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

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

Dissertation submitted by
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28 April 2010

For the degree of Doctor of Philosophy
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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 Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references if given.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

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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 in 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., Gonwanaland 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 asses 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 discontinuites 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 econes 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.

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CHAPTER 1. INTRODUCTION

This chapter sets the background for the dissertation. It gives the reason the study was undertaken and outlines the objectives of the research, reviews the taxonomic status, synonymy, and natural history of sea kraits, and discusses the palaeogeographic and geological context in which the taxon evolved.

1.1. Rationale and Objectives of the Study

Widespread groups of organisms often show considerable morphological variation throughout their geographic ranges; the patterns of variation may serve as clues to their evolutionary history. Homogeneity over extensive areas may indicate recent expansion and/or continuing gene flow among populations and an ability to cross physical barriers that separate populations of other taxa. Demes with similar morphology, but nevertheless with detectable differences, are suggestive of partial isolation (either through vicariance or by dispersal to new areas) with some recent or continuing ameliorating gene flow. The degree of divergence among demonstrably distinct populations indicates the extent of isolation, in time, space, or both, and leads to hypotheses about their genetic affinity and to decisions about their taxonomic status.

Archipelagoes are particularly instructive in that they present a kaleidoscope of habitats of two very different kinds, sea and land, whose interfaces vary in space and change with time, leading to complex patterns of morphological variation among their inhabitants. Unraveling the skein of evolutionary relationships among such archipelagic species depends on an understanding, not only of present-day geography and its effect on dispersal and gene flow, but on how that configuration changed in the past and the effect of those changes in isolating or connecting populations. The objectives of this thesis are to (1) describe the distributions of sea kraits in the *Laticauda colubrina* complex and explain them in terms of historic and present biotic and abiotic influences, (2) analyse geographic patterns of morphological variation, (3) assess the role of present geographic and ecological factors in affecting dispersal and gene flow among populations, (4) interpret the role of palaeogeography and vicariant events in the evolutionary history of the taxa, and (5) identify the most appropriate sources of molecular material to be used for further testing of evolutionary hypotheses.

The advent of biochemical techniques in phylogeography was a major advancement contributing to a revolution in taxonomy and phylogeny from which many important insights were gained that previously were not possible, especially in the estimation of the timing of divergence of taxa. As valuable as these developments were, and are, they have flaws that can be corrected by morphologically based studies. Moor and Gill (2010) pointed out that alone biochemical studies focus on solutions to matrices rather than on homology of characters and that algorithms, not biology are used as the basis of decisions about homology. To that I would add that another difficulty is that biochemical approaches often rely on “taxon sampling”, i.e., haphazardly selecting a few individuals (sometimes only one) to represent a taxon to be used in comparison with other taxa. The present dissertation shows that the *Laticauda colubrina,* as previously known, is not one morphological entity, but a number of them, and hence taxon sampling from this complex, without consideration of the morphological analysis presented in this dissertation, could be misleading (see Chapter 9).

I consider morphological and biochemical approaches to both be necessary for a full understanding of the phylogeny of reptiles and agree with the statement by Zaher *et al.* (2009):

> "Both molecular and morphological data sets will ultimately be necessary to develop a comprehensive phylogeny of snakes and each data source can make a unique contribution. On one hand, molecular methods can provide large quantities of phylogenetically informative data..........On the other hand, only few morphological complexes have been analyzed thoroughly within snakes, and the paucity of broadly sampled morphological characters has prevented the compilation of a large morphological data matrix. We prefer a combination of the two data sources." [pp. 116-117]

Similarly, Scanlon and Lee (2004) have successfully merged morphological and molecular approaches in the study of snakes and opined:

> "Increased reliance on genetic data alone may be seen as avoiding problems due to morphological convergence, but would also entail neglect of much of the currently available phylogenetic evidence, as well as much of the data of biological and evolutionary interest." [p. 359]

I believe that where convergence has occurred a complete understanding is best achieved through a combination of morphological and biochemical approaches.

This dissertation describes variation in morphology and colour pattern in the *L. colubrina* complex and interprets it in geographic and taxonomic terms; phylogenetic inferences are drawn that allow realistic planning of phylogeographic studies and that are serving as hypotheses for testing by biochemical approaches now in progress by Ulrich Kuch and in which I am a participant.

1.2. Taxonomic Status of Sea Kraits

Sea kraits (genus *Laticauda* Laurenti, 1768) are venomous marine snakes of tropical to subtropical coastal waters of Australasia, the western Pacific Ocean and the Bay of Bengal. They have variously been treated as belonging (1) to the family Colubridae, *sensu lato* (e.g., Boulenger, 1896, 1897), (2) to the true sea snakes, family Hydrophiidae (sometimes spelled Hydropheidae) (Cope, 1859, 1886; Golay, 1993), (3) as a separate subfamily (Laticaudinae) of the Hydrophiidae (Smith, 1926, 1943), (4) as the subfamily Laticaudinae within the family Elapidae (McCarthy, 1985, 1986; Dowling, 1967; Cogger and Heatwole, 2006; Sanders and Lee, 2008, see below), (5) in a separate tribe (Laticaudini) in the subfamily Elapinae (Smith *et al.*, 1977; Harding and Welch, 1980) (6) as the tribe Laticaudini within the subfamily Hydrophiinae (Ineich and Laboute, 2002; Heatwole *et al.*, 2005), (7) as a genus within the Hydrophiinae (e.g., Wall, 1909; Dowling, 1959; Underwood, 1967; Mao *et al.*, 1983, and see below), (8) as members of the subfamily Elapinae of the Elapidae (McDowell, 1970; Smith *et al.*, 1977), and (9) as a separate family of their own (Laticaudidae) (Burger and Natsuno, 1974; Cogger *et al.*, 1983).

Within these classifications there have been various interpretations of the relationship of *Laticauda* to other marine and terrestrial genera. Smith (1926) considered *Laticauda* to be more closely allied with *Aipysurus* and *Emydocephalus* than are any of these with *Hydrophis* or other true sea snakes. Lombard *et al.* (1986) found that the ectopterygoids of *Laticauda* and *Aipysurus* were longer than for other sea snakes; most investigators do not support a close relationship between *Laticauda* and these two genera. On the basis of immunological data, Schwaner *et al.* (1985) concluded that *Laticauda* had a separate origin from other marine genera. McDowell (1967, 1969, 1970, 1972, 1974, 1987) suggested that marine genera had independent origins, with the oviparous *Laticauda* being more closely related to some terrestrial Asian and New World elapids (collectively called the "palatine erectors") and the viviparous sea snakes being allied to Australian terrestrial elapids (the "palatine draggers"). Greer (1997) assessed this hypothesis and concluded that southern Asian or American relationships for *Laticauda* were less likely than an Australasian one. Cadle and Gorman (1981) considered both *Laticauda* and *Hydrophis* to have arisen from Asian elapids with *Laticauda* and American *Micrurus* being remote. Mengden (1983) noted a consensus for a close relationship between sea snakes and Australian elapids but felt there was little agreement about the precise relationships of *Laticauda*. Minton and da Costa (1975), using comparative serology, suggested that sea snakes and sea kraits comprised a homogeneous group closely related to Australian elapids. Voris (1977), using 153 qualitative and quantitative characters, concluded that sea snakes consist of three major stocks: (1) *Laticauda*, (2) *Aipysurus* and *Emydocephalus*, and (3) all other species. On the basis of the structure of venom proteins, Tamiya (1985) considered that the simplest classification was into five groups: (1) *Laticauda*, (2) hydrophiine sea snakes, (3) Australian terrestrial elapids, (4) *Dendroaspis*, and (5) other African and Asian terrestrial elapids, with the possibility that *Bungarus* might be a sixth group. Slowinski *et al.* (1997), based on an analysis of amino-acid sequences of venom proteins, also believed that Asian and African elapids constituted a separate lineage; they included *Laticauda* within the Hydrophiinae, but considered this subfamily as diphyletic, one branch being *Laticauda* and the other the remaining hydrophiines, a view consistent with the phylogeny erected by Fry *et al.* (2003) on the basis of three-finger toxins. Rasmussen (1997, 2001) concluded that sea snakes evolved from terrestrial snakes on three independent occasions, once as the *Laticauda* lineage, again as the *Aipysurus*-*Emydocephalus* line, and finally as the *Hydrophis* group. In general, most recent studies have not supported an affinity of *Laticauda* with the Asian, African, or American elapids, but rather have allied this genus to the hydrophiine clade (true sea snakes and terrestrial venomous Australian snakes) (Slowinski and Keogh, 2000; Lawson *et al.*, 2005; Lukoschek and Keogh, 2006; Zaher *et al.*, 2009).

Shine (1991b) suggested that the mode of reproduction in marine venomous snakes reflects their different origins, sea kraits (*Laticauda*) being egg-layers (except possibly *L. crockeri*; see Cogger *et al.*, 1987) with a possible origin from oviparous Asian elapids, and the live-bearing sea snakes with a possible origin from a lineage of

Australian terrestrial elapids that had already become viviparous, perhaps in response to a lowering of temperature about five million years ago (mya) (Shine, 1985). Keogh *et al.* (1998), using sequences of cytochrome b and rRNA, found that the Australian-Melanesian terrestrial elapids clustered into two groups, an oviparous lineage and a viviparous one. *Laticauda colubrina* showed consistent affinities with the oviparous lineage, especially with the Australian genus *Pseudechis*. When *Pseudechis*, however, was removed from the analyses, *Laticauda* clustered with the Melanesian rather than with the Australian terrestrial oviparous species and these authors were skeptical of the *Laticauda-Pseudechis* linkage. In any event, *Hydrelaps*, a viviparous sea snake, consistently clustered with the viviparous lineage and *Laticauda* with the oviparous one, suggesting that sea kraits and true sea snakes represent independent invasions of the marine environment. By contrast, in a review of the evidence from osteology, scutellation, soft anatomy, morphology of the hemipenes, antigens, transferrin immunology, amino-acid sequences of neurotoxins, and base-pair sequences of DNA and RNA, Guinea (2002) concluded that the sea kraits are basal to the true sea snakes and that these two natural groups, along with their sister-group, some Australian-Melanesian terrestrial elapids, collectively form a clade to which all Asian terrestrial elapids are consistently paraphyletic. On the basis of molecular data, Keogh (1998) suggested that sea kraits and true sea snakes had separate origins, with *Laticauda* being a transitional clade between the "palatine draggers" and the "palatine erectors".

Sanders *et al.* (2008) provided a detailed analysis of the phylogeny within the hydrophiines. They showed that after separating from the basal *Laticauda* stock, the remaining Australasian hydrophiines diverged into several rapidly diversifying lineages. These were successively (1) an oviparous clade of terrestrial Melanesian and Australian species with multiple dispersal events between Australia and New Guinea, (2) an oviparous Australian terrestrial lineage within which were generated (3) two separate clades of burrowing forms and (3) two separate viviparous terrestrial lineages, one of which subsequently gave rise to (4) a marine clade, the true sea snakes. Thus, true sea snakes and *Laticauda* were considered to be independent marine radiations. These recent findings were incorporated into a revised taxonomy (Sanders and Lee, 2008) in which the family Elapidae was divided into three subfamilies, the (1) Elapinae containing the African, Asian and American representatives, the (2) Laticaudinae consisting of *Laticauda*, the basal group radiating into Australasia, and (3) its derivative, the Oxyuraninae comprised of the Australasian terrestrial proteroglyphs with the true sea snakes nested within it. Thus, the current classification of sea kraits is: Order Squamata, Suborder Serpentes, Superfamily Colubroidea, Family Elapidae, Subfamily Laticaudinae, Genus *Laticauda*. These designations are employed throughout the remainder of this thesis.

Traditionally, all sea kraits have been assigned exclusively to the genus, *Laticauda*. However, Kharin (1984a) erected *Pseudolaticauda* for the *semifasciata* complex (*semifasciata* and *schistorhynchus*) and later (Kharin and Czeblukov, 2006) reiterated that nomenclature in a revision of the family Laticaudidae, seemingly partly on the basis of the literature without having examined all relevant specimens. This classification has not been generally accepted (see Slowinski, 1989; David and Ineich, 1999) and I agree with Voris' (1977) view that "the genus *Laticauda* is a tight cluster of species very distinct from all other taxa" and concur with McCarthy's (1986) and Rasmussen's (1997) retention of the *semifasciata* group within *Laticauda*. *Laticauda* (*sensu lato*) can be distinguished from all other paddle-tailed snakes by a combination of broad (much wider than long) gastrosteges and by nasal scales that do not contact each other directly but are separated medially by another scale or scales (Heatwole and Cogger, 1994).

Relationships within the genus *Laticauda* also have been subject to various interpretations (Mao *et al.*, 1977; Voris, 1977; McCarthy, 1986; Slowinski, 1989). There seems to be general agreement for a close relationship between *Laticauda laticaudata* and *L. crockeri* and between *L. semifasciata* and *L. schistorhynchus*; interpretations vary as to which of these two groups is most closely related to *L. colubrina* (see reviews by Greer, 1997; Guinea, 2002). Gorman (1981) considered the chromosome number of *L. colubrina* to be primitive for the elapid radiation; thus, it is likely the primitive one for the genus as well and other laticaudid complexes are probably derived from *L. colubrina*. Slowinski *et al.* (1997) supported this grouping as all but one of their gene trees showed an initial split between *L. colubrina* and *L. semifasciata*, with *L. laticaudata* and *L. crockeri* being most closely allied to each other, and both closer to *L. colubrina* than to *L. semifasciata*. Slowinski (1989) later revised this scheme slightly, maintaining *L. colubrina* as the species closest to the ancestor of the genus, but with *L. semifasciata*, rather than *L. colubrina*, closer to the *crockeri-laticaudata* group.

In the present treatise, three species-complexes indicated by Cogger *et al.*

(1987) are recognized: the *Laticauda semifasciata* complex, the *Laticauda colubrina* complex and the *Laticauda laticaudata* complex. The *semifasciata* complex consists of *Laticauda semifasciata* (Schlegel, 1837b [quoting Reinwardt's unpublished work]) and *Laticauda schistorhynchus* (Günther) 1874. The latter sometimes is considered merely a subspecies of the former; McCarthy (1986) opined: "There do indeed seem reasonable grounds for considering the two forms conspecific". *L. semifasciata* occurs from southern Japan southward through Taiwan and the Philippines to some eastern islands of Indonesia (McCarthy, 1986; Slowinski, 1989; Heatwole and Guinea, 1993; Guinea, 2002). *L. schistorhynchus* is found only on Niue Island, Tonga, and Samoa, 6,500 km east of the range of *L. semifasciata* (Slowinski, 1989; Greer, 1997).

The *Laticauda laticaudata* group also contains two species. *Laticauda laticaudata* (Linnaeus) 1758 has an extensive range, being distributed from the Bay of Bengal through the East Indian Archipelago and southeastern coastal Asia northward through the Philippines and Taiwan to southern Japan and eastward through New Guinea and the Solomon Islands to the islands of the southwestern Pacific (McCarthy, 1986). Two subspecies, based mainly on differences in colour pattern, were recognised by Stejneger (1907). They are *L. l. laticaudata*, from the East Indian Archipelago, the Philippines, New Guinea and Oceania, and *L. l. affinis*, from coastal southeastern Asia, Taiwan, and the Ryukyu Islands (see Klemmer, 1963). McCarthy (1986) suggested that variation between eastern and western forms was clinal and subspecific recognition probably not warranted, but if trinomials were to be used, *L. l. muelleri*, a name proposed by Boulenger (1896), but later considered a synonym of *L. laticaudata* (see Cogger *et al.*, 1983), was the appropriate epithet rather than *L. l. affinis*. Embedded in a hiatus in the range of L. *laticaudata* is *Laticauda crockeri* Slevin 1934, a species found only as an isolated population in the slightly brackish waters of Lake Te-nggano on Rennell Island, Solomon Islands (Wolff, 1969, 1970; Cogger *et al.*, 1987; for a coloured photograph see p. 256 in Greer, 1997). McCarthy (1986) noted the close relationship between *L. laticaudata* and *L. crockeri* and considered, but did not resolve, whether the two should be considered subspecifically related. Cogger *et al.* (1987) addressed this question and concluded *L. crockeri* to be a dwarf, melanotic species recently derived from *L. laticaudata*, but now genetically and geographically isolated. Another proposed subspecies, *L. laticaudata wolffi* (Volsøe, 1956a), although considered a full species by Kharin (1984a), had been relegated to the synonymy of *L. crockeri* by its original describer (Volsøe, 1958), a course of action supported by the analysis of Cogger *et al.* (1987).

The *Laticauda colubrina* complex contains four species, *Laticauda colubrina* (Schneider, 1799), *Laticauda frontalis* (De Vis, 1905), *Laticauda saintgironsi* Cogger and Heatwole, 2006, and *Laticauda guineai*, Heatwole, Busack and Cogger, 2005. Cogger and Heatwole (2006) addressed the relationships of some of these species and considered *L. colubrina* as the ancestral species with *L. frontalis* and *L. saintgironsi* as two derivatives closely related to each other; *L. guineai* seems to be the closest of all to *L. colubrina*.

Laticauda colubrina is widespread and relatively abundant, *L. frontalis* is more restricted in distribution and is less abundant, *L. guineai* is known only from southern Papua[1], and *L. saintgironsi* is known only from New Caledonia and the Loyalty islands, where it is common. All except *L. guineai* have been represented by waifs outside their normal breeding ranges. The distribution and geographic variation of these four species forms the subject of the present dissertation.

Laticauda colubrina, the most widespread of the three species, is emphasised. Various authors have noted that some populations of *L. colubrina* differ in one or more characters and Ineich and Laboute (2002) pointed out the need for a reassessment of this species in their statement: "several distinct populations inhabit different regions...most of which should have a separate species status". The present investigation corroborated this view and the analyses described below resulted in the description of *Laticauda guineai* from southern Papua and *Laticauda saintgironsi* from New Caldeonia as well as the resurrection of *Laticauda frontalis* from Vanuatu from synonymy. The synonymy of all species in the *L. colubrina* complex appears in Appendix 1.1.

Various combinations of characters have been used to define and diagnose species of *Laticauda*, including the number, sizes, shapes, and configuration of the various scales (especially of the head), as well as body size, and details of the colour pattern of the head and body. Those most commonly used by various authors over the past two centuries, and of most diagnostic value, are listed by Heatwole *et al*. (2005;

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[1] The designation "Papua" can be confusing. Papua is the southern part of the independent country of Papua-New Guinea located in the eastern half of the island of New Guinea. Papua is also the name of one of the two provinces of Indonesia located on the western part of the island of New Guinea. In order to avoid confusion, in this thesis "Papua" will be used only in reference to the southern part of Papua-New Guinea; the Indonesian part of the island of New Guinea will be designated by its previous name of "West Irian" (Irian Jaya).

their Appendix I). Woodcuts or drawings of whole *Laticauda colubrina* appear in works by Daudin (1803), Cuvier (1846), Jan (1872), de Rooij (1917, 1970) and Taylor (1922), and drawings of the scutellation, colour pattern, or other external features of the head and/or other body parts were presented by Schlegel (1837a,b), Wall (1909), Brongersma (1934, 1956), Bourret (1936b), Smith (1943), McCann (1966a,b), Ota (1985) and McCarthy (1986). Black and white photographs of *L. colubrina* are available in the publications of Volsøe (1956b), Wang (1962), Kuntz (1963), Taylor (1965), Pickwell (1972), Caras (1974), Cogger (1975), Pernetta (1977), Ota (1985), Trutnau (1986), Stuebing (1988), Heatwole and Guinea (1993), and Steinicke and Trutnau (1993), and of *L. saintgironsi* in those of St. Girons (1964, 1990). For a list of coloured photographs of *L. colubrina* and *L. saintgironsi*, see Section 2.2.1.

1.3 Natural History of Species of the *Laticauda colubrina* Complex

The natural history of sea kraits was reviewed by Shine (1991b), Heatwole and Guinea (1993), Greer (1997), and Heatwole (1999) and an extensive bibliography provided by Culotta and Pickwell (1993). Except possibly for *L. crockeri* (Cogger *et al.*, 1987), sea kraits are oviparous. Clutch size is 4-19 (Voris and Voris, 1995). Thin-shelled eggs are laid terrestrially and the shells have a high permeability to oxygen, three times that of chicken eggs and nine times that of the eggs of an iguanid lizard; permeability to water is also high (Guinea, 1995). *L. colubrina* is aseasonal in reproduction in the Philippines (Gorman *et al.*, 1981) but seems to be seasonal in Fiji (Pernetta, 1977) and Sabah (Stuebing, 1988). Preliminary data suggested that *L. saintgironsi* might have seasonal reproduction, with oviposition occurring from December to February (Saint Girons, 1964, 1990). Growth is rapid in young sea kraits but tapers off after sexual maturity is reached (about 18 months in males and 18-30 months in females) and accordingly slows down earlier in males than in females (Saint Girons, 1964, 1990; Guinea, 1986).

Members of the *Laticauda colubrina* complex forage on reefs by searching underwater crevices while tongue-flicking, apparently identifying prey by smell; their diet is almost exclusively of various kinds of eels (Pernetta, 1977; Guinea, 1986; Cogger *et al.*, 1987; Stuebing, 1988; Shetty and Shine, 2002a; Reed *et al.*, 2002), only McCoy (1980) reporting other items. The only known exception to coral reefs as feeding grounds is Rennell Island, Solomon Islands, where this species forages for eels among objects on the muddy bottom of Lake Te-nggano, a mildly brackish body of water (Cogger *et al.*, 1987).

When not foraging for food, sea kraits come ashore (Pernetta, 1977), often in large numbers on small offshore cays (Stuebing, 1988; Voris and Voris, 1995). There they rest, digest food, slough the skin, mate, and oviposit (Shetty and Shine, 2002c). Activity occurs mainly at night and at dusk, with courtship taking place in the morning (Shetty and Shine, 2002b). By day the snakes thermoregulate by shuttling from sun to shade, but in the afternoon they often seek shelter (Voris and Voris, 1995).

Courtship may involve a number of males attending a female simultaneously. The male lies adjacent to the female and contracts his body in pulses of undulating spasms, up to 20 pulses per minute; prior to copulation he may rub his chin against the female's head (Voris and Voris, 1995).

Unlike most sea snakes, sea kraits have retained their broad gastrosteges, and accordingly can crawl effectively on land (Volsøe, 1956b). They share with other sea snakes the aquatic adaptation of a flattened, paddle-shaped tail. *L. colubrina* swim more rapidly than do non-marine elapids, but are slower on land (Shetty, 2000; Shine and Shetty, 2001a). The members of the *colubrina* complex are more terrestrial than are those of the other complexes. *L. colubrina* is the most terrestrial of all and has greater muscular strength and is better able to climb vertical cliffs than can its more aquatic congener, *Laticauda laticaudata* (Bonnet *et al.* 2005). *Laticauda colubrina* spends approximately half its time in each medium, on a roughly 10-day cycle (Shetty and Shine, 2002b) and transfers between land and sea most often at high tides, especially at night (Guinea, 1986; Shetty and Prasad, 1996a; Shetty and Shine, 2002b), sometimes in cohorts (Bhaskar, 1996). Females spend more time on land than do males (Shetty and Prasad, 1996a).

Voris and Voris (1995) noted that *L. colubrina* on Sabah often sheltered in aggregations of 5-15 individuals in rock crevices, under debris, among tree roots, or in tree-holes. Bhaskar (1996) and Shetty and Prasad (1996a) found that in the Andaman Islands, this species primarily used trees, logs, and litter as shelter but was also found under beach vegetation and in crevices of boulders. Crombie and Pregill (1999) noted them in masses of exposed tree roots. I have observed this species sheltering in such diverse places as rock crevices (Ryukyus, Sabah, Indonesia, Thailand, Solomon Islands) and under beach debris such as fallen palm fronds (Fiji), and have seen *L. guineai* sheltering in tree-hollows (Papua-New Guinea). When sea kraits shelter in non-reefal habitats (e.g., mangrove swamps), these sites are invariably adjacent to reefs.

Ineich and Laboute (2002) reviewed the natural history of *L. saintgironsi* (then under the name *L. colubrina*). It inhabits coral reefs where it prefers shallow water (< 20 m) but has been observed as deep as 60 m. It feeds primarily on eels of various kinds (Ineich *et al.* 2007). Of the 60 species of fish recorded from the diet of sea kraits in New Caledonia, all but two were eels of various families; the exceptions were an eel-tailed catfish (*Plotosus lineatus*) and a gudgeon (*Ptereleotris* sp.). *Laticauda saintgironsi* comes onto land, often on small, offshore islands, to oviposit, rest, and digest its meals. It usually traverses beach rock or dead coral (Ineich and Laboute, 2002) but when crossing open sand resorts to side-winding (Heatwole and Abbott, 1998). It has been observed sheltering under mats of halophilous vegetation on beaches, under and between rocks (Saint Girons, 1964, 1990), in outcroppings or coral exposed at low tide (Kuntz, 1963), in cavities in the sand (Heatwole, personal observations) and burrows of petrels; it sometimes enters human dwellings and boats and even climbs trees (Ineich and Laboute, 2002). It has been recorded on the highest points (36-40 m elevation) of some of the offshore islands (Ineich and Laboute, 2002). In New Caledonia *L. saintgironsi* overlaps syntopically with *L. laticaudata*. The latter species is practically restricted to sheltering beneath slabs of beach rock for its terrestrial habitat and *L. laticaudata*, although using a wide range of terrestrial situations, also preferentially uses beach rock.

Unlike *Laticauda crockeri* which is melanotic (Cogger *et al.*, 1987) and *L. laticaudata*, which has a slight tendency toward melanism in older individuals, *L. saintgironsi* retains its banded pattern throughout life (Lorioux *et al.* 2008). The same seems to be true of *L. colubrina* and *L. frontalis* as no melanotic specimens of these species were observed in the present study.

Living in a marine environment, sea kraits require some means of reducing the intake of salt and/or of ridding their bodies of excess amounts of it. Intake is reduced by the fact that the skin is resistant to the inward passage of salt (Dunson and Stokes, 1983). Excesses are excreted, not so much via the kidneys as through a salt gland, once thought to be located in the roof of the mouth (Dunson and Taub, 1967) but now known to lie beneath the tongue; it secretes brine into the tongue sheath and when the tongue is extruded, the brine is ejected into the sea. Even these expedients, however, do not emancipate sea kraits from dependence on freshwater. Guinea (1991) noted that *L. colubrina* drinks from standing freshwater and even from rain or dew drops on leaves. Lillywhite *et al.* (2008) further showed that sea kraits dehydrate in the marine environment and require fresh drinking water; even dehydrated snakes refuse seawater but will drink freshwater and dilute brackish water. In nature it is likely that sea kraits drink from the film of freshwater on the surface of the sea following rain (Lillywhite *et al.,* 2008).

The evaporative water loss in air is lower from *L. colubrina* than from the other sea kraits, an adaptation to its greater terrestriality (Lillywhite *et al.* 2008). In seawater, however, the trend is reversed with the more aquatic species having lower passage of water outward through the skin.

Although some sea snakes seem to be relatively immune from predation, e.g., *Pelamis platurus* (Heatwole, 1975c; Weldon, 1988), there are some sharks and other predatory fish, as well as seals, sea eagles, crocodiles and even marine invertebrates that do eat sea snakes (Heatwole *et al.* 1974, Heatwole 1975c, Heatwole and Finnie 1980, Voris and Voris 1995); Masunaga *et al.* (2008), reported that *Laticauda colubrina* was found in 6.5% of the stomachs of sharks (mostly *Galeocerda cuvieri*) caught in the Yaeyama Islands in the Ryukyu Islands of Japan, *L. laticaudata* in 9.7% and *L. semifasciata* in 19.4%. Bhaskar (1996) reported sea eagles as preying on *L. colubrina*. Leach (1928) noted that there were no remains of *L. saintgironsi* under an osprey nest on an island where these snakes occurred in close proximity to the nest (in contrast to the occurrence of skeletons of sea snakes under sea eagle nests elsewhere); however, Ineich (personal communication) found a skeleton of an undetermined species of *Laticauda* in an osprey nest. Sea kraits are eaten by reef herons (Bauer and DeVaney, 1987) and crabs (Guinea, 1986), and *L. saintgironsi* is taken by juvenile tiger sharks (Rancurel and Intes, 1982).

Sea kraits move faster in water than on land (Shine *et al.* 2003a) and their responses to potential predators varies accordingly (Shine *et al.* 2003b); on land they remain quiet, relying on crypsis, whereas in water they flee.

Perhaps because of their partial terrestriality, sea kraits often have ectoparasitic ticks (*Amblyomma nitidum*) and several species of trombiculid mites (Hayashi and Masuaga 2001); *L. colubrina* also is parasitized by cestodes, trematodes, nematodes and lung mites, and may have a superficial growth of algae

(Pernetta, 1977; Guinea, 1986; Bhaskar, 1996). Chinnadurai *et al.* (2008) reported mortality in captive *L. colubrina* as arising from sepsis associated with (1) necrotizing enteritis, pneumonia, or hepatic lesions, (2) multiorgan granulomas, and (3) multicentric lymphoid neoplasia, and they also noted the presence of hemogregarine parasites and intravascular microfilaria, pulmonary nematodes and trematodes, and intestinal nematodes and protozoa. They attributed death to sepsis arising from immunosupression brought on either by the stress of transport and captivity, or mediated by viral-induced neoplasia.

Sea kraits have powerful neurotoxic venom that has coevolved along with resistances to it on the part of the eels on which they prey (Heatwole and Poran, 1995; Heatwole and Powell, 1998). The properties of the venom have been studied extensively (Mishima, 1965; Uwatoko *et al.*, 1966a,b; Sato *et al.*, 1969; Maeda *et al.*, 1974; Tu and Salafranca, 1974; Kim and Tamiya, 1982; Guinea *et al.*, 1983; Tamiya *et al.*, 1983, 1985; Tamiya and Yagi, 1985; Takasaki *et al.*, 1988; Obara *et al.*, 1989). Death of prey is caused by irreversible presynaptic and postsynaptic blocking of neuromuscular transmission (Tamiya and Arai, 1966; Low, 1979; Singh and Guinea, 1984; Rowan *et al.*, 1989). Although highly venomous, sea kraits are famous for their docility and reluctance to bite humans defensively, a feature early noted by Girard (1858) and Boulenger (1912) and later confirmed for *L. saintgironsi* by Saint Girons (1964, 1990) and Ineich and Laboute (2002), and for *L. colubrina* by many authors (e.g., Keegan, 1960; Heatwole, 1975d; Pernetta, 1977; Bhaskar, 1996). Heatwole (1999) considered *Laticauda* as the least offensive of all venomous marine snakes. Nevertheless, some envenomations of humans by *L. colubrina* have been reported.

1.4. The Geologic Time-Frame of the Origin and Phylogeny of Sea Kraits

The origin of snakes is problematical and still unresolved, with three major hypotheses dominating: descent from: (1) legless, burrowing or terrestrial lizards, (2) legged marine forms, or (3) a common ancestral reptile from which both lizards and snakes evolved (Underwood, 1967; McDowell, 1987; Rage, 1987; Greer, 1989, 1997; Lee and Scanlon, 2002). In the first view, the Scolecophidia (blindsnakes), or burrowing worm-like forms with small mouths and that eat small prey, are primitive and at the base of the phylogeny of extant snakes. These are followed phylogenetically by aniliods (pipesnakes), and then the Macrostomata, or largemouthed snakes that eat large prey. The macrostomes include boas and their relatives as basal members followed by the "advanced" snakes, or Caenophidia.

According to the second view, macrostomes are basal and descended from now-extinct, marine varanoid lizards, with the Scolecophidia adopting the small-mouthed condition as an adaptation to fossorial conditions and a specialized diet (e.g., termites).

Early support for the first hypothesis was Walls’ (1942) discovery that snakes’ eyes were dramatically different from those of lizards and appeared to be reconstructed from remnants of a degenerate eye such as found in fossorial animals. Caprette *et al*. (2004), however, compared the eyes of snakes both with those of fossorial vertebrates and aquatic vertebrates in general and concluded that the characteristics of snakes’ eyes reflected an early evolution in an aquatic, rather than a subterranean, environment.

The ophidian fossil material relevant to this debate is scant (McDowell, 1987; Rage, 1987; Caldwell and Lee, 1997; Lee and Scanlon, 2002; Rieppel *et al.*, 2003; Apesteguía and Zaher, 2006; Scanlon, 2006). Snakes first appeared in the fossil record in the Cretaceous and some of the material is fragmentary, only represented by vertebrae or vertebrae and ribs, e.g., *Lapparentophis* (freshwater) and *Simoliophis* (marine). Several marine snakes, however, left more complete fossils. *Pachyrhachis problematicus* and *Haasiophis terrasanctus* occurred in the mid-Cretaceous to early-upper Cretaceous, about 95 mya and had well-developed pelvises and hind limbs. Although whether or not they should be placed within the Macrostomata, or even considered as snakes, has been questioned (see Rage, 1987), they did have large jaws adapted to feeding on large prey and they were clearly lepidosaurians.

Two related marine families, the Palaeopheidae from the upper Cretaceous to late Eocene and the Nigeropheidae from the Palaeocene and Eocene are mainly known from ribs, vertebrae and fragments of skulls (Rage, 1987). They have been variously believed to be either on the lineage toward pythons and boas (family Boidae), or toward file snakes (family Acrochordidae).

Not all early snakes were aquatic. There were two groups of large, terrestrial, non-burrowing species. Those in the family Dinilysiidae from the upper Cretaceous to the Eocene combined some lizard-like and some snake-like skeletal characteristics (McDowell, 1987). The family Madtsoiidae, believed by most authors to be related to boas and pythons (Rage, 1987), extended from the upper Cretaceous to at least the late Eocene (McDowell, 1987; Rage, 1987). The boids themselves, the Aniliidae, and some early colubroids are the only modern snakes with a fossil history going back as far as the Cretaceous (Rage, 1987); boids are represented in Australia from the middle to late Miocene onward (Smith and Plane 1985).

Although many of the ancient snakes were marine, or at least aquatic, they did not give rise directly to any extant marine taxa of snakes. Rather, all modern marine snakes had terrestrial ancestors and the ancient marine snakes provide no information as to the timing or circumstance of that origin. Modern snakes have secondarily, and independently, returned to the sea several times, i.e., once in the Acrochordidae; several times (at least to brackish situations) in the Colubridae, and once each in the sea kraits and oxyuranine ("true") sea snakes (Heatwole, 1999; Sanders and Lee, 2008).

Several events were important milestones in the evolutionary history of sea kraits:

(1). *Origin of the Caenophidia and the family Elapidae*. The Caenophidia contains the most advanced group of snakes, including the families Acrochordidae (file snakes; sometimes considered a sister group), Viperidae (vipers), Atractaspidae (mole vipers), Colubridae (a large, diverse assemblage of harmless snakes as well as some rear-fanged, mildly venomous to dangerous ones), Elapidae (Asian, African, and American venomous proteroglyphous snakes, such as cobras, mambas, land kraits, coral snakes and others), and Hydrophiidae (sea snakes, sea kraits, and Australian terrestrial, venomous proteroglyphs).

Views on the time of origin of the elapid lineage from the rest of the Caenophidia have been disparate (reviewed by Cadle, 1987; Scanlon and Lee, 2004; Kelly *et al.*, 2009). The earliest known fossils of elapids are from the early Miocene. By the late Miocene some modern genera had appeared and by the Pliocene the fauna had a completely modern aspect (Rage, 1987). One view was that elapids had a basal position among the advanced snakes and that they diverged early in caenophidian evolution (e.g., Storr, 1964; McDowell, 1987; Gravlund, 2001). Proponents of this view often considered Gondwanaland as the origin of the Elapidae and that this family diversified within Australia as that continent separated from Antarctica and drifted northward to abut on the Oriental plate (Slowinski *et al.*, 1997). An opposing view was that elapids dispersed to Australia from Asia as the Asian plate approached the Oriental one in the Tertiary (Cogger and Heatwole, 1981; Heatwole, 1987; Keogh, 1998; Keogh *et al.*, 1998). For a long time, available data did not allow deciding between these alternatives (Scanlon and Lee, 2004). More recently, however, biochemical evidence has dismissed the idea of a Gondwanan origin for elapids and has located that family, not as basal, but rather as a twig on the Caenophidian phylogenetic tree. The Elapoidea originated in Africa from a Eurasian stock in the middle Eocene about 46 mya (51.2-39.5 mya), rapidly diversifying there and dispersing to the Oriental Region in the late Eocene about 41 mya (46.3-34.8 mya) either entirely on land or via “hitch-hiking a ride” on the Indian plate as it moved northward to abut onto Asia. The Elapidae originated from this elapoid prong in the Oligicene about 37 mya (42.8-32.8 mya) and diversified in the mid-Oligocene, beginning about 31 mya (Kelly, *et al.*, 2009).

(2). *The origin of* Laticauda. *Laticauda* is intermediate between the Asian elapines and the Australasian oxyuranine lineage ("hydrophiines") and has been included by some authors in the former (e.g., Smith *et al.*, 1977) and by others in the latter (Keogh, 1998; Slowinski *et al.*, 1997; Slowinski and Keogh, 2000; and see Section 1.2). Lee and Scanlon (2004), on the basis of both phenotypic and molecular data, found *Laticauda* to be the sister group of the other Australasian elapids and thus closest to the stem-group for that clade. Closely related to *Laticauda*, and also a sister group to the true sea snakes and the terrestrial Australian proteroglyphs (Scanlon and Lee, 2004) are some terrestrial Melanesian proteroglyphs. Since *Laticauda* is the oldest extant representative of the lineage diverging from the Asian elapids, and is marine, perhaps the ancestor of that lineage was also marine or littoral and was the agent of dispersal, via the sea, from the Asian to the Australian plate (Scanlon and Lee, 2004; Kelly *et al.*, 2009), where it diverged first to split off *Laticauda*, then the Melanesian terrestrial species, finally leading to the terrestrial Australian species and the oxyuranine sea snakes.

Laticauda is the oldest extant member of the Australasian lineage, and was estimated to have diverged from the Elapinae as recently as 20 mya (Schwaner *et al.*, 1985); the most recent molecular evidence (Kelly *et al.*, 2009), however, suggests that this split occurred in the Oriental Region about the mid-Oligocene, 28 mya (32.4-25.0), followed by overwater dispersal of the stem-group to Australasia. Its arrival was estimated as occurring at least by the Oligocene-Miocene boundary or about 24 mya (Scanlon *et al.*, 2003, Scanlon and Lee, 2004), about the time the Australian tectonic plate began to collide with the Asian one, i.e., about 25 mya (Hall, 2002).

The age of the earliest fossil (tentatively assigned to *Laticauda*) in Australia came from the late Oligocene to early Miocene, about 24-23 mya (Scanlon *et al.* 2003).

The time of the split between *Laticauda* and the oxyuranine radiation has been estimated variously as 23 mya (27.1-18.8 mya) (Kelly *et al.*, 2009), 18.7-13.1 mya (Sanders and Lee, 2008) and 12.6 mya (Sanders *et al.*, 2008) with an extensive, rapid speciation beginning within the oxyuranine radiation about 14.3-10.1 mya. Sanders and Lee (2008) considered the most recent values of these ranges to be the most likely.

1.5 Palaeogeography of the Study Area from the Cenozoic to Recent Times

The distribution of the *Laticauda colubrina* complex covers an extensive area of southeastern Asia and the southwestern Pacific (see Chapter 3), ranging from the edge of the Bay of Bengal southeastward through the East Indian archipelago, Australasia, and islands of the southwestern Pacific, and northward through the Philippines and Taiwan to the Ryukyu Islands of Japan. Tectonically, this is one of the most complex regions of the globe (Fig. 1.1). It begins at the eastern edge of the Indian plate, includes the area of juxtaposition and collision of the Eurasian and Australian plates and finally encompasses the western Pacific rim and the western edge of the Pacific plate.

The literature on the tectonic evolution in this area is vast and the bibliography monitored by the Royal Holloway Southeast Asia Research Group contains approximately 18,000 references. Serendipitously, this group in a series of articles, chapters of books, and online presentations have distilled the available information (Hall, 2002, 2009), based on data from paleomagnetism, isotopic ages, tomography, and GPS observations, to provide a comprehensive model of the geology and plate tectonics precisely for the period (Cenozoic) during which *Laticauda* originated and evolved and for the geographic area (southeastern Asia and southwestern Pacific) encompassed by its present geographic range. These important papers provide excellent, detailed, static maps of the region from 55 mya to the present time at intervals of 5 million years (Figs. 1.1 and 1.2) as well as a continuous animation of the tectonic movements that occurred over that time. These resources, supplemented by information for the Pleistocene, were used as a basis for understanding palaeogeographic changes of relevance to *Laticauda* and as a springboard for interpreting the present distribution and geographic variation of the *Laticauda colubrina* complex. In this section, the tectonic history for the period of interest is summarized briefly.   Events on continental landmasses and in the depths are treated

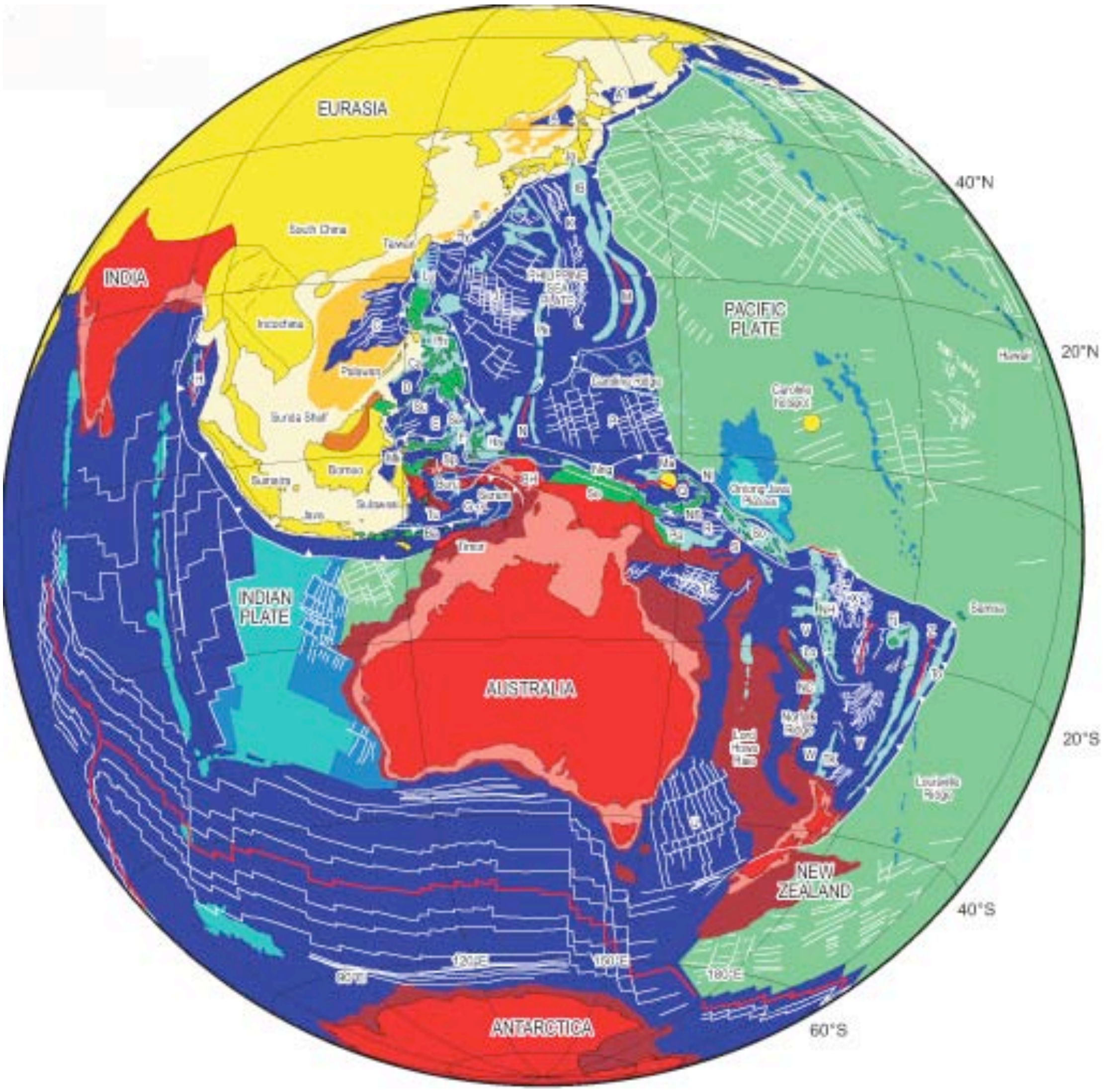


Figure 1.1. Present-day tectonic features of the southeastern Asian and southwestern Pacific regions. Darker colours represent present emergent land with lighter colours indicating submerged continental shelves (red for India, Australia and New Guinea; yellow for Eurasia-Sundaland but with orange representing the deepest part of that continental shelf). The patchwork of colour to the west of Australia can be ignored as not germane to the present study. Otherwise, the large green area indicates the Pacific Plate, small green areas are ophiolitic and accreted material formed at the margins of plates, turquoise areas are arcs and blue is deep water. Jagged white lines indicate marine magnetic anomalies. White lines with triangles denote subduction zones. Other white lines show strike-slip faults. Red lines show active spreading centres. Codes are: A, Kuril Sea and Japan Sea; B, Okinawa Trough; C, South China Sea; D, Sulu Sea; E, Celebes Sea; F, Molucca Sea; G, Banda Sea; H, Andaman Sea; J, West Philippine Basin; K, Shikoku Basin; L, Parece Vela Basin; M, Mariana Trough; N, Ayu Trough; P, Caroline Sea; Q, Bismarck Sea; R, Solomon Sea; S, Woodlark Basin; T, Coral Sea; U, Tasman Sea; V, Loyalty Basin; W, Norfolk Basin; X, North Fiji Basin; Y, South Fiji Basin; Z, Lau Basin; Ba, Banda Arc; BH, Bird’s Head; Ca, Cagayan Arc; Fj, Fiji; Ha, Halamera Arc; IB, Izu-Bonin Arc; Ja, Japan Arc; Lo, Loyalty Islands; Lu, Luzon Arc; Mk, Makassar Strait; Mn, Manaus Island; NB, New Britain Arc; NC, New Caledonia; NH, New Hebrides Arc; NI, New Ireland; Nng, North New Guinea Terranes; Pa, Papuan ophiolite; Pk, Palau-Kyushu Ridge; Ry, Ryukyu Arc; Sa, Sasngihe Arc; Se, Sepik Arc; So, Solomons Arc; Sp, Sula Platform; Su, Sulu Arc; TK,Three Kings’ Rise; To, Tonga Arc; Tu, Tukang Besi Platform. Note the composite nature of New Guinea. Modified slightly from Hall (2002) with permission of Robert Hall.

only insofar as they affected the palaeogeographic configuration of land and shallow waters where sea kraits reside.

As voluminous as these data are, there are still gaps and Hall (2002) himself pointed out several limitations. There are some differences between GPS-derived motions and estimates of long-term motions based on magnetic isochrons, plate boundaries are of different widths in different areas and are deforming in a complex manner and have moved or changed character in the very recent past, some arcs may have disappeared without leaving trace of their existence, and some ocean basins may have subducted as they spread. Consequently, the model may be somewhat simplified. Nevertheless, it supersedes previous ones and is the most comprehensive and complete treatment available.

The two major continental plates involved in the region are the Australian plate and the Asian plate, or more precisely, the Eurasian-Sundaland plate as it encompasses not only Eurasia but also Sundaland (the Indochinese Peninsula, Malaysia and the Indonesian islands of Sumatra, Java, part of Sulawesi, and associated smaller islands). In addition, there are smaller elements, some of terriginous origin and others of marine origin. Crustal fragments, termed terranes, rifted from Gondawanaland during Paleozoic/Cretaceous times, or from the later plates derived from it, such as the Australian Plate. Some of these later accreted to one of the larger plates or became embedded within the Australasian archipelago. (see Burrett *et al*., 1991). Thus, they could have served as “arks” or “stepping stones” carrying terrestrial life northward from Gondwanaland to the Asian region. Other microplates were fragments composed of arc, ophiolitic, and accreted materials formed at plates' margins during the Cenozoic; these contributed to the formation of eastern Indonesia, the Philippines and the northern part of the island of New Guinea.

The western Pacific is a mosaic of microplates, some of oceanic character and some of older terranes. Following are brief descriptions of these events on a region-by-region basis. A comprehensive treatment is not attempted; for that, the reader is referred to Hall's (2002) monograph (but see section 8.4). Rather, the events and the times deemed to be significant for the origin, speciation, dispersal and adaptive radiation within the genus *Laticauda* are emphasised.

The prelude for *Laticauda* coming upon the scene was the dramatic collision of the Indian plate against the Eurasian one. This set in train a series of events that modified the palaeogeography of the region and probably had a profound influence on the course of evolution in *Laticauda*. At 55 mya (Fig. 1.2) in the early Eocene as the Indian plate approached Asia, the Sunda shelf, including the Indochinese Peninsula and much of what was destined to become that part of Indonesia west of the future Wallace's line, was broadly connected to Asia; by contrast the eastern parts of future Indonesia that would eventually lie east of Wallace's line (e.g., Halmahera), as well as

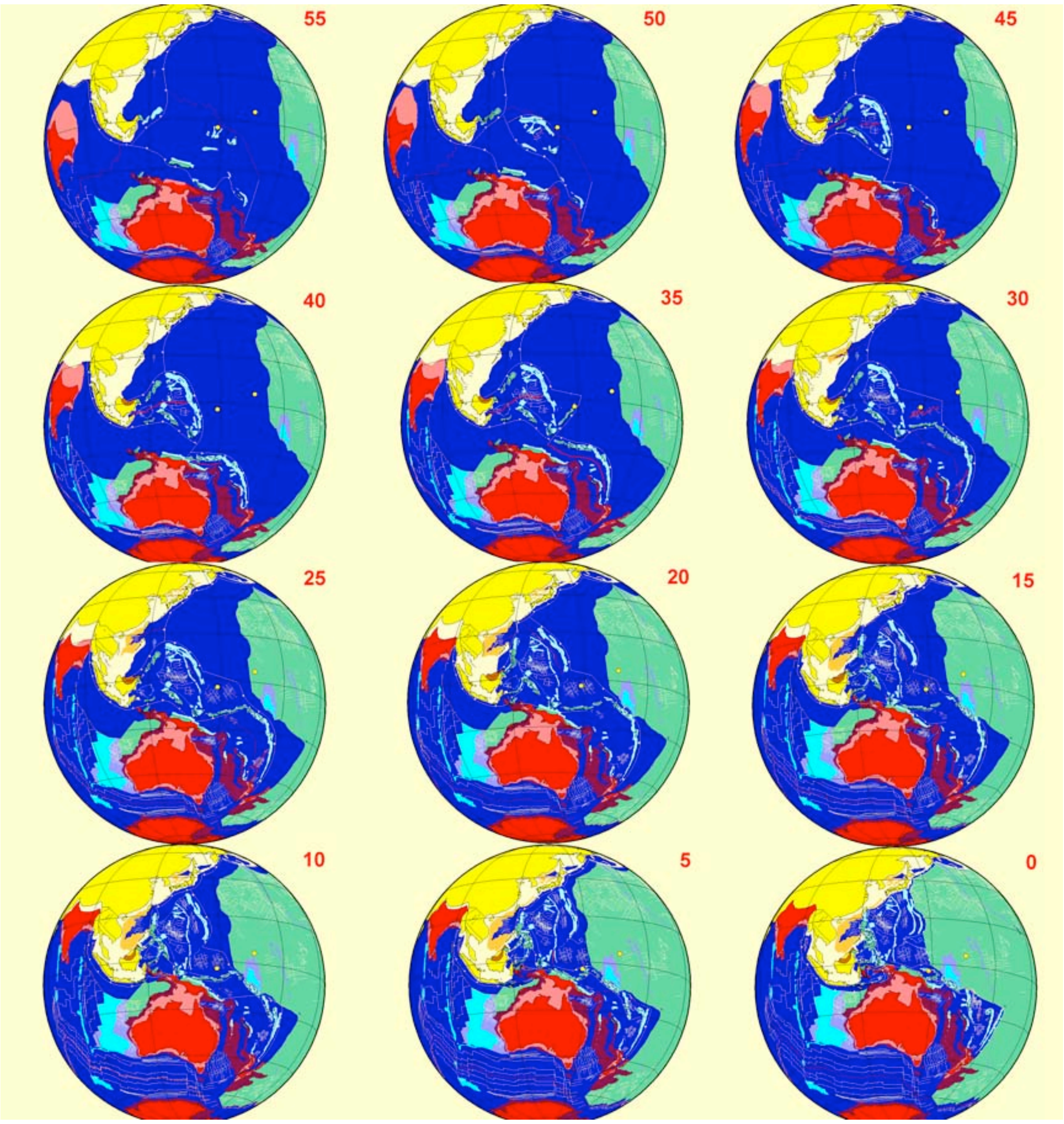


Figure 1.2. Palaeogeographic maps for the past 55 million years from upper left to lower right at five million year intervals. Ages are in red to the upper right of each map in million of years ago (mya). Darker colours represent present emergent land with lighter colours indicating submerged continental shelves (red for India, Australia and New Guinea; yellow for Eurasia-Sundaland). The patchwork of colour to the west of Australia can be ignored as not germane to the present study. Otherwise, the large green area indicates the Pacific Plate, small green areas are ophiolitic and accreted material formed at the margins of plates, turquoise areas are arcs and blue is deep water. Note especially, (1) the movement of widely scattered arcs from west to east to form eastern Indonesia and the Philippines, (2) the composite nature of New Guinea, and (3) the formation and rotation of the Melanesian Arc. For more detailed information on some of the structures shown here, see Figure 1.1. Composite constructed from individual frames from an animated Quicktime animation from the Southeast Asia Research Group (http://searg.rhul.ac.uk/current_research/plate_tectonics/Movies/Quicktime%20movies/globe/globe_2001_vga.mov) with permission from Robert Hall.

northern New Guinea and New Caledonia were represented as ophiolites and island arcs widely scattered over the North New Guinea plate, still quite distant both from Asia and from Australia which had not yet moved far north from Antarctica. Over the next 15 million years, as the Indian plate collided with the Eurasian one, there was a major reorganization of the plates to the east. The Sundaland shelf, including Sumatra, Java and Borneo, extended eastward resulting in subduction that had far-reaching effects. By 50 mya, later in the Early Miocene (Fig. 1.2), the Philippine Sea plate had rotated rapidly and accumulated ophiolitic materials in what was to become the Philippines. There was voluminous boninite magmatism that caused rapid growth of the Izu-Bonin-Mariana Arc. The future Halmahera was still distant from the rest of future Indonesia and was situated well east of Australia. Australia had separated farther from Antarctica and had drawn nearer to groups of ophiolites in the arc in the New Guinea plate that would become northern New Guinea. The eastern one of these, the Papuan ophiolites, had already joined the Australian plate and the western one, the Sepik ophiolites, was very near. The New Caldedonian ophiolites' position, far to the east of Australia, had changed little.

