wrote the entire paper myself and then both co-authors made editorial suggestions.

Cogger, H. and H. Heatwole. 2006. *Laticauda frontalis* DeVis and *Laticauda saintgironsi* sp. nov. representing a new clade of sea kraits from the Republic of Vanuatu and New Caledonia (Serpentes: Laticaudidae). *Records of the Australian Museum* 58: 245-256.

Dr. Cogger was studying the taxonomic relationship of *Laticauda frontalis* to other members of the *Laticauda colubrina* complex and I was examining all taxa of that complex. We combined our databases for *L. frontalis*, *L. colubrina* and *L. saintgironsi* for Vanuatu and New Caledonia to give a wider range of characters than encompassed by either study alone; consequently some of the material for this paper arose from my thesis. We each wrote separate parts of the paper and then combined

them. The contribution by Dr. Cogger to the published paper does not appear in my dissertation.

During the course of my thesis research, two new species were described, *Laticauda saintgironsi* from New Caledonia (Cogger and Heatwole, 2006) and *Laticauda guineai* from southern Papua-New Guinea (Heatwole *et al.*, 2005). Because original descriptions of new species must appear in only one place, and because access to theses is more limited than to published papers, I considered the above two papers a better outlet than my thesis for these original descriptions. The thesis was revised to refer to these taxa by their new specific epithets, rather than as populations of *L. colubrina*.

ACKNOWLEDGEMENTS

I am grateful to Prof. Helene Marsh for the generosity of her time and experience in guiding me through the preparation of this dissertation. Despite other heavy commitments, she willingly gave advice and shared her insights. The research on which this thesis was based took place over a long period of time and was successively funded by a number of different institutions. They are listed in detail in the section entitled " Statement of the Contributions of Others ".

The curators and staffs of many institutions (see "Statement of the Contributions of Others" and Appendix 3.1) provided access to specimens under their care and provided facilities and equipment; their kindnesses were myriad and almost without exception, they facilitated my research in ways beyond normal professional courtesies.

Prof. Arthur Echternacht provided a Visiting Professorship at the University of Tennessee and arranged for that institution to serve as a repository of some of the specimens borrowed from various museums in the United States; he also kindly provided space and facilities.

I benefited from the statistical and technical expertise of colleagues who generously gave their time to tutor me in a particular program with which they were familiar and discuss its application to my work, in some cases actually running a number of iterations through their computers for me (See Publications Arising from this Dissertation and the Contributions made by Co-authors to Them). They should not be held accountable for the hierarchical analysis, which I devised entirely on my own.

Many colleagues and students on various field trips assisted in the collection of specimens. They are too numerous to mention individually, but especially

noteworthy are Nobuo Tamiya, Toru Tamiya, the late André Ménez, Yugi Ishikawa, Kenneth Zimmerman, Michael McCoy, Petah Abbott, Carla Karubaba, and Bryan Stuart.

J. C. Enderman supplied a copy of his unpublished report for my perusal during the early part of the study. Naseem Ostavar, the late Audry Heatwole, Lynda Bridges and Elizabeth Cameron assisted with recording data or entering them into the computer; their dedication and persistence was exemplary. Indraneil Das and Rom Whittaker assisted in locating specimens. Bryan Stuart, Kraig Adler, Benjamin Williams and Christine Giannoni helped procure obscure literature. Yuri Yamamoto, Jason Shih, Andrei Podolsky, and Zola Packman helped in the translation of Japanese, Chinese, Russian and Latin literature respectively.

Barbara and Terry Done and Petah and David Abbott generously welcomed me to their homes and provided logistic support over extended periods.

Most of all I am grateful to my late wife, Audry Ann Yoder Heatwole, for her love and unstinting support of me and my work over 53 years of marriage, and who, without complaint, many times and often for prolonged periods, took time out from her own profession as an artist-potter to efficiently shoulder the responsibilities of rearing children, running a household, and managing finances during my prolonged absences on field expeditions. In addition, she often spent long periods, at night and into the morning hours, helping me collate data, track down literature, proof read, and prepare tables and graphs; she wielded a formidable editorial pen that corrected my tendency toward verbosity. Without her support, I would never have been able to achieve my professional objectives to the extent that I have, nor would I have been able, in the press of other duties, to conduct the research on which this dissertation is based. She was one of the few people who understood why I was compelled to pursue another doctorate. Tragically, her own creative talent was extinguished by a hemorrhagic stroke and she died on 6 March 2008. This thesis is dedicated to her, in loving memory.