By 45 mya in the middle Eocene (Fig. 1.2), there had been a reorganisation of the major plates. Extension continued in the East Java Sea and Sumatra. There was a polarity change in subduction at the eastern margin of the Australian plate, with subduction of the Pacific plate beneath the Australian one initiating the Melanesian arc and bringing the New Caledonian ophiolites into collision with the Australian plate. The arcs and ophiolites in the West Philippine Sea and Celebes Sea become more extensive and new ones formed the East Philippine arc to the south; all of these, as well as the future Halmahera, converged westward toward the Sunda shelf. The Sepik ophiolites became attached to northern New Guinea. The South China Sea began to subduct beneath the Borneo-Luzon margin and the Sunda-Java trench extended far eastward via the East Philippine arc to the Halmahera arc, with northward subduction of the Indian and Australian plates.

At 40 mya (middle Eocene) (Fig. 1.2) spreading had ceased along the Indian-Australian Ridge and India and Australia became parts of a single plate. The size of the Izu-Bonin-Marianas and Melanesian arcs extended as the Pacific Plate continued to subduct and as sea-floor spreading widened the West Philippine Basin. Sea-floor spreading also led to the beginning of the formation of the Solomon Sea south of the Melanasian Arc.

At 35 mya (early Oligocene) (Fig. 1.2) there was extension in the Gulf of Thailand and further extension of the South China-Indochina continental margin. The West Philippine Basin reached its maximum and the eastern margin of the Philippine Sea separated from the Caroline Arc which developed ophiolitic material. Thus, multiple arcs extended intermittently from the Sunda Shelf eastward to Halmahera and then diverged north to the South Caroline Arc and south to the Melanesian Arc. The Solomon Sea widened southward to form the South Fiji Basin.

At 30 mya (mid-Oligocene) (Fig. 1.2) the pressure of the Indian plate indented Eurasia and caused extrusian of the Indochina block and at the same time slab pull from southeastward subduction of the South China Sea formed oceanic crust there; there was extension in the Sea of Japan. The Melanesian arc became more widely separated from Australia but still maintained proximity to the chain of arcs leading to the Sunda Shelf.

At 25 mya in the late Eocene (Fig. 1.2), there was further extrusion of the Indochina block. The East Philippine-Halmahera-South Caroline Arc collided with the Australian Plate at the border of northern New Guinea and the Javan Plateau began to collide with the Melanesian Arc. Sea-floor spreading continued in the South China Sea and occurred in the Parece Vela Basin southwest of the Izu-Bonin-Mariana Arc. These reorganizations of the plates effectively joined the arc systems from the Solomon Islands to the Philippines.

By 20 mya in the early Miocene (Fig. 1.2), there had been additional spreading in the Parece Vela Basin and these combined arcs rotated in a clockwise direction and caused westward subduction of the Molucca Sea beneath northern Sulawesi. Some continental fragments of Australia collided with eastern Sulawesi and the convergence of Australia and Asia caused a counter-clockwise rotation of Borneo and associated Sundaland fragments. Subduction on the border of North Borneo caused major uplift and crustal melting.

At 15 mya in the middle Miocene (Fig. 1.2), the Australian plate had moved farther to the north. The Philippine Sea Plate continued to rotate and the proto-China Sea, which had been getting progressively smaller, was eliminated by the collision of the Cagayan Ridge with Palawan. There were further collisions in Mindoro and southwestern Sulawesi. Some terranes that had formed in the South Caroline Arc docked in New Guinea and continued to move in a slip-strike zone. Although there was some slow sea-floor spreading in the Ayu trough to the east, most of the above events contributed to coalescence of previously dispersed elements toward the future Australasian archipelago.

In the late Miocene, 10 mya (Fig. 1.2), the Australian plate had moved still further to the north and there were collisions in the Philippines and between the Luzon Arc and Taiwan accompanied by intra-plate deformation, strike-slip faulting, and complex subduction zones. Subduction of Jurassic oceanic lithosphere off northwestern Australia induced tension in the overriding plate in Sulawesi. Motion of slivers of the Sumatran forarc was linked to sea-floor spreading in the Andaman Sea. To the east of New Guinea, the Solomon Sea was narrowed by subduction on both sides and the New Hebrides arc was formed, which then rotated and formed the North Fiji Basin.

From 10 mya to 5 mya (end of the Miocene) (Fig. 1.2), there was extensive subduction of the Indian plate at the Sunda and Java trenches, causing rapid hinge rollback in eastern Indonesia and vulcanism in the Inner Banda Arc. At 5 mya there were major changes in motions of the plates. The Philippine Sea Plate moved to its present position, causing subduction in the Manila Trench and collision of the Luzon Arc with the continental margin of China at Taiwan. Subduction began at the eastern edge of the Philippine Sea Trench. Fiji rotated, subduction of the Solomon Sea extended northward from New Hebrides (Vanuatu) to New Britain, and oceanic crust formed in the Woodlark Basin east of New Guinea. The Bismarck Sea began to open. Convergence between the Australian and Pacific plates began in New Guinea and the terranes of the arc accreted and there was significant uplift. Hinge rollback west of New Guinea caused sea-floor spreading in the Banda Sea.

Three areas, Indonesia, New Guinea, and the eastern islands were pivotal to the origin and dispersal of the *Laticauda colubrina* complex and the subsequent speciation within it. The geologic and palaeogeographic features of these three areas now are treated in more detail on a region-by-region basis.

Indonesia: The collision of the Australo-New Guinean Plate with the Asian one in the region of Indonesia was not a simple abutment or a single collision. Rather there was a sequential effect reminiscent of a slow-motion derailment of a train. Western Sulawesi and Kalimantan have been in close proximity to each other since Cretaceous times and are a part of the Asian Plate. Eastern Sulawesi, however, was formerly part of Australian Gondwanaland and in the early Miocene microfragments of that plate collided with southeastern Sulawesi. By the mid-Miocene (about 15 mya) collision of the two plates brought land above water in Sulawesi, followed later by Seram and Ambon at the Miocene-Pliocene boundary and by Obi and Misool (West Irian) in the Pleistocene (Calvert and Hall, 2007). The Moluccas are composed of terranes derived from three sources. The northern Moluccas, centred on Halmahera, are derived from the outer Pacific Arc and hence geologically are related to parts of northern Irian Jaya (West Irian) and to the Solomon Islands and Vanuatu, whereas the southern Moluccas, centred on Seram, is part of the Australian rift system (Michaux, 1991). In addition, a few of the islands from both areas represent the forefront of the New Guinea/Australian craton.

The island of Borneo (Kalilmantan, Sabah, Sarawak) is a composite of at least three microcontinental fragments: southwestern, southeastern, and Sarawak (Michaux, 1991).

Generation of the Sunda Islands occurred in the Miocene and by the end of that period, there was a chain of islands from Java through to Timor at the edge of the Australian Plate. Thus, beginning in the Miocene small parcels of land began to appear near the nexus of the Asian and Australian plates that decreased the width of sea barriers and may have served as "stepping stones" or "staging posts" facilitating terrestrial exchange. The Banda Arc is a composite of an inner arc of volcanic islands extending eastward from Sumatra and Java, and an outer arc representing a fragment rifted from northwestern Australia.

There is a discontinuity between the faunas of the Asian Plate and Australian-New Guinean Plate and seven different lines have been drawn to separate these two faunas (Darlington, 1963; Parenti, 1991). The most famous of these is the Wallace Line that goes between the islands of Bali and Lombok in the Sunda Islands, northward between Kalimantan and Sulawesi and then northeast to separate the Philippines from the Moluccas. Although espoused and made famous by Wallace (1860, 1876, 1880), an almost identical demarcation was proposed earlier by Müller (1846), and later by Murray (1866). Some later workers shifted the line further east; Sclater and Sclater (1899), for example, included Sulawesi on the Asian side, a modification which Wallace himself (1910) approved. Weber (1902) moved the southern portion of the line still further east to include all the Sunda Islands on the Asian side, and Lydekker (1896) proposed that it should be near the edge of the Sahul Shelf, leaving all of Indonesia except the Aru Islands and West Irian and its associated small islands, to the west. The only line that was substantially west of the

Wallace Line was that of Huxley (1868). His line was nearly identical to the Wallace Line in the south, but in the north extended between Palawan and the rest of the Philippine Islands, thereby including most of the Philippines on the Australian side.

These attempts to draw a line precisely separating the Australo-New Guinean fauna from the Asian one were not completely successful as the boundaries differ among taxa, some more nearly conforming to one line, others to another. The ecological requirements and tolerances of taxa differ as do their ability to disperse and invade other areas. A narrowly demarcated line obscures this fact. Perhaps the best approach is to regard the area between the Wallace Line and the Lydekker Line, a region known as Wallacea, as a zone of transition between two quite different faunas in which the exact demarcation varies from taxon to taxon (e.g., see Vane-Wright, 1991). The transition zone for plants, a region called Malesia, is even wider than for animals, and stretches from Sumatra and Peninsular Malaysia to New Guinea and the Bismarck Archipelago (Whitmore, 1981).

The present pattern of sea currents in the region is complex (Hall, 2009; See Section 3.3.2) and presently most flow is from the Pacific toward the Indian Ocean via the Indonesian through-flow. There are two components of the through-flow, one derived from the North Pacific and the other from the South Pacific. (1) The Mindanao Current sweeps southward along the eastern coast of the Philippines and brings well-ventilated water of low salinity from the North Pacific into the Indonesian Archipelago via the Sulawesi Sea and thence through the upper thermocline of the Makassar Strait and along the Denwakang Sill into the Flores Sea where it diverges into eastern and western branches (Gordon and Fine 1996) (Fig. 1.3). The western branch exits the region southward through Lombok Strait while the eastern one eddies and then leaves the area around the eastern end of the Sunda Islands via the Timor Sea. Although some of the Mindanao Current does enter Indonesia further east in the Malaku Sea, it mainly eddies and then turns again northward where it joins the Mindanao Eddy of the North Equatorial Countercurrent to flow eastward across the Pacific. (2) The through-flow in the Moluccas is derived from the South Pacific via the South Equatorial Current where a deflection of water of higher salinity from the Halmahera Eddy flows through the lower thermocline into the Halmahera Sea and Seram Sea and then radiates in several directions, northward along with the return flow from the Mindanao Current, and to the south and west into the Banda Sea. In the

Banda Sea the pattern is further complicated by the fact that the deeper water originates from the Indian Ocean.

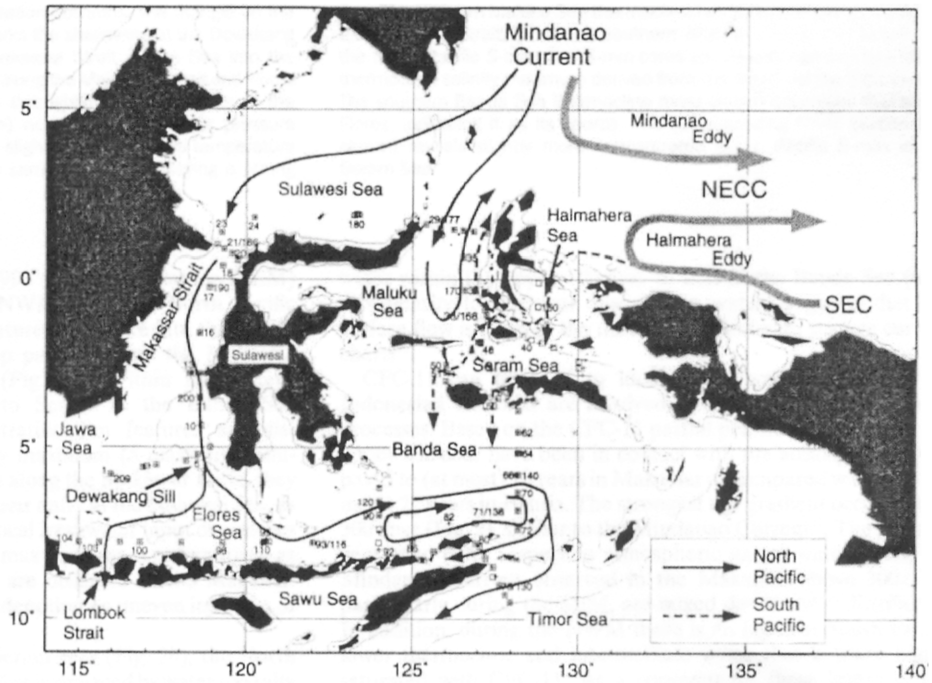


Figure 1.3. Map showing the direction of sea currents in eastern Indonesia. NECC=North Equatorial Countercurrent; SEC=South Equatorial Current. Modified from Gordon and Fine (1996).

The Indonesian through-flow has consequences for present climate (Gordon and Fine, 1996) in that it affects the meridional turnover of the Pacific and Indian oceans and may influence global thermohaline circulation; seepage of warm water out of the Pacific affects the volume of the warm pool in the western Pacific and consequently may influence El Niño events. The complexity of the pattern of flow undoubtedly has a bearing on the dispersal of sea-transported animals (see section 3.3.2). It should be noted, however, that surficial, wind-driven patterns of circulation do not necessarily conform in direction to the deeper flows described above. Dispersal of sea kraits is more likely to be affected by currents in the upper layers of water.

The terrestrial and marine biotas responded somewhat differently to the tectonic events leading to the present configuration of land and sea in Australasia. What may have been barriers to terrestrial organism would have been corridors for marine ones and vice versa. The Indonesian Archipelago, including Wallacea, is an interdigitation of land and water that serves as a faunal and floral filtre for terrestrial organisms dispersing between the Asian and Australian plates; the land is not continuous, but rather is archipelagic. By contrast, the sea is a continuous matrix surrounding points of land isolated within it. Thus, it has served as a corridor allowing mixing of the Pacific Ocean's and the Indian Ocean's marine biotas. Indeed, corals of some taxa, e.g., *Acropora,* reach their highest diversity in Indonesia, because of the presence not only of widespread Indo-Pacific elements, but also a juxtaposition of Pacific elements and Indian Ocean elements, supplemented by endemics that arose from isolation in deep-water refugia during times of eustatic sea-level lowering in the Late Cenozoic (Wallace, 2000). Mantis shrimp also show localisation within the Wallacean region. Although distribution of some mitochondrial DNA haplotypes indicated that gene flow was possible between distant populations, there were some populations only separated by 300 km that exhibited strong genetic breaks across the Wallace Line. These were believed to be relicts of Indian Ocean and Pacific Ocean populations isolated by emergence of the Sunda Shelf during glacial maxima (Barber *et al.,* 2000, 2002). Thus, although Wallace's and other lines originally were defined on the basis of the terrestrial fauna, Wallacea is of biogeographic importance for the marine biota as well.

New Guinea: New Guinea has had a highly complex geologic history and what is now a single island has had multiple origins (Pigram and Davies, 1987). Its two principal components are a southern portion representing the leading edge of the Australian plate, and a northern one consisting of at least 32 terranes of mixed oceanic, continental, and composite affinities. Amalgamation formed composite terranes in oceanic basins, distant from the edge of the Australian plate and as the Australian plate moved northward it encroached on these and entered subduction zones where the terranes had accreted. This led to orogenic events and in the middle to late Oligocene to docking of successive terranes. An initial docking of the Sepik terrain formed the northern part of the island of New Guinea sometime before 25 mya; other terranes subsequently docked onto the periphery of the Sepik one, such as the Finistere that by 10 mya had extended the New Guinean Coastline farther north.

In the east, a series of Cretaceous terranes amalgamated into a single East Papuan Composite by the early Oligocene. By the late Miocene, it had docked onto the eastern part of the Australian plate. The widening of the Coral Sea Basin to its south isolated it as the Papuan Peninsula. Later, its eastern part was fragmented by the opening of the Woodlark Basin and the islands just east of New Guinea resulted.

West Irian also had a complex geologic history. Its accretions consisted of eight terranes of continental origin and two of oceanic origin. Unlike some of the previous terranes of continental origin that may have been displaced fragments of the Australian Plate, at least one, Kemum, and possibly more of the West Irian continental terranes, had an origin from Gondwanaland in the Cretaceous, independent of Australia, but following a similar northward trajectory. After sequential accreting with some other terranes, the combined mass attached to the Australian plate. Attachment of terranes to western New Guinea to form what is now Irian Jaya occurred from before 10 mya to 2 mya.

Eastern Islands: The rises now containing the eastern islands rifted from Australia from the Cretaceous into the Cenozoic (Burrett *et al.*, 1991). In the Oligocene, all these island-groups were distant from Australia and the newly forming New Guinea and hence far from a potential source of waif-dispersed biota. New Caledonia was on the Norfolk Rise and separated from the other islands on the Solomon, New Hebrides and Tonga ridges and the Fiji Platform by an expanse of deep water as wide, or wider, than at present, and it has remained isolated ever since. The Fiji, Vanuatu and the Solomon Islands, however, were in closer proximity to each other than at present, and arranged in a generally linear fashion from northwest to southeast, so that faunal and floral exchange could have occurred among them across short dispersal distances in a stepping-stone fashion. After the late Miocene the three groups drifted toward New Guinea and their respective ridges spread out so that distances between formerly adjacent island groups became wider, especially between Fiji and Vanuatu. The last closely approached the islands east of New Guinea.

1.6 Paleoclimatology, Sea-Level Changes, and Pattern of Oceanic Currents

The Cenozoic was a time of transition from the warm Cretaceous climate to the cooler Quaternary one (Frakes *et al.*, 1992; Kent and Muttoni, 2008; Veron, 2008). Warm, but oscillating, conditions continued into the Cenozoic with two thermal maxima, one (the Late Paleocene Thermal Maximum) reached near the Palaeocene-Eocene border (about 55 mya) and the other at about 50 mya and known as the Early Eocene Climatic Optimum (EECO). In the Late Eocene (about 37 mya) global temperature plummeted into a glacial climatic mode with formation of an Antarctic ice cap about 34 mya, at the Eocene-Oligocene boundary. Thereafter climate trended toward overall cooling but with a somewhat warmer interlude about 15 mya in mid-Miocene and one of lesser magnitude in the Pliocene. The climate then became cooler and more erratic with glacials and interglacials alternating in the Pliocene and Pleistoene.

The causes of these climatic changes are debated and the hypotheses fall into two categories. The most commonly accepted explanation for this general cooling is that the fragmentation of Gondwanaland and subsequent movement of its derivative continents in the Cretaceous caused profound changes in the pattern of sea currents globally. These in turn affected temperatures and generally altered the earth's climate from one of pan-global warmth to a latitudinally stratified one with equatorial warmth and high-latitude cold characterized by polar ice caps. An alternative explanation is that a lowering of atmospheric CO_2 was responsible (Barrett, 2003). The various nuances of these hypotheses have been reviewed by Wang (2004). They include: (1) Variation in the Earth's orbit. (2) Opening and closure of various gateways between the Pacific Ocean and other bodies of water (Ogasawara, 2002), especially closure of the Isthmus of Panama with a consequent strengthening of the northward flowing of the Gulf Stream, thereby delivering greater moisture to the Arctic for formation of ice sheets. (3) Collision of the Indian plate with the Asian one, resulting in uplift in Asia, thereby reversing the continent's westward tilt to an even stronger eastern tilt with consequent change of drainage eastward into the Pacific and northward into the Arctic; this increase in freshwater entering the Arctic would have facilitated formation of sea ice that, in turn, would raise the albedo of the region and insulate the atmosphere from the high heat capacity of the ocean. Another consequence of Asian uplift may have been depletion of atmospheric CO_2 by chemical weathering of the uplifted materials, thereby reducing the "greenhouse effect" and lowering temperatures. (4) Closure of the Indonesian seaway. Cane and Molnar (2001) presented evidence that the northward displacement of New Guinea about 5 mya would have switched the source of flow through Indonesia from warm South Pacific to colder North Pacific waters, thereby cooling sea-surface temperatures in the Indian Ocean and intensifying the monsoon climatic system; also, reduced atmospheric heat transport from the tropics to the higher latitudes would have caused global cooling and stimulated growth of polar ice sheets. More recently Kent and Muttoni (2008) have proposed a modification of the carbon-dioxide hypothesis. They suggested that during the northward movement of India, it passed through the highly productive equatorial belt where carbon-rich pelagic sediments were generated that gave off CO_2 and caused an increase in the greenhouse effect that maintained elevated temperatures during the Early Eocene Climatic Optimum (EECO). With the passage of India further north, it entered the equatorial humid belt where weathering of silicate removed some CO_2 from the atmosphere. Eventually, even a major source of CO_2 was eliminated when the carbon-rich sediments subducted during collision with the Asian plate.

These hypotheses are not mutually exclusive and Molnar and England (1990) suggested that there may be interactive effects and some putative causes may be artifacts. Hay *et al*. (2002) pointed out that it isn't clear whether uplift caused climatic changes, or whether climatic changes produced erosional effects that created an illusion of uplift, and suggested that both erosion and climate in the Miocene may have been altered by the spread of C_4 plants.

Accompanying these climatic changes were glacio-eustatic alterations in sea level (Frakes *et al.*, 1992) with low water occurring when large amounts of the world's water was locked in the polar ice caps, and high water occurring when the caps melted and replenished the oceans. Sea levels were at a peak in the late Cretaceous and then gradually dropped (Frakes *et al.*, 1992). The eustatic fluctuations in sea level were substantial, with estimates of lows as much as 125 m below present levels during brief glaciations as early as the Miocene (5.2 and 4.8 mya) (Frakes *et al.*, 1992; Veron, 2008), and with an overall lowering since the early Eocene (55 mya) with episodic lowerings over short terms of 0.5-3 million years of about 70 m (Kominz *et al*., 1998). Voris (2000) produced a series of palaeogeographic maps of southeastern Asia and Australasia for times when sea level was lowered by 10 m, 20 m, 30 m, 40 m, 50 m, 75 m, 100 m, and 120 m or more below present levels, over the past 250,000 years. During that time sea level was 10 m below present level for 91% of the time, and even below 120 m below present level for 6%. Thus, much of that time water-gaps were narrower than at present and there were many land masses that are now islands that were incorporated into southeastern Asia. The Sunda shelf was largely exposed and formed broad connections between Sumatra, Java and Borneo and these were incorporated into continental Asia; the Sahul Shelf formed a broad connection between Australia and New Guinea. Taiwan was incorporated into the Asian mainland and many of the islands of the Philippines had coalesced and there were two series of "stepping-stone" islands which formed two nearly complete land bridges between the Philippines and Sabah (then part of the Asian mainland). In all, an additional 1.53 million km^2 was annexed to southeastern Asia. At lesser lowering of sea levels these connections were narrower or eliminated altogether.

These changes occurred repeatedly and similar configurations of land and sea recurred at intervals. There were at least 17 cycles of rise and fall in sea level in the Pleistocene (Grigg and Epp, 1989). These oscillations resulted in alternate posing and removing of barriers to dispersal through opening and closing connections between land masses; at higher sea levels some areas that once had a continuous coastline became fragmented into islands, while in other cases, some previous islands became submerged (see Section 8.4).

By the time sea kraits began to differentiate in the Miocene the continents were approaching their present position and hence the major pattern of circulation of oceanic currents had stabilized (Veron, 1995). More regional currents, however, continued to be altered as palaeographic configurations changed, especially with the oscillations of sea level attendant upon the glacial cycles of the Pliocene and Pleistocene (see Section 8.4).

1.7 Recapitulation

- Widespread, archipelagic species are especially useful for studying the causes of geographic variation.
- Morphological and biochemical approaches both are essential for interpreting geographic variation within a taxon. This dissertation provides the former as a springboard to the latter (currently underway).
- Sea kraits have had a checkered taxonomic history but are now considered as a derivative of terrestrial Asian elapid snakes and directly ancestral to the Australian venomous land snakes as well as indirectly to the true sea snakes (derived from Australian venomous terrestrial snakes).
- Sea kraits are in the single genus *Laticauda* which is divided into three complexes, each with one widespread, eurytopic species and one or more species with restricted range.
- The *Laticauda colubrina* complex contains the widespread *L. colubrina*, allopatric to *L. guineai* from southern Papua-New Guinea and to *L. saintgironsi* from New Caledonia. *Laticauda frontalis* is restricted to Vanuatu where it is sympatric, and even syntopic, with *L. colubrina*.
- The species of the *Laticauda colubrina* complex are semi-marine, egg-layers

that prey upon eels and have powerful neurotoxic venom, but are reluctant to bite defensively. They forage on coral reefs but emerge on land for resting, courting and mating, and oviposition. They have salt glands used in osmoregulation but require freshwater for drinking. They are preyed upon by sea eagles, sharks and other predatory fish, and occasionally other animals, and are attacked by ticks and internal parasites.

- The events leading up to the origin and diversification of the sea kraits was: (1) the origin of snakes, perhaps from a marine lizard, by about the mid Cretaceous (*circa* 95 mya), (2) the origin of the Elapoidea in Africa and its dispersal to Asia in the middle Eocene (about 46 mya), (3) the origin of the Elapidae in the Oriental Region in the mid Oligocene (about 31 mya), and its divergence about 28-24 mya into the Laticaudinae as it entered Australasia at the Oligocene-Miocene boundary as the Australian plate approached the Oriental one, (4) the divergence of Oxyuraninae from *Laticauda* about 23-12 mya and finally, (5) speciation within the genus *Laticauda* within the Australasian region and its spread peripherally northward to Japan, westward as far as the Bay of Bengal and eastward throughout the archipelagos of the southwestern Pacific as far as Futuna and Tonga. Thus, the origin, adaptive radiation, and spread of the genus *Laticauda* has taken place from 30 mya to the present time.
- The past 30 million years has been one of intense and complicated activity. During the Cenozoic the plates in the study area shifted rapidly, with some significant tectonic changes occurring within periods shorter than five million years. During movement of the major plates, there was frequent interplay of convergence and extension, driven by subduction. Subduction produced volcanic arcs that maintained chains of islands across the region. While some volcanic arcs disappeared others formed anew. Islands emerged and submerged. Oceanic basins formed and there was subsidence in continental regions. Multiple sutures occurred within eastern Indonesia, New Guinea and the Melanesian arcs. It was against the backdrop of this intense dynamism that *Laticauda* had its origin and extended its range throughout the region.
- The Cenozoic was a time of transition from a warm Cretaceous climate to a cooler Quaternary one. Accompanying these climatic changes were glacio-eustatic alterations in sea level that changed the configuration of land relative

to sea.

CHAPTER 2. MATERIALS AND GENERAL APPROACHES

2.1. Structure of the Dissertation

Figure 2.1 portrays a conceptual diagram of the research on which this dissertation is based. There are six stages: (1) Collection of Data, (2) Collation of Data, (3) Analysis, (4) Synthesis, (5) Construction of Explanatory Hypotheses, and (6) Projection onto Future Research. The first two parts are inductive in that previous data were insufficient to depict the patterns of geographic variation, much less to interpret them or formulate phylogenetic or evolutionary hypotheses; first it was necessary to assemble the relevant information. Once the database was assembled, analysis took place that led to recognition of relationships among populations. Several different approaches to analysis were used and the collective results synthesized to deliver a consistent pattern of geographic variation. The study of distribution went through similar stages and finally the results from both distribution and geographic variation were combined and related to published information on palaeogeography, direction of sea currents, temperature and rainfall to construct an

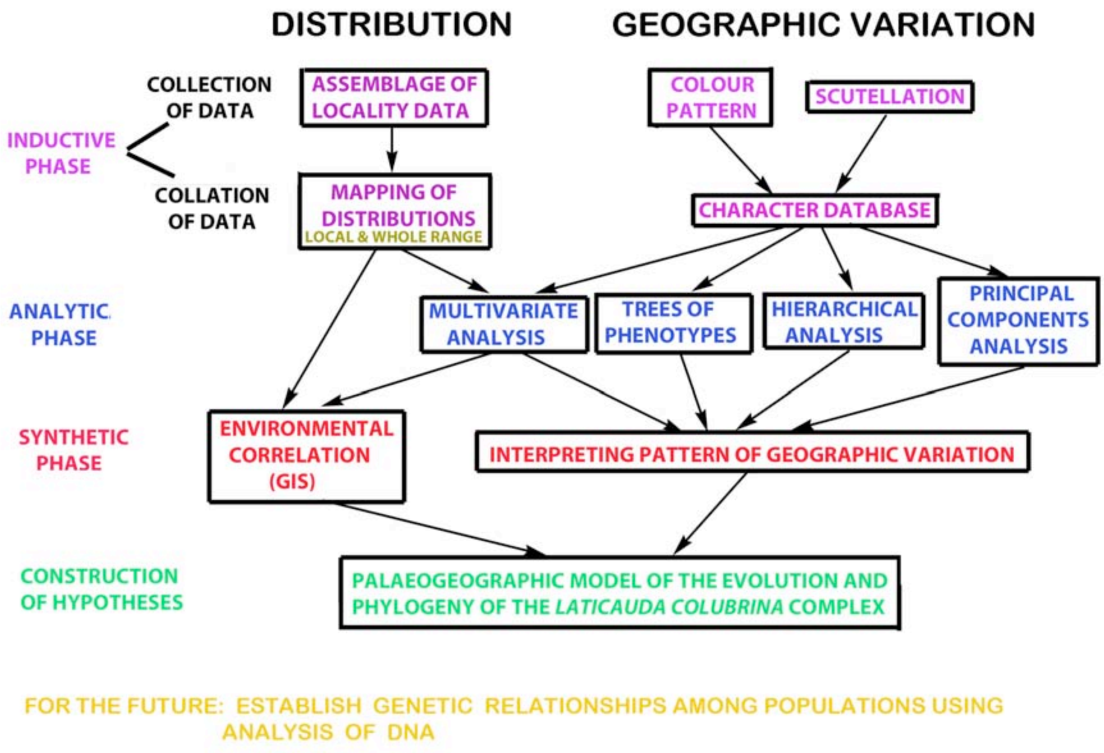


Figure 2.1. Schematic diagram of the research on which the present dissertation is based.

hypothesis of the origin and subsequent diversification of the *Laticauda colubrina* complex. Scientific studies should not only provide answers, but also lead to new questions; consequently, the final stage was a discussion of how the present research projects into the future and how it sets the stage for testing some of the hypotheses generated in this thesis.

Following the background information provided in Chapter 1, the present chapter (2) describes the database, the characters used, and the kinds of analyses employed. Although the morphological terminology used throughout this thesis is standard and will be familiar to most readers, a glossary of terms is provided in Appendix 2.1 for the non-specialist reader. The methods used for each kind of analysis are described. The next five chapters present the analyses, in each case first describing the methods used and then presenting the results. Chapter 3 deals with the distributional pattern of each species in the complex and relates it to environmental parameters, Chapters 4 -7 treat various analyses of the pattern of geographic variation: Hierarchical Analysis (Chapter 4), Principal Components Analysis (Chapter 5), trees based on phenotypes (Chapter 6), and multivariate analysis (Chapter 7). Each of these chapters includes discussion relevant to the material of that individual chapter. Chapter 8 synthesises and discusses the results from all chapters in terms of evolution and adaption and proposes a model for the evolution and dispersal of the complex. Finally, Chapter 9 points the way to future research.

Large portions of this dissertation were extracted from an earlier draft and have already been published as a monograph (Heatwole *et al*., 2005). The geographic patterns of variation revealed by the Hierarchical Analysis are most easily appreciated by reference to the figures in Chapter 4. The data on which those figures were based and the details of the statistical analyses involved were portrayed in a series of tables already published in the monograph cited above. Although not necessary for the narrative of the thesis, these tables do validate the conclusions drawn and therefore it is important they be available for perusal; accordingly, they are included among the appendices to this dissertation.

2.2. The Database

A total of 1,514 specimens was examined between 1982 and

2002: 1,233 *Laticauda colubrina* from 264 localities, 61 *L. guineai* from 14 localities, 192 *L. saintgironsi* from 28 localities, and 28 *L. frontalis* from ten localities (Appendix 2.2), deposited in 49 museums, universities, institutes, and private collections (see “Statement of the Contributions Made by Others”, pp. vi-vii). With the following minor exceptions: (1) a small collection in Bogor, Indonesia, discovered after the analysis had been completed, (2) acquisitions obtained by museums after my visits, and (3) Linnaeus' single specimen of *L. colubrina* (=*Coluber laticaudatus*), of which I examined only a photograph, I studied all worldwide collections of the *Laticauda colubrina* complex of which I am aware.

There were 39 specimens (32 from Indonesia, 3 from Papua-New Guinea, 1 from Fiji, and 3 of uncertain origin) in the Museo Storia naturale Genova "Giacomo Doria" examined after hierarchical analyses and construction of phenetically based trees had been completed. Data from these specimens were not analysed by those methods, but were included in the Principal Components and Discriminant Function analyses, carried out later. To ascertain whether data from the Genoa museum were consistent with the hierarchical analysis, the Genovese specimens were compared statistically to specimens from equivalent localities or regions from other museums; the results are discussed at appropriate places in the following text.

I selected 36 characters of colouration and scutellation and three designations of size, gender and maturity (Table 2.1). Pernetta (1977) indicated that: "if the external scale counts are the major features distinguishing the presently recognised species of *Laticauda*, and it would appear.....that they are, it could well be argued that geographic variation in such parameters should be more closely examined." Accordingly, basic characters historically used to define or diagnose species within the genus *Laticauda* were summarised by Heatwole *et al*. (2005) in order to evaluate consistency throughout the distributional ranges of the species in the *Laticauda colubrina* complex. These characters were included in the present database and are: (1) whether or not the rostral is divided, (2) whether or not an azygous prefrontal is present, (3) how many supralabial scales occur on each side of the head, (4) how many supralabials border the orbit, (5) the number of scale rows around the body, (6) the number of gastrosteges, and (7) the number of subcaudal scales.

An additional suite of easily quantified characters were selected that casual inspection or the literature showed to be variant. These include details of the scutellation, of the head and body, the number and dimension of the dark and light bands on the body and tail, and the colour pattern of the head.

Table 2.1. Summary of characters used in analyses. For details, see text.

CHARACTER	ORDER	CHARACTER STATES
COLOURATION		
Type of Head Pattern	First	28* Qualitative
Number of Dark Bands on Body	First	Quantitative
Number of Dark Bands on Tail	First	Quantitative
Colour of Tip of Tail	First	2 Qualitative
Ventral Spot in Dark Band	First	2 Qualitative
Attenuation of Dark Bands Anterior Mid-body Posterior	Second	3 Quantitative (ratios)
SCUTELLATION		
Configuration of rostral, nasal and internasal scales	First	2 Qualitative
Number of prefrontal scales	First	Quantitative
Number of supralabial scales	First	Quantitative
Supralabial scales contacting orbit	First	Multiple qualitative
Number of temporal scales	First	Quantitative
Number of gastrosteges	First	Quantitative
Number of scale rows around body at 1st gastrostege at 20th gastrostege at 50th gastrostege at 100th gastrostege at 150th gastrostege at 200th gastrostege at last gastrostege	First	7 Quantitative
Scale rows encompassed in dorsal width of dark body band 1st dark band 10th dark band 25th dark band	First	3 Quantitative
Scale rows encompassed in ventral width of dark body band 1st dark band 10th dark band 25th dark band	First	3 Quantitative
Scale rows encompassed in dorsal width of light body band 1st dark band 10th dark band 25th dark band	First	3 Quantitative
Scale rows encompassed in ventral width of light body band 1st dark band 10th dark band 25th dark band	First	3 Quantitative
Scales containing yolk-sac scar	First	Multiple qualitative
Number of subcaudal scales	First	Qualitative
Ratio of gastrosteges to subcaudals	Second	1 Quantitative (ratio)
LIFE HISTORY		
Length Body Tail	First	2 Quantitative
Gender/Maturity	First	3 Qualitative**

*Head pattern contains 23 elements arranged in 28 configurations.
**Males, females, juveniles

Because some specimens were in poor condition (dried, twisted), represented by only a part of the body (e.g., head only), or were otherwise imperfect, not all characters could be assessed on every specimen; one large collection of skins only from the head and neck were used solely for analysis of colour pattern. Some animals were studied alive and subsequently released; characteristics difficult or impossible to obtain reliably from these live animals (e.g., number of gastrosteges) were not recorded. Harold Cogger had studied some specimens from Vanuatu and other eastern islands independently and supplied those data. Although the we treated some characters somewhat differently, those specimens previously studied were not re-examined for the present study. Consequently, when the two datasets were merged some characters were deleted from the older, less extensive dataset. For these reasons, sample size varies somewhat from character to character.

2.2.1. Colour pattern

In life, base-colour of the face, snout, and lips of *Laticauda colubrina* is yellow with other parts of the head similar in colour to that of the body. In preserved specimens, the yellow disappears. Superimposed on the light background colour of the head is a pattern of darker patches, stripes, and bars that connect, in various combinations, with each other or with bands on the body.

Colouration of the body and tail consists of dark bands (black or brownish) alternating with lighter ones (white, cream or yellowish, to grayish or bluish). The dark bands may form a complete, wide ring around the body, or they may narrow toward the underside so that the size of dark bands relative to light ones is greater on the back than on the belly; in extreme cases dark bands are incomplete and do not reach the venter. Boulenger (1912) and Bhaskar (1996) noted that the dark bands of *L. colubrina* do not always meet below and in specimens from Taiwan, Kuntz (1963) observed the dark bands to be incomplete or variable in outline. Fischer (1856) used the failure of dark bands on the trunk to meet on the belly as a distinguishing character for his variety *colubrina*. Wall (1909) incorrectly attributed fading with age as the cause of incomplete bands; I observed some very small specimens that had sharply outlined, distinct, but incomplete, bands.

Bands of both colours may be narrow, or wide, or light ones narrow and dark ones wide, or the opposite. The widths of dark and light bands on different segments of the body are treated in Section 2.2.2 under the subheading "Scale Rows Encompassed in the Width of Coloured Bands", and the attenuation of dark bands and the relative widths of dark versus light bands, are discussed under Section 2.2.5.

Cantor (1847) reported ontogenetic differences in colouration in *L. colubrina*, the young with "Ground color gamboge [yellowish], greenish above, with numerous distinct broad rings of a blue reflecting black color" and adults with "paler colors, lead-grey on the back; the rings impure light blue on the sides and abdomen".

Colour, in life, of light bands on the body and tail of adult *L. saintgironsi* differs from the white to blue of *L. colubrina* and often is a warm brown (personal observation). Saint Girons (1964, 1990) indicated orange for the majority of specimens, but with colour varying "from red to bluish, passing through yellow and white; the young were all blue or white". Bauer and Sadlier (2000) indicated the dorsal ground colour as "pale orange or pinkish to whitish" and Ineich and Laboute (2002) described the light bands as "buff or orangy beige". The distinctiveness in hue of the light bands in these two species can be appreciated by comparing published coloured photographs of adult *L. saintgironsi* (then current name *L. colubrina*) (Bellairs [1971]; p. 741]; Obst *et al.* [1988; p. 484]; Coborn [1991; p. 462]; Shine [1991b; p. 50]; Bauer and Sadlier [2000; Plate 22B]; Ineich and Laboute [2002; pp. 74, 82, 85, 88, 91]) with those of adult *L. colubrina sensu stricto* (Pickwell [1972]; McCoy [1980; Plate 20F]; Mehrtens, [1987; pp. 282, 285]; Heatwole [1990]; Coborn [1991; pp. 462-463]; Shine [1991b; pp. 49, 127, 158]; Mebs [1992; p. 241]; Mara [1993; pp. 206-207]; Heatwole and Cogger [1994; p. 200, but note that the labels of *L. colubrina* and *L. laticaudata* are reversed in error]; Mattison [1995; p. 240]; Das [1996; Plate 34]; O'Shea [1996; pp. 171, 173]; Greene [1997; p. 234]; Cox *et al.* [1998]; Heatwole [1999; Plate 7]; Cogger [2000; p. 723]; Zug *et al.* [2001; p. 530]; Leviton *et al.* [2003]; Reed [2003]). Cuvier (1846) presented an excellent coloured drawing of *L. colubrina* (as *Hydrophis colubrina*). The only photograph featuring *L. colubrina* (*sensu stricto*) with brown background colour is a plate published by Zhao and Adler (1993) of a specimen from Taiwan.

Head pattern---Twenty-three elements of the head pattern (Fig. 2.2) occur in 28 different configurations (Figs. 2.3-2.7) defined by the presence or absence of individual elements, and by the extent of confluency with body bands. These configurations were designated by the letters A-Z and a-b in the order in which they were encountered during the study. The separate elements are as follows. (1) A patch covers the dorsal aspect of the head, sometimes with (2) a light-coloured dot in the centre. This patch is connected, or not, laterally by (3) a dorsal cephalic connection to (4) an orbital bar leading posteriorly from the eye. This bar sometimes connects via (5) a ventral cephalic connection to the lower part of the head pattern, and (in one specimen) via (6) an anterior orbital connection to the anterior part of the head patch. The lower part of the head pattern consists of (7) a labial stripe from the chin along the lateral surface of the lower jaw. This stripe sometimes has a gap part way along the jaw and it may connect, or not, by way of (8) a labial connection to the rest of the head pattern. The posterior part of the head pattern consists of the posterior part of the head patch, the dorsal cephalic connection, the posterior part of the orbital bar, the ventral cephalicconnection and the labial connection, and collectively was designated (9) the head band. It is a complete band if all these components are present and the two sides are connected below by (10) a gular connection, but is saddle-shaped if that connection is absent. The head pattern sometimes is connected to the (11) first body band by the (12) first lateral connection, and sequentially to the (13) second body band, (14) third body band, and (15) fourth body band (not shown in Figure 2.2, but see Figure 2.7) by the (16) second lateral connection, (17) third lateral connection and

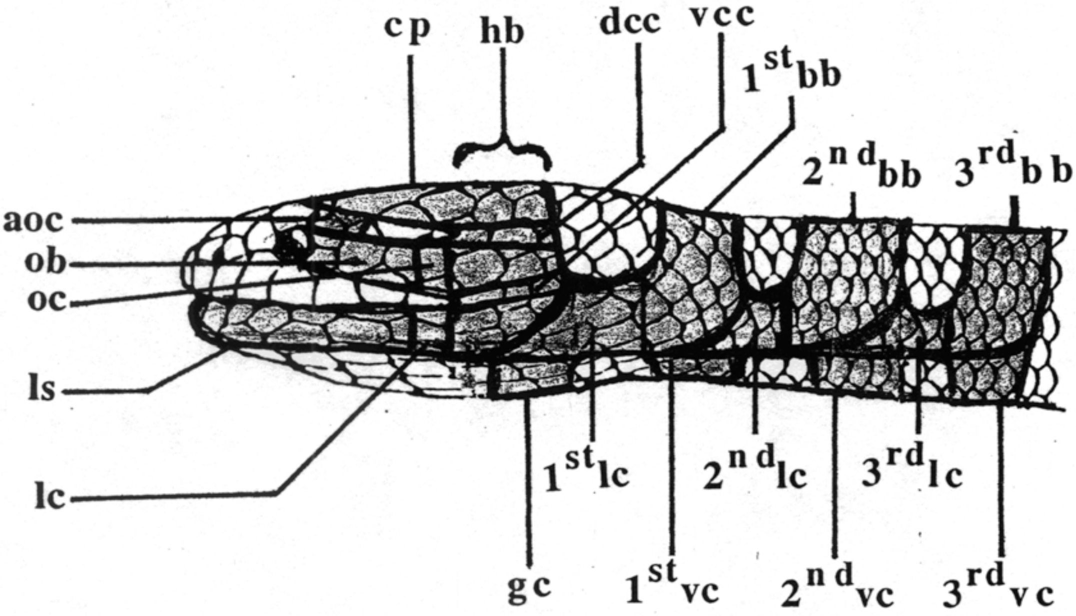


Figure 2.2. Elements of the colour pattern of the head in species of the *Laticauda colubrina* complex. aoc=anterior orbital connection; cp=cephalic patch; dcc=dorsal cephalic connection; gc=gular connection; hb=head band; lc=labial connection; ls=labial stripe; ob=orbital bar; oc=orbital connection; vcc-ventral cephalic connection; 1stbb=first body band; 1stlc=first lateral connection; 1stvc=first ventral connection; 2ndbb=second body band; 2ndlc=second lateral connection; 2ndvc=second ventral connection; 3rdbb=third body band; 3rdlc=third lateral connection; 3rdvc=third ventral connection.

(18) fourth lateral connection (not shown in Figure 2.2, but see Figure 2.7) respectively. Often the body bands involved in the head pattern do not meet ventrally, but sometimes they do via some combination of the (19) first ventral connection (connecting the first body band below), (20) the second ventral connection, the (21) third ventral connection, or the (22) fourth ventral connection. Rarely, there are (23) longitudinal, mid-ventral connections between body bands involved in the head pattern (not shown in Figure 2.2, but see Figure 2.5). When the head pattern was asymmetrical (left and right sides with different patterns), the specimen was given a score of 0.5 for each pattern.

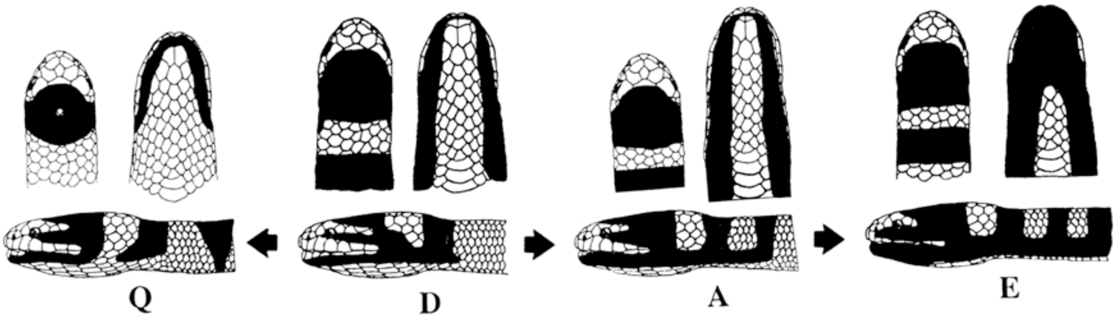


Figure 2.3. Dorsal, ventral and lateral views of the four basic types of head pattern (Q, D, A, E) in the *Laticauda colubrina* complex. Q: Head pattern not connected to any body bands. Note presence of cephalic spot in the centre of the cephalic patch. D: Head pattern connected to the first body band. A: Head pattern connected to the first and second body bands. E: Head pattern connected to the first, second and third body bands. D is considered the primitive pattern (see text). Arrows indicate directions of hypothetical derivation of other patterns from D. Q is derived by loss of the first lateral connection and A and E are derived respectively by progressive establishment of the second and third lateral connections.

Figures 2.3-2.7 present an hypothetical scheme of the derivation of the different head patterns from one another. Pattern D is considered the most primitive as it is the most common and widespread one in *L. colubrina* and also occurs in some *L. saintgironsi*.

L. semifasciata (Stejneger, 1907, plate XXII; Taylor 1922, plate 30; Kuntz, 1963, p. 64) and *L. schistorhynchus* (Günther, 1874, plate XLV) have a pattern that resembles configuration Q, and thus may be derived from Q. As in *L. colubrina*, the head pattern is variable in other species of the genus. In some *L. schistorhynchus* the dorsal cephalic connection is missing. *L. laticaudata* often has a head pattern reminiscent of Q or H but with a dark upper lip; we have observed occasional patterns similar to A, D, I, and L on specimens of this species. Mao and Chen (1980; their Figure 7) show a photograph of an *L. laticaudata* with a pattern similar to C but with an extra first ventral connection.

Number of dark bands (2 quantitative characters)---Dark bands were counted separately for body and tail. The count began with the first dark band on the neck, whether or not that band was also included in the colour pattern of the head, and proceeded posteriorly. A band containing the vent was considered a body band if most of the band was anterior to the vent, and a tail band if most of the band was posterior

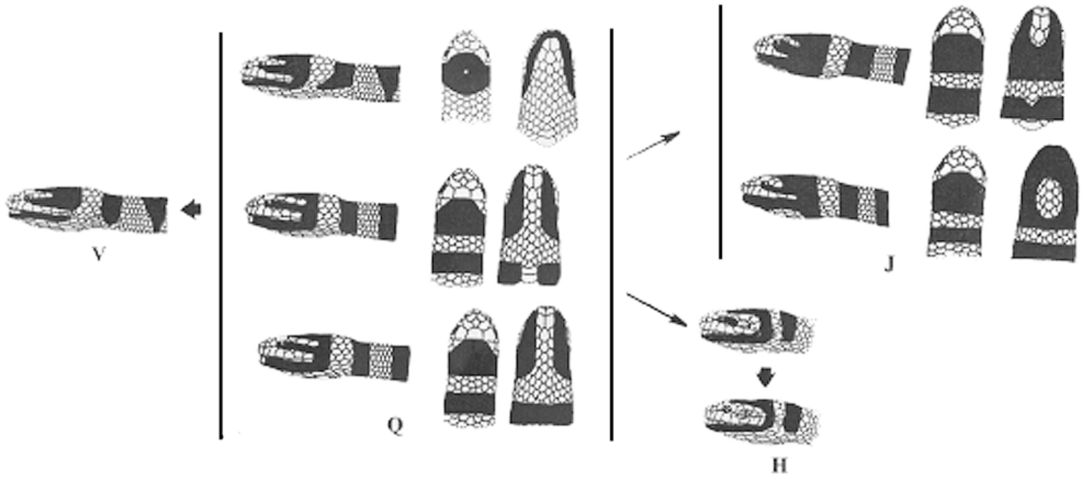


Figure 2.4. Variation in the Q head pattern and its derivatives, J, H, and V. Arrows indicate hypothetical direction of change. Within Q, the width and shape of the various elements differ, and there is variation in how far the first body band extends ventrally, ranging from saddle-shaped to complete encirclement of the body. In both Q and J, the extent and shape of the configuration on the chin and throat varies. J could be derived from Q by formation of a gular connection across the throat, ventrally uniting the head bars on opposite sides of the head. H could be derived from Q by loss of the orbital connection; within H there is progressive loss of the orbital bar until it disappears altogether. V could be derived from Q through loss of the ventral cephalic connection.

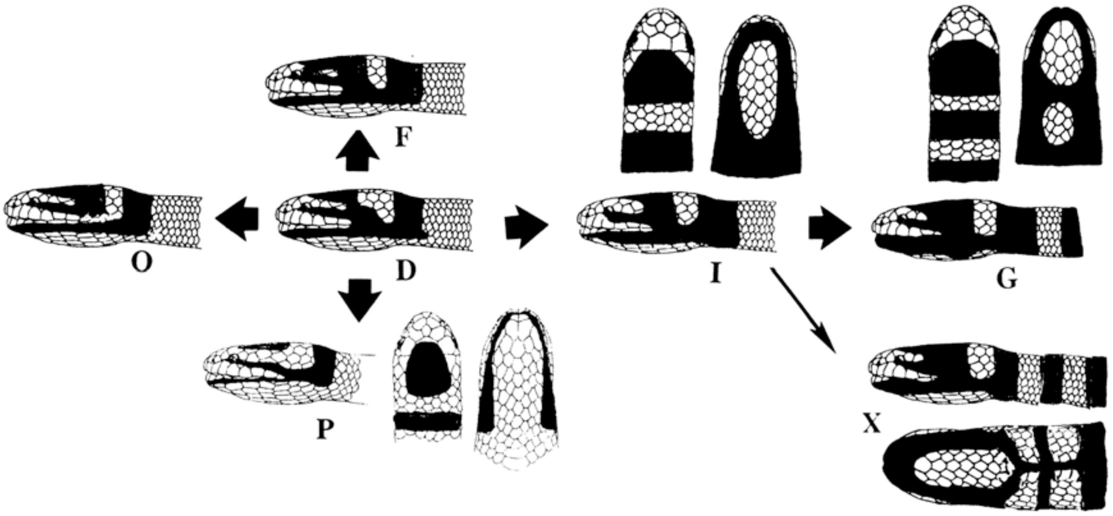


Figure 2.5. Derivatives of head pattern D. Arrows indicate hypothetical directions of change. D could give rise to O through loss of the ventral cephalic connection, to P through loss of the dorsal cephalic connection, and to F by establishment of the anterior orbital connection. D could give rise to I by establishment of the first ventral connection; in turn I could give rise to G by formation of a gular connection, and to X by establishment of mid-ventral connections between the first, second, and third body bands. Note variation in the width of the size and shape of the various elements; such variation occurs within patterns and derivative patterns.

to the vent.

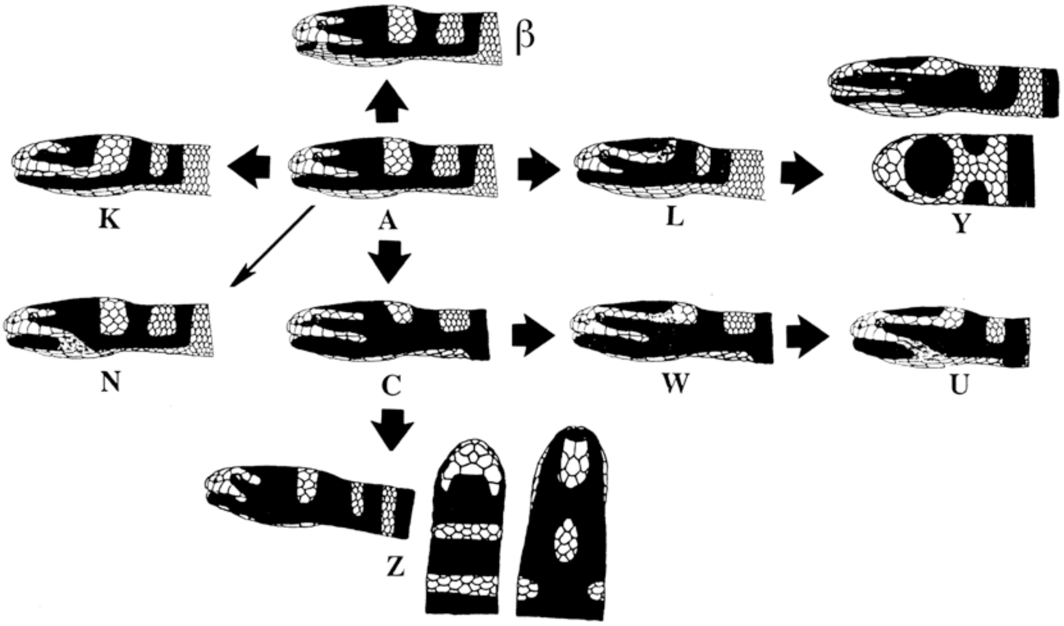


Figure 2.6. Derivatives of head pattern A. Arrows indicate hypothetical directions of change. A could give rise to K by loss of the ventral cephalic connection, to N by loss of the labial connection, to L by loss of the dorsal cephalic connection, to C by establishment of the second ventral connection, and to b by loss of a labial connection in the anterior region of the labial stripe. In turn, L could give rise to Y through loss of the dorsal part of the first body band and development of two light-coloured dots in the centre of the head band. C could give rise to Z through establishment of a gular connection and a first ventral connection and to W through loss of the dorsal cephalic connection, which in turn could give rise to U through loss of the labial connection. Note that alternatively W could develop from L through establishment of a second ventral connection.

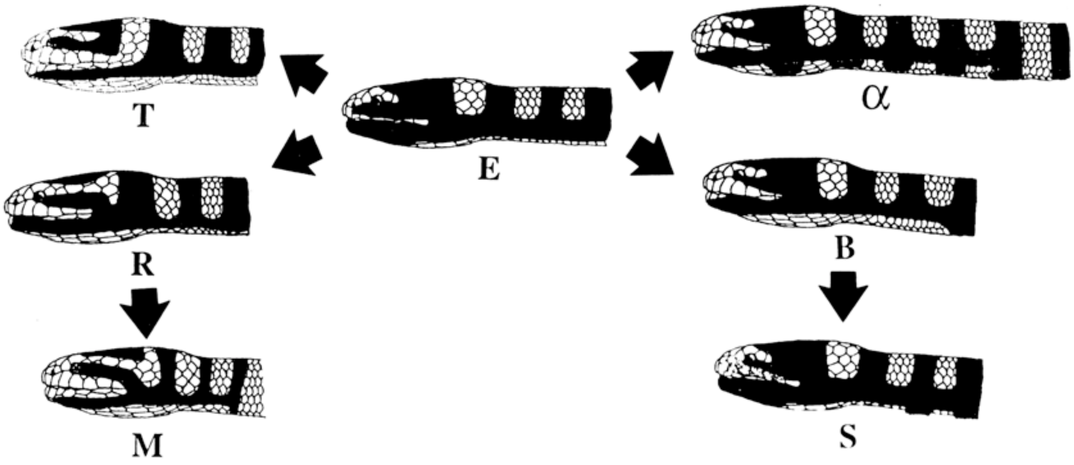


Figure 2.7. Derivatives of head pattern E. Arrows indicate hypothetical directions of change. E could give rise to T through loss of the ventral cephalic connection, to R through loss of the dorsal cephalic connection, to B through establishment of a third ventral connection, and to a by extending posteriorly to the fourth body band and establishment of a gular connection and first, second, third and fourth ventral connections. R, in turn, could give rise to M through establishment of a third ventral connection. B could give rise to S by establishment of a second ventral connection. Note that alternatively, B could give rise to M through loss of the dorsal cephalic connection.

Continuity of dark bands (2 characters, each with two states)---Snakes differed in whether the dark bands completely encircled the body. Complete bands either did or did not contain a central light-coloured spot or other configuration on the venter. Incomplete bands failed to meet either ventrally or (rarely) dorsally.

Tip of tail (1 character, 2 character-states)---Tip of tail either light-coloured (white, cream, yellowish) or dark, in the latter case usually a small dark spot just on the tip.

2.2.2. Scutellation

Rostral, nasal, and internasal scales (1 character, two main character-states)---Lateral to the rostral scale and extending posteriorly are nasal scales surrounding the nostrils. The rostral scale occurs in two character states relative to the nasals; it either extends dorsally to completely separate the nasal scales (Fig. 2.8), or the nasals meet in the midline behind the rostral. In addition, there are several kinds of intercalary scales and some fusions. Lying in the curvature behind the rostral and its flanking nasal scale lie a median pair of internasals (Fig. 2.8). Boulenger (1896) indicated the occasional presence of one or two additional scales between the internasals.

Prefrontal scales (1 character, multiple character-states)---Prefrontal scales (Fig. 2.8) occur in two main character-states: (1) two prefrontals divided by the midline of the head and (2) three prefrontals, with an azygous, central scale lying between two lateral ones. Usually the azygous scale completely separates the two lateral ones, but sometimes it does not do so completely, and the lateral scales meet narrowly in the midline anterior to the azygous scale. There is occasional splitting of individual prefrontals or fusion of prefrontals with other scales.

Number of supralabial scales (1 quantitative character)--- Sometimes the number of supralabial scales (Fig. 2.8) differed on the two sides of the head; accordingly, data were recorded separately for the left and right sides.

Supralabial scales contacting the orbit (1 character, multiple character-states)---Usually the third and fourth labial scales (counting anterior to posterior) form the lower edge of the orbit (3+4) (Fig. 2.8). Character-states less commonly observed were 3rd only, 4th only, 4+5, and 3+4+5.

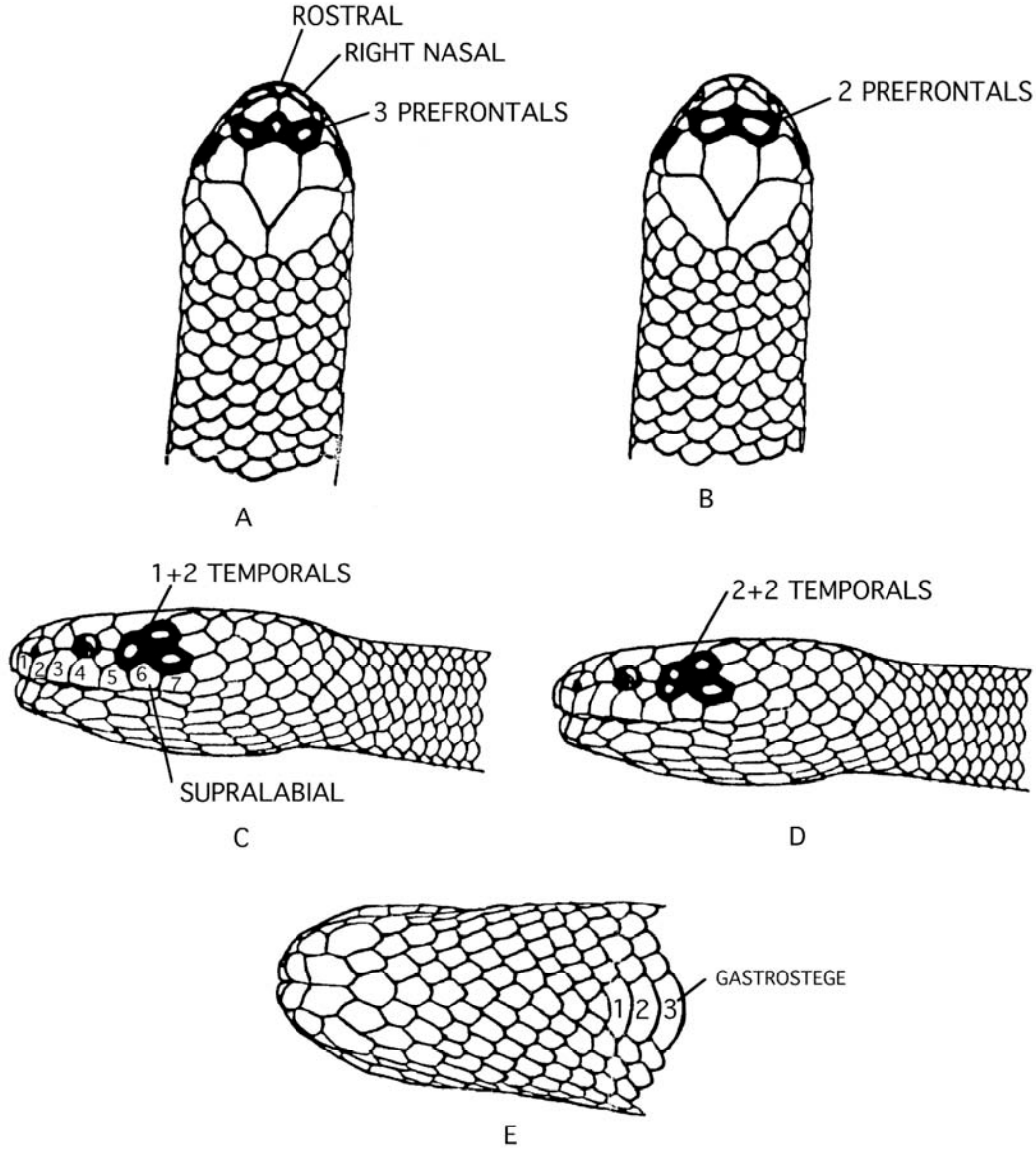


Figure 2.8. Details of the scutellation of the head of *Laticauda colubrina* illustrating some of the character states used in the present study. A, B: Dorsal views showing the rostral completely separating the left and right nasals, and the azygous (A) and non-axygous (B) condition of the prefrontals. Note that the prefrontals are heavily outlined for emphasis. C: Left lateral view showing 1+2 temporal scales (heavily outlined for emphasis) and seven supralabial scales (numbered). Note that supralabial numbers 3 and 4 contact the orbit, the standard condition. D: Left lateral view showing 2+2 temporal scales (heavily outlined for emphasis). E: Ventral view showing the first three gastrosteges (numbered).

Temporal scales (1 character, multiple character states)---On each side of the head one or more anterior temporal scales, is/are followed by a second rank (Fig. 2.8). The most common character-state was one anterior temporal followed by two posterior ones (1+2). Variants, appearing to arise from fusion or splitting of scales within a rank, are: 1+1, 1+3, 1+4, 2+2, 2+3, 2+4, and 3+2. The number of temporals sometimes differed on the two sides of the head and data were recorded separately for right and left sides.

Number of gastrosteges (1 quantitative character)---Gastrosteges, the wide scales covering the venter, were counted, beginning with the first enlarged scale on the underside of the neck and proceeding to the vent (Fig. 2.8). The divided anal scale covering the vent was not included. In some snakes one or more gastrosteges anterior to the anal scale also were divided; these were included. Guinea observed that populations of *L. colubrina* from Fiji and Taiwan differed in number of gastrosteges. The traditional term "gastrostege" is used, rather than the more recent designation of "ventral"; the latter is misleading, as there are other kinds of ventral scales than gastrosteges, e.g., submentals and subcaudals.

Scale rows around the body (7 quantitative characters)---Scale rows around the body were counted at seven different positions. As gastrosteges were counted, insect pins were inserted into the first, 20th, 50th, 100th, 150th, and 200th (when present) scales, and into the last gastrostege just before the vent. At each pin, the scale rows around the body were counted, beginning on the left side of the gastrostege and continuing across the back until the gastrostege on the opposite side was reached. Counts were made diagonally from front to rear for all counts except for that at the level of the last gastrostege. That count was made from back to front, thereby avoiding counting scales on the tail. The gastrostege itself was not included in these counts.

Scale rows encompassed in the width of body bands (12 quantitative characters)---Stejneger (1907) noted that in all three complexes of the genus *Laticauda* dark bands were wider on the back than below and that the dark and light bands often differed in dorsal width. In the present study, dorsal and ventral widths of each colour of band were quantified at three levels: the first, tenth, and 25th band after the head pattern. The unit of measure was the number of scale rows encompassed by the band. At each level the scale rows contained in the width of dark bands on the dorsum were counted from the anterior edge of the band diagonally across the back to the posterior edge, centered on the midline of the back; on the venter, the number of gastrosteges included in the band was counted. After a count on a dark band was made, a similar count was made for the light-coloured band immediately posterior to it. For dark bands, the dorsal count began with the first entirely dark scale abutting on the light band ahead, and continued to include the last completely or partly dark scale. Dorsal counts were made similarly for light bands but with the scale colours reversed. On the venter, a scale was scored dark or light depending on which colour covered the greatest area. If the leading and last gastrostege of a band were both half dark the two were combined and counted as one whole dark scale.

For a given specimen, the sizes of dorsal scales in the dark and light bands appeared the same and consequently the counts were considered equivalent for the two colours of bands. Similarly, dark and light gastrosteges appeared to be the same size in a given individual. The gastrosteges and dorsal scales, however, are of different sizes and are not arranged in the same way. Whereas the scales in dorsal bands occur in diagonal rows, the gastrosteges are arranged in a straight-line sequence along the long axis of the body (Guinea, 2002). Thus, dorsal and ventral scale counts could not be used to directly indicate dorsoventral narrowing or widening of dark bands; for a given band-width (real distance), the ventral counts are usually lower than the dorsal ones.

There are a number of ways that band-width could vary within a given individual: (1) the width of the dark bands, light bands, or both, could change from one location to another along the torso, (2) dark bands could be either narrower or broader than the adjacent light one and this arrangement could differ along the length of the body, and (3) bands of a given colour could either narrow or broaden along the dorsoventral axis. The last type of variation is complicated by the lack of equivalency between dorsal and ventral counts (see above). However, comparisons of the ratio between dorsal and ventral counts did allow assessment of relative narrowing of bands from one body region to another.

When merely the rank in width of the bands in two body regions is of interest, and there is some natural way of pairing data (in the present case by individual animal) then a Wilcoxon Matched-Pairs Signed-Ranks can be used to make comparison over the entire dataset. This test does not require that different localities, genders, or ages vary to the same degree, but merely that the direction of change is consistent among the groups. This test was applied to the first two kinds of variation listed above.

Scales bearing yolk sac scar (1 character, variable character-states)---Yolk sac scars are most prevalent in small snakes but persist in some large animals. Positions of such scars (when present) were indicated by recording the gastrosteges included in a scar, counting anteriorly from the vent. Thus, 21-24 means that a scar extends from the 21st to the 24th gastrosteges anterior to the vent. The mid-point was used for analysis. For example, a scar extending from the 21st to the 24th gastrostege anterior to the vent had a midpoint of 22.5.

Number of subcaudal scales (1 quantitative character)--- In *Laticauda* the subcaudal scales are paired and counts consisted of numbers of pairs, beginning just posterior to the vent and extending to, but not including the large terminal scale on the tip of the tail.

Rare conditions---In addition to the character-states described above, some scales occurred in rarer combinations.

2.2.3. Size

Length (2 quantitative characters)---The snout-to-vent length of the body (S-V length) was measured by placing one end of a string at the tip of the snout and then following the coiling of the body, applying the string to the ventral midline of the animal as far as the opening of the cloaca. The string was then straightened and applied to a metre rule to ascertain its length. The tail was held straight and directly measured from the posterior edge of the vent to the tip of the tail with a ruler. All measurements were to the nearest millimetre.

2.2.4. Gender and Maturity

Life history category (1 character, 3 character-states)---Large snakes were sexed by observing everted hemipenes or hemipenial bulges along the base of the tail (males), and palpating for large eggs and/or noting that the tail just behind the vent was thin (females). When these indications of gender were not clear, the animal was probed in the posteriolateral wall of the vent, with insertion of the probe into the hemipenial sac indicating a male and failure of the probe to enter indicating a female. State of preservation of some specimens sometimes made this procedure difficult and mistakes in designating gender may have been made. Large animals whose sex could not be ascertained were designated as "uncertain gender".

Small snakes whose gender could not be determined in the above manner were listed as juveniles. A number of characters in *Laticauda* display sexual dimorphism (see below) and could perhaps be used to assign juveniles to one sex or the other. However, assigning gender on the basis of a supposedly dimorphic character and then testing that character for sexual dimorphism is circular reasoning. Consequently, juveniles were excluded from analyses of sexual dimorphism.

2.2.5. Second-Order Characters

Second-order characters indicate relative proportions of different characters or changes in characteristics from dorsum to venter or along the length of the body. The ratio of dorsal width of the dark bands to that of the light ones, and the change of this ratio along the body were discussed above.

Attenuation of dark bands on the body (scale rows wide on dorsum/scale rows wide on venter) (3 characters [1 character in each of 3 body regions])---This ratio was calculated at the level of the first, 10th and 25th dorsal bands, and comparisons made among these regions.

Ratio of number of gastrosteges to number of subcaudal scales (1 quantitative character)---This ratio was used as a means of evaluating the relative length of the body and tail.

2.3 Recapitulation

- The database consisted of 1,514 specimens from which 36 characters of colouration and scutellation and three designations of size, gender and maturity were selected for analysis. These included both first order and second order characters. Each character was described.
- A scheme whereby the 28 separate head patterns could be derived sequentially from a primitive pattern was proposed.

CHAPTER 3. GEOGRAPHIC DISTRIBUTION

This chapter details the distribution of the various species in the *Laticauda colubrina* complex and relates distributional patterns to the occurrence of available habitat and favourable environmental conditons.

3.1. Methods

The provenance of all specimens with sufficiently precise locality information were plotted on maps of each individual island-group or country. For a complete list of specimens, see Heatwole *et al.* (2005).

A problem in establishing the precise range of widespread species is that some records are based on old specimens collected when precise locality was not considered an important datum and sometimes collections were labeled as originating from the place from which they were dispatched to a museum, rather than from where they were collected. Also, some old specimens are accompanied by imprecise data such as "Indian Ocean", "China Sea", and "South Seas". Sea kraits are not pelagic species. Consequently, these records probably refer, not to locations of open water, but rather to unspecified coastal areas, peripheral to these seas. Specimens without exact provenance were not plotted on the distribution maps.

Weather data were plotted using Geographic Information System (GIS) so as to ascertain whether geographic patterns of rainfall and/or surface temperatures of the sea showed any relation to the distribution of sea kraits. The layer of mean surface temperature of the periods January - March, April - June, July - September, and October -December was created using data for sea-surface temperatures (SST) for each month between the years 1985 and 2001. The custodian of the SST dataset is the National Oceanic and Atmospheric Administration (NOAA)'s National Oceanographic Data Center, Satellite Oceanography Group (http://nationalatlas.gov/atlasftp.html#sstalli). The grid-cell values represent average seasonal SST in degrees C at a grid scale of approximately 4 km by 4 km. Data on rainfall were obtained for 92 weather stations from NOAA's National Climatic Data Center (http://gis.ncdc.noaa.gov). The mean total rainfall between 1986 and 2004 for each weather station for the periods January - March, April - June, July - September, and October -December were calculated.

3.2. Distribution of Species

Figure 3.1 presents a map showing the geographic area encompassing the distributions of all the species of the *Laticauda colubrina* complex. Collectively, these species are distributed widely within the tropics and subtropics of southeastern Asia and southwestern Oceania, symmetrically around the equator almost precisely within areas bounded by the tropics of Cancer and Capricorn. The only populations lying outside these boundaries are the *L. colubrina* in the Ryukyu Islands, just north of the Tropic of Cancer. The most southern populations (*L. saintgironsi*) occur in New Caledonia, just inside the Tropic of Capricorn.

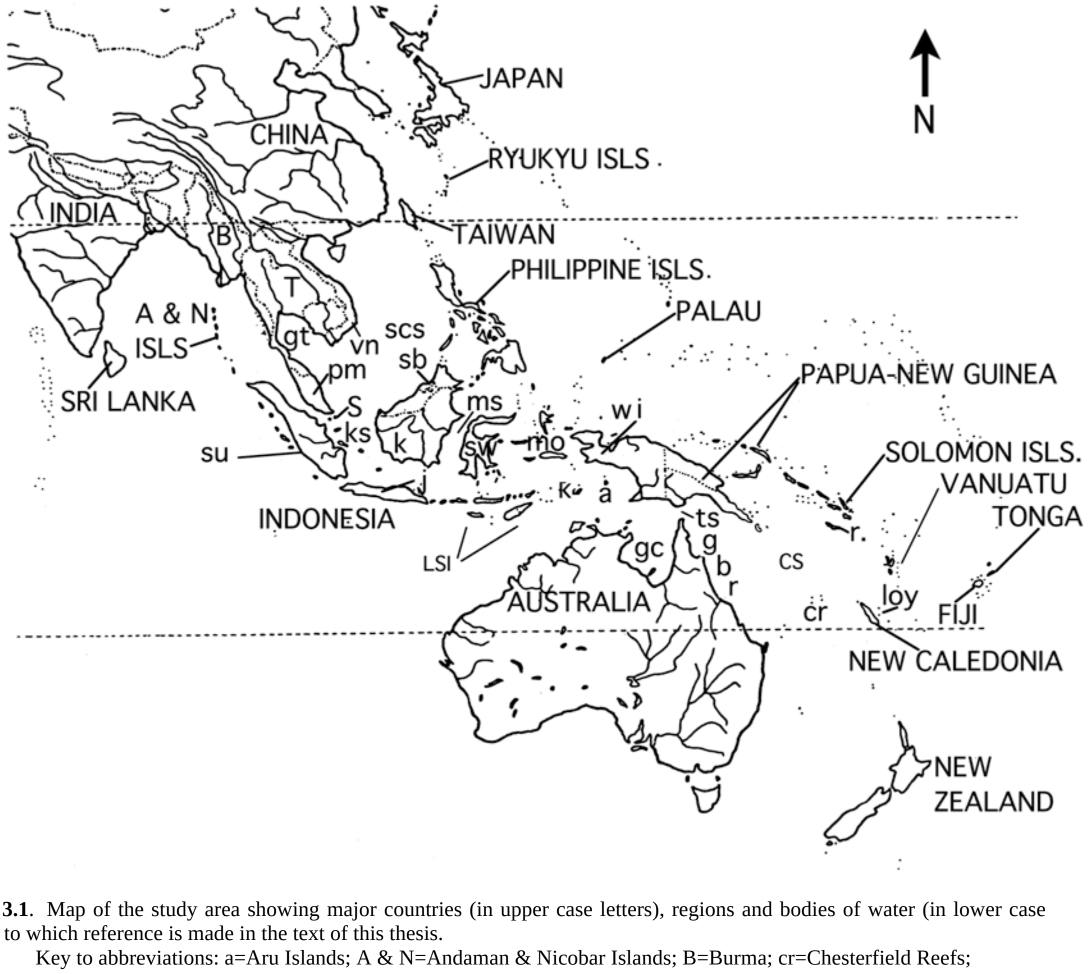


Figure 3.1. Map of the study area showing major countries (in upper case letters), regions and bodies of water (in lower case letters) to which reference is made in the text of this thesis.

Key to abbreviations: a=Aru Islands; A & N=Andaman & Nicobar Islands; B=Burma; cr=Chesterfield Reefs; CS=Coral Sea; gbr=Great Barrier Reef; gc=Gulf of Carpentaria; gt=Gulf of Thailand; k-Kei Islands; ka=Kalimantan (Indonesian Borneo); ks=Karamata Strait; loy=Loyalty Islands; LSI=Lesser Sunda Islands; mo=Moluccas; ms=Makassar Strait; pm=Peninsular Malaysia; r=Rennell Island; S=Singapore; sb=Sabah; scs=South China Sea; su=Sumatra; T= Thailand; ts=torres Straits; VN=Vietnam; wi=West Irian (Irian Jaya). The upper dashed line represents the Tropic of Cancer and the lower one the Tropic of Capricorn.

3.2.1. Laticauda colubrina

Laticauda colubrina has the widest distribution of any species in the complex. Its breeding range extends from the Bay of Bengal (Andaman and Nicobar Islands, Bangladesh and Myanmar), through the East Indian Archipelago and New Guinea eastward to the island-groups of the southwestern Pacific as far as Tonga and Futuna, and northward through the Philippines, Palau and Taiwan to the Ryukyu Islands of southern Japan (Figs. 3.2-3.11). There are a few scattered localities recorded beyond these limits, and their validity is assessed immediately below and in Section 3.3.2.

Mainland China: L. colubrina probably does not occur in the coastal waters of mainland China. A specimen from the imprecise locality of "the China Sea" is old and probably in error (De Rooij (1917) listed China as a locality for *L. colubrina*, but without more specific locality data this record also should be disregarded. More recent general treatments of the Chinese herpetofauna (Hu *et al.*, 1980; Zhao and Adler, 1993) have listed this species only from Taiwan and not from the People's Republic of China.

Mainland of Indian Subcontinent: Although *L. colubrina* has been recorded from the coastal waters of continental India, it is unlikely that it occurs there. Cantor (1847) included "Pondicherry" among the localities of this species and Smith (1926) reported it from Calcutta. The specimens on which those records were based were re-examined for the present study and their identity confirmed. The register of the Indian Museum merely indicates that the Calcutta specimen was purchased there and makes no mention of actual provenance. It could have been brought to that locality by humans and sold, or perhaps it arrived there as a waif and was then captured and sold. In any event, the locality is probably in error.

Modern reviews of Indian herpetology do not include *L. colubrina* in the fauna of continental India. Murthy (1986) listed the Indian distribution for this species as "Bay of Bengal; Andaman and Nicobar Islands". In a checklist, Das (1994, 1996) listed India as included in the range of *L. colubrina* but did not elaborate whether parts of India other than the Andaman and Nicobar islands were indicated. He included Bangladesh in the range of *L. colubrina* and this has been confirmed by a recent unpublished checklist by Khan (undated) who gives a specific locality. Thus, there are no credible records of *L. colubrina* from the mainland of the Indian subcontinent; small islands off the coast of Bangladesh seem to be the westernmost limit of its breeding range. Old records from continental India probably arose from error introduced after specimens were catalogued, labeling specimens from islands of the Bay of Bengal with the more general locality of India, and/or citing the locality as the port from which the specimens were dispatched, rather than where they were collected. The possibility that some specimens may represent waifs dispersed westward from the breeding range, however, cannot be ruled out (see Section 3.3.2).

Reviews of the Sri Lankan sea snake fauna make no mention of *Laticauda* (de Silva, 1994, 2001).

Indochinese Peninsula: A record from the ‘Gulf of Siam’ (=Gulf of Thailand) seems to be in error. In reference to that specimen, Colin McCarthy (personal communication) stated:

> "I have looked at the original register entry and find that a very mixed batch of reptiles and fish were donated at that time by 'The Admiralty through Sir J. Liddell from the voyage of the Herald'. The localities for this material include 'S. Cristoval Id., C. G. Hope and Rio de Janeiro.' 'Gulf of Siam' is written in once for a *Pelamis* (56.7.7.29), the line below this (i.e., the line referring to the *L. colubrina* specimen in question) is blank, there are no ditto marks, so I would regard this evidence as shaky. Two early labels on the bottle itself carry the identification *'Platurus laticauda*tus' and give the locality of 'Gulf of Siam'. There is a later label, in Boulenger's handwriting, merely with '? *Platurus colubrinus'*. I note neither Boulenger cites the specimen in his catalogue nor does Smith in his monograph. Perhaps one reason for this is that they both had doubts about the locality? I note the specimen was retrieved from the 'duplicate collection' on 24th March 1970. Specimens tended to be placed in the duplicate collection by Boulenger and others when there was some doubt concerning provenance."

Thus, it is questionable whether this specimen came from the Gulf of Siam, or even from Thailand at all. Voris and his colleagues have carried out extensive ecological studies on marine snakes in the Gulf of Thailand and have never found *Laticauda colubrina* there (Harold Voris, personal commmunication), nor are there any specimens of this species from that locality in the National Science Museum in Bangkok (Tanya Chanard, personal communication). Murphy *et al.* (1999) do not include any *Laticauda* in their key to the sea snakes of the Gulf of Thailand. Tu (1974) collected over 14,000 specimens of sea snakes from the Gulf of Thailand and found no *Laticauda*. Thus, *L. colubrina* probably occurs in Thailand only on the western coast (Andaman Sea and Strait of Malacca).

Bourret (1936a,b) included *L. colubrina* in the fauna of the Indochinese

Peninsula without reference to specimens or to specific localities other than “Siam” (both north and south of the Isthmus of Kra) and “southern Indochina”. His authority for these inclusions is not clear. Kharin (1984b) reported the only specimen of *L. colubrina* known from Vietnamese waters. Without verification of a breeding population, this individual may merely have been a waif.

Indonesia and Papua New-Guinea: L. colubrina is widespread in Indonesia and Papua-New Guinea. There are some localities, however, that are problematic; those are noted by Heatwole *et al*. (2005).

Japan: The record for *L. colubrina* from Nagasaki, Japan, almost certainly represents a stray individual or is an error. Toriba (1994) in a review of Japanese sea snakes indicated that this species is mainly confined to the Miyako and Yaeyaema island groups in the southwestern part of the Ryukyu Archipelago (also called the Loo Choo islands).

Australia: The records from Australia almost certainly represent waifs rather than breeding populations. The two specific localities, Green Island and Bondi Bay are both heavily populated areas and the waters are well known. It is highly unlikely that an undiscovered breeding population of sea kraits could occur in either area. Consequently, Australia is considered extralimital to the range of *Laticauda.*

Futuna and other Pacific Islands: Only one specimen of *L. colubrina* is available from "Futuna". There are two islands named Futuna in the southwestern Pacific. One (also known as Erronan) is located just east of Tanna Island in Vanuatu, the other in the French possession of Wallis and Futuna Islands (Anonymous, 1992). The data accompanying the specimen did not allow further identification of its provenance and consequently it was excluded from statistical analysis. In 2008, several divers found a live adult female *L. colubrina* while diving on a reef at Futuna of the Wallis and Futuna Islands. I observed it at length at close range (< 0.5 m) and positively identified it as *Laticauda colubrina* (Heatwole, in preparation). The specimen could not be collected because of lack of a collecting permit. This sight record represents a northeastward range extension of 250 km from Fiji or about the same distance northwestward from Niuafo'ou in the Tonga group.

Pacific Islands: Records of *L. colubrina* from several Pacific Islands further east are considered erroneous or perhaps representing waifs.

Overview: It thus appears that the coastal waters of mainland southeastern Asia (People's Republic of China, the Indochinese Peninsula, Gulf of Thailand) are devoid of established populations of *L. colubrina*; only in peninsular Malaysia, the Andaman (western) coast of Thailand, Myanmar and Bangladesh does this species inhabit the coastal waters of the Asian mainland, and even there the precise locality records are from small offshore islands rather than from the mainland itself. Otherwise, *L. colubrina* is widely distributed within its archipelagic range, not only in general, but also within each of the various island groups. There are, however, notable distributional gaps within the archipelagos (see Figs. 3.2-3.11): (1) central Indonesia (eastern Sumatra, most of Java, Kalimantan and most of Sulawesi), (2) the central portion of the southern coast of the island of New Guinea, and (3) the northern and eastern coasts of Australia, including the Great Barrier Reef, and extending to and including the Chesterfield reefs northwest of New Caledonia. Collecting has almost certainly been incomplete in some regions and some absences may reflect that. However, other areas such as the Chesterfield Reefs (Minton and Dunson, 1985) and the various waters of Australia have been the recipients of careful surveys of sea snakes and either *Laticauda* did not occur (Dunson, 1975; Heatwole, 1975e,f; Limpus, 1975; Minton and Heatwole, 1975; Redfield *et al.*, 1978; Wassenberg *et al.*, 1994) or was represented only by waifs, not established populations (Cogger, 1975, 2000; Cogger *et al.*, 1983; Heatwole and Cogger, 1994).

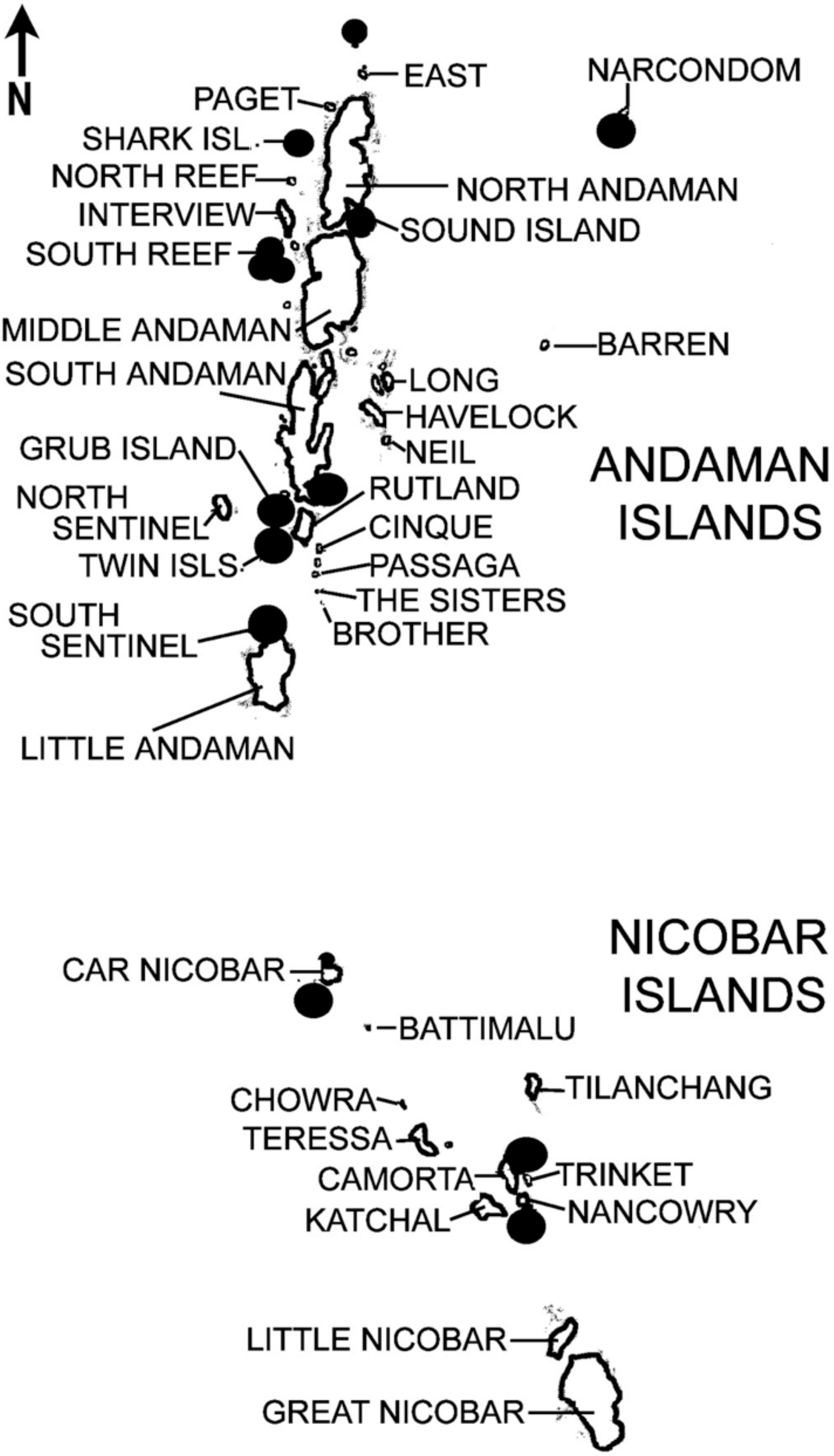


Figure 3.2. Map showing known localities (dots) for *Laticauda colubrina* in the Andaman and Nicobar Islands. Stippled areas indicate coral reefs.

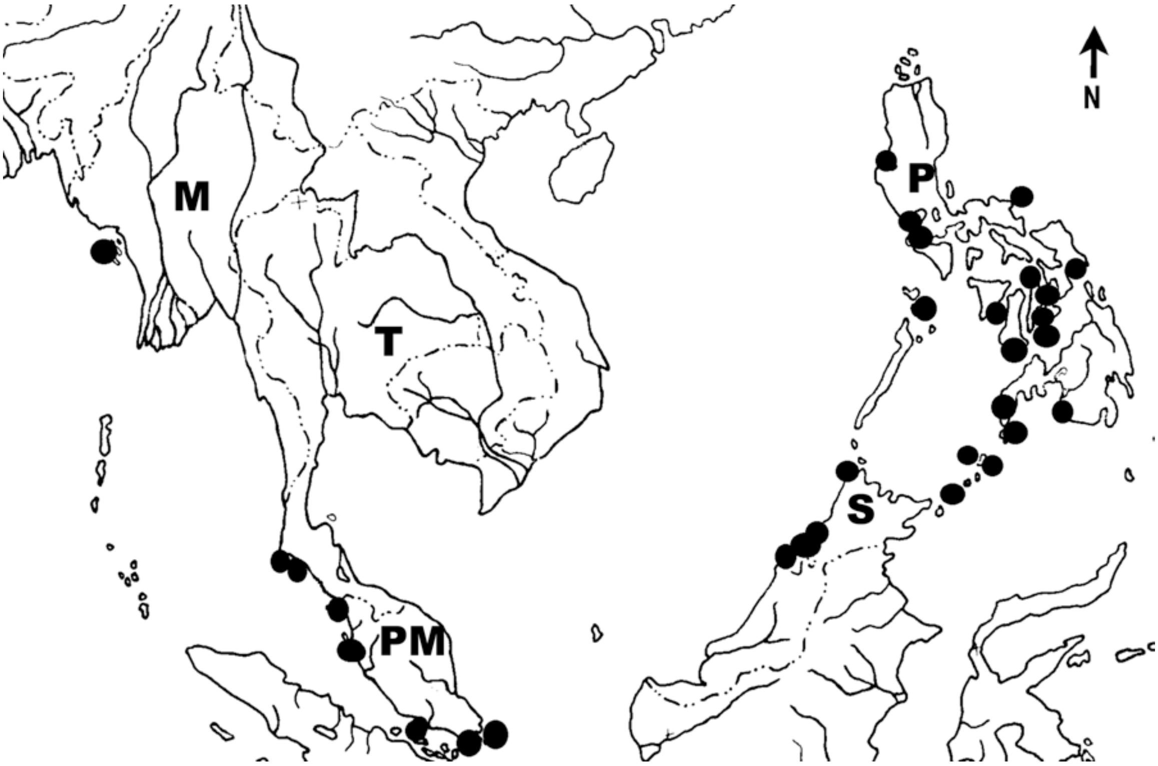


Figure 3.3. Map showing the known localities (dots) for *Laticauda colubrina* in coastal southeastern Asia. M=Myanmar (Burma); T=Thailand; PM=Peninsular Malaysia; S=Sabah; P=Philippine Islands.

Figure 3.4. Map showing the known localities (dots) of *Laticauda colubrina* in Indonesia and neighbouring countries to the north (overlaps with Figure 3.3). T=Thailand; MP=Peninsular Malaysia; SU=Sumatara; J=Java; LS=Lesser Sunda Islands; K=Kalimantan; SA=Sabah; C=Sulawesi (Celebes); M=Molucca Islands; WI=West Irian.

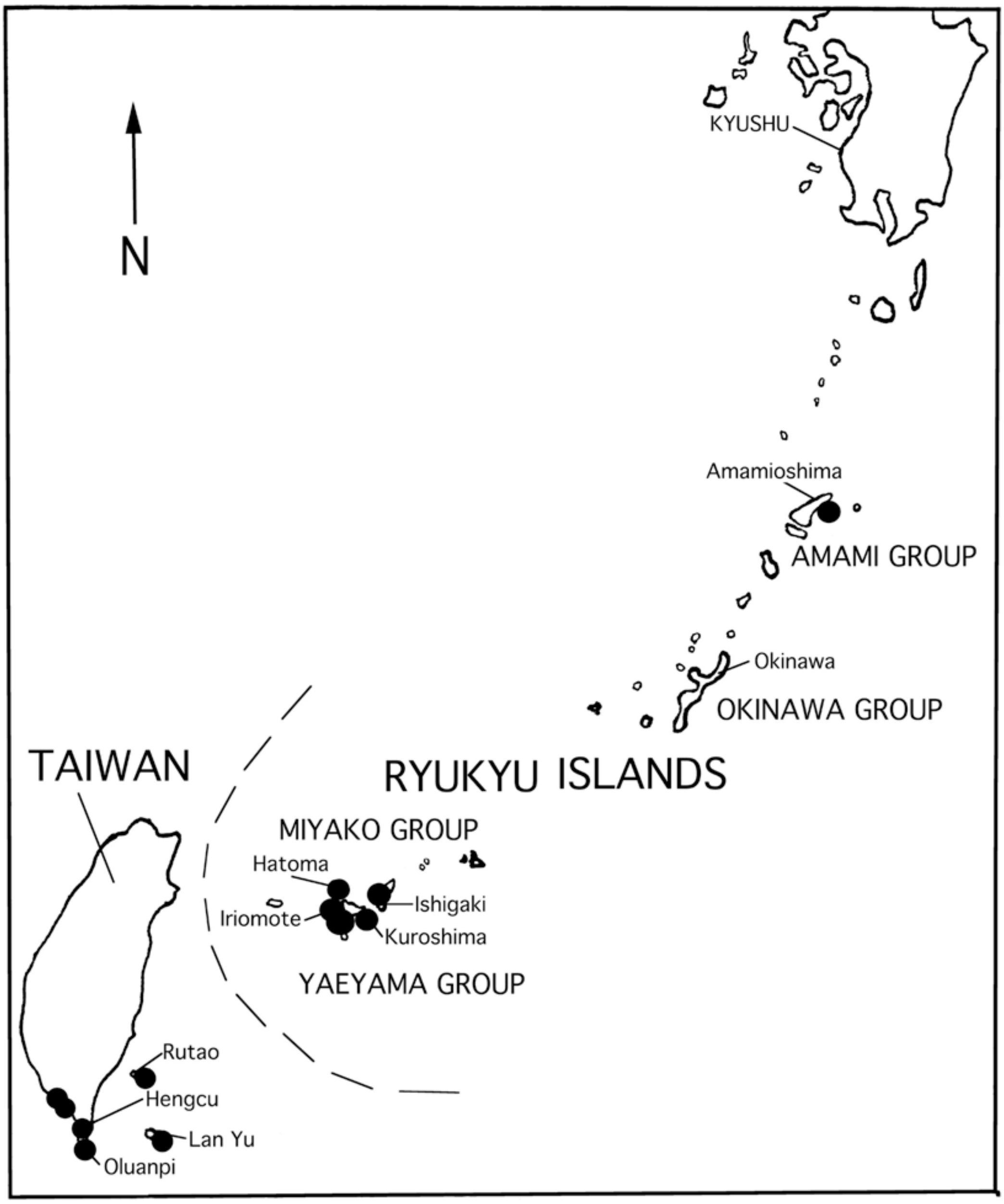


Figure 3.5. Map showing the known localities of *Laticauda colubrina* in Taiwan and the Ryukyu Islands.

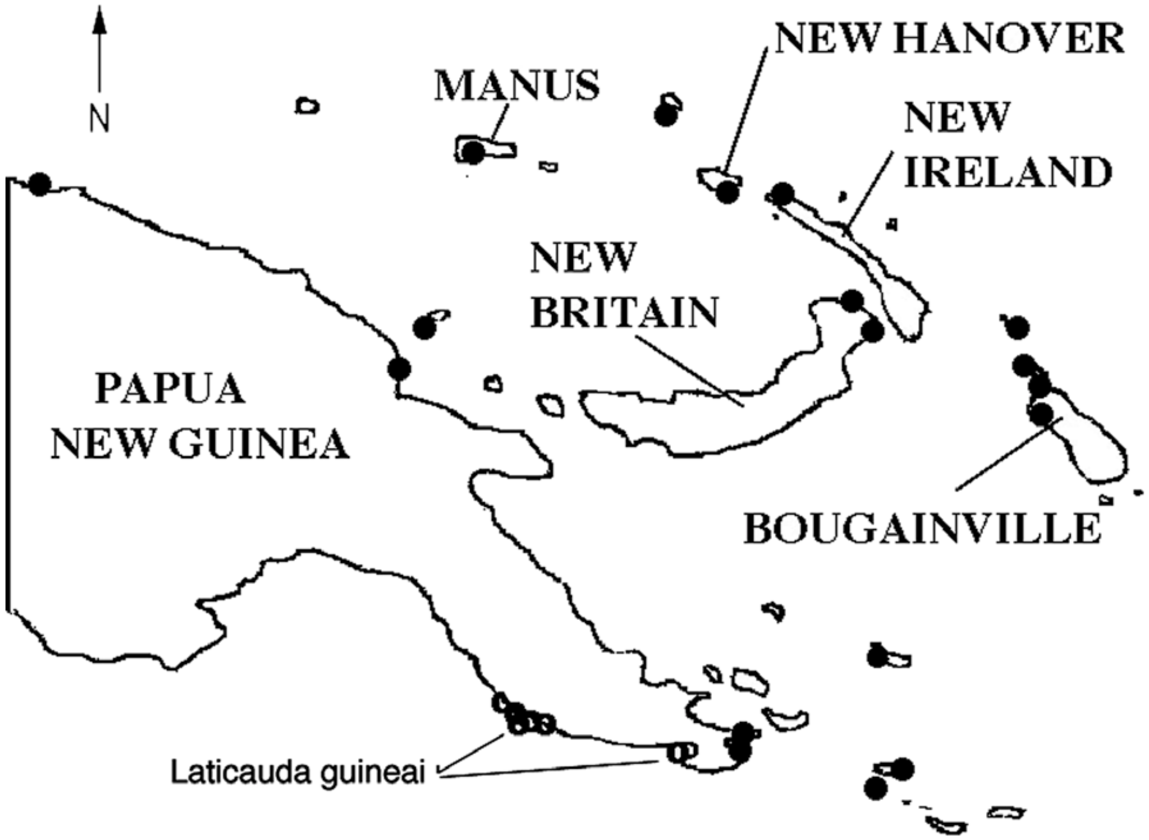


Figure 3.6. Map showing the known localities for *Laticauda colubrina* (dots) and *Laticauda guineai* (circles) in Papua-New Guinea.

Figure 3.7. Map showing the known localities for *Laticauda colubrina* (dots) in the Solomon Islands.

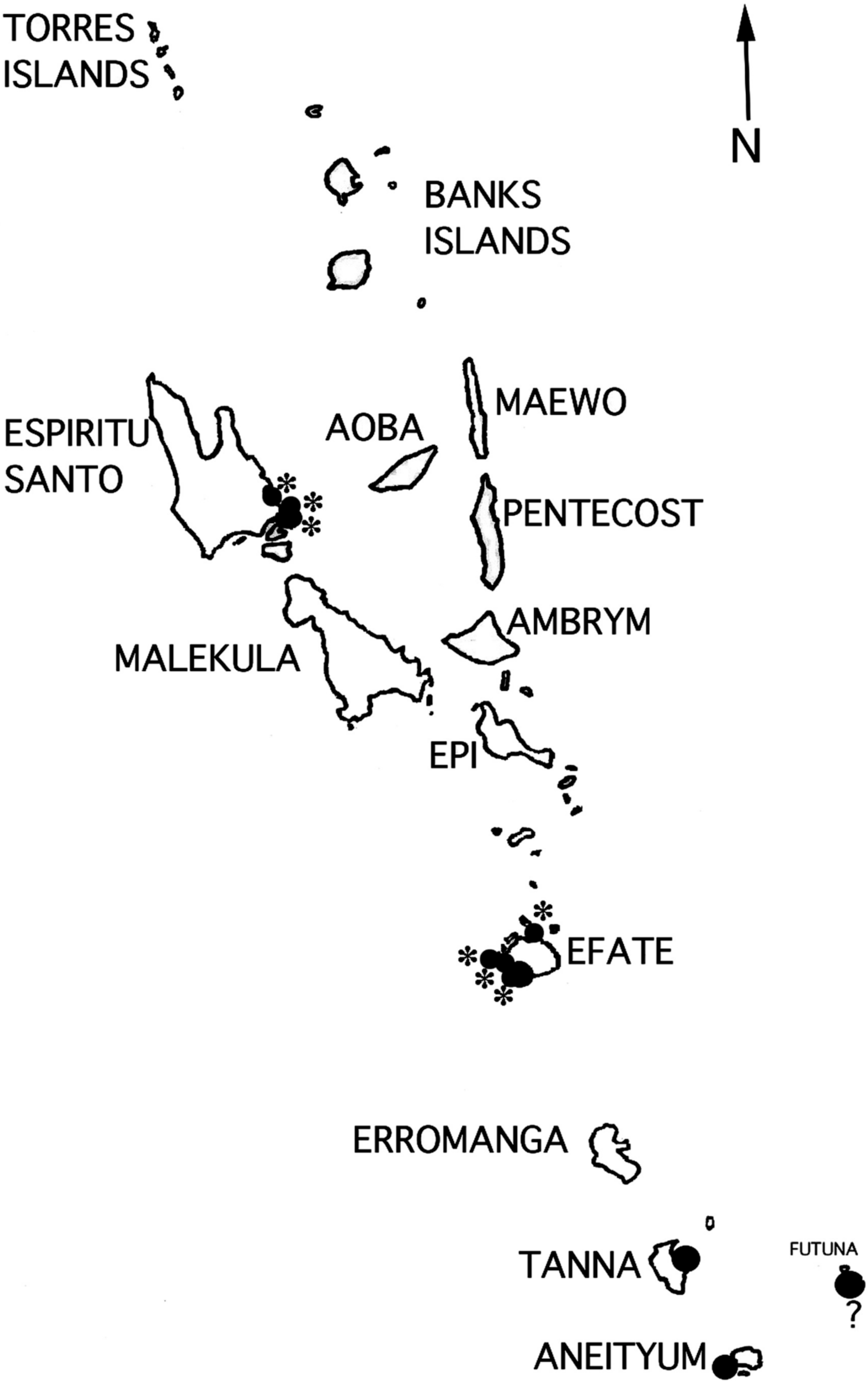


Figure 3.8. Map showing the known localities for *Laticauda colubrina* (dots) and *Laticauda frontalis* (*) in Vanuatu.

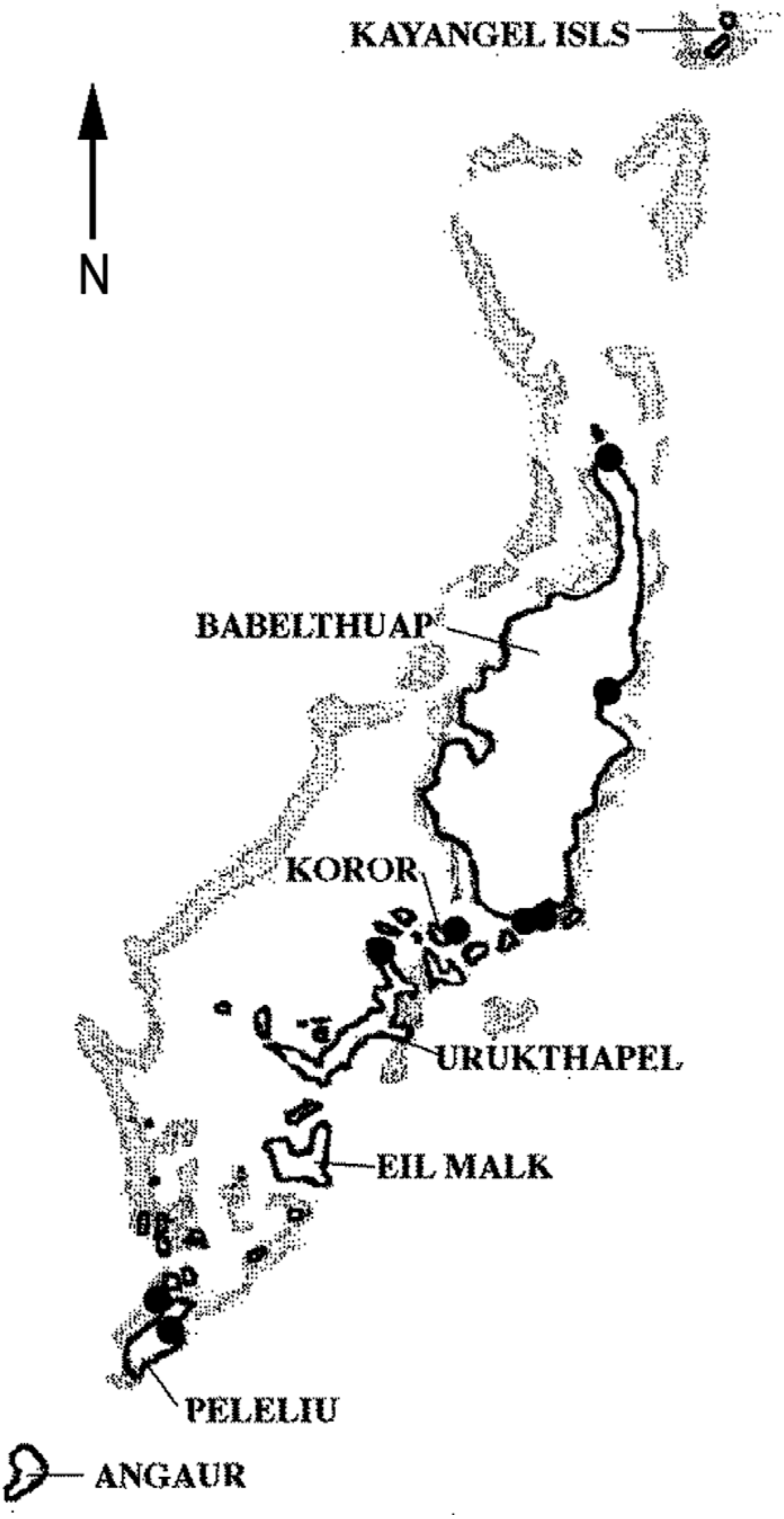


Figure 3.9. Map showing the known localities (dots) for *Laticauda colubrina* in Palau. Gray areas indicate coral reefs.