ABSTRACT

The sea kraits constitute a genus (*Laticauda*) of marine snakes that forage in the sea but come onto land to rest, digest their prey, court, mate and oviposit. There are three complexes: (1) the *Laticauda semifasciatus* complex with two species, (2) the *Laticauda laticaudata* complex with two species, and (3) the *Laticauda colubrina* complex with four species: *Laticauda colubrina*, *Laticauda frontalis*, *Laticauda saintgironsi*, and *Laticauda guineai*, the last two of which were described as new to science as a result of the research presented in this dissertation. The *Laticauda colubrina* complex is far-flung in the tropics and subtropics from the Andaman Islands to Tonga and from New Guinea to the Ryukyu Islands, wherein its species inhabit coral reefs associated with small offshore islands. This area has had an exceptionally complex geologic history involving the collision of the Indian, Eurasian, and Australian tectonic plates, as well as large-scale movements of various marine ophiolites and island arcs and of terranes of various ages and origins (e.g., Gondwanaland and Australia) that became compositely incorporated into the archipelagos now inhabited by sea kraits. The origin, adaptive radiation, and spread of the genus *Laticauda* took place from 30 mya to the present time, thereby bracketing the time-period relevant to the elaboration of the pattern of geographic variation and speciation of the *Laticauda colubrina* complex analysed in this dissertation.

This dissertation describes the distributions and patterns of geographic variation of the species in the *L. colubrina* complex and interprets them in terms of the geologic and palaeogeographic history of the region and of such present-day environmental factors as temperature, directions of sea currents, and distances between areas of suitable habit. The accumulated specimens deposited over several centuries in the museums of the world were used to plot distributions of species and as a source of data on morphological characters and details for use in analysing patterns of geographic variation.

Four approaches to geographic variation in morphology and colour pattern were used: (1) Hierarchical Analysis, (2) Principal Components Analysis and Canonical Discriminant Analysis, (3) construction of phenotypically based trees, and (4) multivariate analysis. The last three are standard techniques, but the first I devised myself. It has the advantage over other morphological techniques of being able to distinguish between populations whose morphologic similarities arise either from (1) convergent evolutionary responses to similar environments or (2) direct effects of similar environments on developmental processes, in contrast to those that (3) reflect genetic relatedness. With the growing recognition that neither morphological nor biochemical techniques alone are sufficient to assess phylogenetic history completely, this technique is an important one in that it bridges the two approaches, and provides a rational basis for selecting target populations for the application of biochemical methods to phylogeographic studies.

The hierarchical approach identified six areas in which populations were relatively homogeneous but which showed discontinuities with adjacent areas. These were: (1) a North-South Axis (Sabah, Philippines, Ryukyus, and Taiwan), (2) an East-West Axis (Andaman and Nicobar Islands, Thailand, Myanmar, Indonesia, Peninsula Malaysia/Singapore, New Guinea excluding southern Papua and West Irian, Solomon Islands), (3) southern Papua, (4) Palau, (5) the Eastern Islands (Vanuatu, Fiji, Tonga), and (6) New Caledonia.

The isolate on New Caledonia was recognized as a new species, *Laticauda saintgironsi* (published elsewhere; Cogger and Heatwole, 2006) as was the one in southern Papua (*Laticauda guineai*; also published elsewhere; Heatwole *et al.*, 2005); *Laticauda frontalis* was elevated from previous synonymy (published elsewhere; Cogger and Heatwole, 2006).

The Principal Components Analysis confirmed these results in a more quantitative way, emphasized the distinctiveness of *L. saintgironsi*, *L. guineai*, and *L. frontalis* and, although confirming the distinctiveness of the other populations demarcated by the hierarchical approach, demonstrated that separation among the two axes

and the eastern islands was not as marked as for the named species, thereby supporting the decision not to recognise those differences nomenclaturally. This approach also identified character displacement between *L. colubrina* and *L. frontalis* on Vanuatu, the only incidence of sympatry among members of the complex.