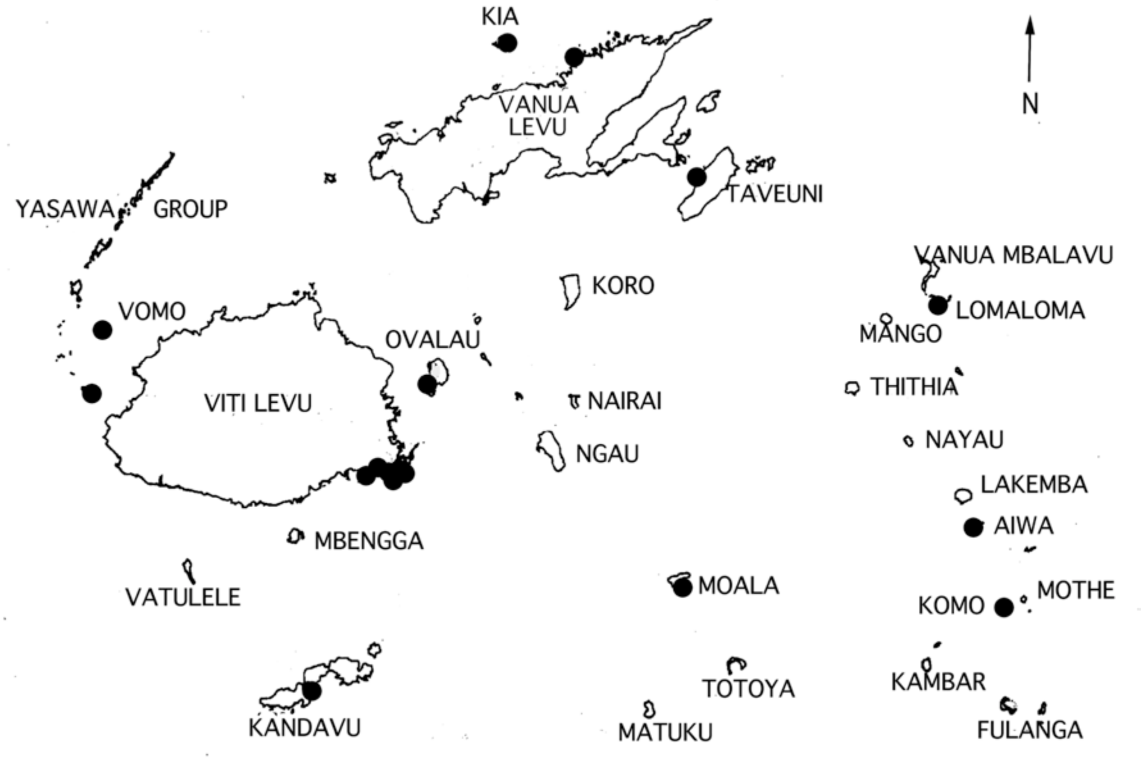


Figure 3.10. Map showing the known localities of *Laticauda colubrina* in Fiji.

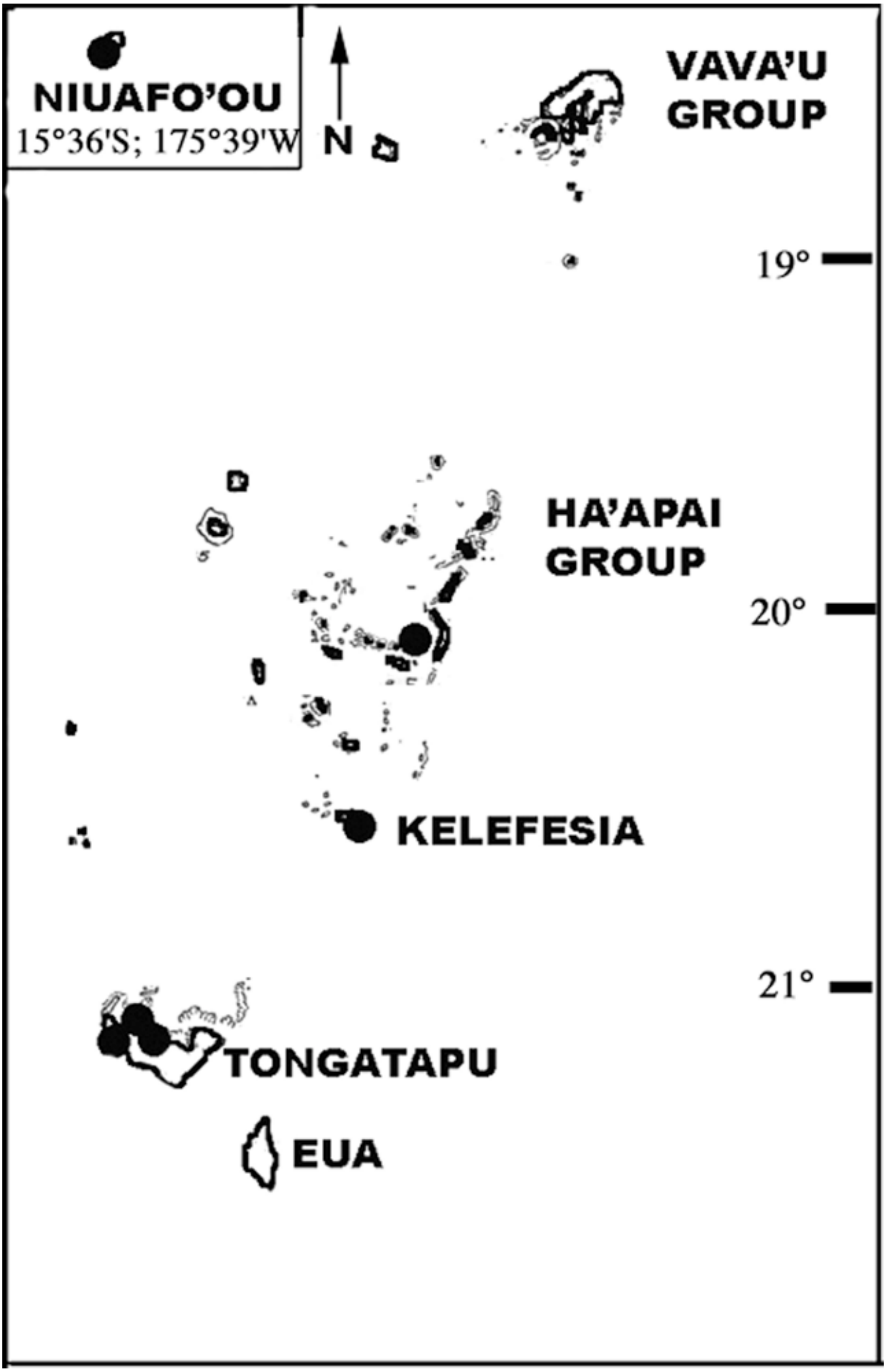


Figure 3.11. Map showing the known localities (dots) for *Laticauda colubrina* in Tonga. Coral reefs are outlined in lighter lines. Inset shows the island of Niuafo'ou from farther north.

3.2.2. Laticauda saintgironsi

Laticauda saintgironsi has a more limited distribution than does *L. colubrina* and is known only from New Caledonia and the Loyalty Islands (Fig. 3.12), except for one specimen each from India, New Zealand, and the Caroline Islands.

The Indian locality was “Malabar”. Malabar could refer either to the vicinity of Bombay (Mumbai) or to the Malabar Coast further south on the western coast of India. The locality is likely in error (see Section 3.3.2). The specimen from New Zealand is likely a waif and the one from the Caroline Islands probably an error (see Section 3.3.2).

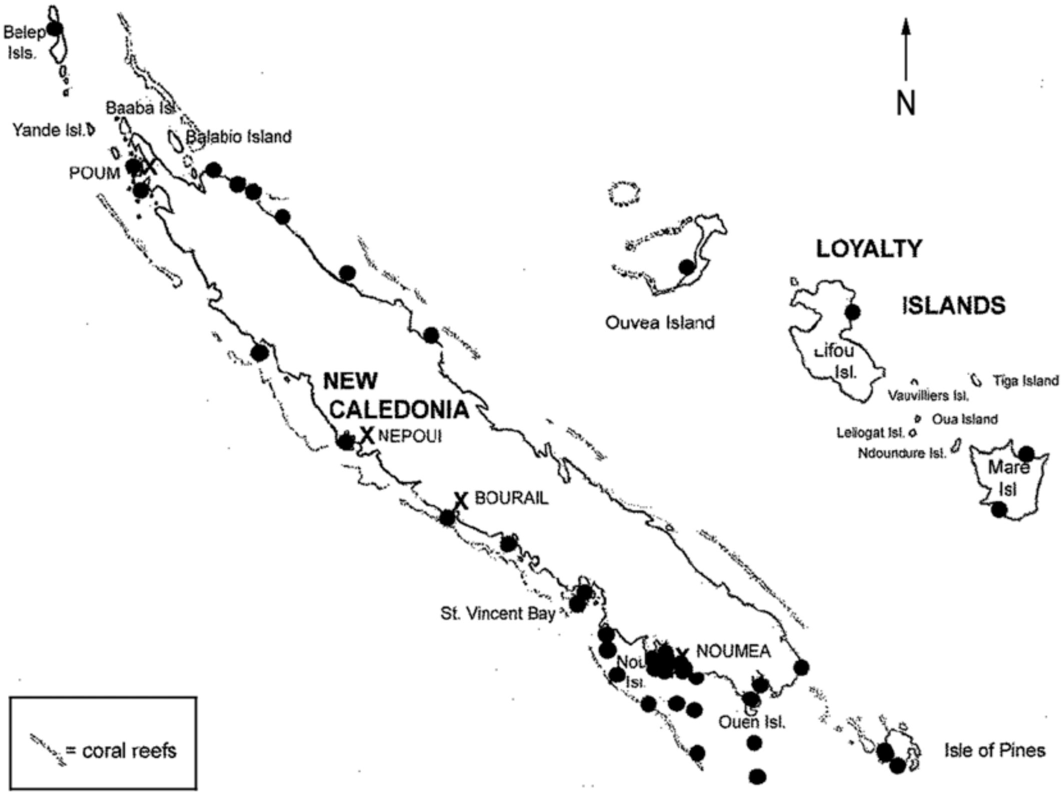


Figure 3.12. Map showing the distribution of *Laticauda saintgironsi* (dots) in New Caledonia and the Loyalty Islands. X indicates a city.

3.2.3. Laticauda frontalis

Laticauda frontalis occurs most commonly in Vanuatu, but is less abundant there than is *L. colubrina*. It also has small outlier populations, or waifs, represented in the Loyalty Islands and perhaps in New Caledonia (the sole specimen listed with the provenance of New Caledonia only had the country designated as the collection locality and hence it may have originated from the Loyalty Islands, rather than from the main island of New Caledonia itself) (Heatwole *et al*. 2005). There are also two extralimital records from Papua-New Guinea, one of which is the type specimen.

3.2.4. Laticauda guineai

Laticauda guineai was recently described by Heatwole *et al.* (2005). Its distribution is southern Papua New-Guinea.

3.3. Factors Affecting Distribution

All species' geographic distributions reflect the (1) taxon’s history as well as a composite of (2) tolerance levels of present physical environmental conditions, (3), behavioural responses to the characteristics of the habitat (habitat selection), (4) ability either to successfully compete with other species, or to circumvent such competition, (5) avoid excessive predation, and (6) competence in dispersing to new sites where environmental requisites can be fulfilled. These influences on the distribution of the *L. colubrina* complex are discussed in turn.

3.3.1. Relation to Climate: Geographic Information System (GIS) Analysis

The *Laticauda colubrina* complex is distributed symmetrically around the equator within the tropics and subtropics (Fig. 3.1). Although this symmetry also applies to surface temperatures of the sea in the sense that mean values at all times of year are higher in a central band along the equator and decline toward both the northern and southern limits of the range of sea kraits (Fig. 3.13), a major asymmetry occurs. During the coolest times of the year in the north (Fig. 3.13 upper right and lower left) cold water extends through the Sea of Japan, along the Korean Peninsula, into the Yellow Sea and southward into the East China Sea and finally as a narrow coastal tongue between the mainland Chinese coast and Taiwan. The presence of this seasonally colder water may be the reason why *L. colubrina* only is found on the milder seaward side of Taiwan and not on the western side facing the mainland. This cool water is in close proximity both to the Taiwanese and the Ryukyuan populations and may well limit their expansion to the northwest. At its southern limits this cold water does not exend far seawards and in fact, both the Taiwanese and Ryukyuan populations lie in an area of milder maritime conditions to the north of the maximum southward penetration of this tongue of cold water. Cool water, however, does not explain failure of these northern populations to spread toward the northeast along the southeastern coast of Japan as at all times of year the mean SST there is similar to that occurring in the Ryukyus and eastern Taiwan (Fig. 3.13). That explanation lies elsewhere (see Section 3.3.2).

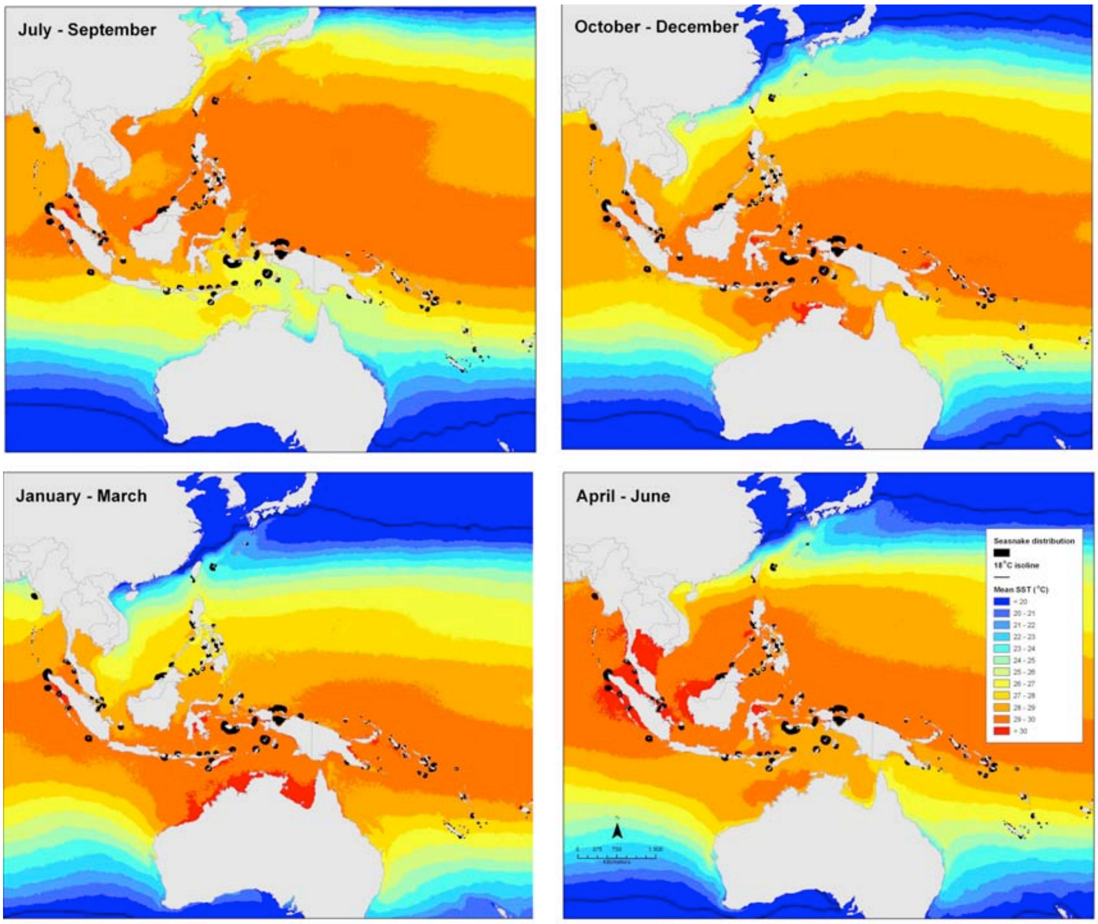


Figure 3.13. Mean surface temperatures of the sea (SST) for different times of year over the geographic range of the *Laticauda colubrina* complex. Black line is the 18°C isotherm. Thermal data from NOAA’s National Oceanographic Data Center, Satellite Oceanography Group (http://nationalatlas.gov).

There is no comparable body of cold water at the southern edge of the range of the *L. colubrina* complex. There the mean sea temperatures during the coolest periods are within the range experienced by the snakes at other times of year (Fig. 3.13). This does not mean that temperature does not limit the distribution of sea kraits in the south, however. Dry land is also a habitat requirement of snakes in the *L. colubrina* complex and the nearest land to the south is New Zealand, which has cooler water surrounding it at least part of the year (Fig. 3.13 bottom). Waif sea kraits come ashore on the New Zealand coast from time to time (see Section 3.3.2) so they are clearly capable of reaching there, yet they do not establish breeding populations. It is likely that lack of land with a suitable year-round temperature is the limiting factor to southward range extension of sea kraits.

The hypothesis of thermal limitation needs to be evaluated from the physiological standpoint. It may not be a simple matter of thermal tolerances, although that should be tested. Dunson and Ehlert (1971) found that the sea snake, *Pelalmis platurus,* appears as live waifs in cool areas, distant from their breeding range, but that the cooler limits of their breeding range is closely confined by the 20° C isotherm of sea temperatures. They suggested that reproduction did not occur below about 20° C and that temperature lower than that at Cape Horn and the Cape of Good Hope was the reason sea snakes have never been able to penetrate the Atlantic Ocean. They found that individuals could survive lower temperatures at least briefly, e.g., >19 days at 15.9-16.6°, 11.5 days at 14.0-14.8°C. The upper tolerance limit of this species lies between 33.2° C and 33.6° C. Thus, their lower thermal limit for indefinite survival must be between 20°C and 17°C (shown as the 18°C isotherm on Figure 3.13).

L. colubrina is likely to be more eurythermic as part of the time it occupies terrestrial habitats where temperatures fluctuate through a wider range than those of the sea's surface. Nevertheless its northern boundary is largely circumscribed by the 20° C isotherm of the cooler months (Fig. 3.13). It occurs in the warmest waters of the region (>30° C; Fig 3.13) so its range does not appear to be limited by high temperatures.

For such a widespread species as *L. colubrina*, it would be worthwhile to investigate whether reproductive cycles are adjusted geographically in ways that avoid breeding during the cooler, less favourable times of year. A species might be able to extend its geographic range into cooler areas where the thermal limits for reproduction were exceeded for part of the year if it altered the timing of its breeding to coincide only with the warmer periods. Some regional, seasonal adjustment has occurred in the *L. colubrina* complex. For example, *L. colubrina* breeds aseasonally (Philippines: Gorman *et al*. 1981; Bacolod, 1983) or twice-yearly (Sabah: Stuebing, 1988) near the central part of its range where mean SST remains at 27°C or higher year round (Fig. 3.13), whereas in Fiji where mean SST seasonally drops several degrees lower (25°C) it breeds only once yearly and then in the warmer months

(Guinea 1981, 1986). An even more peripherally distributed *L. saintgironsi* on New Caledonia oviposits in the austral summer (December to February) (Saint Girons 1964, 1990); it is sedentary during the cold season and its feeding cycle (hunting at sea, followed by digestion on land) then is more than two months in duration.

Temperature may also affect the distribution of sea kraits on a micro-scale. For example, both *L. laticaudata* and *L. saintgironsi* shelter preferentially under rocks of such sizes and at such locations relative to high-tide line that the snakes are buffered against high temperatures, yet remain warm and humid (Bonnet *et al*. 2009).

The relationship of sea kraits' distribution to rainfall is more tenuous than for temperature. The recent finding that sea kraits must drink freshwater in order to keep in water balance (Lillywhite, 2008), suggests that low annual precipitation, or seasonal scarcity of rain might limit their distribution.

Rainfall at sea or on small, low islands often is quite different (usually less) than that on nearby mainlands or large, continental islands and consequently land-based weather stations are a poor guide to rainfall offshore. Most weather stations are located on land and rainfall at sea cannot be assessed via satellites in the same way that temperature can be; consequently, accurate data on rainfall are lacking for many of the small, offshore reefs and islands inhabited by sea kraits and in some cases, data are not even available for adjacent coastal areas. Bearing these limitations in mind, a few very general observations can be made. Precipitation throughout much of the distributional range of the *Laticauda colubrina* complex is as high or higher than for nearby continental areas (Fig. 3.14) and for most localities values are relatively high throughout all four quarters of the year. Some of the insular areas from which sea kraits are not known are also those for which data on rainfall were not available and hence firm conclusions cannot be reached. The present dataset, however, does not demonstrate low rainfall to be a limiting factor for sea kraits and the similarity of precipitation among the four quarters of the year in areas where other factors (e.g. mainland predators or lack of coral reefs; see sections 3.3.3 and 3.3.5) are not limiting distribution suggests that seasonality of rain is not great. What is needed are more detailed and precise data from specific localities, especially for the number of consecutive days without rain. If any locality has bouts of rainlessness that exceeds the maximum time sea kraits can endure without access to freshwater for drinking, then precipitation may be a limiting factor.

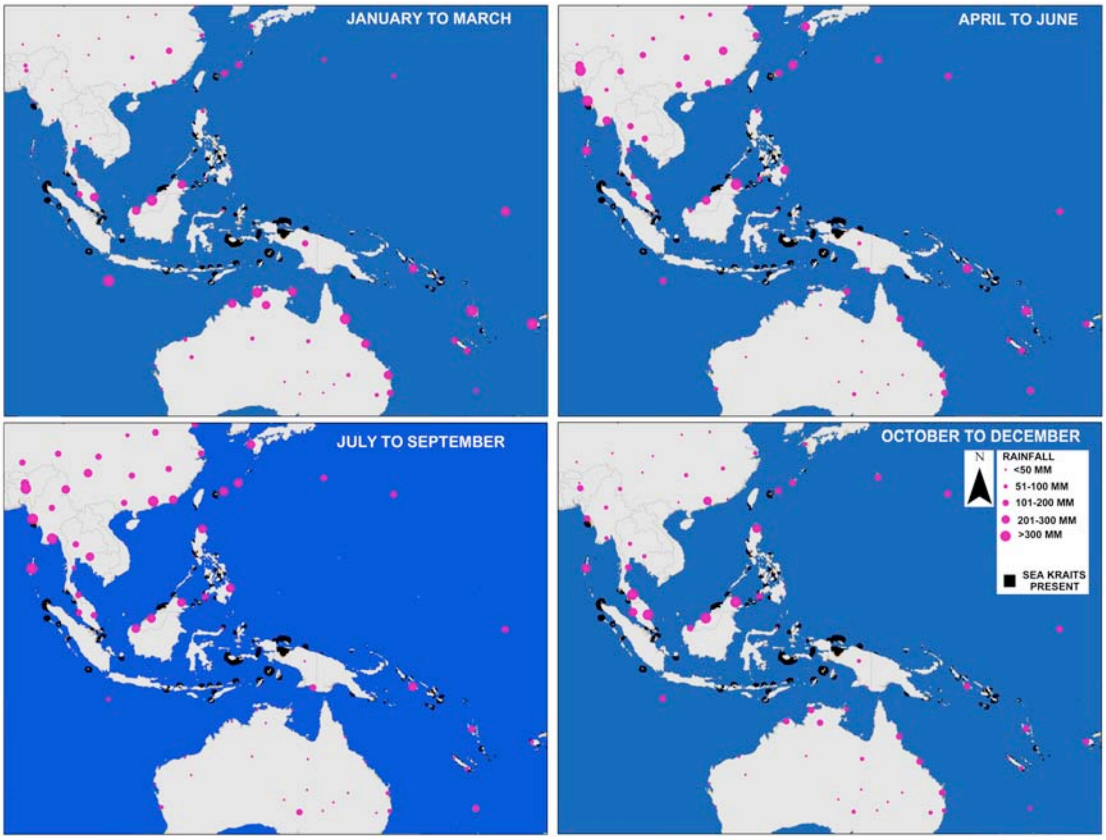


Figure 3.14. Mean quarterly rainfall over the distributional range of the *Laticauda colubrina* complex and adjacent regions for the years 1986 - 2004. Note that mean annual rainfall for a given locality is the sum of the values from these four quarters. Based on data from NOAA's National climatic Data Center (http://gis.ncdc.noaa.gov); see methods (Section 3.1).

Lillywhite *et al*. (2008) showed that the species richness of sea snakes (including oxyuranine sea snakes as well as sea kraits) correlated positively with mean precipitation in tropical Asia and Australasia. Oxyuranine sea snakes would have to depend entirely upon surface films of rain for freshwater whereas sea kraits could go ashore and seek out more permanent. Lillywhite *et al*. (2008) showed that in coastal Taiwan sea kraits are more abundant at localities where there are sources of freshwater such as streams or springs than they are at other nearby locations (also see Section 8.5 for further discussion). The ecology of sea kraits and other marine snakes in relation to water is the subject of a study now in progress by Prof. Harvey Lillywhite and in which I am participating.

3.3.2. Relation to Sea Currents

Stejneger (1907) early noted the likelihood that sea snakes would be borne by currents beyond their natural limits (breeding range). This has likely been the case with the species of the *Laticauda colubrina* complex.

Sea kraits are semi-aquatic and need both terrestrial and marine environments (see Section 1.3). Because of this duality, they are archipelagic to the extent that coral reefs often occur in patches (“islands”) or intermittent strips, and although the sea is not as formidable a barrier to sea kraits as it is to more strictly terrestrial animals, transport by sea currents would be required for dispersal to some areas. Where reefs are more continuous, sea kraits could gradually extend their distribution under their own power along coastal areas.

Specimens of all species of the complex, except *L. guineai*, have been reported from areas extralimital to their known breeding range (see Section 3.2.1), including such distant localities as Central America (see McCarthy, 1986) and even Greece (Steinicke and Trutnau, 1993) (see below).

It is difficult to tell whether seemingly exralimital records represent individual strays, members of small relict populations, far-flung breeding populations established by waifs, or merely specimens mislabeled as to locality. The localities of some specimens are clearly in error and have been discussed in Section 3.2.1; other records may represent waifs and the probable provenances of some were considered on the basis of morphological similarity or Discriminant Function Analysis. The task here is to assess, on the basis of direction of sea currents, the likelihood of waif dispersal for individuals deemed to be extralimital.

The most likely sources of waifs reaching eastern Australia are the islands to the east (Fiji, Tonga, Vanuatu) because of their proximity and their location upstream of major currents directed toward Australia. This interpretation is supported by the Discriminant Function Analysis. Waif dispersal to Australia probably occurs episodically as the known specimens span a period of 91 years.

The record from Nagasaki, Japan, is possibly a waif as the area is well populated by people and well studied and no further specimens have emerged. Taiwan is the likely provenance as the Kuroshio Current sweeps from the islands off Taiwan's southeastern coast, where *L. colubrina* occurs, to Nagasaki; this suggestion is supported by morphological data. The Ryukyus are a less likely provenance as the Kuroshio Current eddies southward from Japan to these islands, i.e., in the wrong direction (Fig. 3.15).

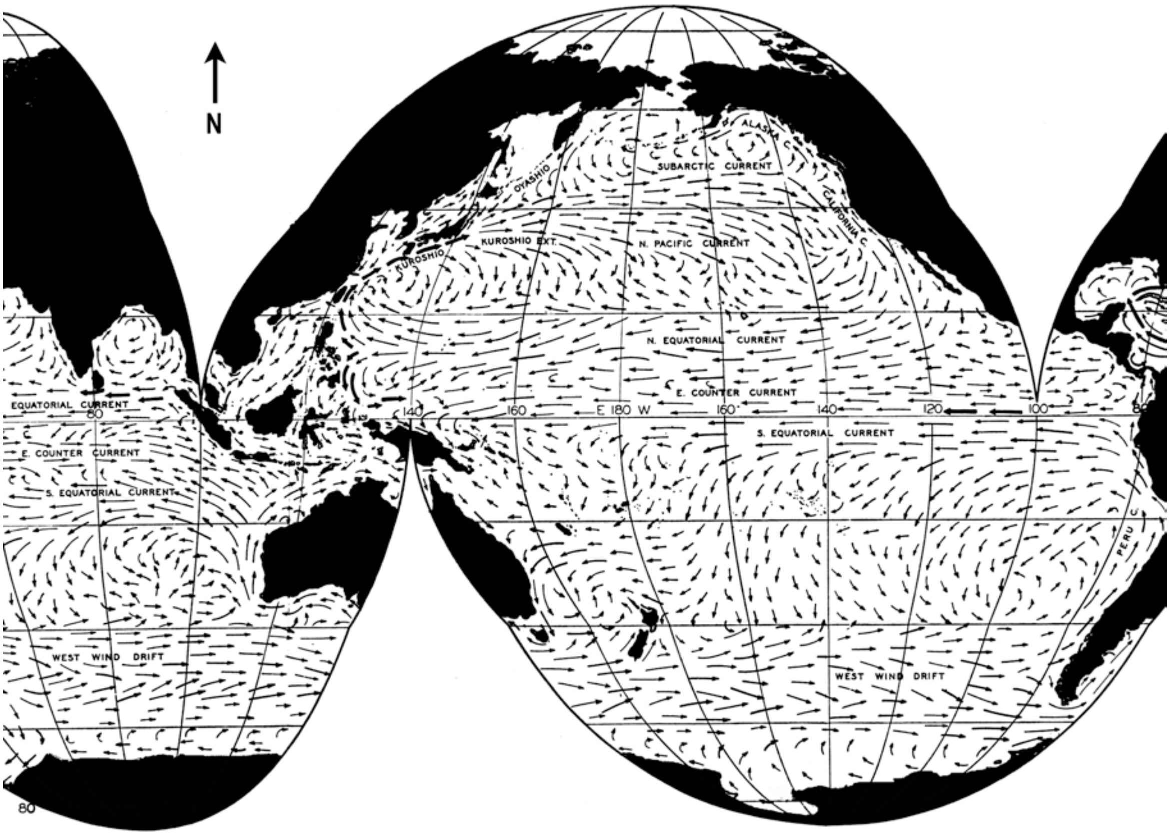


Figure 3.15. Surface currents of the Pacific Ocean and part of the Indian Ocean during the months of February and March. Modified from Sverdrup *et al*. (1942).

The likely provenance of the Vietnamese specimen, if indeed it is a waif, is Taiwan from which a current flows directly to Vietnam (Fig. 3.15). This provenance is supported by morphological data. A locality of "China Sea" is believed to be in error.

Dispersal of a waif *L. colubrina* to Pondichery on the eastern coast of India could occur as currents go directly there from the Andaman Islands (Fig. 3.15). However, the colour pattern and scutellation of this specimen militated against such an interpretation (Heatwole *et al*., 2005); similarly, currents are such that waifs could be carried to Calcutta but morphological evidence was equivocal as to the provenance of the specimen purported to have come from there and waif dispersal is questionable. The other “Indian” localities were not likely to have been reached by dispersal via sea currents; morphological analysis did not provide clear indications of provenance (Heatwole *et al*., 2005).

The dispersal of of *L. saintgironsi* to Malabar, India, from New Caledonia is highly unlikely, not only because of the great distance involved, but because the sea currents militate against such a voyage (Fig. 3.15).

Finally, one *L. saintgironsi* almost certainly was collected in New Caledonia, not Malabar.

A few specimens of *L. colubrina* have been purported to be from Pacific Islands. Ponape in the Caroline Islands lies just downstream along the East Counter Current from Palau (Fig. 3.15) and might receive waifs from that source, or even perhaps from the more distant Philippines. However, there does not seem to be a breeding population in the Carolines. The more distant Pacific islands such as the Society Islands and the Marquesas lie in the south central Pacific, well beyond the path of any currents likely to bear waifs of *Laticauda* (Fig. 3.15). It is likely that the Central Pacific records are erroneous (Heatwole *et al.*, 2005).

Dispersal of *L. saintgironsi* to Ponape, Caroline Islands, is less likely than for *L. colubrina*. Although sea currents are appropriate for transporting animals from New Caledonia as far as Papua-New Guinea, from there on dispersal would be curtailed by a southward deflection of the South Equatorial Current along the Papuan coast, and by East Counter Current further north (Fig. 3.15). Thus, the accuracy of the record of this species at Ponape is in question.

Laticauda colubrina have been reported from four countries in Central America. Villa (personal communication to McCarthy; see McCarthy [1986]) reported this species from El Salvador. Villa (1962) also examined two specimens captured in Nicaragua in 1956 and 1959. Specimens on which these records were based are no longer available (McCarthy, 1986), but the animals from Nicaragua clearly were snakes, not banded eels, as Villa mentioned gastrosteges similar to those of land snakes, and enlarged scales on the head. Some aspects of their scutellation corresponded to that of *L. colubrina* but others did not, nor did the combination of characters he reported conform to any other known species of *Laticauda* or even to any other species of sea snake (Heatwole *et al.*, 2005).

Alvarez del Toro (1982) reported *L. colubrina* from Chiapas, Mexico. He did not collect specimens but indicated that on two occasions he saw examples for sufficient time to identify them; both were near the mouths of estuaries and one escaped by swimming into deeper water. Villa in a personal communication to McCarthy (see McCarthy, 1986) later expressed doubts as to the authenticity of the Central American records for *L. colubrina*.

The only still-extant specimen of *L. colubrina* purportedly from Central America is the one from Guatemala examined for the present study. Wermuth and Schluter in a personal communication to McCarthy (McCarthy, 1986) considered the provenance of this specimen doubtful.

A strong current passes southward by the Philippines to northeastern Indonesia before becoming the Equatorial Counter Current directly crossing the Pacific to impinge upon the coasts of Central America and Mexico before again turning back into the Pacific (Figs. 1.3, 3.15). Thus, the most likely points of origin of waifs dispersed by currents to Central America would be the Philippines, northeastern Indonesia, or Palau. The colour pattern and scutellation of the Guatemalan specimen and the Discriminant Function Analysis indicated possible provenance from several widely spaced localities and was inconclusive (Heatwole *et al*., 2005). In fact, the Guatemalan specimen seemed to have a greater affinity with populations from an area from which dispersal by sea currents is highly unlikely than it does with those from localities upstream of currents leading to Central America; consequently, this specimen may represent a mislabeling; the collector is unknown. At the present time, it cannot be conclusively demonstrated that *Laticauda colubrina* or indeed any species of *Laticauda* has reached Central America. However, Villa's (1962) and Alvarez del Toro's (1982) records do indicate that some marine snake with a banded colour pattern similar to that found in the *Laticauda colubrina* complex occurs (or occurred) there. Villa indicated: "La coloración está compuesta por bandas amarillas, a veces muy pálidas, que alternan con bandas negras or café oscuras. La cabeza es negra con una banda amarilla en la nuca." [The colouration is composed of yellow bands, at times very pale, that alternate with black or dark coffee-coloured bands. The head is black with a yellow band on the neck], and Alvarez del Toro stated: "el color consiste en una serie de anillos negros y amarillos" [the colour consists of a series of black and yellow bands]. The light bands of species in the *Laticauda colubrina* complex span a variety of colours, including yellowish (see Section 2.2.1). *L. colubrina* has a yellow lip (not mentioned by either Villa or Alvarez del Toro), but not a yellow band on the neck. The Central American records of a banded sea snake probably refer to breeding populations, albeit perhaps locally restricted ones, rather than merely to individual waifs dispersed from elsewhere, as local fisherman in both Chiapas and Nicaragua were sufficiently familiar with them to have given them a name, "coral marino" [marine coral snake] in Chiapas, and "serpiente de mar anillado" [banded sea snake], "coral de mar" [coral snake of the sea], or simply "culebra de mar" [sea snake] in Nicaragua. The descriptions of these snakes indicate they are sufficiently distinct that they would not be confused with *Pelamis platurus*, the only other sea snake known from the area. Whether the taxon represents a new species of *Laticauda* derived from waifs dispersed across the Pacific, or is related to some other group of sea snakes, or even locally derived from a terrestrial ancestor, awaits collection of appropriate specimens.

There is a single record of a specimen of *L. colubrina* from the Mediterranean. Steinicke and Trutnau (1993) observed a live individual on the northern coast of the island of Korfu, Greece, and photographed it; their description and the photograph leave no doubt as to its identity. This occurrence almost certainly represents deliberate transport by humans.

Laticauda is known from New Zealand as waifs (McCann, 1966a,b; Gill, 1997). These were repeated events as seven records were obtained over the course of 116 years (Gill, 1997). Of those seven records, five specimens are still extant. Their identity was confirmed as *L. colubrina* on the basis of data supplied by Brian Gill and Raymond Coory (personal communications). The number of dark bands on the body ranged from 27 to 30, making their most likely provenance Fiji or Tonga (see Section 4.3.3). In addition, the present study uncovered one specimen of *L. saintgironsi* from New Zealand, with an obvious provenance of New Caledonia.

McCann (1966a) and Gill (1997) considered the dispersal of marine reptiles (as well as some species of fish) to New Zealand to be via the East Australian Current that flows southward along the eastern coast of Australia, east across the northern Tasman Sea, then southeast along the edge of the northeastern continental shelf of New Zealand's North Island. Gill argued that the scarcity of *Laticauda* in New Zealand waters, as opposed to sea turtles and the sea snake *Pelamis platurus*, was that the likely path of drift proceeds from New Caledonia (for *L. saintgironsi*) or from Vanuatu, Fiji or Tonga (for *L. colubrina*) westward toward Australia and from thence to New Zealand via the East Australia Current (Fig. 3.15). At least some of the *L. colubrina* waifs survived the trip in good condition as after arrival they traveled some distance inland; they were recorded variously as ashore alive "60 m from the sea", "some distance from the sea", "well above high tide line", and "adjoining the Waihou River 44 km in a straight line from its mouth (longer along its meandering course)". Credence is given to Gill's proposed route by the occurrence of a waif at Bondi in

New South Wales, Australia (Heatwole *et al*., 2005).

It is clear that sea kraits are continually dispersing long distances over water. Even after eliminating possible errors from mislabeled specimens, there remains a body of evidence that sea snakes repeatedly appear as naturally dispersed waifs considerable distances from their source. Accordingly, the direction of sea currents must be taken into account in any consideration of the biogeography of sea kraits (see Section 8.4).

Sea currents possibly preclude sea kraits reaching certain areas where reefs occur. A current sweeps along the western and northern Australian coast with branches toward Indonesia and thus dispersal from Indonesia toward western and much of northern Australia would be against the current, an unlikely event (Fig. 3.15). The only potential source of *L. colubrina* upstream of the currents presently sweeping southward along the coasts of southeastern Asia consists of a few small populations in southern and southeastern Taiwan; however, these are located such as to be more likely caught up by offshore currents flowing northward from the eastern Philippine coast than by southerly inshore currents along the Asian mainland (Fig. 3.15). Thus, to reach the Gulf of Thailand and the southeastern Asian coast, dispersal would have to be from the larger source to the south, against the current. As the above current passes Singapore, however, it could pick up waifs of *L. colubrina* on its way into Kerimata Strait and the western Java Sea; also, this current is joined by one sweeping from across the Philippines and Sabah, again potential sources of waifs. Thus, there are sources of *L. colubrina* upstream to flows entering central Indonesia and the distributional gap there must be explained by reasons other than direction of sea currents. Similarly, the absence of kraits from the Great Barrier Reef cannot be explained by sea currents, as the current reaching it comes from the islands to the east where *L. colubrina* occurs. The finding of a few waifs in Australia over the years attests to the fact that dispersal to the region does occur. Rather, it seems that establishment does not take place.

There are several difficulties in interpreting charts of sea currents. One is that they portray average conditions and may not show the details of specific gyres or eddy currents that may be important for dispersal. Also, current patterns in the past, when dispersal was taking place, may have been different from modern ones (see Section 8.4). There also may be seasonal reversals in direction of currents and deep flows may differ from those on the surface. For example, in summer the current flows from west to east between Indonesia and Australia and thence through the Torres Straits between Australia and Papua-New Guinea into the Coral Sea (Fig. 3.15), but reverses to east to west in winter (Webster and Streten, 1972) (see Section 8.4). The Torres Straits are probably not presently important in the dispersal of sea kraits. When the flow is from west to east the current passes between northern Australia and southern New Guinea, both areas barren of sea kraits, although Indonesia is a source of waifs further upstream. When the flow is from east to west, southeastern Papua and points further east are potential sources of waifs, but the current merely carries them to areas of unsuitable habitat unless they are carried all the way to Indonesia.

In east central Indonesia, there are also seasonal changes in current patterns. For example, Tomczak and Godfrey (1994, pp. 246-247) indicated that in the Lesser Sunda Islands, eastern Borneo, Sulawesi, Halmahera, western West Irian, and the southern Philippines the deep throughflow is westward at all times (Pacific to Indian Ocean). In November to March the wind-driven surface flow follows the deeper currents, but in May to September it opposes them. Their maps (their pp. 246-247) compare the surface currents for the months of February and August and there are few that have a common direction in both seasons. There are a number of reversals, and there are eddy currents at one season that do not occur in the other. It seems likely that in much of this area dispersal by surface currents is equally likely in all directions. The same may well apply in other parts of the study area, especially where land and sea are interdigitated in a complex fashion.

In winter, the current flows from the Soloman Islands down the eastern chain of islands, but the rest of the year it is in the opposite direction (Webster and Streten, 1972) (see Section 8.4).

The distance between source and target area may be important in dispersal. In broad coastal areas with only short gaps intervening between populations, not only are there more extensive sources for waifs, but also the target areas are large. Under these circumstances, dispersal is a more likely event than in widely spaced archipelagoes. Tiny areas of reef not only offer fewer potential waifs, but the likelihood of those waifs reaching another small reef in a great expanse of ocean is reduced. Indeed, waifs emanating from Fiji or Tonga would probably have a better chance of reaching a large target, such as Australia, than they would of arriving at a nearer, but much smaller piece of land.

3.3.3. Relation to Habitat

The review of the natural history of the *L. colubrina* complex (see Section 1.3) indicated that all members occupy similar habitats and indeed on Vanuatu *L. colubrina* and *L. frontalis* are syntopic. Although the following discussion will relate specifically to *L. colubrina*, at least some aspects may be applicable to other species in the complex.

The distribution of *L. colubrina* coincides with the occurrence of corals. This is true to the extent that (1) in general corals occur throughout the entire range of the complex (Fig. 3.16), (2) within that area, the snakes occur in conjunction with coral reefs (e.g., Figs. 3.2, 3.9, 3.11, 3.12) and (3) some of the gaps in the range of *L. colubrina* described in Section 3.2 are devoid of corals (Fig. 3.17).

Figure 3.16. Map showing the distribution of coral reefs in the study area. Land is in grey; coral reefs are in blue. Modified from Veron (1986) with permission from J. E. N. Veron and Angus & Robertson Publishers.

Mangroves are the antithesis of coral reefs for *L. colubrina*. Although this species sometimes shelters in mangroves (see Section 1.3), it does so only when reefs are adjacent. Large tracts of mangroves seem to preclude *L. colubrina* and the geographic distribution of these snakes and mangroves seem to be nearly mutually exclusive (Fig. 3.17). Silt is inimical for the development of coral reefs but provides suitable substrate for mangroves. Corals may also be adversely affected by reduced salinity whereas mangrove swamps occur over a wide range of salinities (Veron, 1986; Hutchings and Saenger, 1987). Consequently, large silt-bearing rivers may indirectly influence the distribution of sea kraits through inhibiting corals and promoting growth of mangroves. The southeastern Asian mainland and the main islands of the archipelagoes of the study area are replete with rivers (Figs. 3.1) and have been in the past (Voris, 2000; Inger and Voris, 2001), although because of changes in amount of exposed land their debouchement shifted from time to time. The Irrawaddy, Sittang, Pegu, and Bilin, as well as more minor rivers, empty from Myanmar into the Andaman Sea. Although both corals and kraits occur to the north of the mouths of these rivers, and again further south on the coast of the Malay Peninsula, neither occur along the section of the Burmese coast where these rivers debouche (Figs. 3.1, 3.3, 3.4). The northern Australian coast opposite Indonesia and drained by the Fitzroy, Ord and Katharine rivers is largely devoid of both corals and kraits; similarly, the muddy Gulf of Carpentaria has only a few small, isolated patches of coral and lacks kraits (Heatwole, 1975e; Wassenberg, *et al*., 1994). The south central coast of the island of New Guinea is drained by the large Fly River terminating in a muddy delta (Fig. 3.1), as well as by a number of lesser rivers

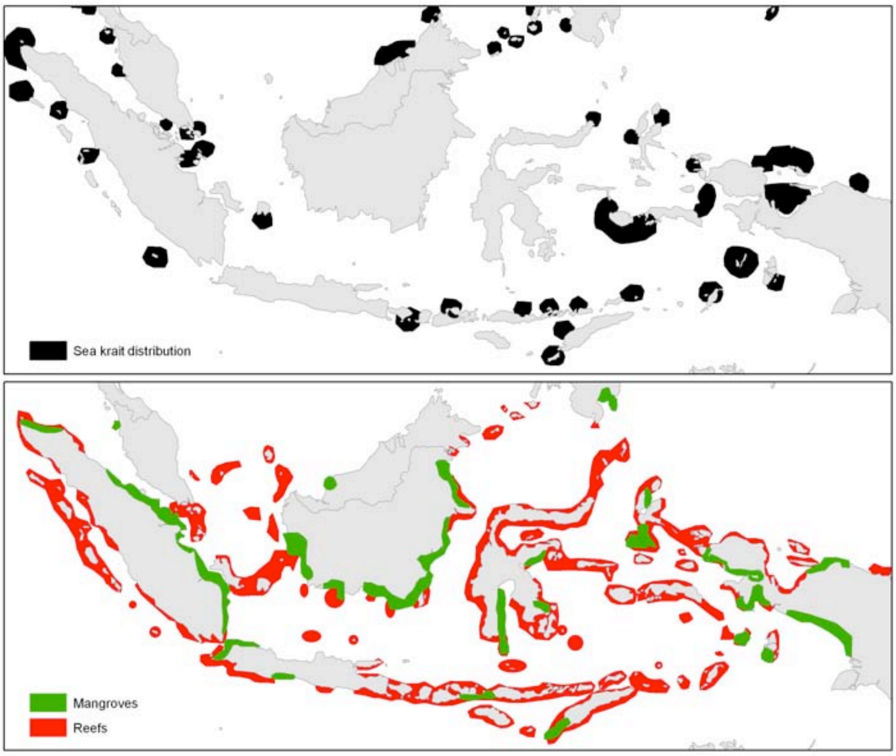


Figure 3.17. The known localities occupied by *Laticauda colubrina* in Indonesia in relation to the distribution of coral reefs (red) and mangroves (green).

debouching through swamps or deltas. This area lacks both corals and kraits (Fig. 3.6).

Gaps in the distribution of *L. colubrina* may occur in areas of extensive drainage by rivers, even when coral is present. There are a number of rivers that flow into the northern and western Java Sea and into the Kerimata Strait between Sumatra and Kalimantan (Borneo) from both these two large islands as well as from Java (Fig. 3.1) and West Irian (see above); nevertheless, there are some reefs in this region (Fig. 3.16, 3.17) but no kraits have been recorded (Fig. 3.4). Similarly, although rivers flow into the Makassar Strait both from eastern Kalimantan and western Sulawesi, corals occur there, but no *L. colubrina* have been reported. The Gulf of Thailand receives the Chao Phraya and other rivers; the mighty Mekong and the Hong River from the Indo-Chinese peninsula and the Xun Jiang and other rivers from China debouche via deltas into the South China Sea in areas climatically suitable for corals and kraits. Some corals do occur in these two bodies of water (Fig. 3.16, 3.17), but not kraits (Fig. 3.3). Finally, the Great Barrier Reef of Australia has an abundance of coral, but no breeding population of kraits. Many of the reefs in the western Java Sea, Kerimata Strait, Gulf of Thailand, South China Sea, and Great Barrier Reef are well offshore and perhaps are beyond the limits of riverine effects, such as silt and reduced salinities, thereby accounting for the presence of coral but leaving the absence of kraits unexplained. There are probably multiple reasons for the absence of kraits in these reefal areas, and the answer may differ from one place to another.

Laticauda colubrina requires terrestrial sites for shelter and ovipositon and although various kinds of cover suffice (see Section 1.3), many of the islands on reefs are sandy cays with only low, sparse vegetation; these lack rocks, woody debris, fallen palm fronds, or other substantial cover. Reefs that are not in close proximity to suitable terrestrial sites seldom have sea kraits. This consideration may apply to various of the more isolated reefs in the South China Sea and central Indonesia. It may also apply to parts of the Great Barrier Reef, but not in its entirety as there are a number of different kinds of islands scattered along its length (Hopley, 1982), including not only sandy cays, but rocky islands as well, some of which have trees, dead wood and other debris. Thus, although lack of suitable terrestrial habitat may exclude sea kraits from some sites, there are places that appear to be climatically suitable and have adequate cover but yet which lack these snakes.

Lack of permanent streams or springs on small offshore islands could be crucial factor limiting distribution of sea kraits, as they require freshwater for survival (see Sections 1.3, 8.5). It may be that this is the answer to the riddle as to why sea kraits do not occur on the cays of the Great Barrier Reef or other localities that otherwise seem to offer suitable habitat.

3.3.4. Relation to Fire

Sea kraits often select small, offshore cays as nesting sites, and although this is probably related to lower incidences of predation there (see Section 3.3.5), lower frequency of fire may also contribute to the safety of such places. Guinea (1986) noted fire to be a source of mortality of *L. colubrina* on Fiji.

3.3.5. Relation to Predators

Inspection of the distribution maps (Figs. 3.2-3.12) and the locality records (Heatwole *et al*., 2005) shows that snakes of the *Laticauda colubrina* complex rarely occur directly on the coasts of mainlands or of the larger islands, but rather on uninhabited smaller islands. Indeed, even at islands, they most often occupy tiny offshore cays, not the islands themselves. There are places where sea kraits inhabit coastlines of larger islands, or where they occur in concert with human populations, but these are exceptions, rather than the rule.

The larger landmasses and islands contain terrestrial predators upon reptiles and/or their eggs, that are lacking on small offshore cays; e.g., mongooses, weasels, civets, large varanid lizards, crocodiles, and feral dogs and cats (Guinea, 1981, 1986; Payne *et al*., 1985; Voris and Voris, 1995). Humans, archenemies of snakes in general, seldom settle permanently on tiny cays. Fiji lacked mammalian predators prior to the introduction of the mongoose by humans in the early 19th century. *L. colubrina* comes ashore on the main island and apparently thrives there in some localities, but is absent where there are now mongooses; in one locality sea kraits are not found on the mongoose-inhabited coast, but commonly occur in the same type of habitat on small offshore cays only 6 km distant (Guinea, 1981). Thus, distribution of kraits along the coasts of large landmasses may depend on nearby havens of small, offshore cays free of terrestrial predators, especially those preying on the vulnerable egg stage.

3.3.6. Relation to Congeners

Voris and Voris (1983) noted that similarity of diet was greater among allopatric species of marine snakes than among those that occurred together, an observation that raises the possibility of avoidance of interspecific competition through ecologic segregation. Glodek and Voris (1982) found that many species of sea snakes were dietary specialists, taking only a few taxa of prey, but that there were some generalists. A generalist overlapped habitat with specialists but two specialists of the same type did not overlap. McCarthy (1986) noted that members of the *Laticauda semifasciata* complex and another group of shallow-water marine snakes (*Aipysurus* spp.) occupy mutually exclusive ranges. He suggested that the hiatus between the main geographic range of *L. semifasciata* and its eastern disjunct populations (*L. schistorhynchus*) was because competitive *Aipysurus* occupied the intervening area. He also suggested that competition with *Aipysurus* might explain the rarity of other *Laticauda* species in Australian waters.

Both *Aipysurus* and *Laticauda* differ from most other marine snakes emanating from the elapid lineage by inhabiting relatively shallow water and by having rather broad gastrosteges, a case of convergent ecologies. Competition for food between *Aipysurus* and *L. colubrina*, however, seems unlikely as the former are either generalists eating a variety of fish (but seldom eels) except for one species specializing on fish eggs and invertebrates, whereas the latter is a specialist on eels and eel-like fish (McCosker, 1975; Voris, 1972; Voris and Voris, 1983) (see Section 1.3). Competition for breeding sites is not an option as *Aipysurus* are all livebearers that give birth in the sea and *L. colubrina* is oviparous and lays its eggs on land. Furthermore, there are some areas in which *Aipysurus* and members of the *Laticauda colubrina* complex do coexist, e.g. *L. saintgironsi* and *A. laevis*, the most common *Aipysurus* on the Great Barrier Reef, are sympatric in New Caledonia (Bauer and Saddlier, 2000). There remains the possibility that on the Great Barrier Reef diffuse competition with the species-rich sea snake fauna in general excludes *L. colubrina*. Again, this seems unlikely because of the occurrence of *L. colubrina* with an even more speciose marine snake fauna in the Philippines, Malaysia, Indonesia, and the Andaman and Nicobar islands (Voris, 1977; Heatwole, 1999). Thus, McCarthy's hypothesis seems to conflict with a number of observations. If competition accounts for the absence of *L. colubrina* from the Great Barrier Reef, it must be of a rather subtle nature. Assessment of the ecological interaction of the species in the *L. colubrina* complex with other marine snakes in various parts of its range might be a rewarding ecological exercise.

Competitive exclusion by congeners does not seem to affect the distribution of sea kraits. Guinea (2002) described the geographic clustering of species of *Laticauda* and noted that (1) three species, *L. colubrina*, *L. laticaudata* and *L. semifasciata,* are all sympatric from Japan to northern Papua-New Guinea, (2) two species, *L. colubrina* and *L. laticaudata*, are sympatric from Tonga to India (but see section 3.2.1 for assessment of Indian localities), and that (3) only in Singapore does *L. colubrina* occur alone. Furthermore, *L. colubrina* occurs syntopically with *L. crockeri* in Lake Te-nggano in the Solomon Islands, and both species even forage in the same crevices (Cogger *et al*., 1987). *L. colubrina* occurs with *L. frontalis* in Vanuatu (Shine *et al*., 2002b; Cogger and Heatwole, 2006). In New Caledonia, *L. saintgironsi* and *L. laticaudata* occur syntopically (Ineich and Laboute, 2002). In the Ryukyus Islands, *L. colubrina*, *L. laticaudata*, and *L. semifasciata* can all be found in the same sea-caves (personal observations). Only *L. guineai* and *L. schistorhynchus* do not overlap with any other member of the genus.

Laticauda colubrina encompasses several econes and this may allow greater population densities because the two sexes occupy separate niches and thereby avoid intraspecific competition for resources. Heatwole (1989) defined a fundamental ecological unit, the econe, as "a species or some component of a species (such as a life history stage, age class, morph or sex), whose members share common patterns of resource utilization and niche characteristics, but differ from other such components or species." Extreme examples are the tadpoles and adults of anurans, in which the two ontogenetic stages are morphologically and ecologically quite different, in some species the young being aquatic herbivores and the adults being semi-aquatic or terrestrial insectivores. Species that display a nearly consistent ecology between both sexes and throughout their ontogeny consist of only one econe. However, many species have markedly different attributes at different ages, or between the sexes, and in such cases a single species may encompass two or more econes. *Laticauda colubrina* and *L. guineai*, and to a lesser extent *L. saintgironsi*, exemplify species with at least two econes, with males and females differing in size, eating different kinds of prey, and occupying different foraging habitats (see Section 1.3). This segregation may allow for greater population densities than could otherwise be sustained. A sexually monomorphic population may be unable to fully exploit the full range of prey sizes either because of inability of large snakes to enter small crevices in search of food there and/or inability of small individuals with limited gape to swallow large prey.

Such ecologic segregation is further complicated in Vanuatu by the presence of an additional species, *L. frontalis*. This species may consist of a single econe. It shows little, if any, sexual dimorphism in size and both sexes are more similar in size to male *L. colubrina* than they are to the larger female *L. colubrina*. How do these three econes relate to each other? Does *L. frontalis* compete with the similar-sized male econe of *L. colubrina*, with both being ecologically segregated from the larger female econe of *L. colubrina*? Character displacement occurs in *L. colubrina* in Vanuatu where it is syntopic with *L. frontalis* (see section 5.2) and this may be a mechanism allowing coexistence of these two species.

Juveniles may constitute a third econe in some sea kraits; Boback (2003) noted that snakes often show distinct ontogenetic shifts in prey throughout their lives, largely because they are gape-limited predators. Werner and Gilliam (1984) regarded body size to be one of the most important attributes of an organism from an ecological and evolutionary point of view. They noted that size imposes important constraints on the manner in which an organism interacts with its enviroment and influences the strength, type, and symmetry of interactions with other species. They elaborated on the concept of an "ontogenetic niche" whereby as animals grow their ecological relations undergo shifts and they play different roles in the biotic community.

The *Laticauda colubrina* complex may have parallels to the evolution of body size in anoline lizards on Caribbean islands (reviewed by Boback, 2003). On islands with a single species of *Anolis*, lizards have an optimum, moderate size (but often with sexual dimorphism in size; personal observation). Invasion by an additional species of anole leads to divergence in body size, presumably in response to selection for reducing competition. In Vanuatu, *L. frontalis* occurs in addition to *L. colubrina* and the two species are of different sizes (Section 1.3). Boback (2003) considered competition and a number of other factors unimportant in the evolution of body size in the insular populations he studied, leaving prey size as the prime determinant of body size. In *Anolis* and *Laticauda*, although prey size seems to be an important determinant of body size, competitive interactions may play a role in the partitioning of species within the size-spectrum of available prey.

3.4. Recapitulation

- The confirmed distribution of *Laticauda colubrina* is from islands in the Bay of Bengal through some offshore islands of Myanmar, to the western part of the Kra Peninsula of Thailand, peninsular Malaysia, Singapore, most of the islands of Indonesia, northward through Sabah to the Philippines, Taiwan and the Ryukyu Islands, and eastward to New Guinea, the Solomon Islands, Vanuatu, Fiji, Tonga, and Futuna.
- *Laticauda saintgironsi* is restricted to New Caledonia and the Loyalty Islands.
- *Laticauda frontalis* is restricted to Vanuatu.
- *Laticauda guineai* is restricted to southern Papua.
- *Laticauda colubrina* have been reliably recorded as waifs (extralimital to the breeding range) in Australia, New Zealand, and Vietnam, as has *L. saintgironsi* in New Zealand.
- Records of *L. colubrina* from continental India, mainland Japan, and the Pacific islands other than those mentioned above, were considered erroneous; other exrtralimal records for the species of the complex may have been either erroneous, or based on waifs.
- Low sea temperatures may limit the geographic distribution of sea kraits in the north. In the south the limiting factor is probably lack of suitable land in a favourable thermal zone.
- The direction of sea currents in the study area were described and related to the dispersal of waifs. An enigmatic population of banded sea snakes in Central America may have originated from Asian sea kraits dispersed as waifs via the North Equatorial Countercurrent.
- The habitat requirements of *Laticauda colubrina* are: coral reefs (where males forage); deeper off-reef waters (where females forage); with both in proximity to islands free of large terrestrial predators and recurrent fire, but with sources of freshwater and with terrestrial cover suitable for concealment and oviposition. Gaps in the distribution of sea kraits can occur if any one of these requirements is lacking.
- Interspecific competition does not seem to limit the distribution of sea kraits.

Males and females, and possibly juveniles, are in different econes, and therefore are ecologically segregated, thereby allowing maintenance of denser populations.

CHAPTER 4. GEOGRAPHIC VARIATION: HIERARCHICAL ANALYSIS

This chapter describes a new method for analyzing geographic variation that allows detection of morphological discontinuties along a geographic continuum, and thereby identifying possible convergences among distant populations. The method is then applied to the sea kraits of the *Laticauda colubrina* complex and patterns of variation compared among various characters. Similarity of patterns among different characters allowed grouping of homogeneous populations, separated from other such groups by sharp discontinuities in multiple characters.

4.1. Methods

Analysis was undertaken in an hierarchical fashion. Data were inspected and all characters that were identified as invariant, or practically so, were not subjected to further analysis except for tabulating the frequency of rare departure from the standard condition, separately by geographic region.

Combining data from males and females to analyse patterns of geographic variation is valid only if there are no significant differences between the sexes. Consequently, for all characters, comparisons of males and females were made by two-tailed t-tests, first on the dataset as a whole. Then, for all localities for which the sample sizes of adults of both sexes combined were ten or greater, a two-tailed t-test of sexual dimorphism was applied for each specific locality (e.g., Port Moresby, Papua-New Guinea, not New Guinea as a whole). Data from juveniles and from animals that could not be sexed were excluded. On the basis of these results, data were divided into two groups: characters that did not display sexual dimorphism and those that did. For those that did not, the data from juveniles were replaced in the dataset and a two-tailed t-test comparing juveniles and adults was conducted for all localities with a total pool of ten or more specimens and in which juveniles and adults were both represented. Most characters analysed in the present study do not change ontogenetically (see Guinea, 2002); however, if there is strong selection for or against a certain character state, this might be detected by significant differences between juveniles and adults. For traits showing sexual dimorphism, ontogenetic comparisons could not be made as the gender of the juveniles could not be ascertained.

Dimorphic and non-dimorphic characters were both used in hierarchical analyses. For characters without sexual dimorphism, all data, including those from juveniles, were used in an analysis of variance (ANOVA) addressing variation among specific localities within a given country (e.g., among different islands in the Fiji Island group; see Heatwole *et al*. (2005) for the localities in each country). When the ANOVA indicated overall significant differences within a country, *post hoc* Fisher Protected Least Significant Difference (PLSD) tests were used to compare each locality with every other locality within the same country. The ANOVA and PLSD analyses were performed using a SAS StatView package. For sexually dimorphic characters juveniles were excluded and then the suite of ANOVAs and Fisher PLSD tests were performed separately for adult males and adult females. On those few occasions when only two localities were available for comparison, a t-test was used. For small samples, nonparametric tests were employed, either a Mann-Whitney U test (for two localities) or a Kruskal-Wallis test (for three or more localities).

Using a number of characters, Pernetta (1977) did not find any significant differences among localities in Fijian *L. colubrina*. In the present study, sometimes there were two or more areas within a country that differed significantly from each other for a given character, but with each being internally homogeneous. In such cases, the country was deemed to contain several areas, not just one. Once the numbers of internally homogeneous areas were identified for a given country, wider groupings were analysed. Geographically adjacent homogeneous areas in different countries were compared with their extralimital nearest neighbours to ascertain how far homogeneity extended. Thus, regions of similarity could be circumscribed and the location of discontinuities (significant differences) between areas identified.

For some specimens, locality data were missing, in error, or vague, or the locality could not be identified (Heatwole *et al*., 2005). These specimens were excluded from geographic analyses. Other localities were general and although excluded from the comparisons among localities, were included at higher regional levels (e.g., a specimen with only "Sabah" as a designated locality could not be used for comparisons among localities within Sabah, but could be grouped with more specific Sabah localities for comparison between Sabah and Peninsular Malaysia).

Some aspects of colour pattern could not be analysed in the same way as other characters. Localities were characterized by frequencies of occurrence of different colour patterns. To test for sexual dimorphism, localities for which there were 100 or more adults of known gender were used in a comparison between males and females by a chi-squared test using relative frequencies (Johnson and Bhattacharyya, 1992). Then tests were conducted comparing geographic regions, either grouping all specimens, or treating males and females separately, as judged appropriate from the above test. Each of the three species was tested against either adjacent or sympatric populations of the other species, and for *L. colubrina* various regions were tested against conspecific populations from the adjacent region(s). For these tests, rare patterns were lumped into the category "other" so as to comply with the restriction against small numbers in "expected" categories. Because of differences in patterns among different areas, the types of colour patterns were not always the same. For example, colour patterns A, C, and D were relatively common in many localities and constituted major categories in many tests. By contrast, in comparisons among *L. frontalis*, *L. colubrina* from Vanuatu, and *L. saintgironsi*, category "A" occurred in low frequency and was relegated to the category "other", whereas category "I" occurred at high frequency and was included as a major category.

In portraying statistical analyses, the degrees of freedom appear as subscripts to “P” for chi-squared tests and parametric tests, but not for nonparametric statistics that use ranking.

4.2. Results and Discussion: Stable Characters

The range of values for meristic characteristics for the species of the *L. colubrina* complex are presented in Appendices 4.1-4.3, the means and maximum body lengths in Appendix 4.4, and a summary of the ANOVAs testing for geographic differences in *L. colubrina* for all quantitative characters, separately by gender, in Appendix 4.5.

Several characters proved to be relatively stable within the entire complex, and therefore more useful in defining this species-group than in emphasizing intraspecific patterns of geographic variation. There were, however, some geographic correlates. The characters were (1) the condition of the rostral relative to the nasals, (2) the number and arrangement of the temporals, and (3) the number and disposition of supralabials. These will be treated in turn.

4.2.1. Snout (Rostral and Nasals)

In *L. colubrina*, *L. guineai*, *L. saintgironsi* and *L. frontalis* a single rostral scale usually protrudes upward and completely separates the nasals (Fig. 2.8), a feature that has been used to distinguish these species and the *laticaudata* complex from the *semifasciata* complex (Appendix 1.2; also see Chapter 2). A few other rare configurations, however, do occur in the *L. colubrina* complex.

One is for the rostral to only touch the nasals or to incompletely separate them, with the nasals coming into contact above the tip of the rostral. This condition was found in *L. colubrina* in one specimen each from Thailand and the Philippines, three specimens each from Fiji and Tonga, two from Vanuatu, six from the Solomon Islands, and one specimen each from four localities in Indonesia (Ambon, Java, Kei, Wetar). It was also found in 13 of *L. guineai* from Papua-New Guinea (of which 12 were from the vicinity of Port Moresby), for a total of only 32 specimens in the complex. Thus, this was a widespread variant, but rare except for *L. colubrina* in the Solomon Islands (11.5% of the local specimens) and for *L. guineai* (25% of the local specimens).

Another rare condition was for the rostral to be divided into an upper and a lower scale (as in the *semifasciata* complex), with the upper one occurring as an intercalary between the nasals. In *L. colubrina*, this condition occurred in one specimen each from Tonga (Niuafo'ou), Vanuatu, Fiji and the Philippines, two from the Solomon Islands, and one each from four scattered localities on the island of New Guinea (including one from Biak, West Irian), for a total representation of ten; in addition, this condition occurred in one of the specimens of *L. saintgironsi* from New Caledonia. It was not observed in *L. guineai* or *L. frontalis*. Seven specimens of *L. colubrina*, one from Ambon, Indonesia, two from Fiji, and four from Biak, West Irian, had either two or three small scales above the rostral and intercalated between the nasals. Boulenger (1912) also mentioned the occasional occurrence of one or two azygous scales between the internasals.

In one specimen (from Mindanao, Philippines) the nasal on the right side was divided into two smaller scales. In one from West Irian, the right internasal extended downward along the right edge of the rostral and contributed to the separation of the nasals.

Finally, in eight specimens of *L. colubrina* there was an asymmetrical pattern in which the first supralabial from one side extended upward and both that extension and the rostral separated the nasals. In five of these, the first supralabial and the rostral were retained as separate scales (one from the Philippines, one from Fiji, and three from Biak, West Irian), and in the remaining two (both from Biak) the first supralabial and the rostral were fused.

Biak, West Irian, seems to be an area in which there is considerable lability in the scutellation of the snout. Not only did that locality produce a number of specimens with intercalary scales between the nasals (12.5% of the specimens from that locality), but there was also a number in which the first supralabial participated in the division of the nasals (15.6%). Brongersma (1934, 1956) also noted variation in the scutellation of the snouts of specimens from West Irian and provided drawings of a number of them, including some of those noted above.

In conclusion, most variants of the configuration of the rostral were rare in *L. colubrina,* usually less than 1% but local pockets of higher incidences were scattered throughout the range. One of these rare variants, a divided rostral, is the same configuration found in the *semifasciata* complex. Thus, separation of the two complexes by this character is not absolute. The fact that certain areas, such as Biak, seem to have high incidences of a number of different fusions of scales, raises the question as to whether certain populations have a greater propensity than others for fusion in general. It is also possible that high incidences of fusions may be artifacts of collecting. Because sea kraits often aggregate on small islands, a collection from such aggregations may include a high proportion of siblings with related features not representative of the population in general.

Guinea (2002) noted that in specimens from Mabualau Island, Fiji, two of seven females had the nasal scale divided on one side only, in another the nasal scales met and excluded the internasal scales, and a fourth individual possessed an azygous internasal scale. Ota *et al.* (1985) presented drawings of variation in the placement of the nostril within populations of *L. colubrina* from the Ryukyu Islands, its location ranging from the posterior half of the nasal scale to its centre.

4.2.2. Temporals

The *colubrina* and *laticaudata* complexes have been distinguished from the *semifasciata* complex on the basis of the number of temporals. There is some variation in this character, however, within the *colubrina* complex. The most frequent configuration of the temporals in *L. colubrina* is for one anterior temporal to be followed by two posterior temporals (1+2) (Fig. 2.8; Appendix 4.6). A second common pattern is the presence of two anterior temporals and two posterior temporals (2+2). Six other combinations were observed (1+1, 1+3, 1+4, 2+3, 2+4 and 3+2) but all these are relatively rare. Tonga is the region with the greatest variety of temporal counts; all the known variants occurred there except 1+1. In Fiji, one specimen had the upper posterior temporal fused with the parietal. One specimen from an unknown locality had a temporal fused with a postocular. Brongersma (1956) described and provided drawings of some of these variants in specimens from West Irian.

Asymmetries, in which there was one configuration on one side of the head and a different one on the other, occurred in many localities. The incidence of asymmetry for *L. colubrina* was 6.9% over the entire database. The areas of highest local incidences of asymmetry (>10% of local specimens) were Tonga, Palau, and Taiwan (Appendix 4.6), and Rennel Island in the Solomon Islands (Appendix 4.7).

The 1+2 pattern was 70% or greater for species in *L. colubrina* at most localities throughout its range. However, there were exceptions. In Tonga fewer than half of the specimens had 1+2 temporals and almost a third had 2+2 (Appendix 4.6). There were three centres in which the configuration 2+2 was dominant, with local incidences >50%: *L. colubrina* in the Philippines (Appendix 4.6) and Papua-New Guinea and *L. guineai* in southern Papua-New Guinea (Appendix 4.7). Within the Solomon Islands the pattern was confused and there was some interdigitation of populations characterized by different numbers of temporals. Larger sample sizes are needed to elucidate the details of variation in that archipelago. Palau to the east of the Philippines, also had nearly equal values of 1+2 and 2+2.

It would appear that rare variants from the dominant 1+2 pattern emerge throughout the range of *L. colubrina*, with 2+2 being the most frequent one, occurring in rather high incidences in some localities, even to the point of becoming the most prevalent type. Four variants were recorded for *L. saintgironsi* of which 1+2 was the dominant in about the same frequency as over most of the range of *L. colubrina* (Appendix 4.6). In several individuals, all collected at the same time from reefs southwest of Noumea, the upper tier of the posterior temporals was fused to the scale immediately behind.

In summary, the most common number of temporals in the *Laticauda colubrina* complex is 1+2, with 2+2 being a common variant in *L. guineai* and some populatons of *L. colubrina* and *L. saintgironsi;* all other configurations are relatively rare. The only condition known for *L. frontalis* is 1+2.

4.2.3 Supralabials

All species of *Laticauda* have been characterized as having seven supralabials on each side of the head, with numbers three and four entering the orbit (Fig. 2.8; Appendix 1.2). In the *L. colubrina* complex, however, the number varies (see description and drawings in Brongersma [1956]), in the present study from three to nine (left side of the head) and six to nine (right side) with different scales participating in the border of the orbit. Seven was the predominant number in all three species of the complex and at all localities, always75% or higher and often exceeding 90% (Appendix 4.8); overall (including specimens without specific locality locality data) 90.6% of the specimens had seven supralabials. The second most common number was eight, with an overall incidence of 8.5%; all other counts were extremely rare with a collective representation of <1%. When counts exceeded seven, the extra supralabials were usually not full-sized scales but rather occurred as small triangular intercalary scales only about half as large as the adjoining supralabials that met above them. Counts lower than seven appeared to represent fusion of adjacent supralabials; in the single extreme case of three, the upper lip somewhat resembled that of *Emydocephalus annulatus*.

Over the entire database of *L. colubrina*, the two sides of the head differed in number of supralabial scales in 6.7% of the specimens (Appendix 4.8). No asymmetry was noted in the extreme western (Andaman Islands to Thailand) or extreme northeastern (Ryukyu Islands) parts of this species' range. Low incidences (<5%) occurred in Singapore and Indonesia and northward through the Philippines and Taiwan, and increased southeastward into New Guinea, the Solomon Islands, Vanuatu, Fiji and Tonga to values of about 9-16%.

The supralabials entering the orbit were nearly uniform throughout the complex, with less than 2% of the specimens at any locality departing from the state in which supralabials 3+4 directly bordered the orbit.

No departures from the standard condition were observed in *L. frontalis*.

4.2.4 Yolk Sac Scar

The overall range of scales involved in the yolk sac scar was from the 15th gastrostege anterior to the vent to the 29th one; for a given animal as few as a single scale could be involved or as many as six, but most often three or four.

The position of the mid-point of the scar appeared to be sexually dimorphic, with its location being slightly further anterior in females than in males. Since the scar cannot be detected in all animals, especially adults, the data are limited and were not statistically testable for many localities. The difference between the sexes was found to be significant only for *L. colubrina* in the Philippines and for all regions combined, and for *L. saintgironsi* (Appendix 4.9). Were there no consistent differences between the sexes, one would expect that by chance males would have larger values in half the regions and females in half; the metadata in Appendix 4.9 can be used to test that supposition. Without exception, the mean values for males were lower than those for females from the same region, a highly significant finding (Wilcoxon matched-pairs, signed-ranks test, two-tailed; P<<0.01, pairing observations by region). Thus, position of the yolk sac scar was treated as a sexually dimorphic character and its geographic variation treated separately for males and females.

In *L. colubrina*, an ANOVA indicated no significant geographic variation for either sex, either when tested using specific localities (males F=1.25, $P_{34,68}$=0.262; females F=l.52, $P_{28,44}$=0.186) or by general regions (males F=1.20, $P_{11,68}$=0.304; females F=2.73, $P_{11,52}$=0.699). There were insufficient specimens showing umbilical scars in other species for comparisons among specific localities.

Neither males (F=3.37, $P_{3,122}$=0.471) nor females (F=0.79, $P_{3,94}$=0.200) exhibited interspecific differences in the midpoint of the umbilical scar.

4.2.5. Length of the Body and Tail

The snout-vent lengths of two neonate *L. colubrina* incubated artificially were 275 and 307 mm (Guinea, 1986) and the smallest young encountered in the field have been reported as 300 mm (Fiji; Guinea, 1986, Shetty, 2000) and 317 mm (Ryukyu Islands; Ota *et al.*, 1985); the snout-vent length of the smallest individual of *L. saintgironsi* reported by St. Girons (1964, 1990) was 300 mm. In the present study the smallest individuals encountered had S-V lengths of 210 mm (*L. colubrina*; Appendix 4.1), 276 mm (*L. saintgironsi*), 280 (*L. guineai*) (Apppendix 4.2), and 293

(*L. frontalis*, Appendix 4.3). Ineich and Bonnet (personal communication) indicated that of several hundred *L. saintgironsi* they measured, the smallest was 380 mm S-V for females and 335 mm S-V for males. Allowing for growth of animals before first encounter, these three species do not seem to be greatly different in size at hatching.

Sexual dimorphism in body size of snakes has often been noted (e.g., Bergman, 1955, 1962a,b; reviews by Shine, 1978, 1994). It was found in the genus *Laticauda* by Smith (1926), and subsequently the greater length and weight of females have been confirmed repeatedly by a number of authors for *L. colubrina* as well as for some members of the other complexes within the genus (see review by Greer, 1997). Saint Girons (1964, 1990) and Ineich and Laboute (2002) found sexual differences in size in the New Caledonian populations later named *L. saintgironsi*. The present study compares the degree of sexual dimorphism in size in the species in the *colubrina* complex and examines whether there is intraspecific geographic variation of this trait.

Based on the entire dataset for each species, a t-test revealed that the differences between adults of the two sexes were significant for *L. colubrina*, *L. saintgironsi* and *L. guineai* but not for *L. frontalis* (Appendices 4.1-4.3), although Shine *et al.* (2002a) did find a small degree of dimorphism in the last species. The former two species differ in the extent to which the sexes diverge. *L. colubrina* and *L. guineai* (especially females) grow larger than *L. saintgironsi*, and *L. frontalis* is a dwarf species by comparison (Appendix 4.4).

The distribution of S-V lengths among those specimens of *Laticauda colubrina* for which the bodies were sufficiently intact and undamaged to permit accurate measurement is shown for all localities collectively in Figure 4.1 for *L. colubrina* and in Figure 4.2 for *L. saintgironsi*. Most juveniles of both species were between 300 and 350 mm. Some individuals in that size range could be reliably sexed and the number of identifiable males was increasingly represented in the larger body sizes until a peak at 700 mm S-V (Figs. 4.1, 4.2). Some females also could be reliably sexed within the juvenile size-range and they became increasingly represented at larger body sizes, reaching a peak at about 1100 mm in *L. colubrina* (Fig. 4.1) and 850 mm in *L. saintgironsi* (Fig. 4.2) but with some individuals growing

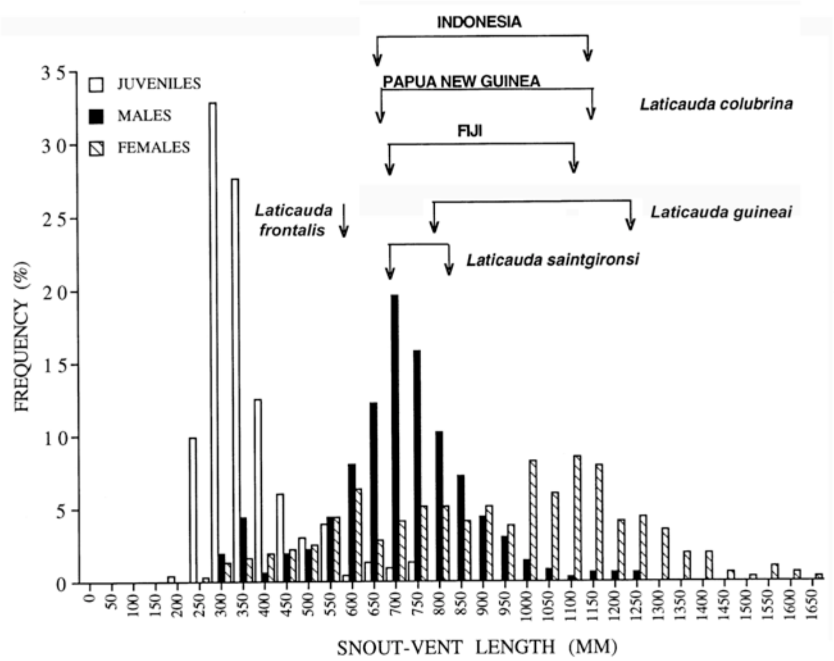


Figure 4.1. Frequency of snout-vent lengths of *Laticauda colubrina* from all localities. The superimposed horizontal lines indicate the span between peaks for males and female for the three regions for which there were more than 100 specimens of *L. colubrina* (Indonesia, New Guinea and Fiji) and for all specimens of *L. guineai*, *L. saintgironsi*, and *L. frontalis*. In each case, the arrow on the left end of the horizontal line indicates the position of the peak for males and the arrow on the right denotes the location of the peak for females. In *L. frontalis*, the peaks for both sexes coincide at the arrow.

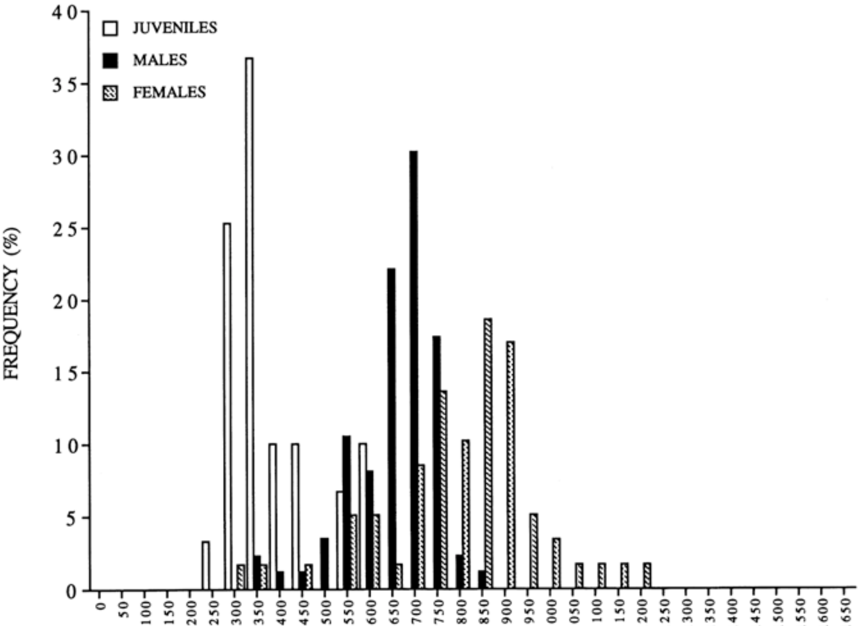


Figure 4.2 Frequency of snout-vent lengths of *Laticauda saintgironsi*.

much larger.

Sexual dimorphism in size extends to all parts of the geographic range of *L. colubrina*. At all specific localities in which both sexes were represented by a collective sample size of ten or greater, the mean and maximum sizes of females were always greater than those of males (Appendix 4.4).

The body size of *L. colubrina* did not seem to differ greatly throughout the range of the species. Three regions for which the sample size of *L. colubrina* exceeded 100, and which represented nearly the complete longitudinal extent of the species' breeding range, were used to construct individual frequency histograms of snout-vent lengths. The locations of the peak frequencies of the two sexes were superimposed on the collective frequency-histogram of all examined specimens of *L. colubrina* (Fig. 4.1). There was a strong congruence of frequency histograms among these localities. Vanuatu, however, may depart from the condition found in most parts of the range as Shine *et al.* (2002a) found sexual dimorphism in size in *L. colubrina* there to be less pronounced than in Fiji, perhaps because of character displacement with syntopic *L. frontalis* at the former locality. By contrast, *L. saintgironsi* showed a different pattern. The maximum snout-vent length of males of this species was somewhat shorter than that of *L. colubrina* (Appendices 4.2, 4.3) but the mean S-V and shape of the frequency curve and position of the peak was similar (Fig. 4.2). Females, however, differed from those of *L. colubrina* by not showing such a strong divergence in body length from males; the largest female *L. saintgironsi* examined was only 1210 mm (mean S-V 823 mm; Appendix 4.5) and Ineich and Laboute (2002) reported maximum S-V lengths of 890 cm and 1120 cm for males and females respectively). Furthermore, the frequency of S-V length of females peaked about 250 mm shorter than those of *L. colubrina* (Figs. 4.1, 4.2) and the span between the peaks for males and females was much narrower than in populations of *L. colubrina* (Fig. 4.1).

Clearly, sexual dimorphism in snout-vent length is less pronounced in *L. saintgironsi* than it is in *L. colubrina*. *Laticauda guineai* has about the same span between males and females in peak body length. This species also appears to be somewhat larger than other species (Fig. 4.1), but this may be an artifact of the smaller sample size for this species than for *L. colubrina*.

Laticauda frontalis is a smaller species. Over its entire distribution, the range in S-V length of animals whose gender could be ascertained was 293-717 mm, the maximum just reaching the level of the peak S-V for male *L. colubrina* and *L. saintgironsi* (Appendix 4.4; Figs. 4.1, 4.2). There was no obvious sexual dimorphism. Indeed, the S-V lengths of females averaged about the same as those of males and the difference between the two was not significant (Appendix 4.4), although the maximum size recorded was for a female.

As early noted by Günther (1864) and subsequently verified by many authors, e.g., Bhaskar, 1996; Shine and Shetty, 2001b), relative tail length varies between the sexes in *Laticauda colubrina*, with males having longer tails than do females of equivalent body length (Fig. 4.3). The difference is not so great in juveniles but as animals grow, males and females diverge in relative tail length. In all species of the complex, the tails of males are longer than in females of equivalent body length (Fig. 4.3).

Each species was subjected to a regression analysis of tail length against S-V and an analysis of covariance (ANCOVA) relating tail length to S-V and sex. In *L. colubrina,* S-V explains 63% of the variation in tail length of males and 64% in females; the slopes of the lines for the two sexes are significantly different (F=15.95; $P_{1,646}$<0.0001). In *L. guineai,* S-V explained 49% of the variation in tail length in males and 65% in females. The slopes of the lines for the two sexes were significantly different (F=64.53; $P_{1,44}$<0.001). In *L. saintgironsi* S-V accounted for 68% and 86% of the variation in tail length for males and females respectively and the slopes of the lines did not differ significantly between the sexes (F=572.27; P1, 144<0.0001). In *L. frontalis*, sample sizes were small and S-V explained only 6% for males but 91% for females. Nevertheless, the slopes of the regression lines of tail length against S-V length were significantly different between the sexes (F=1024.90; $P_{1,15}$=0.0013).

It is not valid to include different species in an analysis of covariance if they cluster around different portions of the regression line or if they differ by two-fold or more in the RMS residuals (unexplained variation). *L. frontalis* was excluded from interspecific comparisons on the first basis as it was a smaller species than the others. The residuals were similar for *L. colubrina* (males 15.0, females 19.7) and *L. guineai* (m 20.8, f 12.8), with both being higher than either *L. saintgironsi* (m 8.9, f 6.4) or *L. frontalis* (m 8.4, f 4.3). Consequently, the only ANCOVA that could be carried out with species as a variable was between *L. colubrina* and *L. guineai*. In that analysis, the species-effect was not significant (F=0.002, $P_{1,690}$=0.964) and thus these two species do not differ. Although formal comparisons could not be made with the other species, it is unlikely that the length of the tail relative to body length differs significantly among any of the species as the slope of the regression lines for males was identical for males of three species (0.121), with only *L. guinea* being slightly (but not significantly at least from *L. colubrina*) different (0.131). For =females the slopes varied from 0.083 to 0.094, with *L. frontalis* and *L. colubrina* both having 0.094.

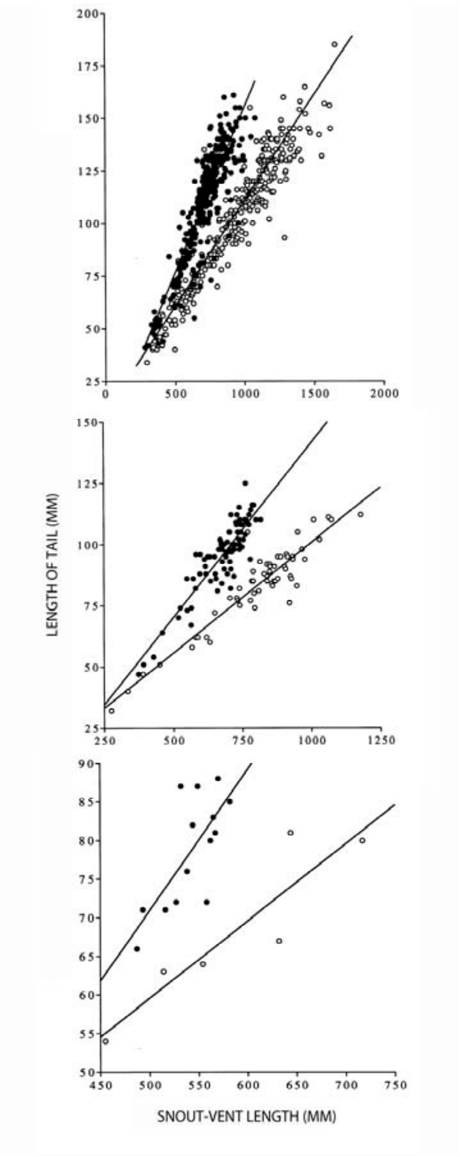


Figure 4.3 Relationship of tail length to snout-vent length in *Laticauda colubrina* (upper), *L. saintgironsi* (centre), and *L. frontalis* (lower) collectively from all localities. *L. guineai* not shown as analysis indicated it did not differ significantly from *L. colubrina*. Sizes of these species differ so the axes are at different scales in the three graphs.

Sexual dimorphism in relative tail length is known for various other snakes, including terrestrial and aquatic species (e.g., Bergman, 1962a,b), but it seems especially pronounced in some *Laticauda*.

The ratio of the number of gastrosteges to the number of subcaudals can be used as an index of relative tail length for comparisons among taxa or geographic areas. In the total dataset for *L. colubrina*, females had a higher ratio of gastrosteges to subcaudals (6.72 ± 0.04) than did males (5.4 ± 0.03) and the difference was significant (t=-29.5; P_{637}<0.0001). Within each sex there was significant variation in the ratio among countries (females F=3.38, $P_{18, 287}<0.0001$; males F=0.03, $P_{20, 308}<0.0001$). In males, the values for Peninsular Malaysia/Singapore (5.56) and Fiji (5.79) were higher than for other countries (range 5.02-5.47). In a PLSD analysis, Fiji differed significantly from ten other countries ($P_{1, 1\text{-}100}<0.0001$ to 0.006), including its nearest neighbours, Tonga, Vanuatu and the Solomon Islands. Peninsular Malaysia/Singapore differed significantly from four other countries ($P_{18\text{-}46}=0.009\text{-}0.040$): Palau, the Philippines, the Ryukyus, and Vanuatu. There was only one other significant pair-wise comparison: Palau versus Singapore/Peninsular Malaysia ($P_{33}=0.016$).

For females, Peninsular Malaysia/Singapore again had a higher mean ratio (7.26) than for most countries (range 6.47-6.99), but Fiji (6.34) had lower values, the reverse of the condition in males. New Guinea, also had a lower value (7.07). The PLSD analysis revealed that Fiji differed significantly from ten other countries individually ($P_{79\text{-}108}<0.0001$ to 0.044) and Peninsular Malaysia/Singapore from seven ($P_{18\text{-}50}=0.006\text{-}0.030$); no other pair-wise combinations exhibited significant differences. Thus, as in males, females in Fiji and Peninsular Malaysia/Singapore had significantly different ratios than those occurring elsewhere. The direction for females was the same as for males for Peninsular Malaysia/Singapore (higher than elsewhere), but reversed for Fiji (lower than elsewhere).

There were also significant differences among species in ratio of gastrosteges to subcaudals. Overall, there were significant differences among species both for males (F=9.13; $P_{3, 456}=0.001$) and for females (F=19.74; $P_{3, 372}<0.0001$). In females, *L. saintgironsi* (7.29) and *L. guineai* (7.20) had relatively shorter tails (higher ratios) than did *L. frontalis* (6.32) and most *L. colubrina* (6.72). In pair-wise PLSD tests the two long-tailed species did not differ significantly from each other ($P_{305}=0.141$) nor did the two shorter-tailed species differ between themselves ($P_{79}=0.595$); however, each of the long-tailed species had significantly different ratios than did either of the short-tailed ones ($P_{27\text{-}357}<0.0001\text{-}0.002$).

The males showed a similar trend with *L. saintgironsi* and *L. guineai* having higher ratios (5.64 and 5.53 respectively) than did *L. frontalis* and *L. colubrina* (5.32 and 5.40 respectively). In PLSD tests, *Laticauda guineai* differed significantly from *L. colubrina* from Papua-New Guinea (mean 5.18; $P_{44}=0.022$) as well as from Fiji, Palau, the Philippines, and Vanuatu ($P_{3\text{-}27}=0.001\text{-}0.017$) but otherwise differences between *L. guineai* and *L. colubrina* were not significant ($P_{28}=0.189\text{-}0.513$). *L.*

saintgironsi differed significantly from the two species with relatively long tails (low ratio) (P_{329}=0.016 with *L. colubrina* and P_{93}<0.001 with *L. frontalis*).

4.3. Results and Discussion: Variable Characters

4.3.1. Preliminary Analysis

Ranges.---Appendices 4.1-4.3 show the total ranges of values for measurements and meristic characters, as well as ranges separately by gender and state of maturity, over the entire dataset for each species. In view of the large number of specimens examined from all parts of their geographic distributions, it is likely that these ranges approach the limits of variation for these species.

Sexual dimorphism.---If there were strong sexual dimorphism, it would be expected to be revealed not only by comparison of the sexes directly, but to also be expressed in significant differences between adults of either gender (containing only male or female attributes) and juveniles (collectively containing characteristics of both sexes).

In the preliminary analysis of the entire dataset for *L. colubrina* (Appendix 4.1), the number of prefrontal scales, number of dark bands on the body, and numbers of scale rows in dorsal dark and light bands showed no significant differences between males and females or between either sex and juveniles, suggesting sexual dimorphism to be unlikely for those characters. By contrast, the number of dark bands on the tail, number of gastrosteges, and number of subcaudal scales consistently showed significant differences between males and females and between males and juveniles and females and juveniles. The numbers of scale rows around the body were significantly different between males and females at all levels of the torso; usually juveniles differed from either gender of adults, with the exceptions that there were no significant differences between juveniles and females at the level of the first gastrostege, and between juveniles and males at the level of the 20th and 150th gastrosteges. The number of scale rows in the ventral dark bands (at all levels of the torso) always showed significant differences between males and females, but never between females and juveniles; males and juveniles differed significantly in this regard only at the level of the first dark band. The number of supralabials did not differ significantly between the sexes on either side of the head, but juveniles differed significantly from females on the left side of the head and from males on the right side of the head.

Although it seems that all but a few of the meristic characters are likely sexually dimorphic and the sexes should be treated separately for most analyses of geographic variation, it must be recognized that this is a crude analysis, and the intersexual comparisons on such a broad basis do not necessarily imply that all populations have the same degree of dimorphism, or even that all populations are sexually dimorphic. It merely indicates that the males and females from the entire dataset show significant differences in many characters. The comparisons of adults of the two sexes with juveniles are less definite as degree of resemblance to either sex would depend upon the ratio of immature males and females in the juvenile group. Thus, less weight was placed on this comparison than upon the direct comparison of adult males and adult females at particular sites. In the treatment of individual characters (see below), where sample sizes are sufficient to do so, the analysis is refined and interpreted on a detailed locality-by-locality basis.

Geographic variation: Because of the demonstrated likelihood of sexual dimorphism in a number of characters, a second preliminary analysis consisted of an analysis of variance (ANOVA) for each character, separately for males and females (Appendix 4.5). The snout-vent length, tail length, band widths at various levels of the body, and numbers of gastrosteges, prefrontal scales, subcaudal scales, and dark bands on the body and on the tail all showed highly significant variation among countries, both in males and in females. This test did not indicate that all countries varied from every other, but that merely over the entire geographic range there were countries that differed significantly from others. In this analysis, as well as an overall probability value for the geographic variation over the range as a whole, each country was compared with every other. Some of these pair-wise comparisons revealed significant differences; others did not. The details of the specific regions are discussed below where a more detailed treatment of individual characters is presented.

In the complete dataset of *L. saintgironsi* the number of gastrosteges, subcaudal scales, and dark bands on the tail differed significantly between males and females. There were no significant intersexual differences in number of dark bands on the body or in number of prefrontal scales. In these regards this species resembles *L. colubrina*. It differed from *L. colubrina* in that the differences between males and females in widths of body bands and in the number of scale rows around the body were not significant in most regions of the torso (Appendix 4.2). *Laticauda guineai*, unlike the other species, showed slight sexual dimorphism in the number of supralabial scales and, like the others, was dimorphic in body size and relative tail length

4.3.2. Prefrontals

Prefrontal scales appear in two main configurations in *L. colubrina*. In one, there are two prefrontals, symmetrical across the midline; in the other there are three prefrontals, a central azygous scale flanked on each side by a lateral one (Fig. 2.8). In addition, there are two rare conditions. Six individuals from widely scattered localities had the azygous prefrontal divided so as to form a total of four prefrontals. Three of the six snakes with this condition, however, came from a single region, Velitoa Island, Tonga. Two snakes had all prefrontals fused into a single scale (Appendix 4.10). One snake from Ternate, Indonesia, had the prefrontals and internasals fused. Brongersma (1956) provided drawings of variation in the arrangement and shape of the prefrontals in specimens from West Irian.

Neither the dataset as a whole nor the 13 major regions for which there were adequate data for *L. colubrina* for testing, showed a significant difference in mean number of prefrontals between the sexes (Appendix 4.11). In seven of these comparisons, males and females had identical values, in six the males had slightly higher means, and in 16 females had the larger values. Neither *L. saintgironsi*, *L. guineai* nor *L. frontalis* showed any significant sexual differences in number of prefrontals (Appendix 4.11). In none of these species did juveniles differ significantly from adults (Appendix 4.12). Consequently, data on prefrontals from both sexes can be lumped together with those from juveniles for analysis of patterns of geographic variation.

The preliminary ANOVA on the entire dataset of *L. colubrina* (Appendix 4.5) showed that males and females separately demonstrated significant geographic variation in number of prefrontals; combining the data for all sexes and states of maturity in a similar ANOVA confirmed this conclusion ($F=3.83$; $P_{14, 785}<0.0001$). The proportions of snakes with an azygous prefrontal (three prefrontals), without an azygous prefrontal (two prefrontals) and with other configurations were calculated for each geographic region. In all regions, the azygous condition was the prevalent one. For regions with small sample sizes the proportion of individuals with the azygous condition ranged from 75% to 100%. For the more accurate data from large samples, most values were between 88% and 95% with no discernible consistent geographic pattern (Appendix 4.10). There were two exceptions, one with an unusually low proportion of azygous prefrontals (Singapore 66%) and the other, Sabah, with only that configuration (100%). These two localities are not far apart but are on opposite sides of the southern end of the South China Sea. It would appear that the number of prefrontals does not show consistent geographic trends, a conclusion in agreement with the opinion of McCarthy (1986). Guinea's (2002) results from Fiji also showed high incidences of azygous prefrontals.

Laticauda saintgironsi, *L. guineai* and *L. colubrina* had similar proportional representation of prefrontal types (Appendix 4.10), with the azygous condition being predominant, two prefrontals relatively uncommon and other types rarely occurring. In addition to the four-prefrontal condition, however, *L. saintgironsi* had two variants not observed in *L. colubrina*. These were (1) fusions of the central (azygous) prefrontal with the frontal and (2) one of the paired prefrontals fused with an internasal. Only the azygous condition was noted for *L. frontalis*.

Of the 11 localities for *L. colubrina* that could be tested, three showed identical mean numbers of prefrontals for juveniles and adults; in five of the remaining eight localities juveniles had higher numbers of prefrontals than did adults and in three the reverse was true. For no locality were the differences between the life stages significant (Appendix A-12). Clearly, juveniles and adults of *L. colubrina* do not differ significantly with respect to prefrontals and natural selection upon this character is either absent or too feeble for detection with the samples sizes at hand. Similarly, the two life stages did not differ significantly in number of prefrontals for *L. saintgironsi*.

4.3.3. Number of Dark Bands on the Body

In *L. colubrina* the crude preliminary analysis of the entire dataset did not reveal any significant sexual dimorphism but more refined analysis indicated that there were geographic differences in sexual dimorphism. In the western (Peninsular

Malaysia, Singapore, Indonesia), south-central (New Guinea) and far northern (Taiwan and Japan) parts of the species' range, no significant differences were found between males and females at any individual locality or for all localities collectively in a particular region for which there were adequate data for testing. Similarly, Bhaskar (1996) found no significant difference between the sexes in the total number of dark bands (body + tail) in the Andaman Islands. In an arc including the eastern (Tonga, Fiji, Vanuatu, Solomon Islands) and north-central (Palau, Philippines, Sabah) portion of the range, however, at least some individual localities, and sometimes an entire archipelago, tested significantly for sexual dimorphism in number of body bands (Appendix 4.13). Pernetta (1977) also found significant sexual differences in number of dark bands on the body in two localities in Fiji. Because some regions are sexually dimorphic in this character, males and females were treated separately for analysis of geographic variation.

Taylor (1965) earlier noted an extraordinary geographic variation in the number of dark bands in *L. colubrina*. In the present study, when all specific localities for *L. colubrina* throughout its range were collectively subjected to an analysis of variance, the number of dark body bands of females showed significant geographic variation (F=28.24; $P_{71, 163}<0.0001$). When ANOVAs were performed on particular countries taken individually some were found to show significant variation in dark body bands within the country, and others not. Those that were internally homogeneous were: Taiwan (F=0.41; $P_{2, 13}=0.672$), the Philippine Islands (F=2.04; $P_{6, 17}=0.145$), Palau (F=0.12; $P_{4, 8}=0.967$), the Solomon Islands (F=2.50; $P_{5, 19}=0.081$), Vanuatu (F=0.26; $P_{1, 19}=0.772$), Fiji (F=1.35; $P_{12, 63}=0.221$), and Tonga (F=1.41; $P_{5, 10}=0.358$). The Andaman and Nicobar Islands showed a significant result (F=7.31; $P_{14, 27}=0.04$), but this arose from the locality of South Sentinal Island, represented by only one specimen being a significant outlier from two other localities. This was deemed a trivial result and the Andamans and Nicobars consequently are treated here as an homogeneous area. The Ryukyu Islands had females from only one locality so that area was considered homogeneous.

Other countries did, however, show genuine internal variation, e.g., variation among Indonesian females (F=4.58; $P_{9, 32}=0.005$) that PLSD analysis showed to be attributable to division into three groups of islands, (1) Sumatra and its offshore islands in the west, (2) West Irian and its offshore islands in the east, and (3) a central group that encompasses the rest of the Indonesian archipelago. Differences among these three groupings were highly significant (F=13.66; $P_{2, 34}$<0.0001). PLSD comparisons among them showed highly significant differences in all combinations (West Irian vs. Sumatra P_{19}=0.0002; West Irian vs. central islands P_{22}=0.023; Sumatra vs. central islands P_{6}=0.018).

Snakes from Malaysia/Singapore also showed overall geographic heterogeneity (F=22.25, $P_{5, 29}$<0.0001). This resulted from two distinct groupings, (1) Sabah and (2) Peninsular Malaysia/Singapore that differed significantly from each other (t=9.70; P_{27}<0.0001).

Laticauda colubrina from New Guinea showed significant geographic variation within the country (Appendix 4.13). The PLSD analysis, however, indicated that all the significant pair-wise comparisons involved localities with sample sizes of three or less and the result was considered inconclusive of significant variation in this character.

Laticauda guineai differed significantly from *L. colubrina* from the rest of New Guinea (t=9.70, P_{39}<0.0001) and all of its PLSD pair-wise comparisons with New Guinean populations of *L. colubrina* were significant ($P_{23\text{-}31}$<0.0001 to 0.019).

The above results show that a number of countries, or subregions within countries, are internally homogeneous. These are now compared with adjacent countries or subregions to ascertain how far homogeneity extends.

Beginning at the western end of the range, there are no significant differences among the Andaman/Nicobars, Thailand, Peninsular Malaysia/Singapore, and the central part of Indonesia and these can be lumped as one homogeneous area. Sumatra (including its offshore islands) does not differ significantly from the Andaman and Nicobar Islands to the northwest (t=1.21; P_{18}=0.249), but does differ significantly from central Indonesia to the southeast (see above). Thus, there may be a clinal change from northwest to southeast along the Sumatran coast.

It was formerly mentioned that Peninsular Malaysia/Singapore differed significantly from Sabah (see above). Similarly, central Indonesia also differs significantly from Sabah (t=-6.38; P_{46}=<0.0001). Thus, there is a discontinuity between the central and northwestern limb of the geographic range and the branch that extends northward; that break occurs between Sabah and its western and southern neighbours. There is significant variation proceeding northward along the northern limb (F=35.67; $P_{3, 71}$<0.0001). PLSD analysis shows that one break accounts for that result. It occurs between the Philippines and Taiwan. Sabah and the Philippines do not differ significantly ($P_{39}=0.354$), but the Philippines and Taiwan do ($P_{37}<0.0001$); Taiwan and the Ryukyus are not significantly different ($P_{33}=0.225$). Palau lies to the east of the junction between the northern and southeastern arms of the range of *L. colubrina*, but is different from all its nearest neighbours, the Philippines to the northwest (t=-11.77; $P_{33}<0.0001$), West Irian to the south (t=-5.96; $P_{33}<0.0001$), and the Solomon islands to the southeast (t=-2.01; $P_{34}=0.053$, bordering on significance).

Proceeding now along the southeastern branch of the geographic range, *L. colubrina* from West Irian is significantly different from New Guinea (t=2.13; $P_{34}=0.039$). *Laticauda guineai* is not only significantly different from *L. colubrina* from the rest of New Guinea ($P_{41}<0.0001$) but differs from that species in the Solomon Islands (t=12.42; $P_{45}<0.0001$). Populations of *Laticauda colubrina* from New Guinea do not differ significantly from those in the Solomon Islands (t=0.77; $P_{38}=0.447$) and these two areas can be considered homogeneous. Progressively, southeastward along the southeastern chain of islands, the Solomon Islands populations of *L. colubrina* are significantly different from those in Vanuatu (t=6.06; $P_{52}<0.0001$), which in turn differ significantly from those in Fiji (t=-14.82; $P_{100}<0.0001$). The final two island groups in the chain, Fiji and Tonga, do not differ significantly (t=0.06; $P_{82}=0.950$).

The distributional pattern of the number of dark body bands in female *L. colubrina* is summarised in Figure 4.4.

Male *L. colubrina* showed a somewhat different pattern in number of dark body bands. Overall, there was significant geographic variation (F=33.12; $P_{37, 218}<0.0001$). The following countries were internally homogeneous: Ryukyu Islands (males from only one locality), Taiwan (F=0.004; $P_{1, 7}=0.949$), Philippines (F=1.14; $P_{8, 27}=0.382$), Andaman and Nicobar Islands (F=0.33; $P_{1, 2}=0.667$), Myanmar (only one male specimen), Thailand (F=0.25; $P_{2, 31}=0.817$), Indonesia (F=1.09; $P_{16, 28}=0.450$), Vanuatu (F=0.004; $P_{1, 22}=0.948$), and Tonga (F=1.87; $P_{3, 13}=0.198$).

Localities in Fiji did not differ significantly overall (F=2.13; $P_{7, 76}=0.051$). When the localities were grouped into the four Fijian major districts, again the statistical test was near the border of significance (F=2.64; $P_{3, 76}=0.052$). Means did not differ greatly in magnitude among districts (27.0-29.0). For comparisons with other island groups, the Fijian populations were treated as homogeneous, although recognizing that slight divergence in this character might be occurring.