The construction of phenetically based trees supported the interpretation that *L. frontalis* and *L. saintgironsi* were closely related but did not contribute much otherwise to an understanding of geographic patterns of variation within the complex.

Multivariate analysis revealed that there was a strong latitudinal component to the variation of *L. colubrina* and that the latitudinal effect varied with longitude. Addition of rainfall and surface temperature of the sea as variates explained little additional variation.

There was sexual dimorphism in many characters, perhaps related to the ecological segregation of males and females into distinct ecomes with different foraging habits and diets. *L. frontalis* was less dimorphic than the other species. There was also differences in some characters between juveniles and adults, perhaps reflecting different selective forces operating on juveniles and adults (the two groups are different in the time they spend on land as opposed to in the sea).

A model of the phylogeny and dispersal of sea kraits was developed. It indicates origin of *Laticauda* in New Guinea from an Asian elapine ancestor. Subsequent radiation involved successive cycles of dispersal during periods of lowered sea levels and isolation during elevated sea levels, giving rise first to the three complexes of the genus, then to the species within complexes, and most recently to the groupings of the east-west axis, north-south axis and eastern islands. These events took place within the past 30 million after most of the formative tectonic and vicariant events of the region had already taken place. Rather, distribution and geographic patterns of variation relate to configuration of land and sea in the area from 30 mya to the present.

TABLE OF CONTENTS

Title Page	i
Statement of Sources	ii
Electronic Copy	iii
Statement of Access	iv
Treatment of Animals	v
Statement of the Contribution Made by Others	vi
Publications Arising from this Dissertation and the Contributions Made by Co-Authors	viii
Acknowledgements	x
Abstract	xii
Table of Contents	xv
List of Tables	xviii
List of Figures	xviii
List of Appendices	xxii
Chapter 1. Introduction	1
1.1. Rationale and Objectives of the Study	1
1.2. Taxonomic Status of Sea Kraits	3
1.3. Natural History of Species of the <i>Laticauda colubrina</i> Complex	9
1.4. The Geologic Time-Frame of the Origin and Phylogeny of Sea Kraits	13
1.5. Palaeogeography of the Study Area from the Cenozoic to Recent Times	17
1.6. Paleoclimatology, Sea-Level Changes, and Pattern of Oceanic Currents	28
1.7. Recapitulation	31
Chapter 2. Materials and General Approaches	34
2.1. Structure of the Dissertation	34
2.2. The Database	35
2.2.1. Colour Pattern	38
2.2.2. Scutellation	44
2.2.3. Size	48

2.2.4. Gender and Maturity	48
2.2.5. Second-Order Characters	49
2.3 Recapitulation	49
Chapter 3. Geographic Distribution	50
3.1. Methods	50
3.2. Distribution of Species	51
3.2.1. <i>Laticauda colubrina</i>	51
3.2.2. <i>Laticauda saintgironsi</i>	65
3.2.3. <i>Laticauda frontalis</i>	65
3.2.4. <i>Laticauda guineai</i>	66
3.3. Factors Affecting Distribution	66
3.3.1. Relation to Climate: Geographical Information System (GIS) Analysis	66
3.3.2. Relation to Sea Currents	70
3.3.3. Relation to Habitat	78
3.3.4. Relation to Fire	81
3.3.5. Relation to Predators	81
3.3.6. Relation to Congeners	82
3.4. Recapitulation	85
Chapter 4. Geographic Variation: Hierarchical Analysis	87
4.1. Methods	87
4.2. Results and Discussion: Stable Characters	89
4.2.1. Snout (Rostral and Nasals)	89
4.2.2. Temporals	91
4.2.3. Supralabials	93
4.2.4. Yolk Sac Scar	93
4.2.5. Length of the Body and Tail	94
4.3. Results and Discussion: Variable Characters	101
4.3.1. Preliminary Analysis	101
4.3.2. Prefrontals	103
4.3.3. Number of Dark Bands on the Body	104
4.3.4. Number of Dark Bands on the Tail	111
4.3.5. Subcaudal Scales	115
4.3.6. Scale Rows Around the Body	120
4.3.7. Width of Bands	127
4.3.8. Gastrosteges	141
4.3.9. Colour Pattern of the Head and Tip of Tail	146
4.4. Synthesis	150
4.5. Recapitulation	150
Chapter 5. Geographic Variation: Principal Components Analysis	152
5.1. Methods	152
5.2. Results and Discussion	154
5.3. Recapitulation	157

Chapter 6. Geographic Variation: A Tree of Phenotypes	158
6.1. Methods	158
6.2. Results and Discussion	158
Chapter 7. Multivariate Analysis	162
7.1. Methods	162
7.2. The Analyses: Results and Discussion	162
7.3. Recapitulation	167
Chapter 8. General Discussion and Conclusions	168
8.1. Taxonomic Conclusions	168
8.1.1 Definition of Taxa	168
8.1.2. Morphologic Lability and Diversity	169
8.1.3. Delimiting Type Locality	171
8.2. Sexual Dimorphism	171
8.3. Ontogenetic Variation	181
8.4. “Patchy” Distributions	183
8.5. Factors Affecting Patterns of Geographic Variation	184
8.5.1. Latitudinal and Developmental Effects	191
8.6. Role of Palaeogeography and Palaeoclimate in the Distribution of Sea Kraits and their Derivatives	194
8.6.1. Comparison with other Taxa of Reptiles	203
8.7. General Conclusions	204
8.8. Recapitulation	206
Chapter 9. Future Research	209
9.1. Relationship of Morphological and Biochemical Approaches	212
9.2 Widening the Scope of Morphological Studies	214
References	216
Appendices	243

LIST OF TABLES

Table 2.1. Summary of characters used in analyses.	37
Table 5.1. Ranking of characters by percentage of variation explained in the Principal Components Analysis.	154
Table 7.1. Coefficients of correlation between the two major factors and the scores of four simple surrogates.	164

LIST OF FIGURES

Figure 1.1. Present-day tectonic features of the southeastern Asian and southwestern Pacific regions.	18
Figure 1.2. Palaeogeographic maps for the past 55 million years.	20
Figure 1.3. Map showing the direction of sea currents in eastern Indonesia.	26
Figure 2.1. Conceptual diagram of the dissertation.	34
Figure 2.2. Elements of the colour pattern of the head in species of the <i>Laticauda colubrina</i> complex.	40
Figure 2.3. Dorsal, ventral and lateral views of the four basic types of head pattern.	41
Figure 2.4. Variation in the Q head pattern and its derivatives, J, H, and V.	42
Figure 2.5. Derivatives of head pattern D.	42
Figure 2.6. Derivatives of head pattern A.	43
Figure 2.7. Derivatives of head pattern E.	43
Figure 2.8. Details of the scutellation of the head of <i>Laticauda colubrina</i> illustrating some of the character states used in the present study.	45
Figure 3.1. Map of the study area showing major countries, localities, and bodies of water.	51
Figure 3.2. Map showing the known localities for <i>Laticauda colubrina</i> in the Andaman and Nicobar Islands.	56
Figure 3.3. Map showing the known localities for <i>Laticauda colubrina</i> in coastal southeastern Asia.	57

Figure 3.4. Map showing the known localities of <i>Laticauda colubrina</i> in Indonesia and neighbouring countries to the north.	57
Figure 3.5. Map showing the known localities for <i>Laticauda colubrina</i> in Taiwan and the Ryukyu Islands.	58
Figure 3.6. Map showing the known localities for the <i>Laticauda colubrina</i> and <i>Laticauda guineai</i> in Papua-New Guinea.	59
Figure 3.7. Map showing the known localities for <i>Laticauda colubrina</i> in the Solomon Islands.	60
Figure 3.8. Map showing the known localities for <i>Laticauda colubrina</i> and <i>Laticauda frontalis</i> in Vanuatu.	61
Figure 3.9. Map showing the known localities for <i>Laticauda colubrina</i> in Palau.	62
Figure 3.10. Map showing the known localities for <i>Laticauda colubrina</i> in Fiji.	63
Figure 3.11. Map showing the known localities for <i>Laticauda colubrina</i> in Tonga.	64
Figure 3.12. Map showing the distribution of <i>L. saintgironsi</i> in New Caledonia and the Loyalty Islands.	65
Figure 3.13. Mean surface temperatures of the sea over the geographic range of the <i>Laticauda colubrina</i> complex.	67
Figure 3.14. Mean quarterly rainfall over the distributional range of the <i>Laticauda colubrina</i> complex and adjacent regions.	70
Figure 3.15. Surface currents of the Pacific Ocean and part of the Indian Ocean during the months of February and March.	72
Figure. 3.16. Map showing the distribution of coral reefs in the study area.	78
Figure 3.17. The known localities occupied by <i>Laticauda colubrina</i> in Indonesia in relation to the distribution of corals and mangroves.	79
Figure 4.1. Frequency of snout-vent lengths of <i>Laticauda colubrina</i> from all localities.	96