The localities in the Solomon Islands differed significantly (F=15.12; $P_{7, 29}<0.0001$), but this was attributable almost entirely to Choiseul (Figure 3.7),

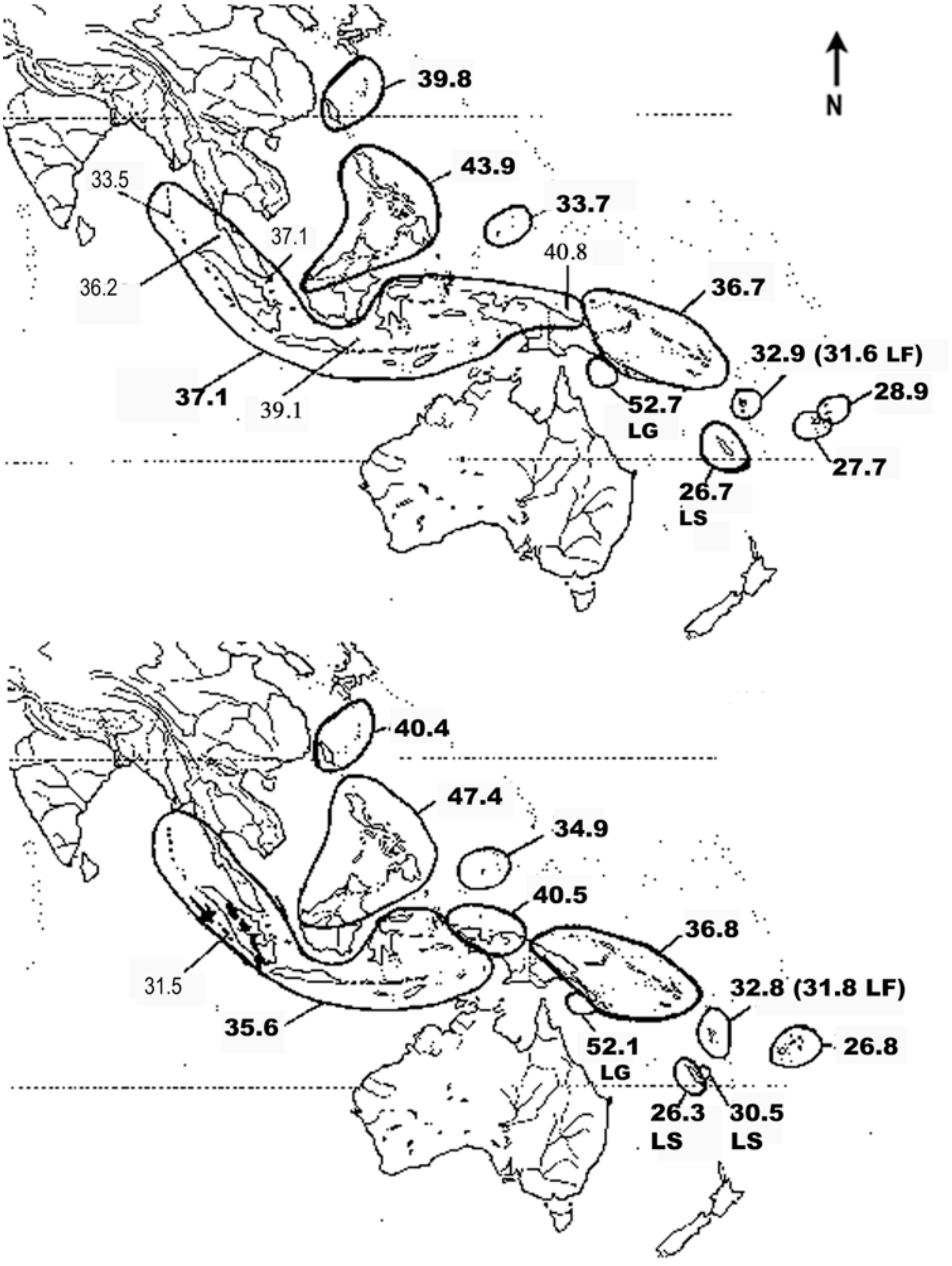


Figure 4.4 Distribution of numbers of dark bands on the bodies of male (upper) and female (lower) *Laticauda colubrina*, *Laticauda saintgironsi* (LS), *Laticauda guineai* (LG), and *Laticauda frontalis* (LF). Non-italicized numerals indicate means for the entire area enclosed by the indicated polygon. Smaller italicized numerals indicate means for the corresponding subregion within a polygon. Arrows indicate possible clinal variation. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

represented by only one male specimen, being an outlier of most of the other localities in the PLSD analysis. This result was treated as trivial. When the analysis was performed after eliminating the one specimen for Choiseul, there were no longer any significant differences among localities within the Solomon Islands ($F=2.18$; $P_{6, 28}=0.085$). Consequently, the Solomon Islands are treated as homogeneous.

Several countries did show significant variation internally. Sabah differed significantly from Peninsular Malaysia/Singapore ($t=6.46$; $P_{33}<0.0001$) and neither showed significant variation internally (Sabah $F=2.38$; $P_{4, 16}=0.101$; Peninsular

Malaysia/Singapore F=0.55; $P_{1, 12}=0.474$). Thus, these two regions can be considered as distinct. New Guinea varied overall (F=3.61; $P_{8, 14}<0.032$) and the PLSD analysis of specific localities showed this to be attributable to the distinctiveness of two regions, (1) northern Papua, and (2) eastern Papua and the offshore islands (rest of Papua-New Guinea). The rest of Papua-New Guinea did not show any significant variation within its region (F=1.81; $P_{5, 18}=0.180$); northern Papua had too few localities with males for individual testing. The difference between these two groupings was highly significant (t=3.28; $P_{21}=0.004$).

The identifiably homogeneous regions were then compared with adjacent ones to ascertain whether homogeneity extended beyond their borders. The entire region extending from the Andaman Islands along the southern arm of the inverted T of the geographic range of the species to northern Papua tested as having no significant differences among component homogeneous regions (F=0.76; $P_{34, 73}=0.605$). Despite the lack of statistical significances among localities over this wide area, there does seem to be clinal variation as the means of the various subregions show a progressive increase from northwest to southeast: Andaman Islands (33.5) to Thailand (36.2) to Peninsular Malaysia/Singapore (37.1) to Indonesia (39.1) to northern Papua (40.8) (Fig. 4.4). Extending eastward, northern New Guinea, and eastern and insular Papua-New Guinea differed significantly from each other (see above), but the last-mentioned did not differ significantly from the Solomon Islands (t=-1.62; $P_{48}=0.112$). The Solomon Islands did differ significantly, however, from Vanuatu (t=4.61; $P_{64}<0.0001$), which in turn differed significantly from Fiji (t=-12.08; $P_{119}<0.0001$). Fiji was significantly different from Tonga (t=-2.31; $P_{100}=0.023$).

Considering now the northern limb of the geographic range, Sabah was significantly different from Peninsular Malaysia/Singapore to the west (see above) and from Indonesia to the south and east (t=-5.23; $P_{57}<0.0001$), but not from the Philippines (t=0.92; $P_{48}=0.364$). Thus, the latter two countries can be considered as homogeneous with respect to the number of dark body bands in males. The Philippines did differ significantly from Taiwan (t=3.21; $P_{40}=0.003$), but Taiwan and the Ryukyu Islands did not differ significantly from each other (t=1.67; $P_{14}=0.116$).

Finally, Palau is an isolate in regard to this character as it differed significantly from all its neighbours: the Philippines to the west (t=-9.37: $P_{47}<0.0001$), West Irian to the south (t=5.33; $P_{29}<0.0001$) and Papua-New Guinea exclusive of northern Papua, to the southeast (t=2.94; $P_{36}=0.006$). Palau also differed significantly from the waifs from the Pacific to the east (t=-4.58; P_{19}=0.0002).

In *L. colubrina*, the numbers of dark bands on the body were higher in females than in males at all localities (Fig. 4.4). The pattern of variation differed between the sexes in that (1) the males differed between Tonga and Fiji but the females did not, (2) West Irian females differed from those of the rest of Indonesia but males did not, and (3) the females in the Sumatran population may have been somewhat different but not the males. In both sexes, high values in the Philippines-Sabah homogeneous group decreased to the north (Taiwan-Ryukyus), south (Indonesia and western countries) and progressively decreased southeastward along the insular chain to Tonga.

Shetty and Prasad (1996b) previously demonstrated geographic variation in number of dark body bands in that their specimens from the Andaman Islands had higher counts than did those from Taiwan, Fiji or New Caledonia (the last now *L. saintgironsi*). Similarly, Guinea (1981) noted that Fijian and Taiwanese populations differed in number of bands on the body and tail.

Laticauda saintgironsi showed no sexual dimorphism in number of dark body bands at any locality for which there were sufficient data to test, nor for all New Caledonian localities combined (Appendices 4.11, 4.14). For males, females and juveniles combined, there were no significant differences among localities within New Caledonia itself (F=1.002; $P_{17, 127}$=0.462). Animals from the Loyalty Islands, however, had significantly greater numbers of dark bands on the body (29.3±1.20) than did those from New Caledonia (26.6±0.15; t=-3.36, P_{167}=0.001). There was no significant difference in number of dark body bands between juveniles (26.9±0.43) and adults (26.5±0.16; t=-1.10, P_{168}=0.274).

The outstanding feature of *L. guineai* is that both sexes have an exceptionally high number of dark bands (the highest of any of the species in the complex). It did not show any sexual dimorphism in number of dark body bands (Appendix 4.13), nor did its population differ from each other. There were significant differences between it and *L. colubrina* from all parts of New Guinea, including Bougainville as shown by PLSD ($P_{1, 2\text{-}14}$<0.0001 in all cases).

In Vanuatu, *Laticauda frontalis* did not display sexual dimorphism in number of dark body bands nor were there significant differences among localities (Tables 4.7, 4.9). Neither were juveniles and adults significantly different (juveniles: mean=30.7 ± 0.53; adults: mean=31.7±0.359; t=0.94; P_{26}=0.359). Consequently, both sexes and all stages of maturity were grouped for assessing variation throughout the entire geographic range. Overall, the differences among countries were not significant (F=2.00; $P_{3, 26}$= 0.143).

4.3.4. Number of Dark Bands on the Tail

Given that males of *L. colubrina* have relatively longer tails then do females (see above), it is to be expected that the number of dark bands on the tail would also exhibit sexual dimorphism. This result was suggested by the preliminary analysis and confirmed by more detailed analyses of specific localities and regions (Appendix 4.14). Of the 40 tests conducted, in only two did females have a higher mean value than did males, and then not significantly so. In one test males and females had identical means. In the 37 remaining tests, males had a greater mean number of dark tail bands than did females, with these differences being significant in all but one test. Clearly, this character is highly dimorphic in *L. colubrina*. Consequently, males and females of this species are treated separately in the analysis of geographic variation.

Sexual dimorphism in number of dark bands on the tail also occurred in *L. saintgironsi*, *L. guineai* and *L. frontalis* at all testable localities (Appendix 4.14).

For female *L. colubrina*, the following countries did not show any significant variation in number of dark tail bands among localities within the country: Andaman/Nicobar Islands, New Guinea, Solomon Islands, Vanuatu, Fiji, Tonga, Palau, Philippines, Taiwan, and the Ryukyus (Appendix 4.14). Thailand and Myanmar had sample sizes for females too small for testing. In Indonesia, the differences among localities bordered on significance for females (F=2.60; $P_{10, 34}$=0.044), but the PLSD analysis showed that this result was attributable entirely to a single specimen from the Celebes being an outlier to seven other localities; when this specimen was omitted from analysis, no residual differences among localities remained. Consequently, Indonesia is considered as having no significant internal geographic variation in this character.

By contrast, females exhibited significant variation of this trait among specific localities in Malaysia/Singapore (Appendix 4.14). In Malaysia/Singapore, all the significant pair-wise comparisons were between localities from Sabah and those from Peninsular Malaysia/Singapore. These two regions differed significantly from each other, but within each there were no significant differences.

Turning now to an assessment of differences in *L. colubrina* among adjacent countries or regions, a number of homogeneous regions can be identified. The entire east-west axis of the southern distribution, extending from the Andaman Islands through Thailand, Indonesia, Papua-New Guinea, Palau and the Solomon Islands was homogeneous for the number of dark bands on the tail. There was no overall significant difference over this area (F=0.63; $P_{5,105}$=0.680). Continuing eastward, Vanuatu differed significantly from the Solomon Islands (t-2.90; P_{52}=0.006). Vanuatu, Fiji, and Tonga did not differ significantly overall (F=1.38; $P_{2,113}$=0.255).

In the east-west axis, Peninsular Malaysia/Singapore was an isolate. It differed significantly from Sabah to the east (see above). When included with the rest of the countries indicated above as homogeneous (Andamans and Nicobars, Thailand, Indonesia, Papua-New Guinea, Palau, and the Solomons) the combination was no longer homogeneous (F=2.21; P=0.038) and in the PLSD pair-wise analysis Peninsular Malaysia/Singapore did differ significantly from three of the countries in this group: Indonesia, its nearest neighbour to the south (P_{56}=0.035), Thailand (P_{18}=0.015), and the Solomon Islands (P_{39}=0.038). None of the other regions differed significantly from any other in the pair-wise comparisons. For these reasons Peninsular Malaysia/Singapore was considered to be an isolate from this larger group (Fig. 4.5).

In the northern geographic axis, Sabah and the Philippines did not differ significantly (t=1.22; P_{40}=0.228), but the Philippines did differ significantly from Taiwan (t=3.33; P_{38}=0.002). Taiwan and the Ryukyus did not differ significantly (t=0.17; P_{33}=0.867).

For males of *L. colubrina*, the following countries did not show any significant variation in number of dark tail bands among localities within them: Andaman and Nicobar Islands, Thailand (H=3.00; P=0.223), New Guinea (F=0.123; $P_{8,22}$=0.352), Indonesia, Vanuatu, Fiji, Tonga (all means were identical, and values varied overall only between three and four), Palau (F=3.40; $P_{5,14}$=0.131), Philippines (F=1.81; $P_{8,27}$=0.137), Taiwan (z=-0.24; P=0.814), and the Ryukyus Islands (only one locality with data for tails of males, all identical at 5).

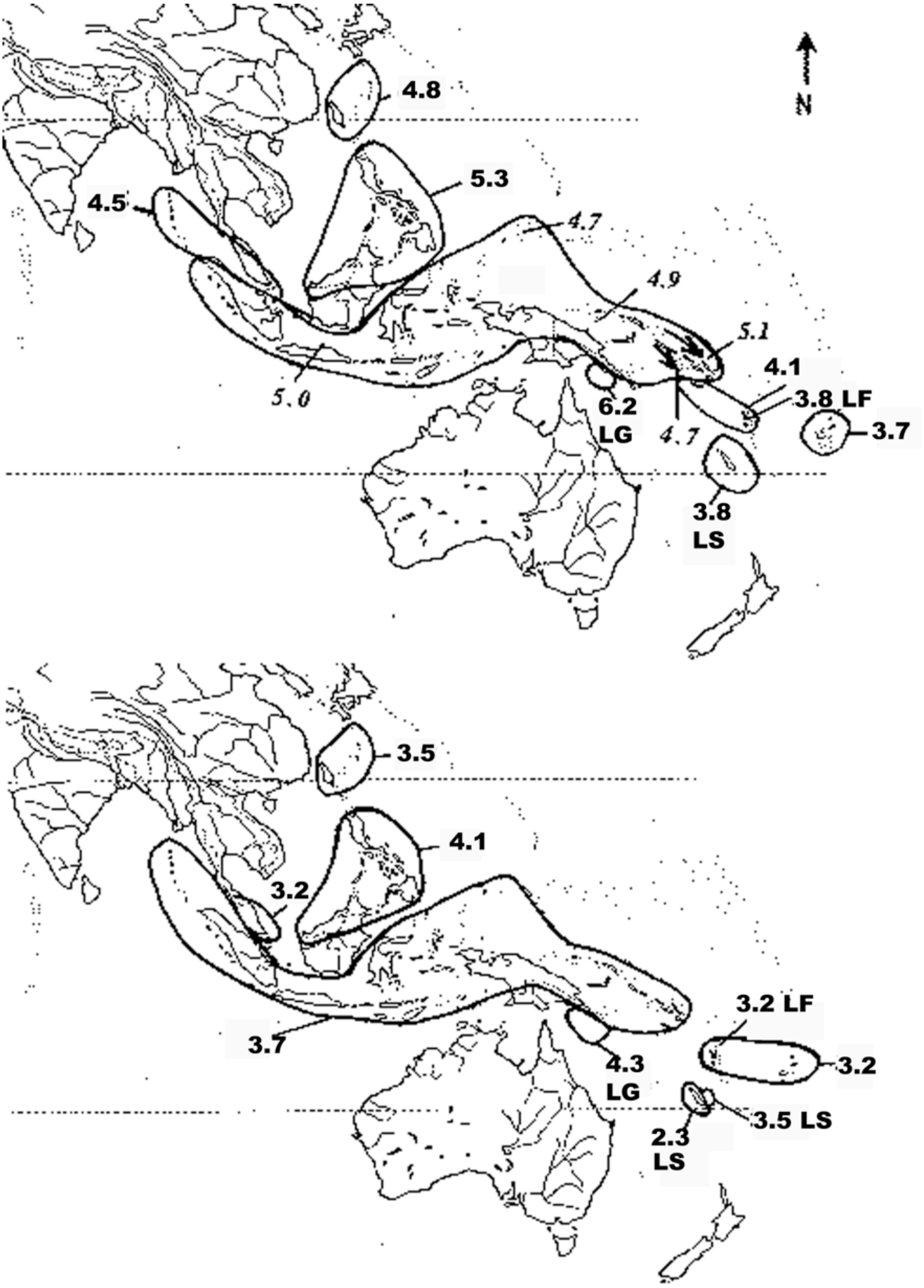


Figure 4.5. Distribution of numbers of dark bands on the tails of male (upper) and female (lower *Laticauda colubrina*, *Laticauda saintgironsi* (LS), *Laticauda guineai* (LG), and *Laticauda frontalis* (LF). Non-italicized numerals indicate means for the entire area enclosed by the polygon. Smaller italicized numerals indicate means for the corresponding subregion within a polygon. Arrows indicate possible clinal variation. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south)

Malaysia/Singapore and the Solomon Islands were the only countries that showed overall significant internal differences in number of dark tail bands in males (Appendix 4.14). In Malaysia/Singapore, the internal differences arose from two areas that differed markedly from each other, but which were each homogeneous within: Sabah and Peninsular Malaysia/Singapore. In the Solomon Islands, after disregarding one locality (Laumon) represented only by one specimen that was found to be an outlier, the internal variation arose from three general areas that differed significantly from each other overall (F=10.93; $P_{2, 29}$=0.003) and in each of the pair-wise PLSD analyses (eastern chain of islands vs. western chain of islands, $P_{1, 20}$=0.039; Rennell Island vs. eastern chain of islands, $P_{1, 14}$<0.001; Rennell vs. western chain of islands, $P_{1, 20}$=0.004).

Investigation as to whether the limits of similarity extended beyond the borders of countries revealed that there were no significant differences among the Andaman/Nicobars, Myanmar, Thailand, and Peninsular Malaysia/Singapore (F=0.52; $P_{4, 24}$=0.671). Both the Andaman/Nicobar Islands (t=-2.39; P_{39}=0.023) and Peninsular Malaysia/Singapore (t=2.86; P_{49}=0.007) differed significantly from Indonesia, their nearest neighbour to the southeast. It has already been established (see above) that Peninsular Malaysia/Singapore differs significantly from Sabah to the east. Indonesia, Papua-New Guinea, Palau, and the Solomon Islands (exclusive of Rennell Island) did not differ significantly (F=0.32; $P_{2, 64}$=0.80, although recall that the eastern and western Solomons tended to diverge from each other. The Solomon Islands overall differed significantly from Vanuatu (F=9.28; $P_{1, 63}$=0.0003), but the PLSD analysis showed that this was because of a strong, significant difference from both the eastern Solomons (P_{10}=0.0002) and the western Solomons (P_{16}=0.003); there was no significant difference between Vanuatu and Rennell Island (P_{11}=0.524). Recall that it was previously shown that Rennell Island was significantly different from the rest of the Solomon Islands (see above). Vanuatu differed significantly from Fiji to the east (t=-4.37; P_{117}<0.001) but Fiji and Tonga did not exhibit significant differences (t=-1.34; P_{98}=0.182).

Turning now to the northern limb of the geographic range, Sabah and the Philippines do not differ significantly (t=-0.92; P_{48}=0.927), but the Philippines do differ significantly from Taiwan (t=3.05; P_{39}=0.004) and from Palau (t=-3.56; P_{34}=0.0009); there is no significant difference between Taiwan and the Ryukyu Islands (t=1.30; P_{15}=0.213).

In *L. colubrina* in all areas, males had higher numbers of bands in the tail than did females (Fig. 4.5). The geographic pattern differed between the sexes in that (1) males from Vanuatu differed from those from Fiji-Tonga but no such differences occurred in the females, (2) Rennel Island grouped with Vanuatu for males but not for females, (3) Peninsular Malaysia-Singapore was an isolate in females but not in males, and (4) males from the Andaman-Nicobar islands differed from those in Indonesia but females from these areas did not differ (5) the Andaman-Nicobar Islands were linked to Peninsular Malaysia-Singapore via males but not via females. In both sexes high values in the Philippines-Sabah region decreased progressively in all directions, with the exception that the southern Papuan population had higher values than any other region.

In females of *L. saintgironsi*, there were no significant differences in number of dark tail bands among localities within New Caledonia but New Caledonia and the Loyalty Islands did differ significantly (Appendix 4.14). Males showed no significant difference in the number of dark bands on the tail among localities within New Caledonia nor, contrary to the situation in females, between the Loyalty Islands and New Caledonia.

L. guineai, restricted to southern Papua, differed significantly from *L. colubrina* in Papua-New Guinea (males $t=-6.43$; $P_{47}<0.0001$; females $t=-4.08$; $P_{41}=0.0002$) and from *L. colubrina* in the Solomon Islands, its nearest neighbour to the east (males $t=8.69$; $P_{43}<0.0001$; females $t=2.89$; $P_{44}=0.006$).

In *L. frontalis*, there were no significant differences among localities within Vanuatu, either for males ($F=1.17$; $P_{4,14}=0.226$) or females ($Z=-.050$; $P=0.617$). When comparisons were made between Vanuatu and those few specimens from other regions (Papua-New Guinea, New Caledonia and the Loyalty Islands), again there was no significant geographic difference in either sex (males $F=0.16$, $P_{4,13}=0.700$; females $F=0.36$, $P_{3,6}=0.576$).

4.3.5. Subcaudal Scales

Preliminary analysis suggested that *Laticauda colubrina* is sexually dimorphic in number of subcaudal scales with males having higher numbers than females (Appendices 4.10-4.12). This was verified by the more detailed analyses, locality by locality (Appendix 4.14); in 30 (93.8%) of the 32 tests, male *L. colubrina* had higher numbers of subcaudal scales that did females, 27 (84.4%) significantly so. In only two tests (6.3%) did females have higher values than males and in neither case was the difference significant. In *L. colubrina* most males have 39 or more scales and most females have 38 or fewer (Fig. 4.6). About 10% of males have values of 38 or fewer and about the same percentage of females have values in the male range. The actual error of sexing animals by number of subcaudal scales may be somewhat smaller than these data would suggest because of possible errors in sexing by the primary method. In all tests of *L. saintgironsi*, *L. guineai* and *L. frontalis*, males had significantly higher numbers of subcaudal scales than did females (Appendix 4.10). In *L. saintgironsi* most males have 35 or more subcaudals and most females have 35 or fewer (Fig. 4.6). Again, however, there is a small amount of overlap and sexing by this criterion is not absolute. Data were insufficient for *L. frontalis* to assess whether number of subcaudals would unequivocally differentiate between the sexes.

Because of the marked sexual dimorphism in subcaudal scales in these species, only adults of known sex were used for analyses of geographic variation, and the sexes were treated separately.

For female *L. colubrina* there were no significant differences among specific localities within nine of the ten countries for which there were sufficient data for testing at that level (Andaman Islands, Indonesia, New Guinea, Solomon Islands, Fiji, Tonga, Philippine Islands, Palau, and Taiwan; the sole exception was Vanuatu (Appendix 4.15). The PLSD analysis indicated that Tanna and Espiritu Santo, each represented by only one specimen, were outliers from the main body of data from Efate. Consequently, Vanuatu also is treated as homogeneous for number of subcaudal scales. Inspection of the means for the countries included in this area indicated a slight increase in number of subcaudal scales from northwest toward the southeast and especially northward into the Philippines (Fig. 4.6). Thus, there seems to be a slight cline with the Philippines being the most divergent country in this group.

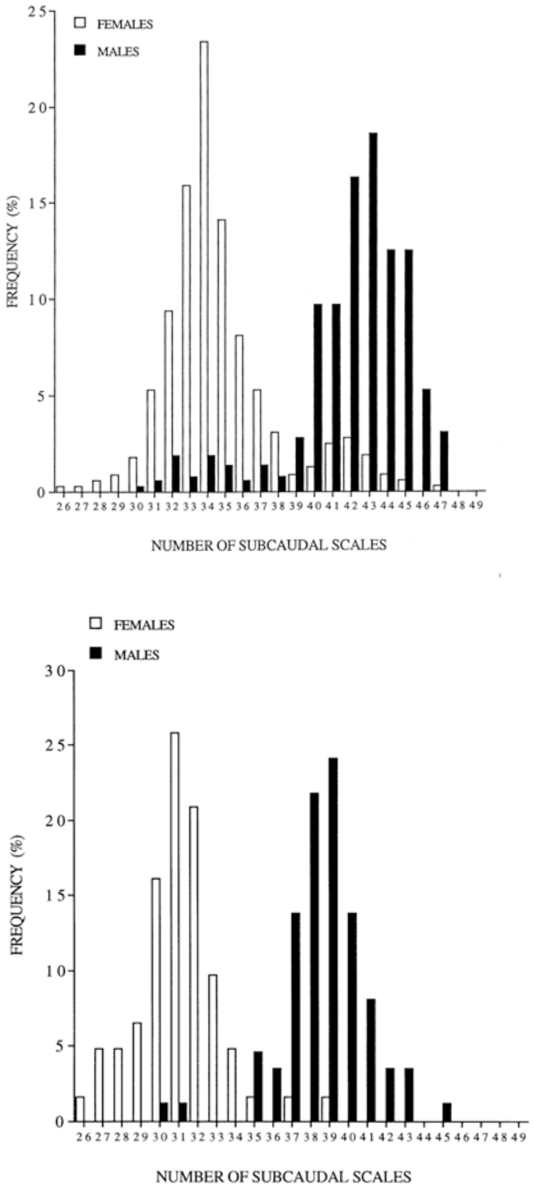


Figure 4.6. Comparison of the frequencies of number of subcaudal scales in male and female *Laticauda colubrina* (upper) and *Laticauda saintgironsi* (lower).

The countries from the Andamans through the Isthmus of Kra, Malay Peninsula, Indonesia and the Philippines were indicated by ANOVA to be homogeneous (F=1.84; $P_{4,81}$=0.112). The Philippines in the PLSD pairwise tests, however, did differ significantly from three countries: the Andamans (P_{31}=0.018), Indonesia (P_{48}=0.033) and Singapore (P_{33}=0.014). Thus, although, the Philippines seem to link with this major group in general, it is somewhat different and may be clinally related to the rest of the group as well as among the islands within its own borders (Fig. 4.7).

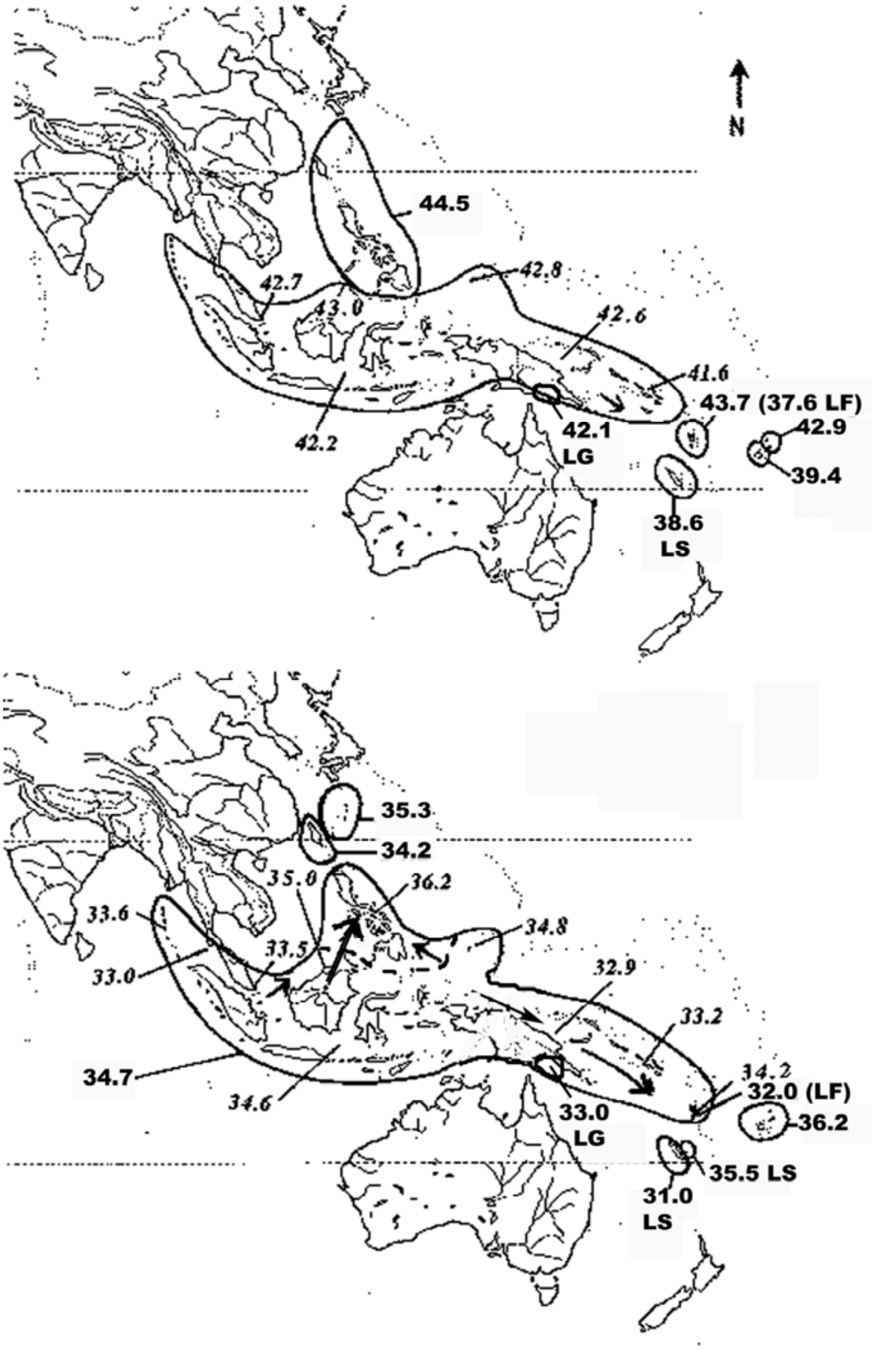


Figure 4.7. Distribution of numbers of subcaudal scales in male (upper) and female (lower *Laticauda colubrina*, *Laticauda saintgironsi* (LS), *Laticauda guineai* (LG), and *Laticauda frontalis* (LF). Non-italicized numerals indicate means for the entire area enclosed by the polygon. Smaller italicized numerals indicate means for the corresponding subregion within a polygon. Arrows indicate possible clinal variation. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

Taiwan and the Ryukyu Islands were significantly different (t=2.13; P_{34}=0.040). Although the mean value for this combination was the same as that for the central parts of the species' range (Fig. 4.7), Taiwan differed significantly from its neighbouring country in that region, the Philippines (t=3.73; P_{37}=0.0006), and thus a break occurs between the two, again indicating a somewhat distinctive status for the

Philippines in regard to this character.

Proceeding now to the southeastern limb of the geographic range, Papua-New Guinea differed significantly from Palau to the northwest ($t=-3.34$; $P_{29}=0.002$), bordered on significance with Indonesia to the west ($t=2.06$; $P_{55}=0.045$) and with the Solomons to the southeast ($t=-2.03$; $P_{39}=0.045$) and did differ significantly from Vanuatu, ($t=-3.62$; $P_{49}=0.0007$) further away in that direction. The Solomons and Vanuatu did not differ significantly ($t=-0.71$; $P_{52}=0.484$). Thus, there seems to be a cline from New Guinea through the Solomon Islands and perhaps even to Vanuatu in one direction and Indonesia in the other.

For males, the entire east-west axis of the inverted T-shaped distribution tested as homogeneous from the Andaman Islands through the Solomon Islands ($F=1.03$; $P_{6,110}=0.415$). The Solomon Islands had a slightly lower mean relative to the other countries in this group (Fig. 4.7), and in the PLSD analysis it was the only country that differed from any other in pair-wise comparisons; it was significantly different from one other region, Malaysia/Singapore ($P_{39}=0.036$). Proceeding eastward, the Solomon Islands were significantly different from Vanuatu ($t=-3.56$; $P_{63}=0.0007$), which in turn was significantly different from Fiji (-5.76; $P_{117}<0.0001$). Fiji and Tonga also differed significantly ($t=-3.25$; $P_{99}=0.002$). There was a discontinuity between the east-west axis and the northern one in that the Philippine Islands differed from all their neighbouring components of that axis, Sabah to the southwest ($t=2.88$; $P_{38}=0.006$), Indonesia to the south ($t=-4.13$; $P_{65}=0.0001$), New Guinea to the southeast ($t=-4.32$; $P_{51}<0.00001$), and Palau to the east ($t=-3.16$; $P_{47}=0.003$). On the north, there were no significant differences among the Philippines, Taiwan and the Ryukyu Islands ($F=2.06$; $P_{2,45}=0.388$).

The pattern of variation differed between the sexes (Fig. 4.7) in that (1) the Philippines were allied with Taiwan and the Ryukyus in males, but loosely with the eastern-central axis in females, (2) Taiwan and the Ryukyus were distinct in females but not in males, (3) there was either a break or a cline between Indonesia and Papua-New Guinea in females but not in males, (4) Vanuatu was clinally related to the Solomons in females but was an isolate in males, and (5) Fiji and Tonga were grouped in females but separate in males. The region with the highest values for females (Fiji) had one of the lowest values for males. In females, the number of subcaudals averaged just over 36 in the Philippines and decreased in all directions from there, the progressive decrease in the eastern chain reversing to another peak above 36 in Fiji-Tonga. In males, the northern axis of the range had high values that decreased slightly toward the southwest and southeast (Fig. 4.7).

In male *L. saintgironsi*, overall there were significant differences in number of subcaudals among specific localities and even within each of three localities, Atira, Redika, and Signal, all near Noumea; differences were significant (Appendix 4.15). Thus, this character seems to be rather labile in males of this species and significant differences occur over short distances, at least in the vicinity of Noumea. This was not the case for females which overall did not show significant variation in number of subcaudal scales within New Caledonia (Appendix 4.15). Because of variability within the New Caledonian population, it was not possible to compare males from New Caledonia with those from the Loyalty Islands for this character. However, Appendix 4.15 shows that males from the Loyalty Islands had relatively low means for males and the females had unusually high ones compared with New Caledonian localities with larger sample sizes. The difference between New Caledonia and the Loyalty Islands for females was significant (t=-3.062; P_{59}=0.004).

In *L. guineai*, there were no significant differences among localities in southern Papua New Guinea (Appendix 4.15), and unlike most characters, in this one this species did not differ significantly from neighbouring populations of *L. colubrina* in New Guinea (males t=0.82; P_{44}=0.420; females t=-3.92; P_{40}=0.697).

In *L. frontalis* the number of subcaudals was geographically stable. Individual localities within Vanuatu did not exhibit significant differences among themselves (Appendix 4.15); males from the Loyalty Islands differed significantly from those from Vanuatu (Z=-1.02; P=0.308); there were no females from the Loyalties.

4.3.6 Scale Rows around the Body

In *Laticauda* as the body enlarges posteriorly from the neck, the increased girth is at least partly accommodated by adding successive rows of scales around the body, rather than merely increasing the size of the scales (McCarthy, 1986; Guinea, 2002). Thus, the number of scales will vary depending on where along the torso the count is made. Traditionally, the count is made at mid-body. In the present study, counts were made at a series of locations to ascertain which region was the most stable, and hence most suitable for comparing species or localities.

Laticauda colubrina (all localities) had a greater number of scale rows around the body in all regions of the trunk than did the comparable sex in *L. saintgironsi* (Fig. 4.8). These differences were significant (males: $P_{337-429}<0.0001$ throughout the torso except at the last gastrostege where $P_{339}=0.0012$; females: $P_{298-374}<0.0001$ except at the last gastrostege where $P_{290}=0.0004$). Male *L. colubrina* also had significantly higher numbers of scale rows around the body than did male *L. frontalis* at all parts of the torso (males: $P_{279}=0.0014$ at the anterior gastrostege, $P_{281}=0.004$ at the vent and $P_{346-362}<0.0001$ elsewhere). Female *L. colubrina* and female *L. frontalis* did not differ significantly in the number of scale rows at the vent ($P_{256}=0.291$), but elsewhere along the torso the former species had higher counts than did the latter ($P_{313-320}<0.0001$ from the 20th to the 200th gastrostege; $P_{264}=0.006$ at the neck).

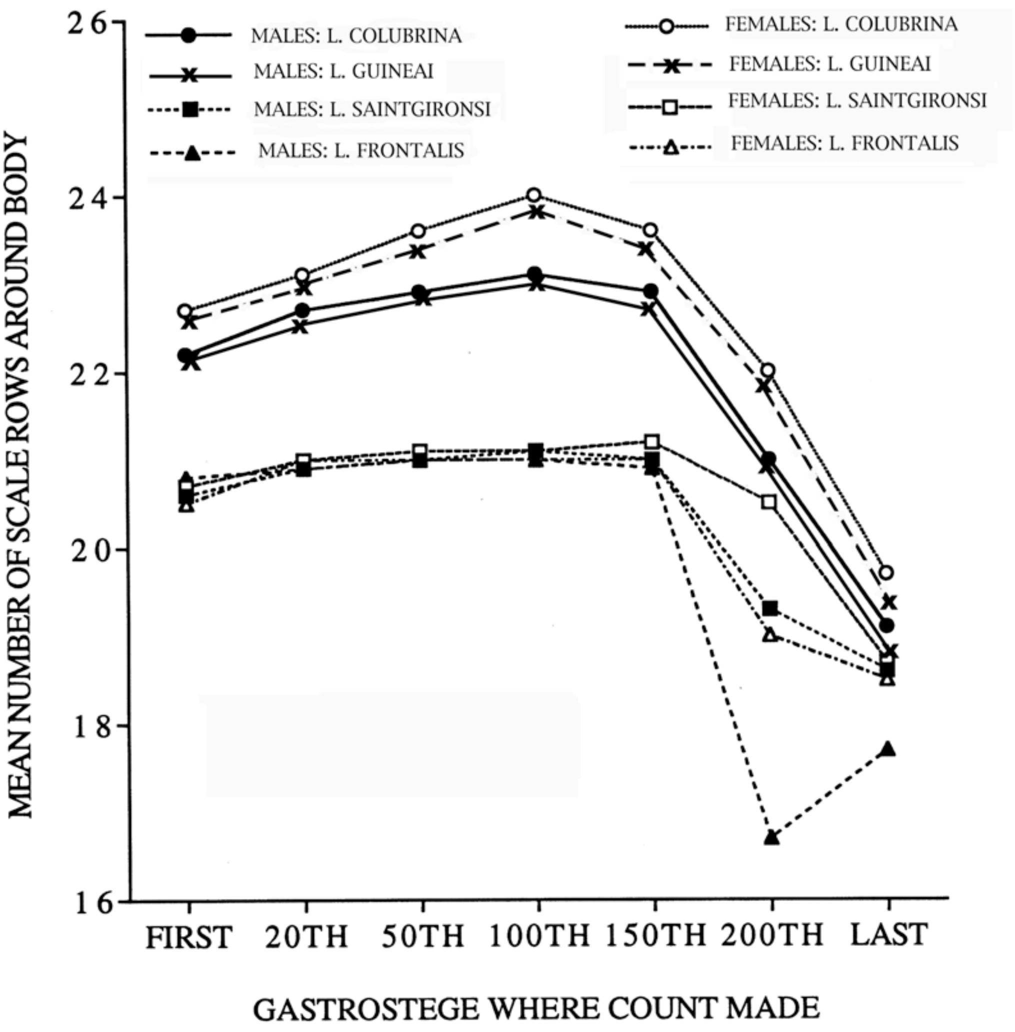


Figure 4.8. Change along the torso in the number of scale rows around the body of species in the *Laticauda colubrina* complex. Note that at the level of the 200th gastrostege in *L. frontalis*, the results were less precise because of reduced samples size; not all snakes had 200 gastrosteges.

In both sexes of *L. colubrina* the mean number of scale rows increased from the neck posteriorly until the level of the 100th gastrostege, after which it declined gradually to the 150th gastrostege and then precipitously toward the vent. At each level of the body, females consistently had higher counts than did males (Fig. 4.8). Although these sexual differences were small, with means usually differing by less than one scale row, they were significant throughout the length of the body (Appendices 4.1, 4.16).

Laticauda guineai had a nearly identical pattern to *L. colubrina* in that for both sexes there was a gradual increase in rows up to the level of the 100th gastrostege, posterior to which there was a much sharper decline; sexual differences were small, although at all levels of the torso the number of scale rows were higher in female *L. guineai* than in males but these differences were significant only from the level of the 100th gastrostege posteriorly (Appendix 4.16).

An analysis of covariance supported the above conclusions and indicated that (1) there were significant differences among species (F=254.82, $P_{3,\,5688}<0.0001$) and (2) at different positions along the torso (F=267.25, $P_{6,\,5688}<0.0001$). In addition, (3) the interactive terms of sex•species (F=5.094; $P_{3,\,5688}=0.0016$), (4) sex•torso position (F=9.33, $P_{1,\,5688}=0.0023$), and (5) species•torso position (F=11.77, $P_{3,\,5688}<0.0001$) were all significant. (6) The three-way interaction sex•species*torso position was not significant (F=1.34, $P_{3,\,5688}=0.260$).

Numbers of scale rows were higher in *L. colubrina* than in *L. guineai* at all levels of the body (Fig. 4.8), and significantly so in females at all levels ($P_{331-337}=0.0002-0.043$) except for the anteriormost ($P_{284}=0.096$) and posteriormost ($P_{273}=0.106$) ones. The interspecific differences were not significant in males ($P_{294-371}=0.063-0.986$) except at the level of the 20th ($P_{374}=0.007$), 150th ($P_{365}=0.005$) and last ($P_{296}=0.036$) gastrosteges. Both of these species had much larger numbers of scale rows than did *L. saintgironsi* and *L. frontalis* and the pattern of change was different. In the latter two species the number of scale rows did not change markedly over the torso until posterior to the level of the 150th gastrostege, at which point there was a sharp reduction in number of scale rows toward the vent (Fig. 4.8). In *L. saintgironsi* differences between the sexes were not significant over much of the torso (Appendix 4.11), but were significant at the 100th and 200th gastrosteges and near significance at the 150th gastrostege. *L. frontalis* was practically identical to *L. saintgironsi* (Fig. 4.8) except that the decline in number of scales was more precipitous in the latter. Differences between these two species were not significant from the neck to the 150th gastrostege, either for males ($P_{68\text{-}99}$=0.363-0.892) or females ($P_{36\text{-}64}$=0.145-0.936), but were significant at the level of the 200th one (males: P_{93}<0.001; females: P_{60}=0.004). At the last gastrostege the difference was borderline for males (P_{68}=0.051) and not significant for females (P_{36}=0.763).

In *L. frontalis* sexual dimorphism was not prevalent. The only level at which the sexes differed significantly was at the 200th gastrostege (Appendix 4.3), but there the sample size was small (and hence less reliable) because not all individuals had 200 gastrosteges.

Similar results were obtained from analysis of individual localities (Appendix 4.16) in that (1) sexual dimorphism was less pronounced in *L. saintgironsi* than in *L. colubrina*, and (2) in the former, differences were more often significant toward the center of the trunk than at the ends; in *L. saintgironsi* the only significant differences occurred near the posterior end (level of the 200th gastrostege). Appendix 4.16 indicates one very important point, namely that the smaller sample sizes often were unable to demonstrate sexual dimorphism. Differences were slight with the ranges being similar for both sexes (Appendices 4.10, 4.11), but with females tending to have values in the upper end of that range and males toward the lower end. Were results available only from, say, Tavarua Island, Fiji, one would conclude sexual dimorphism to be lacking in this character. However, relying only on Kia or Buiba islands (both also in Fiji) the opposite conclusion would have been drawn. Every island group throughout the entire range of the species had at least one locality in which sexual dimorphism in number of scale rows around the body was significant at least on some part of the trunk. Accordingly, it is likely that sexual dimorphism in this trait is a common feature of *L. colubrina* and failure to demonstrate it in some localities may represent a statistical artifact rather than biological lability. Because of the prevalence of significant differences in scale counts at many localities, the number of scale rows around the body was treated as a sexually dimorphic trait and males and females were analyzed separately. The analysis was carried out only on the 100th scale row, near the middle of the body where this character is most often assessed, and where differences between the sexes were most often significant (subsequently referred to merely as "scale rows around body").

For most countries, there were no significant differences among individual localities in the number of scale rows around the body of *L. colubrina*, in either males or females (Appendix 4.17). In those countries in which inter-locality differences in a particular sex reached significant levels overall, as judged by an analysis of variance, the individual tests of each locality against each other by Fisher PSLD tests showed that those differences depended upon one or a few localities represented only by one or two specimens, each registering as an outlier from one or more other localities. For example, in Indonesian females the differences among localities was accounted entirely by a single specimen (an outlier) from Timor differing from the females from all other specific localities. No Timorese male specimens were available. Within Vanuatuan females, a single specimen from the island of Tanna was an outlier in comparison to other islands in that country. Similarly, among Indonesian males significant inter-locality differences were dependent solely on one specimen from Wetar being a significant outlier from those of 16 other localities. In the males from the Philippines, two specimens from Cebu and one from Subic Bay were significant outliers from those of six of the remaining seven other localities. These few outliers based on so few specimens were considered insufficient to indicate regional variation in number of scale rows and the various localities were grouped into geographic regions of larger sample sizes. When this was done, no significant differences among regions within a country were detected for males, but three countries did show significant inter-regional differences for females. Grouping Peninsular Malaysia with the small adjacent island of Singapore into a single "country" indicated that Sabah differed significantly from Peninsular Malaysia/Singapore ($t=3.11$; $P_{20}=0.006$). Thus, the only notable discontinuity in number of scale rows at the level of the 100th ventral that occurs within the boundaries of any country is between Peninsular Malaysia+Singapore and Sabah, and then significant only in females. It would appear that populations on opposite sides of the southern South China Sea seem to have begun to differentiate in regard to this character.

For both sexes of *L. colubrina* the differences among means for different countries were less than two scale-rows in magnitude. Yet, even these slight differences allowed discrimination among three separate regions for females, (1) the north-south axis, (2) most of the east-west axis, and (3) the eastern chain of islands. In females, the east-west axis tested as homogeneous from the Andaman Islands through the Solomon Islands ($F=1.13$; $P_{5,\,111}=0.351$). The range in means over the area was only 23.3-24.2 but there was a general decrease in mean values from west to east. Hence, the slight differences in this part of the east-west axis may be clinal (Fig. 4.9).

The eastern islands differed from the east-west axis, with the discontinuity

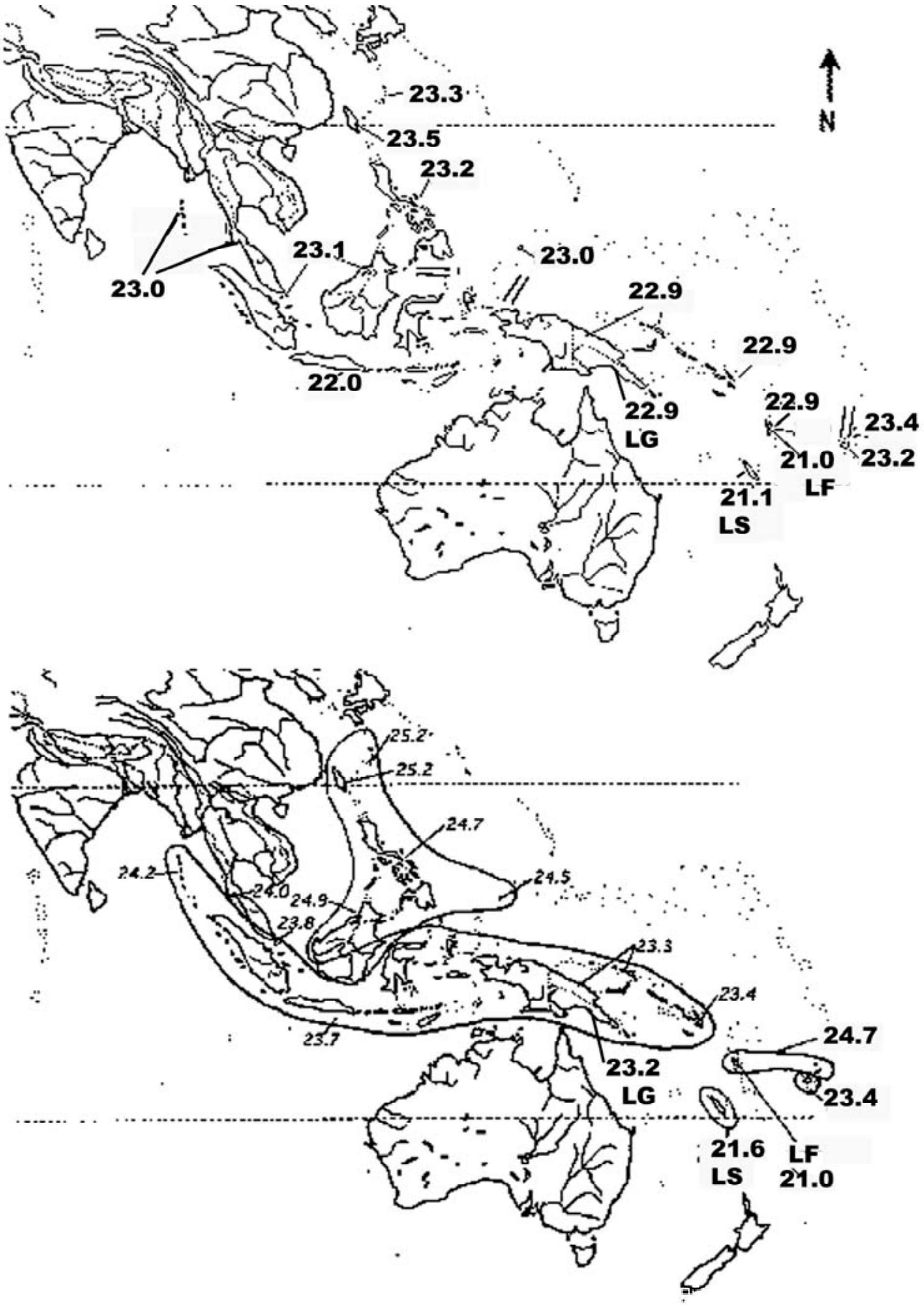


Figure 4.9. Distribution of numbers of scale rows around the body at the level of the 100th gastrostege in male (upper) and female (lower) *Laticauda colubrina*, *Latidauda saintgironsi* (Ls bold), *Laticauda guineai* (Lg bold) and *Laticauda frontalis* (Lf bold). For males, numerals indicate means for the areas indicated. Parallel bars indicate discontinuities (significant differences) between the regions on either side of the bars. For females, non-italicized numerals indicate means for the entitre area enclosed by the indicated polygon. Smaller italicized numerals indicate means for the indicated subregion within a polygon. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

occurring between the Solomon Islands and Vanuatu (t=-6.31; $P_{51}<0.0001$). Furthermore, there was significant variation among the countries within the eastern islands (F=29.2; $P_{2, 113}<0.0001$). Both Vanuatu (t=-7.98; $P_{98}<0.0001$) and Tonga (t=-5.47, $P_{81}<0.0001$) differed significantly from Fiji, but they did not differ from each other (t=0.40; P_{43}=0.689).

The means for the countries in the north-south axis ranged from 24.5-25.2 (Fig. 4.9). This axis differed significantly from the east-west one. For example, Sabah differed from Peninsular Malaysia/Singapore (see above), the Philippine neighbours in the east-west axis, Indonesia to the south (t=-3.13 P_{44}=0.003) and New Guinea to the southeast (t=-6.65; P_{25}<0.0001).

There was no significant variation among the countries within the north-south axis (Sabah, Philippines, Taiwan and the Ryukyus) (F=1.81; P_{5}=0.156).

Palau differed from Indonesia to the southwest (t=-2.14; P_{49}=0.039), New Guinea to the south (t=-5.01; P_{30}<0.0001), and the Solomon Islands to the southeast (t=4.29; P_{34}=0.0001) and thus was separate from the east-west axis. It did not differ significantly from the Philippines to the west (t=0.86; P_{31}=0.399).

In summary, for females the north-south and the east-west axes were different, with each showing slight internal clinal variation, and there were isolations in the eastern chain of islands

Variation in number of scale rows at the 100th gastrostege among males was of even smaller magnitude than for females, with means for countries ranging only from 22.9 to 23.5 (Fig. 4.9). Despite this small range of values there was significant variation among countries overall (F=2.01; $P_{14, 325}$=0.014). Although the north-south axis was joined to the east-west one in the west by lack of differentiation between the Philippines and Sabah and other western regions (Peninsular Malaysia-Singapore, Myanmar, Thailand, Andaman and Nicobar Islands (F=0.54l $P_{4, 59}$=0.748), there was a partial separation of these two axes in the east; in the PLSD pair-wise comparisons there were discontinuities between the Philippines and both Indonesia to the south (P_{53}=0.013) and New Guinea to the southeast (P_{49}=0.004). In PLSD pair-wise comparisons among islands of the eastern chain, Vanuatu differed significantly from Tonga (P_{16}=0.007).

In *L. saintgironsi*, the number of scale rows around the body did not differ significantly between New Caledonia and the Loyalty Islands, either for males (t=0.34; P_{86}=0.736) or females (t=0.78; P_{56}=0.440). Similarly, in *L. frontalis* there were no significant differences among countries (New Guinea, Vanuatu, Loyalty Islands, New Caledonia) for either males or females (Z=0; P>0.999 in both cases) although the sample sizes were small.

Both sexes of *L. saintgironsi* and *L. frontalis* seem to resemble the masculine condition of *L. colubrina* more than the feminine pattern, whereas both genders of *L. guineai* closely matches those of *L. colubrina*.