Figure 4.2. Frequency of snout-vent lengths of <i>Laticauda saintgironsi</i> from all localities.	96
Figure 4.3. Relationship of tail length to snout-vent length in <i>Laticauda colubrina</i> , <i>Laticauda saintgironsi</i> , and <i>Laticauda frontalis</i> .	99
Figure 4.4. Distribution of numbers of dark bands on the bodies of male and female <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	108
Figure 4.5. Distribution of numbers of dark bands on the tails of male and female <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	113
Figure 4.6. Comparison of the frequencies of number of subcaudal scales in male and female <i>Laticauda colubrina</i> and <i>Laticauda saintgironsi</i> .	117
Figure 4.7. Distribution of numbers of subcaudal scales of male and female <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	118
Figure 4.8. Change along the torso in the number of scale rows around the body of species in the <i>Laticauda colubrina</i> complex.	121
Figure 4.9. Distribution of numbers of scale rows around the body at the level of the 100 th gastrostegite in male and female <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	125
Figure 4.10. Distribution of the dorsal width of the first dark band and first light band in <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	131
Figure 4.11. Distribution of the ratio of dorsal widths of dark and light bands and of the ratio of the dorsal and ventral widths of the first dark band on the bodies of <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	141
Figure 4.12. Distribution of the number of gastrosteges in male and female <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	144
Figure 4.13. Distribution of the dominant colour patterns of the head in <i>Laticauda colubrina</i> , <i>Laticauda guineai</i> , <i>Laticauda saintgironsi</i> and <i>Laticauda frontalis</i> .	147

Figure 5.1 Principal Components Analysis of the <i>Laticauda colubrina</i> complex.	155
Figure 5.2. Comparison of discriminant scores for adult <i>Laticauda colubrina</i> sympatric with <i>Laticauda frontalis</i> on Vanuatu and for allopatric <i>L. colubrina</i> , separately for males and females.	157
Figure 6.1. A phenotypically based tree showing clustering of female specimens of the species of the <i>Laticauda colubrina</i> complex from different regions.	159
Figure 6.2. A phenotypically based tree showing clustering of male specimens of the species of the <i>Laticauda colubrina</i> complex from different regions.	160
Figure 7.1. Quadratic surface relating cumulative principal scores in the multivariate analysis to latitude and longitude for males.	165
Figure 7.2. Quadratic surface relating cumulative principal scores in the multivariate analysis to latitude and longitude for females.	166
Figure 8.1. Contours showing the average age of extant reef coral genera.	195
Figure 8.2. The configuration of land and sea and the distribution of mangrove swamps (in green) in Sundaland during the height of the last glaciation, 18,000-20,000 years ago and similar to that occurring during repeated cycles of sealevel-lowering during the late Pliocene and Pleistocene.	197
Figure 8.3. Palaeogeographic maps showing configuration of land and sea from 30 million years ago (mya) to 15 mya and the events in the history of <i>Laticauda</i> that are postulated to have occurred during that time.	198
Figure 8.4. Palaeogeographic maps showing configuration of land and sea from 10 million years ago (mya) and 5 mya and the events in the history of <i>Laticauda</i> that are postulated to have occurred during that time.	199
Figure 8.5. Palaeocurrents and distribution of corals in the Eocene before the origin and dispersal of <i>Laticauda</i> and in the Miocene when these events were postulated to have begun.	199
Figure 8.6. Patterns of Australasian sea currents in winter and summer at the present day and at maximal sea level lowering during glacial periods.	202