Ota *et al.* (1986) showed that within a sample of *L. colubrina* from Japan, females not only had a greater augmentation in scale rows than did males but that the subsequent reductions occurred further posteriorly in females.

4.3.7. Width of Bands

Width of bands was measured in terms of the numbers of scales encompassed by the width of the bands, not by actual distances (see Section 4.1) and hence bands in different-sized snakes are comparable. Consequently, in the following text “width” of a band is used as an abbreviation for “the number of scales in the width” of the band.

Kuntz (1963) indicated that in Taiwan the distal bands of *L. colubrina* were nearly uniform in width, but slightly narrower in the neck region. In the present study, however, quantitative comparisons detected no significant differences in the dorsal widths of the dark bands along the torso in either *Laticauda colubrina, L. guineai, L. saintgironsi,* or *L. frontalis* (Appendices 4.18- 4.20). Hence, the values of the first, tenth and 25th bands were not used as independent measures, but rather one of them (the first) was selected for detailed assessment of geographic variation. In *L. saintgironsi* the width of the first dorsal dark band did not differ significantly from that of the tenth one. The 25th dorsal dark band, however, encompassed fewer scale rows (was "narrower") significantly more often than either the first or tenth bands (Appendix 4.20). In *L. guineai* also, the 25th band tended to be narrower than the 10th one (Appendix 4.18). Because of this variation along the torso in two of the species, with the variability being greatest toward the posterior end, the first band was used for comparisons among species and for analyzing geographic variation within a species.

In contrast to the dark bands, the dorsal width of the light bands did differ along the body in all species but *L. guineai* (Appendices 4.18-4.20). In the other three species there was a posterior widening. In *L. colubrina*, it occurred progressively throughout the torso; in *L. frontalis* the widening occurred before the 10th band with no further change posteriorly and in *L. saintgironsi* there was first a widening between the first and tenth bands before narrowing again. For making geographic and interspecific comparisons of dorsal width of light bands, the first dorsal light band was used.

The relative dorsal widths of dark and light bands differed significantly in all four species (Appendices 4.19-4.21). In *L. colubrina*, *L. guineai* and *L. saintgironsi* the light bands were wider significantly more often than the dark ones all along the body. In *L. frontalis* the dorsal width of the dark and light bands did not differ significantly at the level of the first band, but posteriorly the light bands were significantly more often the wider.

The ventral widths of the dark bands varied significantly along the torso in *L. colubrina*, first narrowing and then widening again; in *L. saintgironsi* the pattern was the reverse, with first a significant widening from the anterior end toward mid-body and thereafter a narrowing. In *L. guineai* there was no detectable difference in ventral width of the dark bands from one part of the torso to another (Appendix 4.18).

First dorsal dark band.---The preliminary analysis suggested no significant differences in width of the first dorsal dark band between the sexes for any of the three species (Appendices 4.1-4.3). This was substantiated by individual analyses of the specific localities for which there were sufficient data (Appendix 4.21). There were 18 such localities for *L. colubrina*, and these were widely scattered over the entire range of the species. There were two localities with sufficient data for *L. saintgironsi*, and a single one each for *L. guineai* and *L. frontalis*. Males and females did not differ significantly in any of the species at any locality and it can be concluded that there is no sexual dimorphism in the width of the first dorsal dark band.

There were no significant differences between juveniles and either males or females for *L. colubrina*, *L. guineai*, or *L. saintgironsi* in the preliminary analysis (Appendices 4.1-4.2). However, when localities were tested individually (Appendix 4.22) for *L. colubrina*, juveniles and adults differed significantly. Recall that this character doesn't change during the life of a particular individual so differences between adults and juveniles result from changes in frequencies of traits within the population. If there were no real differences between juveniles and adults in this character, one would expect that by chance the means would be higher for juveniles than for adults in half of the observations and the reverse in the other half. The departure from expectation was significant (Wilcoxon Matched Pairs Signed Ranks test, pairing the data by locality; $0.02>P>0.01$). The pattern of differences is also interesting. In localities from all regions but two the juveniles had the higher mean values; the reverse was true for localities in Fiji and Tonga.

Although the widths of the tenth and 25th bands did not differ significantly from that of the first band in *L. colubrina* and *L. frontalis* (Appendices 4-18, 4-19), the tenth and 25th bands were tested separately to see whether the same pattern of differences between juveniles and adults existed at those levels of the torso (Appendix 4-22). At the level of the tenth dark band only one locality showed significant differences between juveniles and adults (Biak, West Irian). However, in all but two localities mean values for juveniles were greater than for adults, a result far exceeding expectations based on randomness (Wilcoxon Matched Pairs Signed Rank test: $P=0.01$). Again the exceptions were from Fiji and Tonga (Appendix 4-22) with adults having wider bands than juveniles at some localities, although not significantly so. At the level of the 25th band, at all Tongan and Fijian localities adults had greater dorsal width of the dark band than did juveniles whereas at all other localities but one (Andaman and Nicobar Islands; juvenile sample of only one) the reverse was true, with the difference being significant for one locality (Palau; Appendix A-22). Thus, at all three levels of the torso the sea kraits in the Fiji-Tonga region seem to have wider dark bands than do those everywhere else.

Juvenile *L. guineai* had significantly wider 25th bands than did adults at the single testable locality. There were no significant differences between juveniles and adults in either of the two testable localities for *L. saintgironsi* (Appendix 4.22); shortage of juveniles of *L. frontalis* prohibited testing of that species.

Because of possible differences between adults and juveniles in at least some localities of *L. colubrina*, the analysis of geographic patterns of variation in this character was carried out using only adults; data from males and females were combined. In *L. colubrina* overall, there were significant differences among localities in the width of dorsal dark bands ($F=15.29$; $P_{14.\ 568}<0.0001$). When individual countries were tested, some did not show any significant differences among localities, whereas others did (Appendix 4.23). The latter were further analyzed to ascertain internal patterns of variation. Within Malaysia/Singapore when each locality was compared with every other, about a fifth of the pairings showed significant differences (Appendix 4.23). Inspection of these revealed that all of the significant differences were between localities in Peninsular Malaysia/Singapore versus localities in Sabah, but that no localities within either of these regions were significantly different from each other. Thus, it appears that Sabahan populations and those from Peninsular

Malaysia/Singapore, are each internally homogeneous, but differ from each other. This was verified by lumping the data for each region and comparing the two regions (t = -5.02; P_{46}<0.0001).

In Indonesia over 10% of the locality-by-locality comparisons were significant. The Fisher's PLSD tests were inspected and localities that did not differ significantly were grouped by geographic regions and then those regions compared, much as explained above for Malaysia and Sabah, but more complex because of the greater number of localities involved. The regions were: Sumatra, Lesser Sundas, Arafura Sea, Moluccas and West Irian. The only misfit was Ambon which differed significantly from one other locality in the Moluccas but was placed in that group because it is geographically part of it, was represented only by a small sample (two specimens) and also differed by as much or more from localities in other adjacent regions. There was significant inter-regional variation (F=5.21; $P_{4, 69}$=0.0014). This was attributable to Sumatra differing from each of the other four (PLSD: $P_{6\text{-}34}$<0.0001-0.019); none of the other four regions differed from each other and when Sumatra was excluded from the Indonesian database, there were no longer any significant differences among regions (F=0.76; $P_{3, 53}$=0.523). Thus, on the basis of the first dorsal dark band, there seem to be two geographic groups of *L. colubrina* in Indonesia (1) Sumatra and (2) the rest of Indonesia.

In New Guinea there were significant differences among localities (Appendix 4.23). The PLSD pair-wise comparisons revealed that these differences were attributable to New Hanover having significantly higher values than many other localities, Bougainville and Karkar having lower ones and Panaeti and Kunua differing. All these significant comparisons involved localities with three or fewer specimens and consequently were considered trivial. Thus, New Guinean *L. colubrina* were treated as homogeneous for this character.

In the Solomon Islands, more than a fifth of the individually paired localities demonstrated significant differences in dorsal width of dark bands (Appendix 4.23). Most of the significant differences among specific localities were between eastern and western islands rather than within either of those regions. No significant differences occurred between any eastern localities but two islands with small sample sizes in the western group were outliers. When eastern and western regions were compared the differences were significant (t=2.54; P_{30}=0.017).

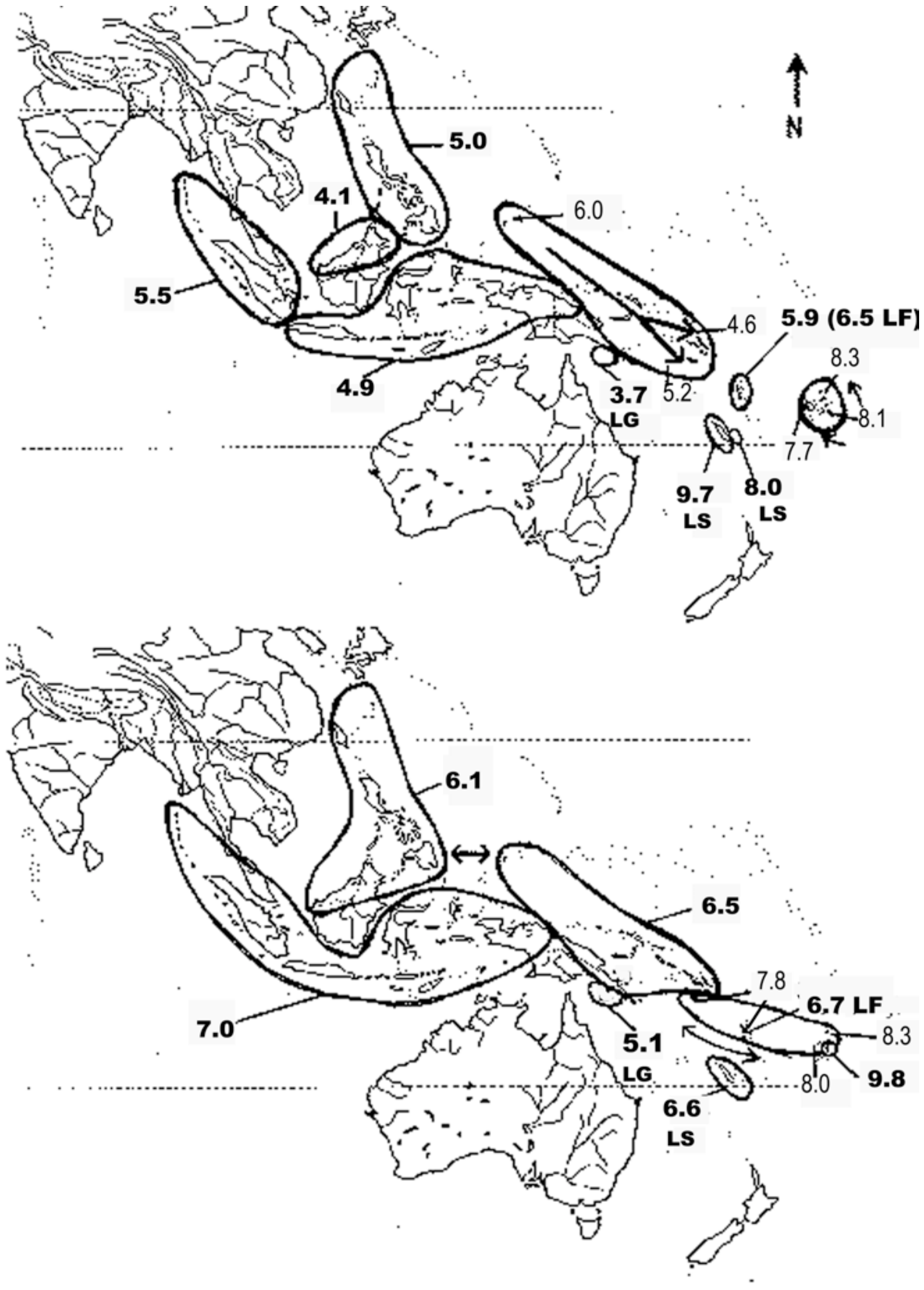


Figure 4.10. Distribution of the dorsal width of the first dark band (upper) and first light band (lower) in *Laticauda colubrina*, *Laticauda guineai* Lg), *Laticauda saintgironsi* (Ls) and *Laticauda frontalis* (*Lf*). Non-italicized numerals indicate means for the entire area enclosed by the indicated polygon. Smaller italicized numerals indicate means of the indicated subregion within a polygon. Arrows indicate possible clinal variation. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

In Fiji, almost a fourth of the individually paired comparisons showed significant differences among localities (Appendix 4.23). Two sites with only one specimen each (Masi and Lomaloma) were outliers. Grouping the localities into northern, eastern, southern and western regions gives a grouping in which no localities within any region differ significantly (except for the single outlier specimen from Lomaloma). The regions, however, differ significantly (F=2.95; $P_{3,112}$=0.036).

The western and southern regions are similar and do not differ significantly from each other (PLSD P_{69}=0.196), and similarly the eastern and northern regions do not differ significantly (P_{42}=0.582). However, the western region differs significantly from both the northern (P_{58}=0.010) and eastern (P_{27}=0.042) ones. It would seem that there are two geographic groupings (1) a southwestern one and a northeastern one (Fig. 4.10).

Now that the variation within countries has been described and statistical tests applied, only the task of linking up countries remains to complete the assessment of geographic variation in this character. To do this, adjacent regions or countries were compared so as to identify sharp discontinuities in attributes.

The Andaman and Nicobar Islands, Myanmar, Thailand, Peninsular Malaysia/Singapore, and Sumatra did not differ significantly among themselves (F=1.26; $P_{4, 61}$=0.298) and this complex can be taken as a single entity in regard to this character (Fig. 4.10). Regions within these general areas did differ significantly from adjacent ones outside the area. Thus, Peninsular Malaysia/Singapore differs significantly from Sabah (see above) and from "Rest of Indonesia" (t=2.05; P_{100}=0.043); Sabah and "Rest of Indonesia" differed significantly from each other (t=-4.85; P_{94}<0.0001).

Continuing eastward, the "Rest of Indonesia" did not differ significantly from Northern Papua (Z=-1.40; P=0.161) and Bougainville did not differ significantly from either the Eastern Solomon Islands (t=2.14; P_{12}=0.054) or the Western Solomon Islands (t=-0.68; P_{23}=0.506), but note that the former is near the rejection level. The changes in width of the first dorsal dark band does not have such sharp boundaries as in most other characters. It is likely that the changes are more clinal in nature from Eastern Papua to the Eastern Solomons. The two ends of this cline (Eastern Papua and Eastern Solomons) showed a strongly significant difference (t=8.28; P_{40}<0.0001) but with less marked differences at shorter geographic distances within the cline.

The Western Solomon Islands differed significantly from the nearby *L. guineai* (t=-7.47; P_{68}<0.0001. In the Solomons, the eastern islands differed significantly from the western ones (see above), with the western ones showing a closer relationship with Bougainville than with the eastern ones. Thus, the eastern Solomons seem to have differentiated from the western ones and to a lesser degree from Bougainville. Both regions of the Solomons differed significantly from Vanuatu (Eastern Solomons, t=-5.79; P_{61}<0.0001; Western Solomons, t=-3.60; P_{71}=0.0006). Vanuatu differed significantly both from southwestern (t=11.16; P_{120} <0.0001) and northeastern (t=13.07; P93<0.0001) Fiji. Neither region of Fiji differed significantly from Tonga (southwestern Fiji: t=-0.36; $P_{98}=0.136$; northeastern Fiji: t=0.91; $P_{71}=0.367$). Since the southwestern region of Fiji differs from the northeastern one but neither differs significantly from Tonga, the best interpretation seems to be that there is a cline from Tonga to southwestern Fiji to northwestern Fiji. For these reasons Tonga and Fiji are combined as a single group containing a cline.

Returning now to the northeastern part of the geographic range of *L. colubrina*, the Philippine Islands differed significantly from Sabah (t=-4.37; $P_{68}<0.0001$), again leaving Sabah as an isolated population. The Philippines. Taiwan and the Ryukyu Islands did not differ significantly from each other (F=0.09; $P_{2,102}=0.910$) nor did any of these differ from any other in PLSD paired combinations (P ranged from 0.673 to 0.917) and they all can be considered members of a common group. Palau differed significantly from all three members of this group (Philippines: t=5.42; $P_{81}<0.0001$. Taiwan: t=4.95; $P_{59}<0.0001$. Ryukyus: t=4.74; $P_{55}<0.0001$), its nearest neighbours to the west and northwest, as well as from its neighbours to the southwest (Rest of Indonesia; t=-6.0; $P_{96}<0.0001$) and south (northern Papua: Z=-1.76; P=0.08) and was at the borderline of significance with its nearest neighbour to the southeast (Eastern Papua; t=2.05; $P_{62}=0.05$). This puts Palau on the northwestern end of the cline Palau-Eastern Papua-Bougainville-Solomon Islands. In this cline Palau borders on significance with the next island area in the geographic sequence, Eastern Papua (see above) or Bougainville (P=0.206) but differs significantly from the most distant ones: Bougainville (t=-1.08; $P_{35}=0.290$), Western Solomons (t=3.63; $P_{52}=0.0007$), Eastern Solomons (t=-5.45; $P_{42}<0.0001$).

In summary, based on the dorsal width of the first dark band, there seem to be seven distinct geographic subgroups of *L. colubrina*, (1) the western part of the range from the Andaman Islands through Sumatra, Thailand and Peninsular Malaysia, (2) the central part of the range including the remainder of Indonesia and northern Papua, (3) Sabah, (4) the Ryukyus, Taiwan and the Philippines, (5) a cline running from Palau through eastern Papua, to Bougainville and then the Solomons, with the southeastern end of this cline diverging into the Eastern Solomons and the Western Solomons, (6) Vanuatu, (7) a cline running from Tonga to Fiji and diverging in the latter place (Fig. 4.10).

The final stage in the hierarchical analysis was to compare each of these groups with each other by an ANOVA accompanied by PLSD comparisons of each group with every other. Note, however, that including an entire cline in a single group for such an analysis is not strictly valid, and interpretations based on such lumping should be interpreted in light of the variation within the group.

As anticipated, there was significant variation exhibited among the groups (F=164.79; $P_{7, 551}$<0.0001). There were 28 paired-comparisons (each group compared individually with every other group); differences between members of pairs were significant in 23 (82.1%) of the cases. Four of the five comparisons that lacked significance were between pairs of groups remote from each other in the archipelago. Since direction of change in values of this character altered from west to east (see below), this does not affect the validity of the groupings. The single exception of two adjacent groups not being significant was between the eastern cline and Vanuatu. Values in the cline decrease from northwest to southeast. Vanuatu has significantly higher values (see Fig. 4.10) than the southeastern localities nearest it, but resemble the higher values in the remotest part of the cline. Thus, lumping the different parts of the cline was probably responsible for a spurious result, and the original grouping is retained.

In *L. saintgironsi* there were no significant differences in the width of the first dorsal dark band among localities within New Caledonia (F=1.50; $P_{16, 106}$=0.118), but New Caledonia did differ significantly from the site in the Loyalty Islands (t=2.45; P_{109}=0.016). There were no significant differences among localities in width of the first dark band in either *L. guineai* (F=1.09; $P_{1, 41}$=0.302) or *L. frontalis* (F=2.42; $P_{5, 20}$=0.086).

First dorsal light band.---The dorsal width of the first light band did not differ significantly between the sexes for any of the localities with sufficient data for testing in any of the three species (Appendix 4.24). This confirmed the preliminary, rough analysis for *L. colubrina*, *L. guineai* and *L. saintgironsi* (Appendices 4.10, 4.11). The preliminary analysis suggested that there was sexual dimorphism in this character for *L. frontalis* (Appendix 4.3) but the more refined analysis reversed this conclusion. Thus, the width of the first light band does not appear to be sexually dimorphic in any of the three species and data from both sexes can be combined for geographic comparison.

Comparison of juveniles and adults of all individual localities from which both stages were sufficiently represented indicated that at most places differences between juveniles and adults of *L. colubrina* were not significant (Appendix 4.25). However, for two localities (Singapore and Suva) differences were significant; the conservative approach was taken and juveniles were excluded from the analysis of geographic pattern of variation in this character.

An ANOVA testing all specific localities over the entire range of *L. colubrina* revealed that there was highly significant geographic variation in this character ($F=5.52$; $P_{103, 454}<0.0001$). When countries were tested individually, it was found that fewer showed differences among localities internally than was the case for dorsal width of the first dark band and in those that did, the percentage of paired localities with significant differences was usually lower (compare Appendices 4.23 and 4.26). It appears that the dorsal width of the first light band is more stable geographically than is that of the first dark band.

All seven countries that showed no significant internal differences in dorsal width of the first dark band in *L. colubrina* also lacked significant variation among internal localities in the dorsal width of the first light band (Appendices 4.24, 4.27). One country, Indonesia, that had significant internal variability in the first dark band, had geographically homogeneous light ones and hence was not divided into regions. In Malaysia-Singapore there were significant differences among specific localities (Appendix 4.26); all these differences were between localities on peninsular Malaysia/Singapore and those on Sabah, but not among localities within either of those regions. When the localities from each area were combined and peninsular Malaysia/Singapore compared with Sabah the two regions differed significantly ($t=-4.42$; $P_{46}<0.0001$), as was the case with dorsal width of the first dark band.

There were no significant differences among localities in Papua-New Guinea (Appendix 4.26). Differences among specific localities within the Solomon Islands were significant (Appendix 4.26). PLSD analyses showed that this resulted mainly from Rennell being significantly different ($P_{9\text{-}17}=0.002\text{-}0.043$) from all but two of the other islands (Shortlands and Laumona; $P_{11, 11}=0.141\text{-}0.392$). The only other significant difference was the single specimen from Choiseul being an outlier to two other localities ($P_{3, 3}=0.012\text{-}0.033$). Thus, for this character, there seems to be two distinct populations in the Solomon Islands, one on Rennell Island and the other occurring everywhere else. The difference between these two groups was highly significant ($t=3.65$; $P_{29}=0.001$).

There were significant differences among specific localities within Fiji

(Appendix 4.26) but PLSD analysis showed that all of these resulted from the single specimen from Masi being an outlier from all localities in the northern, western and southern districts, and Aiwa (again a single specimen) being an outlier from all localities but one (Vomo) in those districts. Both Masi and Aiwa are in the eastern district and thus the eastern district may differ somewhat in this character from the other districts. This was borne out by a PLSD comparison of these districts after combining all the localities within each district; the eastern district differed significantly from all three others ($P_{22\text{-}48}<0.0001\text{-}0.0002$), but none of those three differed among themselves ($P_{55\text{-}81}=0.551\text{-}0.749$). For further geographic comparisons of this character, Fiji was deemed to consist of two areas, one encompassing the northern, western, and southern districts, and the other consisting of the eastern district alone.

Based on the above assessments the different regions were altered for four countries from that used in analyzing the dorsal width of the first dark band: (1) Indonesia is treated as a single region, (2) the Solomon Islands are separated into Rennell Island alone and all others combined, and (3) Fiji is considered as consisting of an eastern district separate from all others combined. Using these new boundaries, an ANOVA indicated significant overall variation among regions (F=15.99; $P_{18, 504}<0.0001$). However, not all regions differed from each other. The Andaman Islands, Myanmar, Thailand, Peninsular Malaysia/Singapore and Indonesia did not differ significantly from each other (F=0.49; $P_{4, 130}=0.743$) and these can be considered to constitute a single group. Sabah differed significantly from its western (Peninsular Malaysia-Singapore: t=-4.42; $P_{46}<0.0001$) and southern (Indonesia: t=4.43; $P_{85}<0.0001$) neighbours but not from its northeastern one (Philippines: t=-0.54; $P_{68}=0.609$). Sabah, the Philippines, Taiwan and the Ryukyus showed no significant differences among themselves (F=1.25; $P_{2, 100}=0.243$).

Papua-New Guinea, Palau, and the Solomon Islands (excluding Rennell; see above) were not significantly different overall (F=0.22; $P_{68}=0.805$) and they can be considered as a homogeneous group for this character.

Palau was significantly different from its nearest neighbour to the southwest (Indonesia; t=2.44; $P_{97}=0.017$), and was near the border of significance with the Philippines to the west (t=1.78; $P_{80}=0.079$). Although Palau was more similar to Papua-New Guinea than to the Philippines, its lack of significance with the latter suggests at least a clinal relationship between the two.

Rennell Island not only was significantly different from the rest of the Solomon Islands (see above), but was also significantly different from its northwestern neighbour, Papua-New Guinea (t=-4.27; $P_{44}<0.001$). It did not differ from its neighbour to the southeast, Vanuatu (t=-0.11; $P_{59}=0.910$). Thus, in this character, Rennell is allied to Vanuatu, but not to the rest of the Solomon Islands.

Overall there was no significant difference among the islands of the chain: Rennell-Vanuatu-Fiji (excluding the eastern district)-Tonga (F=1.97; $P_{3, 221}=0.120$). However, there was a progressive increase in mean values along this series (Fig. 4.99). Thus, this region may be clinal (Fig. 4.10). The eastern district of Fiji differed significantly both from the other districts of Fiji (see above) and from Tonga (t=2.25; $P_{34}=0.032$) and appears to be an isolate.

The number of scale rows in the dorsal width of the first light band is highest in the southeastern part of the geographic range of *L. colubrina* and decreases to the north and west, with the far west again showing a slight increase (Fig. 4.10).

There were fewer groupings for light bands for *L. colubrina* than for dark bands (Fig. 4.10). The light bands combined Sabah with the Philippines-Taiwan-Ryukyu group, whereas the dark bands did not. In dark bands there was also a break between Sumatra and the rest of Indonesia that did not occur in the light bands. Rennel Island was part of the Solomon Island grouping for dark bands, but was allied with the extreme eastern islands for light bands, and finally, the affinities in the Vanuatu-Fiji-Tonga group aligned differently for the two colours of bands.

For *L. saintgironsi* there were no significant differences among localities within New Caledonia proper (H=24.6; P=0.138) nor did New Caledonia did differ significantly from the Loyalty Islands (t=-0.72; $P_{109}=0.472$). Neither *L. guineai* (F=0.017; $P_{1, 41}=0.897$) nor L. *frontalis* (H=2.13; P=0.831) showed significant variation among localities.

Ventral light bands.---Since the dark "bands" in some specimens from these localities were in fact "saddles" in that the dark marking did not extend all the way to the ventral side, the ventral width of some dark bands was zero and that of the corresponding light ones "indefinite" (beyond the limits of the band-unit being considered). For this reason, statistical analysis could not be applied to the ventral widths of light bands. Rather, the frequency of occurrence of incomplete bands was ascertained.

L. colubrina, *L. guineai* and *L. saintgironsi* from all localities had a preponderance of individuals in which all the dark bands completely encircled the body. Indeed, in all but two countries, values exceeded 85%; the two exceptions were the Solomon Islands and Tonga, and even in these more than 65% of the snakes had complete dark bands (Appendix 4.27). The situation was just the opposite in *L. frontalis* in which all animals had at least some bands incomplete and frequently, most or all bands did not meet below. In the other species, when incomplete bands occurred, there were usually only a few bands that were incomplete, whereas in *L. frontalis* many, and sometimes all, the bands failed to meet below.

The mean incidence of incomplete bands varied along the torso in all three species, the percentage being highest anteriorly and then decreasing toward the tail (Appendix 4.28).

Relative dorsal widths of light and dark bands on the body.---Fischer (1856) indicated that the dark bands on the body of *L. colubrina* were almost twice as wide as the intervening light bands, whereas Boulenger (1912) considered the dark bands equal to or narrower than the width of the light interspaces. Inspection of Figure 4.10 suggests that the dorsal widths of the dark and light bands do not vary in exactly the same ways geographically. The following analysis was undertaken to quantify the relative widths of the two colours of bands. Relative band-width was expressed as the ratio obtained by dividing the number of scale rows in the dark band by the number in the light band. Hence, values greater than one indicate that the dark band is the wider of the two and values less than one indicate a relatively greater width of the light band. Because width of band was not sexually dimorphic for either colour of band, males and females were combined for calculation of ratios between the widths of the two types of bands.

A preliminary analysis of the whole dataset indicated that different localities differed significantly in ratio of widths of the first dark and the first light bands ($F=7.67$; $P_{99, 446}<0.0001$). For further analysis, the smallest geographic units testing as homogeneous for either band colour alone were first used in testing for homogeneity of ratios. For example, the Andaman and Nicobar Islands, Thailand, Peninsular Malaysia/Singapore, and Sumatra tested as a homogeneous unit for width of dark bands (Fig. 4.11) and that unit was used rather than the larger one for light bands that in addition included the rest of Indonesia. Thus, the maximum number of possible units was tested.

The Andaman and Nicobar Islands, Myanmar, Thailand, Peninsular Malaysia/Singapore and Sumatra were homogeneous for ratio of band widths (F=1.70; $P_{4,64}$=0.162), as was the group composed of the Ryukyus, Taiwan and the Philippines (F=1.02; $P_{2,90}$=0.363). Given the clinal nature of the width of the first dark band in the region from Palau to the Solomon Islands, and in Fiji-Tonga, the ratios of widths for the eastern islands were not tested for homogeneity, but are portrayed separately for the various island groups or subregions within an island group (Fig. 4.11). In general, dark bands in *L. colubrina* were relatively narrower than light ones in the entire north-south axis, western part of the east-west axis, and the region from the Solomon Islands through Vanuatu in the east. In Palau, the islands and eastern coast of Papua, Tonga, and most of Fiji, dark and light bands were nearly equal in width (Fig. 4.11) despite regional differences in the absolute values of those widths (Fig. 4.10).

The ratio of dorsal width of the two colours of bands showed no significant differences among localities either for *L. guineai* (F=1.09; $P_{2,52}$=0.362) or for *L. frontalis* (H=8.14; P=0.149).

Because the dorsal width of the dark bands of *L. saintgironsi* differed significantly between New Caledonia and the Loyalty Islands, but that of the ventral ones did not, it was anticipated that the ratio of these two measures would also differ significantly between these two regions, and such proved to be the case (t=2.77; P_{112}=0.006).

De Vis (1905) in the original description of *L. frontalis* indicated that the dark bands were narrower than the light spaces between them. The present study confirmed this conclusion (Appendix 4.19; see above). The mean dorsal width of the light bands was greater than that of the dark band at all levels of the torso tested: first band (dark=6.4 scales; light=6.7 scales), tenth band (dark=5.8; light=7.3) and 25th band (dark=5.4; light =7.4). However, the effect was less pronounced anteriorly than in the middle part of the body (Appendix 4.19); the differences between mean widths of bands of different colour were not significant at the levels of the first (t=-1.24; P_{46}=0.220) band but was at the tenth (t=-5.59; P_{45}<0.0001) and 25th band (t=-8.00; P_{45}<0.0001).

Dorsal-ventral attenuation of the dark bands on the body.---In each of two animals (one from the Solomon Islands and the other from the Nicobar Islands) one dark band failed to meet dorsally. In one from Halmahera there was one incomplete band that occurred only on the venter and the left side. A single specimen from Java had two dark bands that were offset with the right and left semicircles failing to meet either ventrally or dorsally. In one animal from southern Papua the dark bands flared wider ventrally. Except for these rare variants the dark bands took one of two forms, either (1) encircling the body completely and with their widths remaining unchanged, or (2) narrowing on the sides, sometimes to the extent of failing to meet below, thereby forming dorsal "saddles" or "blotches" on the dorsum.

As an expression of the dorsal-ventral attenuation of complete dark bands, the dorsal width of the first dark band was divided by its ventral width. Thus, the higher the value, the greater is the degree of attenuation of band-width from the dorsum to venter. Because width of dark bands was not sexually dimorphic (Appendix 4.21), both sexes were combined for analysis of attenuation, but because of the possibility of differences between juveniles and adults (Appendix 4.22), only adults were used. There was variation in the degree of attenuation along the body. Attenuation was greatest at the level of the tenth dark band (mean=3.4) and decreased both anteriorly (3.0 at first band) and posteriorly (2.9 at 25th band). Each of these regions was significantly different from every other ($P_{54\text{-}57}$<0.0001 to 0.021). For geographic comparisons (Fig. 4.11), data from the first band were used and the regions were those defined by statistical analysis of the width of dark bands.

In *L. colubrina*, there were no significant differences in attenuation among the Andaman and Nicobar Islands, Myanmar, Thailand, Peninsular Malaysia/Singapore and Sumatra (F=0.87; $P_{5, 58}$=0.490), or between the rest of Indonesia and northern Papua (z=-1.31;P=0.183), but there were significant differences among the Ryukyu Islands, Taiwan and the Philippines overall (F=12.83; $P_{2, 91}$<0.0001). These differences arose from the Philippines differing significantly from both Taiwan (PLSD P_{68}=0.001) and the Ryukyus (P_{64}<0.0001); the Ryukyus and Taiwan did not differ significantly (P_{49}=0.174). Because of the clinal nature of variation in dorsal width of dark bands in the Palau-eastern Papua-Solomon Island area and in Tonga-Fiji, no statistical tests for internal homogeneity were conducted and means for individual subregions are presented (Fig. 4.11).

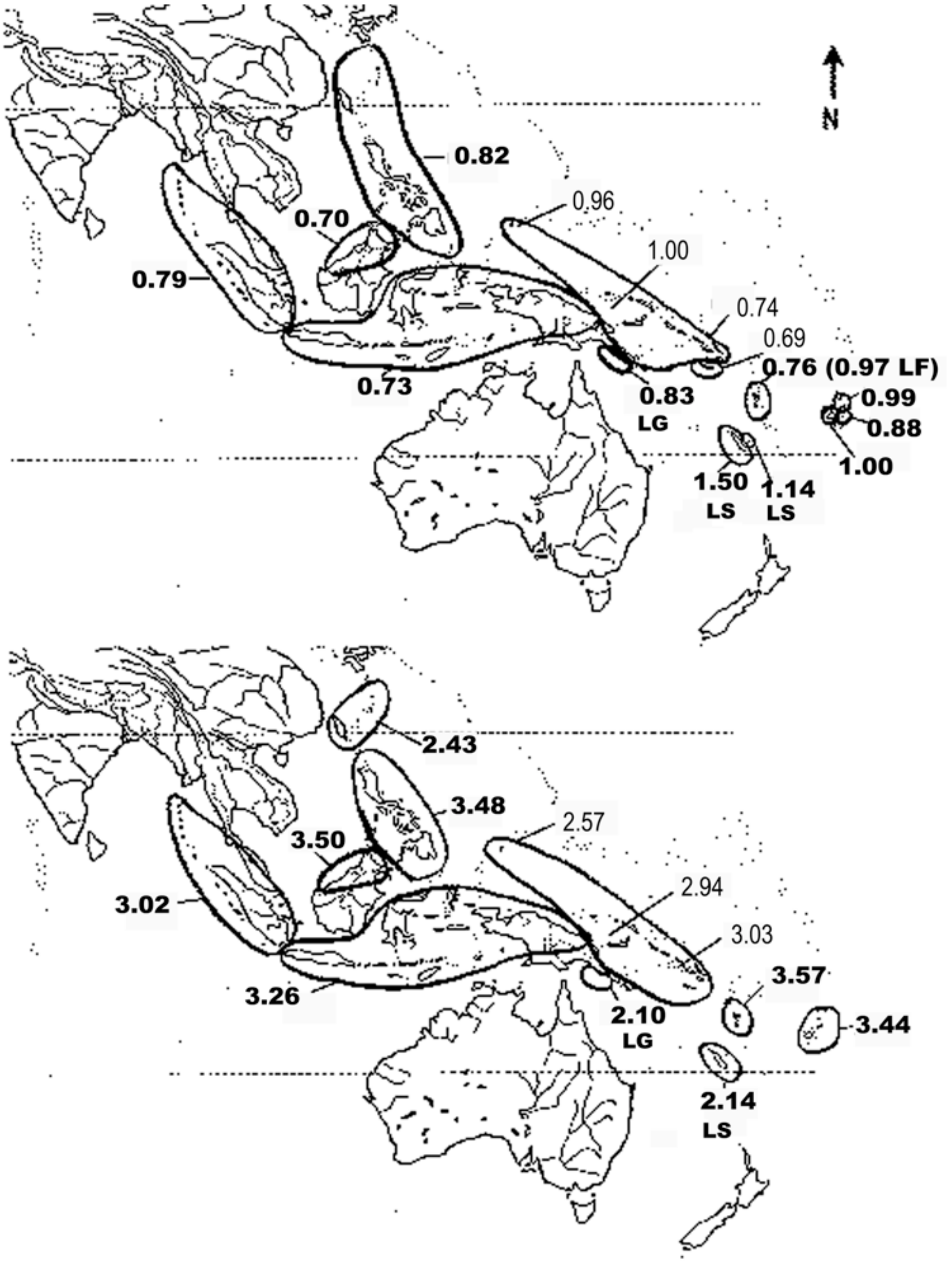


Figure 4.11. Distribution of the ratio of dorsal widths of the first dark and first light bands (upper) on the bodies of *Laticauda colubrina*, *Laticauda guineai*, *Laticauda saintgironsi* and *Laticauda frontalis* and of the ratio of the dorsal and ventral widths of the first dark band (lower) on the bodies of *Laticauda colubrina*, *Laticauda guineai*, and *Laticauda saintgironsi* (in *Laticauda frontalis* the body bands are saddles and seldom meet below). Non-italicized numerals indicate means for the entire area enclosed by the indicated polygon. Smaller italicized numerals indicate means for the indicated subregion within a polygon. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

4.3.8. Gastrosteges

The preliminary analysis (Appendix 4.1) suggested a sexual dimorphism in number of gastrosteges in *L. colubrina*. This was confirmed by t-tests between the sexes at each locality for which both sexes were represented and the combined number of specimens was ten or greater (Appendix 4.29). At 18 of the 19 such localities, females had higher mean counts of gastrosteges than did males, a result that was highly significant (Wilcoxon Sums Matched-pairs Signed-ranks test, pairing data by locality; Z=3.76, P<<0.0001) and half of these localities individually exhibited significant differences between the sexes (Appendix 4.29). Those nine localities were scattered throughout the range of the species' distributional range. At Kia, Fiji, the only locality at which males had a higher mean count, the difference between the sexes was slight (only 1.5 scales) and was not significant. In one rare variant (from West Irian) there were incomplete sutures partly splitting some of the gastrosteges.

The preliminary analysis also suggested sexual dimorphism in this character for *L. saintgironsi* (Appendix 4.2). At all three localities that were testable individually, females had higher mean counts than did males, and at two of them the differences were significant (Appendix 4.30). The situation was less clear for *L. frontalis* as the range of values did not differ greatly between males and females (Appendix 4.3) and in the sole locality that could be tested individually, females had a higher mean count than did males, but the difference was not significant (Appendix 4.30).

The preliminary analysis also suggested sexual dimorphism in this character for *L. guineai*, with females having the higher counts (Appendix 4.11), a conclusion supported by the more detailed analysis (Appendix 4.29).

In view of the fact that all three species exhibited higher counts of gastrosteges in females than in males and that in *L. colubrina*, *L. guineai* and *L. saintgironsi* these differences achieved significance overall and/or at many individual localities, this character was considered sexually dimorphic. Consequently, only adults were analyzed for geographic variation, and the sexes were treated separately.

For *L. colubrina* females, no country for which there were adequate data for testing (Andaman Islands, Indonesia, Malaysia, Papua-New Guinea, Solomon Islands, Fiji, Tonga, Philippine Islands, Palau and Taiwan) showed significant interlocality differences in number of gastrosteges (F=0.62-5.22; H=3.98-5.07; $P_{2,\ 13-12,\ 60}$=0.070-0.773).

For males, there were no significant interlocality differences in eight of the testable countries: Thailand, Indonesia, Vanuatu, Fiji, Tonga, Philippine Islands, Palau, and Taiwan (F=0.19-1.96; $P_{1, 22 – 13, 37}$=0.076-0.818; Thailand H=1.80, P=0.407; Taiwan Z=-1.68, P=0.093).

Males of three countries (Malaysia-Singapore, Papua New Guinea, Solomon Islands) did show overall interlocality differences that were significant. In Malaysia-Singapore (F=3.42; $P_{4, 19}$=0.029) the significant pair-wise PLSD differences involved pairing of localities between Sabah and Peninsular Malaysia-Singapore, except for one locality with only one specimen. When Sabah was compared with Peninsular Malaysia/Singapore overall, however, the difference was not significant (t=-0.062; P_{22}=0.951). For these reasons, Malaysia was treated as homogeneous with respect to this character despite the overall significant F-test. In Papua New Guinea the overall differences among localities were significant (F=3.62; $P_{8, 22}$=0.017 but all but one of the significant PLSDs represented differences between either Admiralty or Karkar with only two and one specimen(s) respectively; again it was treated as a homogeneous region.

The significant overall variation among males in the Solomon Islands (F=2.55; $P_{7, 28}$=0.046) arose from two sources, (1) a significant PLSD pair-wise comparison between Rennell Island and New Georgia (P_{14}=0.036) and (2) the island of Choiseul (sample of only one specimen) being an outlier to seven other islands. The latter result is treated as trivial. The former suggested that Rennell Island might be somewhat isolated, but when Rennell was compared to the rest of the Solomon Islands collectively, the result was not significant (t=1.09; P_{22}=0.285) and that hypothesis was rejected.

In contrast to the weak variation in number of gastrosteges among localities within countries, the overall variation among countries was highly significant both for females (F=26.99; $P_{13, 296}$<0.0001) and males (F=5.69; $P_{14, 331}$<0.0001).

For females, 69% of the PLSD pair-wise comparisons among countries were significant at a 5% rejection level. Comparisons between adjacent countries allows geographic groupings to become evident. The Andaman Islands, Thailand, and Indonesia did not display significant differences with each other in any pair-wise combination (P_{12-48}=0.269-0.917), but all three were each significantly different from Malaysia-Singapore (P_{11-47}<0.0001-0.042), and the Philippines (P_{22-58}<0.0001-0.027).

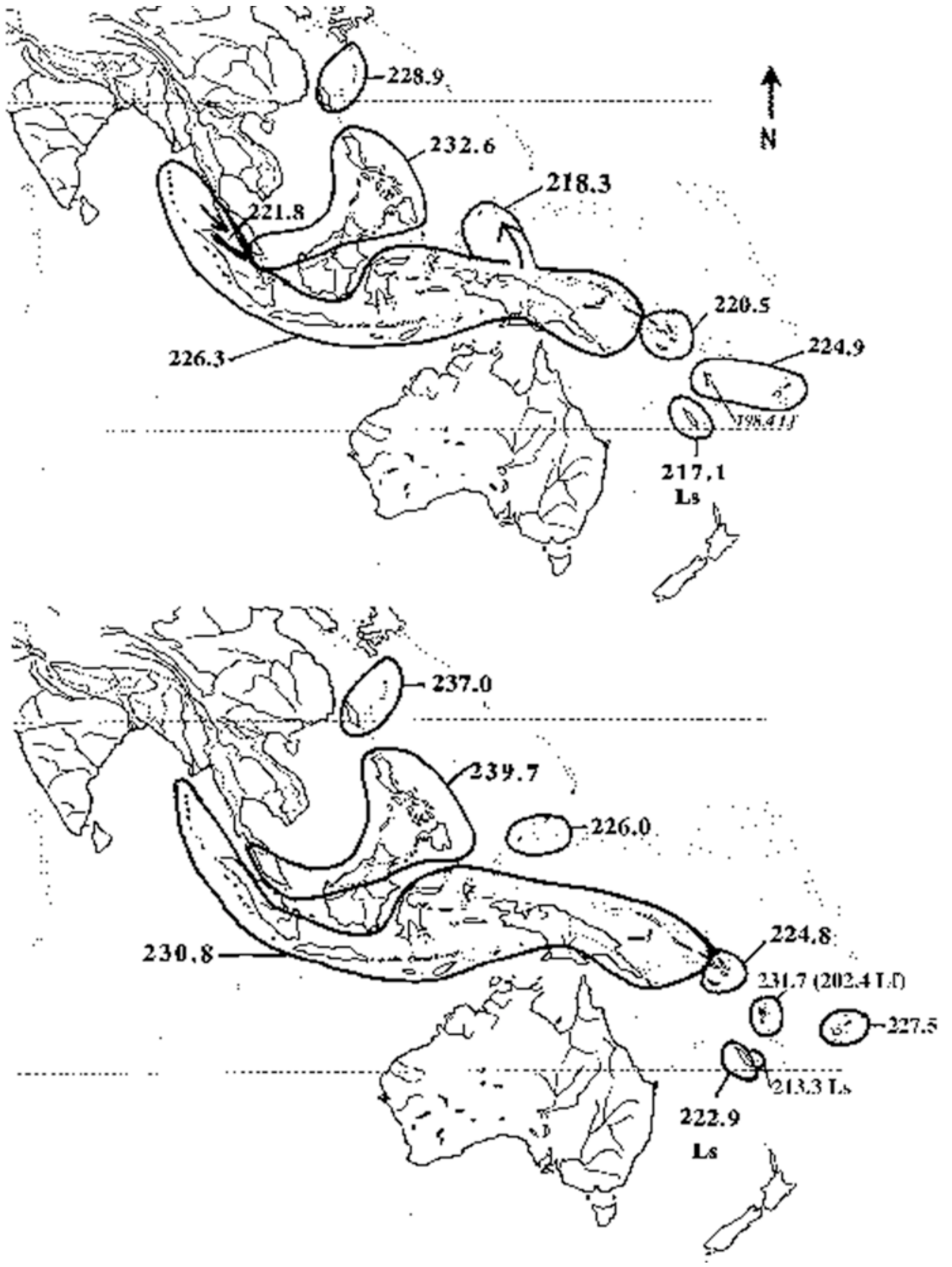


Figure 4.12. Distribution of the number of gastrosteges in male (upper) and female (lower) *Laticauda colubrina* , *Laticauda guineai*, *Laticauda saintgironsi* (Ls), and *Laticauda frontalis* (Lf). Non-italicized numerals indicate means for the entire area enclosed by indicated polygon. Smaller italicized numerals indicate means for the indicated subregion within a polygon. Arrows indicate possible clinal variation. Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

The latter two countries were not significantly different ($P_{41}=0.643$) and thus constitute a single geographic unit with respect to this character (Fig. 4.12). The latter two countries showed significant differences from their nearest neighbours to the north and east (Philippines vs. Taiwan, $P_{37}=0.017$; Philippines vs. Palau, $P_{34}<0.0001$; Indonesia vs. Palau, $P_{51}=0.012$; Indonesia vs. New Guinea $P_{54}=0.010$).

Taiwan and the Ryukyus were not significantly different ($P_{34}=0.066$) and constituted a small northern isolate. New Guinea did not differ significantly from the Solomon Islands ($P_{38}=0.652$) but the latter differed significantly from Vanuatu to the southeast ($P_{53}<0.0001$). Vanuatu, in turn differed significantly from Fiji ($P_{100}<0.001$). At the southeastern end of the species' range, Fiji and Tonga did not differ significantly from each other ($P_{82}=0.096$).

For males overall, there were significant differences among countries ($F=24.23$; $P_{14, 331}<0.0001$). Fifty-nine% of the PLSD pair-wise comparisons among countries were significant at a 5% rejection level. The Andaman Islands did not differ from either Indonesia ($P_{46}=0.580$) or Thailand ($P_{7}=0.347$), but the latter bordered on significance with Indonesia ($P_{48}=0.056$) and Thailand may be beginning to diverge clinally (Fig. 4.12). Myanmar, represented only by one specimen and situated between the Andaman Islands and Thailand, did not differ significantly either from the Andamans ($P_{3}=0.331$) or from Thailand ($P_{5}=0.116$). Papua New Guinea did differ significantly from Indonesia ($P_{66}<0.0001$). Malaysia-Singapore and the Philippine Islands did not differ significantly ($P_{43}=0.457$). This group showed significant divergence from Thailand, its nearest neighbour on the west (Malaysia-Singapore vs. Thailand, $P_{18}<0.0001$), Indonesia on the south (Malaysia-Singapore vs. Indonesia, $P_{57}<0.0001$; Philippines vs. Indonesia, $P_{73}<0.0001$), Papua New Guinea to the southeast (Philippines vs. Papua New Guinea, $P_{52}<0.0001$), Taiwan to the north (Philippines vs. Taiwan, $P_{41}=0.017$), and Palau to the east (Palau vs. Philippines, $P_{38}<0.0001$). Taiwan and the Ryukyus did not differ significantly ($P_{17}=0.846$). Palau bordered significance with New Guinea, its nearest neighbour to the south ($P_{41}=0.049$), but not from the presumed waifs of the Pacific ($P_{19}=0.245$). Proceeding southeasterly from New Guinea, that region did not differ significantly from the Solomon Islands ($P_{52}=0.909$), but the Solomons differed significantly from Vanuatu ($P_{65}=0.0011$). Vanuatu, Fiji, and Tonga formed a homogeneous group, with none differing significantly from any of the others ($P_{51\text{-}100}=0.417\text{-}0.881$).

Considering both sexes of *L. colubrina* (Fig. 4.12), the populations of the north-south axis had higher numbers of gastrosteges than did those of the east-west axis. Within the latter, there was first a trend of increasing scale counts, followed by a decreasing one from east to west in males and alternate highs and lows in females.

Laticauda guineai in southern Papua differed from adjacent *L. colubrina* in Papua New Guinea, both for females ($t=7.54$; $P_{36}<0.0001$) and for males ($t=9.56$; $P_{42}<0.0001$).

In a more detailed analysis than presented here, Cogger and Heatwole (2006) showed that in neither *L. frontalis* nor *L. saintgironsi* did males and females differ significantly in number of gastrosteges. *L. saintgironsi* overlapped with *L. colubrina*, but *L. frontalis* had significantly fewer gastrosteges than either of the other two species.

4.3.9. Colour Pattern of the Head and Tip of Tail

Before analyzing geographic variation in colour pattern of the head (Figs. 3.1-3.6), it was necessary to ascertain whether this character showed sexual dimorphism. Only two regions had the requisite number of specimens for testing *L. colubrina* and in neither of them were there significant differences between males and females (Appendix 4.30). In *L. saintgironsi* from New Caledonia both sexes overwhelmingly had the same dominant head pattern, but they differed significantly with respect to incidences of the less common ones, and in further analyses for that species, males and females are treated separately. There were too few specimens of *L. guineai* and *L. frontalis* to test for sexual differences and the two genders were treated collectively.

Of the 27 colour patterns of the head and neck, most were uncommon (less than 10%), and in a given region there usually were four or fewer that were represented at high incidences in the population. For the complex as a whole, the most common types were A, C, D, and I; in addition, types H, and Q sometimes occurred in moderate or high frequency (Appendix 4.31). *L. colubrina* had 25 patterns, all except Z and a. *L. saintgironsi* had 13 patterns (A, C, D, F, G, H, I, J, Q, X, Y, Z, a), *L. guineai* had 11 (A, B, C, D, E, L, M, N, P, W, b) and *L. frontalis* only two, H and I, the latter represented by one individual only. Shine *et al.* (2002b) noted that head pattern was a reliable criterion for separating *L. colubrina* from *L. frontalis* in the field.

The four species differed markedly in colour pattern, with both sexes of *L. saintgironsi* having predominantly the I pattern, *L. frontalis* having configuration H in which the head pattern did not connect with any of the body bands, and the Vanuatu population of *L. colubrina* (sympatric with *L. frontalis* and nearest neighbour to *L. saintgironsi*) having the D pattern as dominant. In *L. guineai*, the A pattern was dominant.

In *L. colubrina*, there was geographic variation in the incidence of head patterns. There was no significant difference between Tonga and Fiji, but otherwise each region was significantly different from its nearest neighbours (Appendix 4.31). These differences reflected variations in the relative abundance of particular types, especially of the more minor ones, even though the dominant form was the same in many adjacent regions. The D pattern is the most common one as it was the dominant pattern along the entire east-west axis, except for two pockets (Thailand and Palau-to-West-Irian) where C was dominant. It should be noted that the sample from Thailand was smaller (10) than those from other regions and its characterization therefore less reliable.

In the north, from the Ryukyu Islands of Japan through Taiwan and the Philippines to Sabah, type A was the dominant form and showed an infusion into the Indonesian region, including West Irian, as a moderately large component (Fig. 4.13).

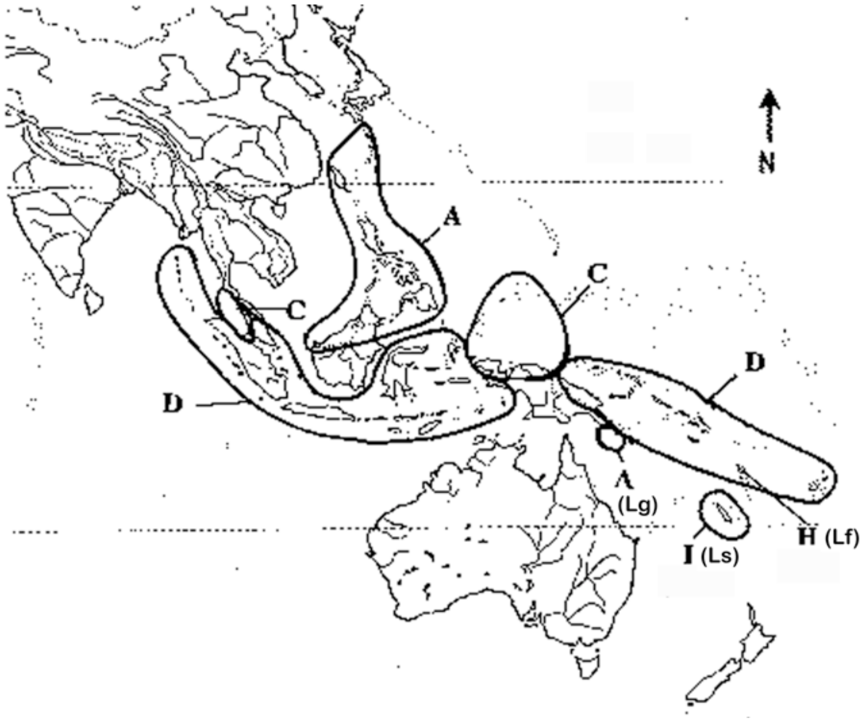


Figure 4.13. Distribution of the dominant colour patterns of the head in *Laticauda colubrina*, *Laticauda guineai* (Lg), *Laticauda saintgironsi* (Ls) and *Laticauda frontalis* (Lf). Dotted lines indicate the Tropic of Cancer (north) and the Tropic of Capricorn (south).