LIST OF APPENDICES

Appendix 1.1. Synonymy of the species of the <i>Laticauda colubrina</i> complex.	243
Appendix 2.1. Glossary	245
Appendix 2.2. Numbers of specimens of the <i>Laticauda colubrina</i> complex examined from different countries.	248
Appendix 4.1. Range of values of measurements and meristic characters in <i>Laticauda colubrina</i> .	249
Appendix 4.2. Range of values of meristic characters in <i>Laticauda saintgirons</i> and <i>Laticauda guineai</i> .	250
Appendix 4.3. Range of values of measurements and meristic characters in <i>Laticauda frontalis</i> .	252
Appendix 4.4. Mean and maximum snout-vent lengths of male and female sea kraits of the <i>Laticauda colubrina</i> complex.	253
Appendix 4.5. Results of an ANOVA testing for differences among the various major localities for all characters used in this study, separately by gender for <i>Laticauda colubrina</i> .	255
Appendix 4.6. Geographic variation in the temporal scales of <i>Laticauda saintgironsi</i> , <i>Laticauda frontalis</i> and <i>Laticauda colubrina</i> .	256
Appendix 4.7. Geographic variation in the temporal scales <i>Laticauda colubrina</i> and <i>Laticauda guineai</i> in Papua-New Guinea and the Solomon Islands.	257
Appendix 4.8. Geographic variation in the number of supralabials in species of the <i>Laticauda colubrina</i> complex.	258
Appendix 4.9. Sexual dimorphism in the position of the midpoint of the yolk-sac scar.	259
Appendix 4.10. Proportions of individuals with different numbers of prefrontal scales in species of the <i>Laticauda colubrina</i> complex.	260
Appendix 4.11. Comparison of the number of prefrontals in males and females of species in the <i>Laticauda colubrina</i> complex.	261

Appendix 4.12. Comparison of the number of prefrontals in juveniles and adults of the species in the <i>Laticauda colubrina</i> complex.	262
Appendix 4.13. Sexual dimorphism and regional differences in the number of dark bands on the body in adults of the <i>Laticauda colubrina</i> complex.	263
Appendix 4.14. Sexual dimorphism and regional differences in the number of dark tail bands on the body in adults of the <i>Laticauda colubrina</i> complex.	265
Appendix 4.15. Sexual dimorphism and regional differences in the number of subcaudal scales in adults of the <i>Laticauda colubrina</i> complex.	267
Appendix 4.16. Probability values tests of sexual dimorphism in number of scale rows around the body at the level of the 100 th gastrostege in species of the <i>Laticauda colubrina</i> complex.	269
Appendix 4.17. Statistical significance of geographic variation in the number of scale rows around the body at the level of the 100th gastrostege in <i>Laticauda colubrina</i> as tested by ANOVA.	270
Appendix 4.18. Comparisons along the torso and from dorsum to venter of the widths of the dark and light-coloured bands in <i>Laticauda colubrina</i> and <i>Laticauda guineai</i> .	271
Appendix 4.19. Comparisons of dorsal widths of the dark and light bands along the torso in <i>Laticauda frontalis</i> .	272
Appendix 4.20. Comparisons along the torso and from dorsum to venter of the widths of the dark and light-coloured bands in <i>Laticauda saintgironsi</i> .	273
Appendix 4.21. Comparison between males and females of the dorsal width of the first dark band.	274
Appendix 4.22. Comparison between juveniles and adults in the number of scale rows in the dorsal widths of black bands.	275
Appendix 4.23. Variation among specific localities in dorsal width of first dark band of adult <i>Laticauda colubrina</i> .	277

Appendix 4.24. Comparison between males and females of the dorsal width of the first light band.	278
Appendix 4.25. Comparison of the number of scale rows in the dorsal width of the first light band between juveniles and adults.	279
Appendix 4.26. Variation among specific localities in dorsal width of first light band of adult <i>Laticauda colubrina</i> .	280
Appendix 4.27. Geographic variation in the colour pattern of the cephalic shield, body bands, and tip of the tail in species of the <i>Laticauda colubrina</i> complex.	281
Appendix 4.28. Incidence of incomplete dark bands at different levels along the torso in species of the <i>Laticauda colubrina</i> complex.	282
Appendix 4.29. Comparison between males and females of the number of gastrosteges.	283
Appendix 4.30. Colour pattern on the heads of male and female <i>Laticauda colubrina</i> and <i>Laticauda saintgironsi</i> .	284
Appendix 4.31. Statistical comparison of head colour patterns of species in the <i>Laticaudacolubrina</i> complex among adjacent geographic regions.	285