There were several rather abrupt changes in incidence of colour patterns. The two sides of the Thai-Malaysian peninsula differed markedly, the Thai side having predominantly a C pattern and the Malaysian side having mainly type D. There was also a marked difference between peninsular Malaysia/Singapore (mostly type D) on the western side of the South China Sea and Sabah (type A) on the eastern side.

West Irian and Palau had a predominantly type C pattern, with a moderately large secondary one of type A, perhaps influenced by gene flow from the adjacent northern regions that carried A as the dominant pattern. The effect of the West Irian populations can be seen in the secondary, rather large incidences of type C to the southeast in northern and eastern New Guinea and the Solomon Islands. The Solomon Islands had rather high incidences of types A and C as well as the dominant pattern D. The high values of C may represent gene flow from the area of predominantly type C in West Irian via northern New Guinea (see Appendix 4.31, Fig. 4.13).

It is likely that the pockets of predominantly C pattern in Thailand and West Irian were independently derived because of the distance separating them and the barriers to dispersal between them.

The incidence of the cephalic spot was low in most localities for all three species. Only Tonga, at the extreme eastern end of the geographic range of *L. colubrina*, had an incidence exceeding 10%.

In summary, the inverted T-shaped distribution of *L. colubrina* is characterized by an east-west axis characterized by a predominance of pattern D and a north-south axis mainly of type A. Superimposed upon this are pockets of type C in Thailand and West Irian. The latter two appear to export their predominant pattern type to adjacent regions where they are reflected by moderately high secondary incidences; the Solomon Islands seem to be affected by infusions of type C from northern and eastern New Guinea.

The incidence of asymmetry in head pattern was low in *L. colubrina* (6.0% of the specimens) and *L. saintgironsi* (4.7%) but somewhat higher in *L. guineai* (14.6%). No asymmetry of head pattern was observed in *L. frontalis*. In total, there were 20 different combinations in *L. colubrina* in which one pattern was present on the left side of the head and a different one on the right side. Pattern D was most often involved, participating in 32.8% of the asymmetrical occurrences. Patterns A (23.1%) and C (16.8%) also were well represented; all other pattern-types individually participated in 4.5% or fewer of the asymmetrical occurrences. The most common individual combination was C+D, accounting for 29.9% of the asymmetrical occurrences; A+D was second and accounted for 23.9%. Each of the other individual combinations accounted for 7.5% or fewer of the specimens with asymmetrical patterns. Patterns J, S, T, and V occurred as an asymmetrical partner with another pattern, once each, but never accounted for the pattern on both sides of the head in any specimen.

In *L. saintgironsi*, most (62.5%) of the asymmetrical configurations involved head pattern H on one side, most often in combination with I (37.2%)%), but also linked with D and Q. D was the second most common participant in asymmetrical configurations (25.0%) and was linked with H, Q, and F. J was the only other head type in this species that was observed to participate in an asymmetrical configuration (with I). In *L. guineai*, the asymmetrical colour patterns were mainly A+B (50%), but A+L, A+K, B+D, and L+W were represented by 12.5% each.

In addition to variation in the number and widths of the dark and light bands (see above), there were differences among species in features of the colour pattern on the body. There were several variants of the details of the ventral colouration of *L. colubrina*. Four specimens from Fiji had small, darker, backwardly-directed markings that resembled nicks in the anterior edge of the gastrostege. There was one on each side, about half way between the midline and the lateral margin of the gastrostege. The collective appearance of these markings was of a pair of interrupted ventral lines running the length of the body.

In the great majority of *L. saintgironsi* there was a mid-ventral, light-coloured marking in the centre of the dark band. Most often this marking was circular, but occasionally it was oval and rarely of other configurations (oblong, cross-shaped, a series of flecks, or two oval or oblong markings). In *L. guineai*, a ventral light spot occurred only rarely, and in *L. colubrina*, not at all (Appendix 4.27). Because the dark bands fail to meet ventrally in *L. frontalis*, this character is not applicable to this species.

A light-coloured tip of the tail was the only condition observed in *L. saintgironsi* and *L. frontalis* (Appendix 4.27). In *L. colubrina*, this form was predominant, but in addition in most localities some individuals had a black tip to the tail. The proportion of black tail-tips was 13% or less in all localities but three. In Thailand a third of the specimens had black tips (but sample size was rather small). Perhaps reflecting gene flow from southern Papua, the nearby Solomon Islands had a slightly elevated incidence of black tail-tips (17%). By contrast, Pernetta (1977) noted incidences of black tips of 23-83% in two Fijian populations; he reported that the sexes differed significantly. In the present study, *L. guinea* had nearly equal numbers of black-tipped (43%) and light-tipped (57%) tails (Appendix 4.27).

4.4. Synthesis

The various characters showed similar patterns of geographic variation for *L. colubrina*, but with minor difference among them. The commonalities were (1) an east-west axis stretching from the islands in the Bay of Bengal stretching eastward through the Malay Peninsula, Indonesia, and the island of New Guinea to the Solomon Islands, (2) a north-south axis from Sabah through the Philippines and Taiwan to the Ryukyu Islands, (3) the eastern chain of islands from Vanuatu to Fiji to Tonga, and (4) Palau, which had some characteristics of the north-south axis and others of the east-west one. Within, each of these areas, there were discontinuities in a few characters. The most common breaks occurred between Taiwan and the Philippines, Indonesia and New Guinea, and Sumatra and the rest of Indonesia. The eastern islands showed less cohesiveness than either of the two axes, with discontinuities in some characters between Vanuatu and Fiji/Tonga and between Fiji and Tonga.

4.5. Recapitulation

- An hierarchical method was developed for assessing geographic patterns of variation by progressively connecting populations along a geographic continuum into areas homogeneous for particular characters, separated from other such homeogeneous areas by sharp discontinuities. Congruences of homogeneous areas and discontinuities for different characters served as a basis for describing new species and for identifying morphologically distinct, geographically discrete units within species. The method allows distinguishing between populations whose morphological similarities are likely based on gene flow between them and those whose similarities probably arise from convergent responses to selection by similar environments, or influenced by environmental influences upon developmental processes.
- Some characters (e.g., configuration of the rostral, nasals, supralabials, position of yolk sac scar) were relatively stable in *Laticauda colubrina*, with rare departures not showing a consistent geographic pattern. They were not, however, as reliable as previously believed for consistently separating the *L.*

colubrina complex from other complexes in the genus.

- Most variable characters were sexually dimorphic, thereby demanding that the two sexes be subjected to separate analyses.
- In some populations, juveniles differed significantly from adults in characters that do not change ontogenetically, the significance of which is discussed in Chapter 8.
- Two new species, *Laticauda saintgironsi* and *Laticauda guineai* were discovered (and described elsewhere) on the basis of the hierarchical analysis and the specific status of *Laticauda frontalis* was confirmed.
- *Laticauda colubrina* is broken up geographically into four main morphologically distinguishable groups, (1) an east-west axis from the Bay of Bengal to the Solomon Islands, (2) a north-south axis from Sabah to the Ryukyu Islands, (3) an eastern island group including Vanuatu, Fiji, and Tonga, and (4) Palau, somewhat intermediate between 1 and 2. The eastern islands are less homogeneous than are the two axes.

CHAPTER 5. GEOGRAPHIC VARIATION: PRINCIPAL COMPONENTS ANALYSIS

This chapter applies Principal Components Analysis to the dataset as a further means of (1) defining the taxa of the *Laticauda colubrina* complex and (2) assessing sexual dimorphism, as well as (3) quantifying the degree of morphological divergence among the taxa and of (4) evaluating the relative importance of different characters in defining patterns of geographic variation.

5.1. Methods

While there were four taxa involved in the study, two of them, *Laticauda frontalis* and *L. saintgironsi,* had relatively few specimens (see above). Consequently, I utilized principal component analysis to assess the degree of sexual dimorphism within *L. colubrina* and to suggest which variables within the dataset might best describe variation among species within *Laticauda*. First, all juveniles and specimens with incomplete data were removed from the dataset, and then "input" original data from the 26 continuously-distributed characters (number of prefrontal scales; supralabials on the left; supralabials on the right; dorsal scale rows included in dark bands 1, 10, and 25 and light bands 1, 10, and 25; number of dark bands on the body; number of dark bands on the tail; number of gastrosteges; number of gastrosteges included in dark-coloured bands 1, 10, and 25 and light-coloured bands 1, 10, and 25; number of scale rows around the body at the levels of the first, 20th, 50th, 100th, 150th, 200th and last gastrostege; and number of subcaudals) were used for a principal component analysis.

Examination of derived factors allowed construction of a preliminary list of each character's importance to that factor (the variable with the highest loading on a factor "defines" the factor). The variable with the highest loading in each of the 26 factors was selected as representative of that factor and all 26 variables were arranged in a sequential listing with the variable having the highest loading in factor one being first, and the variable in factor 26 being last. When a variable that had already appeared on the list had the highest loading on a second factor, the variable with the next highest loading was selected as representative of that factor. This variable list was then used as the initial character-loading sequence for various iterations of the discriminant function analysis. As in the principal component analysis, original data derived from each specimen were used as "input" data.

Eighteen geographic entities were represented in the original dataset: Andaman and Nicobar Islands; Fiji; Vanuatu; Indonesia (including West Irian); Peninsular Malaysia/Singapore; Sabah; Rest of New Guinea (New Guinea excluding Irian Jaya and SE Papua); SE Papua; Palau; Philippines; Ryukyus; Solomon Islands; Taiwan; Thailand; Tonga; Myanmar (Burma); New Caledonia; and the Loyalty Islands. These entities were used both individually, and then as condensed into six localities grouped as (1) the North-South Axis (Sabah, Philippines, Ryukyus, and Taiwan), (2) the 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) Eastern Islands (Vanuatu, Fiji, Tonga), and (6) New Caledonia.

Males and females were examined separately by Discriminant Function analysis. The initial data matrix included all available data for each of the 26 characters, the locality, and the species name for all species in the complex. As the ultimate goal was to create one matrix each for males and females that would assign the maximum number of specimens to the localities from which they originated, I began by using all characters and eliminated characters one by one to achieve that goal. Later these matrices were modified to include only *Laticauda colubrina* and the classification function of discriminant function analysis was used to predict the provenance of waifs and specimens whose exact locality was unknown or suspected to be in error.

The computer-based statistical package SYSTAT 9.0 for Windows (2000) was used for all these analyses.

The Principal Components Analysis eliminates any specimen that lacks data for any of the characters included in the database. Data could not be obtained for all characters for every specimen (see Chapter 3) and the sample size was reduced by the number of specimens with missing data, and by the fact that sexual dimorphism necessitated eliminating juveniles. One can increase the sample size, however, by reducing the number of characters included in the database. Accordingly, different numbers of characters were used for different comparisons in order to optimize the analysis. Such reductions were not believed to weaken the conclusions because even the six most important characters accounted for 95% of the variation (Table 5.1).

Table 5.1. Ranking of characters by percentage of variation explained in the Principal Components Analysis.

GENDER/ORDER OF COMPONENTS	VARIATION EXPLAINED		
	%	CUMULATIVE %	CHARACTER
MALES			
1	65.9	65.9	Number of gastrosteges
2	18.7	84.6	Number of subcaudals
3	5.7	90.3	Number of dark bands on body
4	1.8	92.1	Number of dark bands on tail
5	1.6	93.7	Scales in width of 25th dark band (dorsal)
6	0.9	94.6	Number of scale rows at 200th gastrostege
7-26	5.4	100.0	All other characters
FEMALES			
1	61.6	61.6	Number of dark bands on body
2	20.2	81.8	Number of gastrosteges
3	6.5	88.3	Number of subcaudals
4	2.8	91.1	Scales in width of 25th light band (ventral)
5	2.1	93.2	Scales in width of 25th dark band (dorsal)
6	2.1	95.3	Number of scale rows at 150th gastrostege
7-26	4.8	100.1	All other characters

5.2. Results and Discussion

Complete data for 211 adult males and 219 adult females of *L. colubrina* were condensed to five significant (eigenvalue representing at least as much variation as might be contributed by a single variable) principal components that explain 68% of the variance within the dataset.

The most important character alone accounted for over 60% of the variation, with diminishing improvement obtained by adding further characters, such that the use of more than the six top characters added little to the analysis (Table 5.1). The most important characters were the same for both sexes, but the rank order changed. For example, for females the number of gastrosteges, number of subcaudals, and number of dark bands were the top three characters and ranked in that order; for males, the same three characters occupied the top spot but number of dark bands ranked first, gastrosteges second and subcaudals third. Further rankings were less similar, but both sexes included in the following three, ranked some measure of band-width and number of scale rows. When factor scores from the five significant components identified in the principal component analysis were used as "input" data, 93% of adult males, and 88% of adult females were correctly classified to sex by discriminant function. Graphic examination of the first and second principal components clearly demonstrates the degree of dimorphism between the sexes (Fig. 5-1) and confirms the necessity of treating males and females separately in geographic comparisons. A discriminant function analysis using eight characters

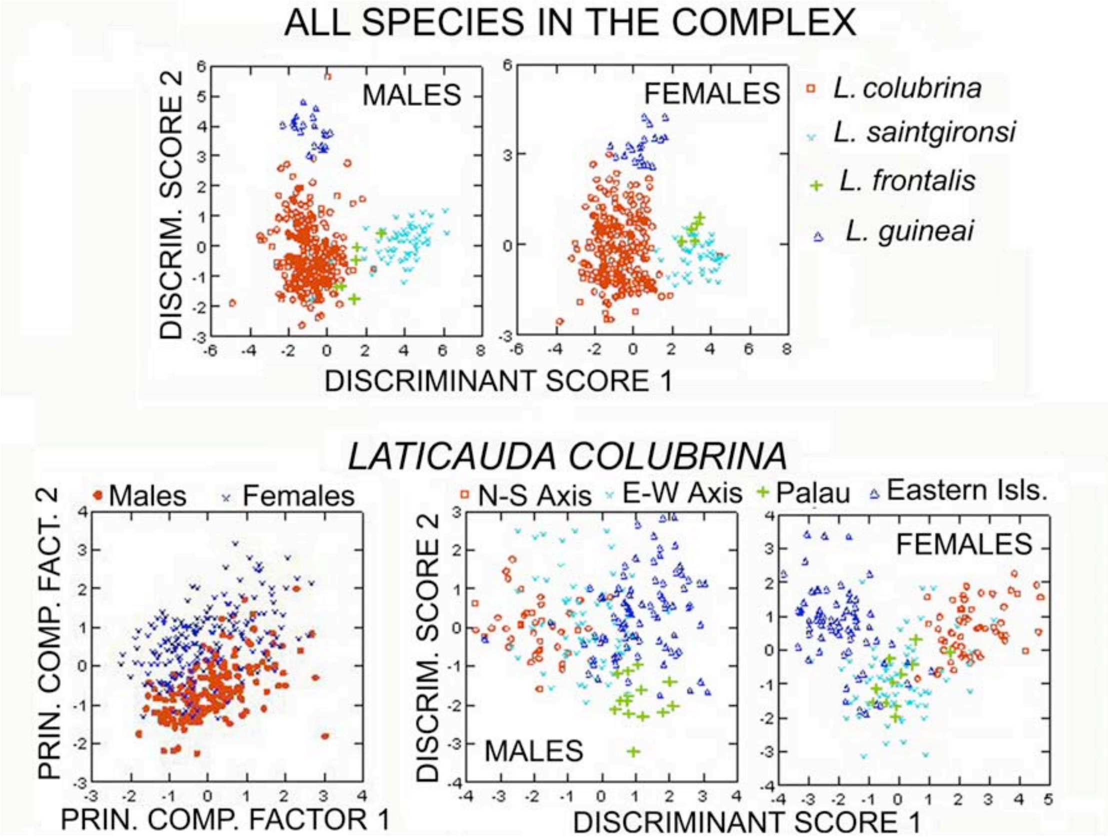


Figure 5.1. Upper: Relationship of the first and second principal component factors for adult males (left) and females (right) of *Laticauda colubrina*, *L. saintgironsi*, *L. frontalis*, and *L. guineai*. The database consists of all specimens with complete data for the 13 (males) and 12 (females) most important characters (see Methods). Females: N=233 (*L. colubrina*), 43 (*L. saintgironsi*), 21 (*L. guineai*), and 11 (*L. frontalis*). Lower: Relationship of the first and second principal component factors for adult male and female *L. colubrina* from all localities combined (left) and for adult male (centre) and female (right) *Laticauda colubrina* from different geographic regions.

(numbers of dorsal scale rows included in dark band 25; dark bands on the body; dark bands on the tail; gasrosteges; scale rows around the body at the levels of the 100th and 150th gastrosteges; subcaudals) for females and seven (number of dorsal scale rows included in dark and light band 25; dark bands on the body; dark bands on the tail; gastrosteges; scale rows around the body at the level of the 150th gastrostege; subcaudals) for males assigned specimens correctly to species with 93% and 95% accuracy respectively.

Laticauda colubrina occupies the central position in the scattergram (Fig. 5.1) with only marginal overlap with *L. guineai* on the one hand and *L. saintgironsi* on the other; *L. frontalis* is separate from *L. colubrina* and quite distant from *L. guineai*, but overlaps broadly with *L. saintgironsi*. This pattern is consistent with the view that *L. colubrina* is the primitive member of the complex, having given rise to *L.*

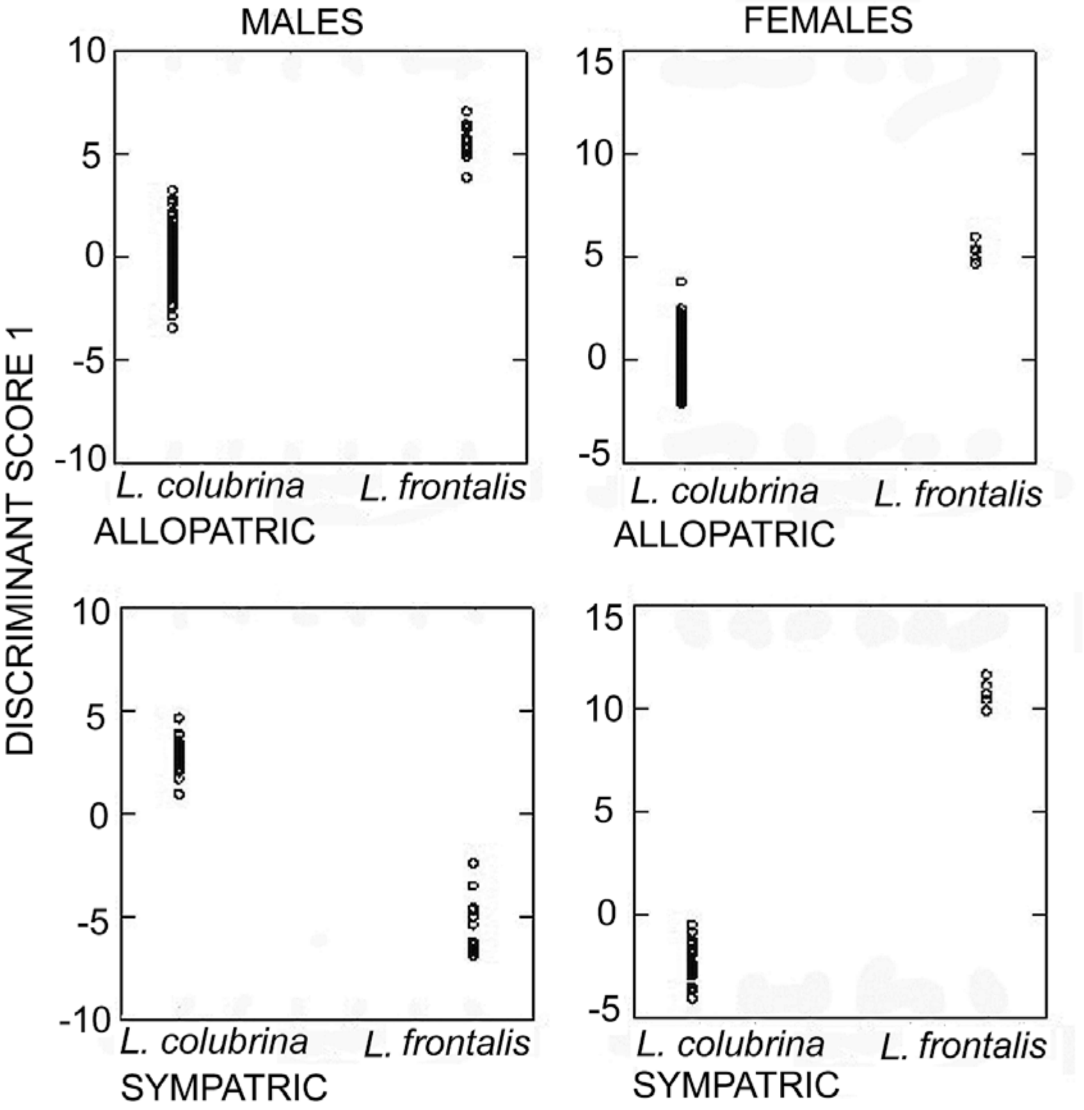


Figure 5.2. Comparison of discriminant scores for adult *Laticauda colubrina* sympatric with *Laticauda frontalis* on Vanuatu and for allopatric *L. colubrina* (all localities but Vanuatu) separately for males (left) and females (right). Note that because there are only two groups, the analysis can provide only one discriminant score. The database consisted of all specimens with complete data for the eight most important characters. Females: N=242 for allopatric *L. colubrina*, 23 for sympatric *L. colubrina* and 5 for *L. frontalis*. Males: N=268 for allopatric *L. colubrina*, 24 for sympatric *L. colubrina* and 13 for *L. frontalis*.

saintgironsi, which in turn, after isolation in New Caledonia, gave rise to *L. frontalis* (Cogger and Heatwole 2005). *L. guineai* seems to be an independent, and more recent, offshoot from *L. colubrina*. *Laticauda colubrina*, *L. saintgironsi* and *L. guineai* are all allopatric. By contrast, *L. colubrina* and *L. frontalis* are broadly sympatric in Vanuatu, to which the latter is probably restricted. For this reason, these two species were compared in more detail; first *L. frontalis* was compared only with sympatric *L. colubrina* (from Vanuatu) and then only with allopatric *L. colubrina* (all localities but Vanuatu). In the allopatric comparison, 99.5% of the female specimens were assigned to the correct species (one *L. colubrina* was misclassified as *L. frontalis*); in the sympatric comparison 100% were correctly classified. For males, 99% of the specimens were correctly classified in the allopatric comparison and 100% in the sympatric one. The two species are clearly separated morphologically. For females, the minimum separation between *L. frontalis* and allopatric *L. colubrina* is about one unit of Discriminant Function Score 1 (Fig. 5.2). By contrast, sympatric *L. colubrina* and *L. frontalis* have a minimum separation of about ten-fold. In males, the ranges in discriminant function scores between allopatric *L. frontalis* and *L. colubrina* nearly abut, whereas sympatric populations show a minimum separation of more than two discriminant function scores. Thus, there seems to be marked character displacement in *L. colubrina* in sympatry with *L. frontalis*.

A Principal Components analysis for adult *L. colubrina* by general region assigned 77% of females and 72% of males to the correct region. The north-south axis was broadly separated from the eastern islands with only marginal overlap in either sex (Fig. 5.1). The east-west axis fell between those two groups and broadly overlapped with both. Thus, although clear distinctions could be made between the two geographic extremes, neither the north-south axis nor the eastern islands could be consistently distinguished from the geographically intermediate east-west axis. This reinforces the decision by Heatwole *et al.* (2005) not to recognize these populations nomenclaturally.

5.3. Recapitulation

- Only six characters, but with different combinations and rankings for the two sexes, accounted for 95% of the morphogical variation in *Laticauda colubrina*; eight characters could assign specimens to species with 93-95% accuracy.
- There was generally strong sexual dimorphism in *L. colubrina*.
- The species of the complex were strongly separated on scattergrams whereas the separation of populations from different geographic regions were less distinctly separated, thereby confirming the taxonomic and nomenclatural decisions.
- There was characer displacement between *L. colubrina* and *L. frontalis* in Vanuatu.

CHAPTER 6. GEOGRAPHIC VARIATION: A TREE OF PHENOTYPES

This chapter applies the technique of constructing phylogenetic trees based on phenotypes, as a means of analysing geographic variation in sea kraits in the *Laticauda colubrina* complex.

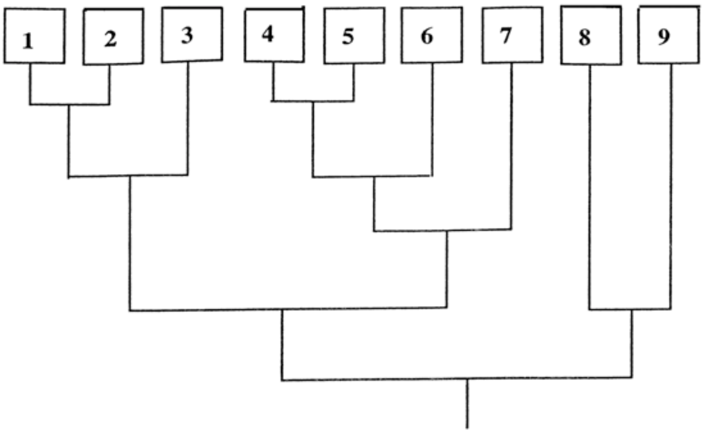
6.1. Methods

Phylogenetic trees based on morphological phenotypes were constructed as a means of assessing morphological trends and evaluating possible correlates with patterns of geographic variation. Because of the prevalence of sexual dimorphism in the species involved, separate trees were constructed for males and females. All waifs, specimens from general localities (e.g. "South Seas" or "Indian Ocean"), and specimens that would cluster merely because they shared many blank data-entries (e.g., specimens represented only by the skin from the head, with all characters from the torso missing) were excluded from the analysis. After cropping the database in this way, morphological scorings were converted to pair-wise Euclidean distances and clustered using UPGMA (Unweighted Pair-Group Method Using Arithmetic Averages) (Swoford, 1996).

This tree clusters individuals that are most similar, with each individual ultimately forming a twig on the tree (as many twigs as specimens examined). These coalesce into progressively larger trunks. The proportional representation of localities was ascertained for each major trunk.

6.2. Results and Discussion

Separate phenograms were generated by the computer for the two sexes. In these, there was progressive branching into finer and finer branches until the apical twigs led to individual specimens. Visual inspection of these phenograpms identified nine major trunks (clusters) for females (Fig. 6.1) and six for males (Fig. 6.2). Among females, *L. saintgironsi* and *L. frontalis* are the only species found in Trunk 7 and for both it is the trunk in which they find their major representation, *L. frontalis* exclusively so; *L. saintgironsi* also has a minor representation in Trunk 8 (Fig. 6.1). These results suggest that morphologies of females may reflect a closer relationship between *L. saintgironsi* and *L. frontalis,* than between either of them with the other species, a conclusion also reached by Cogger and Heatwole (2006).



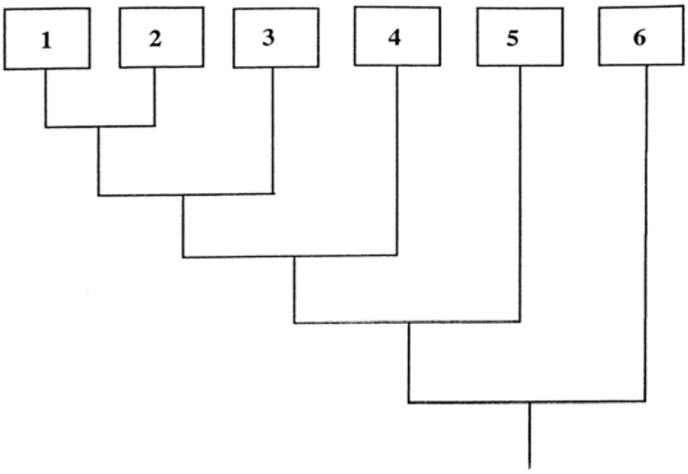
PERCENTAGE OF SPECIMENS FALLING INTO PHENETIC CATEGORY NUMBER:

REGION/TAXON	1	2	3	4	5	6	7	8	9
Andaman & Nicobar Isls.	8.3	0	25.0	0	**41.7**	25.0	0	0	0
Thailand	0	0	0	0	**100.0**	0	0	0	0
Indonesia	26.9	0	**73.1**	0	0	0	0	0	0
Peninsular Malaysia & Singapore	0	0	0	0	**57.1**	28.6	0	14.3	0
New Guinea	0	0	6.3	**75.0**	0	0	0	6.3	12.5
SE Papua *L.guineai*	0	24.0	0	**76.0**	0	0	0	0	0
Solomon Islands	0	0	0	0	**81.3**	18.8	0	0	0
Sabah	30.0	5.0	5.0	10.0	0	0	0	0	**50**
Philippine Islands	0	8.3	0	**66.7**	16.7	0	0	8.3	0
Taiwan	0	0	0	0	**64.3**	28.6	0	7.1	0
Ryukyu Islands	0	0	0	0	**62.5**	25.0	0	12.5	0
Palau	0	0	0	**100.0**	0	0	0	0	0
Vanatu *L. colubrina*	0	0	0	0	40.6	**59.4**	0	0	0
Vanuatu *L.frontalis*	0	0	0	0	0	0	**100.0**	0	0
New Caledonia *L. saintgironsi*	0	0	0	0	0	0	**83.8**	16.2	0
Fiji	25.4	0	**70.2**	0	0	0	0	0	4.5
Tonga	0	0	0	0	**90.0**	10.0	0	0	0

Figure 6.1. A phenotypically based tree showing clustering of female specimens of the species of the *Laticauda colubrina* complex from different regions. All localities refer to *L. colubrina* unless otherwise indicated.

L. guineai clustered mainly in Trunk 4, along with the majority of specimens from its nearest neighbour (New Guinea) and Palau.

There was no clear correlation in this analysis between morphological clustering and geographic distribution for female *L. colubrina*. All the major trunks, except Trunk 7, contained specimens from widely separated regions. Trunk 1 contains specimens from scattered regions near the eastern and western extremes of



PERCENT OF SPECIMENS FALLING INTO PHENETIC CATEGORY NO:

REGION/TAXON	**1**	**2**	**3**	**4**	**5**	**6**
Andaman & Nicobar Isls.	0	0	0	33.3	0	**66.7**
Burma	0	0	0	**100.0**	0	0
Thailand	0	20.0	0	**60.0**	0	20.0
Indonesia	3.3	6.7	**53.3**	10.0	26.7	0
Peninsular Malaysia & Singapore	**38.5**	15.4	7.7	30.8	7.7	0
New Guinea	21.4	**35.7**	17.9	3.6	17.9	3.6
Southeastern Papua (*L. guineai*)	27.3	4.5	0	**54.6**	13.6	0
Solomon Islands	0	24.1	**48.3**	3.5	20.7	3.5
Sabah	30.0	10.0	0	**50.0**	10.0	0
Philippine Islands	23.3	16.7	10.0	**43.3**	6.7	0
Taiwan	14.3	0	0	28.6	**42.9**	14.3
Ryukyu Islands	**100.0**	0	0	0	0	0
Palau	15.8	**42.1**	5.3	21.1	15.8	0
Vanatu (*L. colubrina*)	16.2	**35.1**	**35.1**	2.7	8.1	2.7
Vanuatu (*L frontalis*)	0	0	0	0	**100.0**	0
New Caledonia (*L. saintgironsi*)	13.8	**39.1**	23.0	1.2	18.4	4.6
Fiji	8.9	17.9	5.4	**39.3**	23.2	5.3
Tonga	0	28.6	0	**64.3**	7.1	0

Figure 6.2. A phenotypically based tree showing clustering of male specimens of the species of the *Laticauda colubrina* complex from different regions. All localities refer to *L. colubrina* unless otherwise indicated.

the geographic range, and no region is represented by a majority of the individuals. Trunks 2 and 8 also have various localities represented, but from a more limited geographic area, and none has its greatest representation in these trunks. Trunk 3 has a number of localities represented with two widely separated regions (Indonesia and Fiji) both having their greatest representation in this trunk. In Trunks 4 and 5, several regions have their greatest representation, and share this trunk with individuals from many widely dispersed localities. Specimens from the centrally located localities of New Guinea, the Philippine Islands and Palau are mostly clustered in Trunk 4. Trunk 5 includes specimens from the extremes of the north-south and east-west axes, as well as lesser representations from across the geographic range. Two trunks, 6 and 9, each contain the majority of specimens from a single region, Vanuatu and Sabah, respectively. No single trunk, with the possible exception of Trunk 4, conformed to expectations based on geographic distances between regions.

The pattern for males was even less conclusive (Fig. 6.2). All trunks contain representatives sampled from multiple, widely-spaced regions. Male *L. saintgironsi* fall into multiple clusters and show no strong similarity to male *L. frontalis*. Instead, *L. frontalis* males are found only in Trunk 5 along with *L. colubrina* from various localities, including many from Taiwan.

The inconclusiveness of these phenetically based trees probably arises from their inability to detect convergence in morphological characteristics of geographically and genetically distant populations. Hence, they do not provide as precise a pattern as the hierarchichal analysis that can make such distinctions.

6.3. Recapitulation

- Females diverged into more major trunks of a phonetically based tree than did males.
- *Laticauda saintgironsi* and *Laticauda frontalis* mainly were associated with each other on the same major trunk of the tree, confirming their close relationship.
- Otherwise, and especially for *L. colubrina*, most clustering on the trees was inconclusive.

CHAPTER 7. MULTIVARIATE ANALYSIS

In this chapter, various characters of morphology and colouration are related to each other and to temperature of the sea's surface (SST) and to latitude. The purpose of the study was to ascertain the relative importance of different characters in explaining geographic variation in *Laticauda colubrina* and to assess whether the environmental variable of SST and the geographic ones of latitude and longitude had a significant impact on the pattern of variation.

7.1. Methods

Multivariate analysis of geographic variation was performed on the widespread *Laticauda colubrina* but not on the three species with very restricted distributions. In addition to characters of scutellation and colour pattern, variables included latitude and longitude, temperature of the surface of the sea, and rainfall. The dataset was pared by eliminating stable characters (i.e., those for which there were only rare departures from the norm, or which occurred in only one or a few isolated localities (see Section 4.2). All analyses were carried out using SAS 9.1.3 Sevice Pack 4, SAS Institute Inc., Cary, NC, USA.

The data on temperatures were obtained from the "Coral Reef Watch Operational 50 km satellite Nighttime Climatologies" of the National Oceanic and Atmospheric Administration (NOAA) of the United States (coralreefwatch.noaa.gov/satellite/hdf/index.html). Their software (Coast Watch) was used to convert data files into binary floating-point files and finally into Fortran. This provided temperatures for each month from nine years of satellite date (1985-1993). These were smoothed by taking the average over a 5° x 5° grid of nearest cells, thereby correcting for missing values of some locations.

Data on mean precipitation in mm per day from 2.5° x 2.5° grids over a 30-year period (1979-2008 with no missing values) were obtained from the Global Precipitation Climatology Project (GPCP) of the National Aeronautics and Space Administration (NASA) (precip.gsfc.nasa.gov) of the United States.

7.2. The Analyses: Results and Discussion

An orthogonal transformation matrix was constructed and a factor analysis revealed that three common factors explained 30% to 80% of the variance in these characters. Upon using a varimax rotation to accentuate the large effects, these three factors exhibited localized behaviour among these variables. The first factor was composed largely of the number of scales in the width of the first, tenth and 25th light bands dorsally and ventrally (wband1, wband10, wband25, vband1w, vband10w, vband25w); the second factor was composed largely of the dark band widths (bband1, bband10, bband25, vband1b, vband10b, vband25b); and the third factor was composed largely of ventral markings (vent20, vent50, vent100, vent150, vent200). The third factor was quickly identified as largely an artifact of sexual dimorphism, and a linear classification rule was developed, based on a simple summary (the sum of the five ventral measurements) and two more variables (number of tail bands and number of subcaudal scales) with a cross-validation misclassification rate of 67/645 or about 10%.

The number of scale rows around the body, at the various levels, and the numbers of black bands on the tail were the best indicators of the sex of adult animals. Snout-to-vent length and tail length also are indicators of gender in adults (females are much larger than males). Little improvement in predicting the gender of animals is achieved by adding other variables. Since size cannot be used to sex juveniles, the single best character for predicting the gender of immature animals is the number of scale rows around the body.

Dropping those five variables whose common variation was closely linked with gender, the factor analysis was repeated in two ways: separate analyses for each category (male, female, juvenile), and then with these 12 characters adjusted for differences in gender. These analyses produced the same results, with the first two factors explaining 95% of the total variation in these 12 variables, and the commonalities (fraction of common variance to total variance for each variable) ranging from 0.44 to 0.82. Again, the factor loadings showed a pattern related to band colour. This suggested using the sample means of the widths of the dorsal and ventral light and dark bands as simple surrogate summaries of the patterns of variation. Table 7.1. indicates the correlation among the two factor scores and these simple scores.

These four simple scores contained nearly the same information as the two dominant factors, and three of the four simple surrogates (DWSS, DBSS, VWSS) had stronger relationships to latitude and longitude than did the two factor scores. In fact, their sum (FSS), showed a stronger relationship than any single summary. Moreover, this simple summary is not adjusted for gender.

Table 7.1. Coefficients of correlation between the two major factors (Factor 1 and Factor 2) and the scores of four simple surrogates: dorsal light bands simple score (DWSS), dorsal dark bands simple score, (DBSS), ventral light bands simple score (VWSS), ventral dark bands simple score (VBSS). Not adjusted for gender.

Correlations	**Factor 1**	**Factor 2**	**DWSS**	**DBSS**	**VWSS**	**VBSS**
Factor 1	1.000	0.037	0.853	0.626	0.976	0.018
Factor 2	0.037	1.000	0.220	0.758	0.001	0.964
DWSS	0.853	0.220	1.000	0.593	0.776	0.199
DBSS	0.626	0.758	0.593	1.000	0.561	0.616
VWSS	0.976	0.001	0.776	0.562	1.000	-0.049
VBSS	0.018	0.964	0.199	0.616	-0.049	1.000

Then, because many of the characters exhibited sexual dimorphism, analyses were conducted separately for males and females. To do this it was necessary to pare the data again, this time to eliminate all juveniles and other specimens whose gender (for whatever reason) could not be determined. The remaining 17 characters formed the basis of the multivariate analysis. These were: scale rows around the body at the 20th gastrostege, 50th gastrostege, 100th gastrostege, 150th gastrostege, and 200th gastrostege; number of scales in the width of the dorsal side of the first (bband1), 10th (bband10), and 25th (bband25) dark bands and of the first (wband1), 10th (wband10) and 25th (wband25) light-coloured bands; the number of scales in the width of the ventral side of the first (vband1b), 10th (vband10b) and 20th (vband25b) black band; the number of scales in the width of the ventral side of the first (vband1w), 10th (vband10w) and 25th (vband25w) light band (eliminating values where the black band did not meet below). Any specimen with data missing for any of these characters was also eliminated. This trimmed dataset contained 203 female and 225 male *L. colubrina*.

When first scores were plotted against latitude there was a decline in values from south to north without a reversal in direction across the equator. This result, however, could have been confounded by longitudinal, or other, effects and when both latitude and longitude were considered together (Figs. 7.1 and 7.2), the U-shaped trough expected on the basis of thermal adaptation occurred at all levels

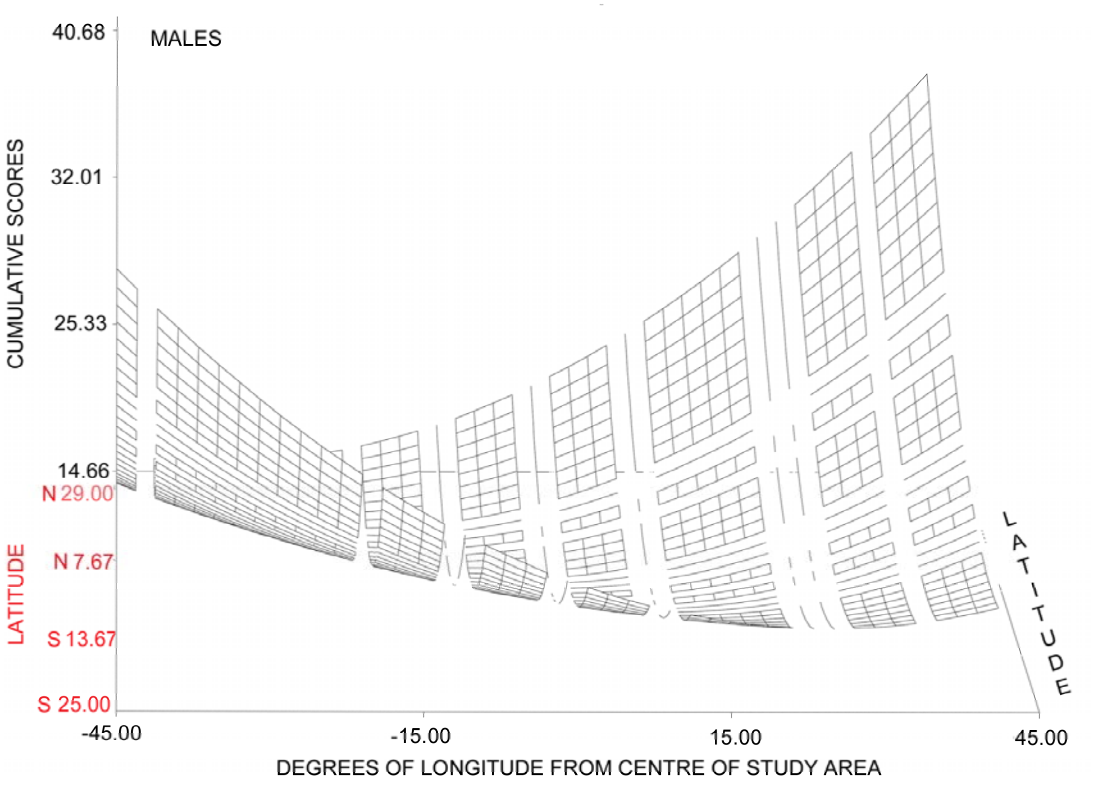


Figure 7.1. Quadratic surface relating cumulative principal scores in the multivariate analysis to latitude and longitude for males. Values of latitude are actual degrees of latitude north (N) and south (S). Values of longitude are expressed, not as actual longitudes, but as degrees of longitude east of the centre of the study area (positive values) and degrees west of the centre of the study area (negative values). For both measures, fractions of degrees are expressed on a decimal scale rather than as minutes and seconds.

of longitude for both of the two major sets of characters that contributed to factors 1 and 2. The unexpected results were that the trough was not symmetrical around the equator and the longitudinal effect was even stronger than the latitudinal one. For both sexes, in the east the latitudinal effect was greater with higher cumulative scores in the north, whereas in the west, the reverse was true and the highest cumulative scores were in the south. Thus, the northern and southern populations may be responding to the thermal gradient but within the context of longitudinal effects. In this regard, it is important to note that the thermal environment is not entirely symmetrical around the equator (Fig.3.13) and that there is marked longitudinal difference in the pattern of isotherms. In part of the western segment of the range of *L. colubrina* the temperatures are more variable than elsewhere, alternating seasonally between unusually warm to unusually cold in relation to the rest of the species' range; Peninsular Malaysia and western Indonesia are the hottest places anywhere in the range of the species in April to June whereas in January to March a tongue of cool water penetrates southward into the same region and conditions become cooler there than anywhere else in the range of the species except for the two most northern localities (Taiwan and the Ryukyus). The isotherms are in a more confused pattern there at all times and are less evenly stratified latitudinally than farther east where nearly parallel isotherms merely shift northward or southward with the seasons.

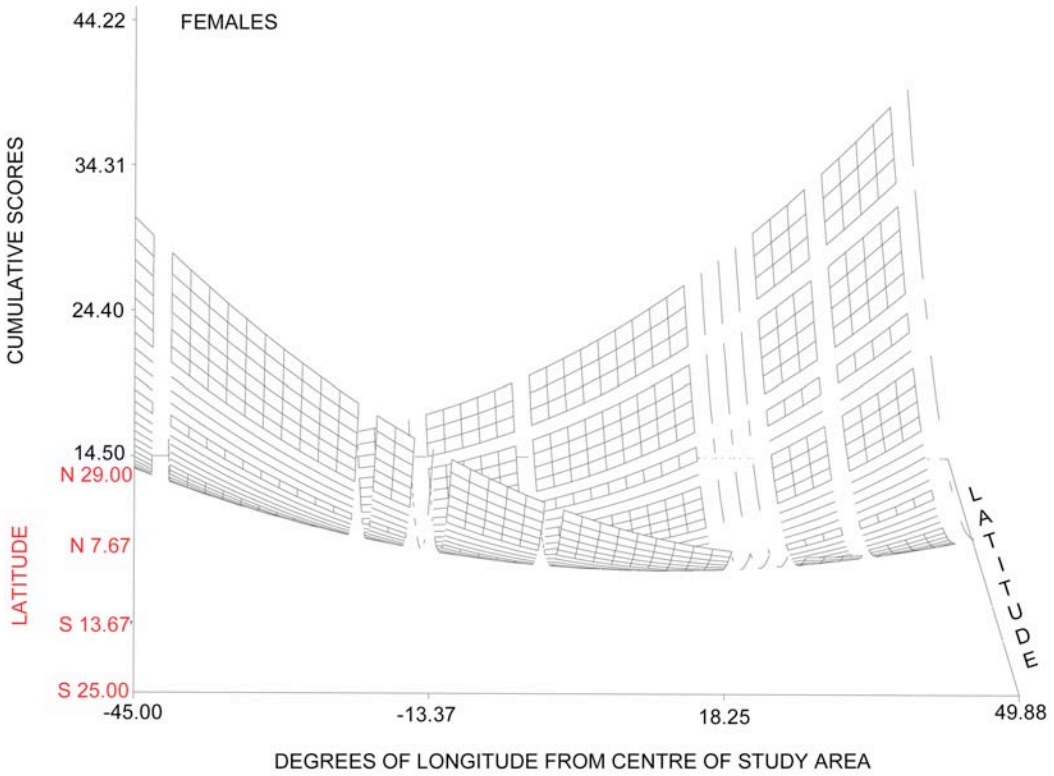


Figure 7.2. Quadratic surface relating cumulative principal scores in the multivariate analysis to latitude and longitude for females. Values of latitude are actual degrees of latitude north (N) and south (S). Values of longitude are expressed, not as actual longitudes, but as degrees of longitude east of the centre of the study area (positive values) and degrees west of the centre of the study area (negative values). For both measures, fractions of degrees are expressed on a decimal scale rather than as minutes and seconds.

To further investigate the role of climatic variables, the data on temperature and precipitation were included in the analysis. A multiple regression was conducted and the variables for inclusion were selected on the basis of their explanatory power. There were five geographic parameters (latitude, longitude, latitude^2, longitude^2, and latitude x longitude) 12 for surface temperatures of the sea (means for each of 12 months) and 12 for precipitation (means for each of 12 months) for a total of explanatory variables of 1 (intercept) + 5 + 12 + 12=30. The data were also analysed using means based on the averages of three months and using various harmonics of the fundamental data, e.g., sine/cosine.

With 428 observations of FSS (=sum of DW, DB, VW; see Table 7.1), the quadratic geographic model achieved a reasonable fit with R^2=0.76. Although a variety of statistical variable selection methods (forward, backward) and criteria (e.g. Cp) were considered for building a more sophisticated model to include precipitation and surface temperatures of the sea, none of the models improved R^2 beyond 0.80, and among the models that produced a modest improvement in fit, none appeared to be scientifically defensible. The variation in both precipitation and surface temperature of the sea is too tied to the geography to offer much improvement to the simple quadratic geographic model. Moreover, explaining variation in FSS using precipitation and/or sea temperatures alone, i.e. without geography, could not match the quadratic geographic model.

7.3. Recapitulation

- Multivariate analyses were carried out using various morphological, geographic, and climatic variables as a means of assessing their importance in explaining geographic variation in *Laticauda colubrina*.
- Common factors and simple scores relating go features of the pattern of banding in the snakes, and not adjusted for gender, showed strong relations to longitude and latitude’
- The number of scale rows around the body was the best indicator of gender in adult snakes (other than body and tail sizes and direct observation of genitalia) and was the best single character for predicting the gender of immature snakes, but could not do so with absolute certainty.
- Because of sexual dimorphism in many characters, a second analysis was performed separately for males and females.
- Quadratic surfaces relating cumulative scores for morphological characters to latitude and longitude showed a strong latitudinal conponent but an even stronger longitudinal one in which the direction of the latitudinal one was reversed between east and west and was not symmetrically centered on the equator.
- Adding the climatic variables of surface temperatures of the sea and precipitation raised the R^2 to 0.80, only a modest improvement over the value of 0.76 from using only latitude and longitude.

CHAPTER 8. GENERAL DISCUSSION AND CONCLUSIONS

Chapter 1 outlined the general biology of species in the *Laticauda colubrina* complex and discussion of individual topics occurred in each of the above chapters. The present chapter provides an overall discussion encompassing material from more than one chapter and synthesises the material from the dissertation as a whole. The major taxonomic conclusions arising from all the analyses are integrated, followed by a discussion of the significance of the sexual dimorphism and the ontogenetic variation in various characters. Then a model of the origin of the genus *Laticauda* and its subsequent divergence into three species complexes, and more specifically into the four species of the *Laticauda colubrina* complex, is developed and related to palaeogeographic events of the past 30 million years and to present sea currents and configuration of land and sea.

8.1. Taxonomic Conclusions

Although assembling the morphological information leading to the present thesis was biogeographically motivated, the extensive database that resulted is valuable in taxonomic terms, as it provides a better definition of the various taxa and a more conclusive understanding of their relationships (see Chapter 1 for a discussion of the taxonomy of sea kraits).

8.1.1. Definition of Taxa

One of the taxonomic findings arising from the present study was extension of the number of known species of the *Laticauda colubrina* complex from one to four by the description of two new species, *Laticauda guineai* (Heatwole *et al*. 2005) and *Laticauda saintgironsi* (Cogger and Heatwole, 2006) and the resurrection of another (*Laticauda frontalis*) from synonymy with *L. colubrina* (Cogger and Heatwole, 2006). These taxonomic changes are not formally made in this thesis but rather were published elsewhere for several reasons: (1) original descriptions of new species and changes in synonymies need to be published where they are readily accessible and a dissertation is less accessible than are most professional journals, (2) several herpetologists had learned of the discovery of the new species and were anxious to have the new names available as soon as possible to use in their own publications and (3) the analysis of *L. frontalis* overlapped with work in progress by a colleague and collaboration was the professionally courteous approach.

Morphologically and geographically identifiable populations at the infraspecific level were recognized and could have been designated as from three (east-west axis; north-south axis; eastern islands) to as many as ten (Andaman Islands through Sumatra; Rest of Indonesia-Thailand-Singapore-Peninsular Malaysia; New Guinea-Solomon Islands; Vanuatu; Fiji; Sabah; Philippines; Taiwan; Ryukyus; Palau) named subspecies, according to one's taste either as a "lumper" or a "splitter". Trinomials were not applied, however, as it was felt to be premature. Designations based solely on morphological evidence are subject to considerable modification and the decision was taken to describe this geographic variation in detail and await pending molecular studies for final assessment in taxonomic terms. It is likely that some of these variants will be designated full species, as has so often been the case when detailed morphological and molecular studies have combined. Cluttering up the literature with subspecific epithets likely to be changed in the near future seemed undesirable.

8.1.2. Morphhologic Lability and Diversity

Another important taxonomic finding was that some of the characters previously believed to be relatively constant within a species and therefore useful in distinguishing among them, proved to be somewhat more labile than supposed. For example, condition of the rostral scale is often used to separate different complexes and yet in *L. colubrina*, uncommon variants characteristic of the *semifasciata* complex were found (see Section 4.2.1). Thus, these features alone do not always distinguish complexes, even though those species are readily identifiable on general appearance (much as one can identify one's friends without being able to name any single unique feature) and on combinations of characters. In other cases, ranges of quantitative values, e.g., number of gastrosteges, overlapped among species, such that small numbers of individuals could not be identified solely on this character. This condition is common among ophidian taxa. An important finding in the present study, is that the species accepted by most recent researchers as the most primitive member of the genus (*L. colubrina*;

see Section 1.2), is the most labile in terms of some of these "invariant" characters. Thus, it seems that *L. colubrina* has retained more of its genetic (or at least phenetic) diversity compared to the other, putatively derived complexes.

This is in keeping with its extensive geographic range. A species capable of occupying a large geographic area must be able to cope with a wider range of conditions than one limited to a smaller area. It is likely that divergence of the original stock into the three complexes followed waif dispersal of a single gravid female or a small number of individuals to a previously uninhabited reef (see Section 8.4). These original founders of a new, derivative species would have carried only a limited subset of the ancestral genotype (the "founder principle") and as a result, genetic diversity would have been reduced. Within such initially small populations random genetic changes (genetic drift) and inbreeding occur and can lead to fixation of some characters and elimination of others. Finally, adaptive genetic change may have occurred in response to selection by the new environment. It is likely that all three of these processes (adaptation, founder principle, genetic drift) converged in reducing or altering the genetic diversity of the derived, geographically restricted species. After formation of the different complexes had occurred, the derived species gradually extended their ranges until they overlapped much of the geographic range of *L. colubrina* (see Section 8.4) but despite that, they still are less diverse morphologically than is the parental *L. colubrina*. They, in turn, generated additional species with restricted distributions within each of their respective complexes. Molecular studies may make it possible to identify which geographic segment of the *L. colubrina* population is genetically closest to the ancestor of each of the other complexes.

Divergence within the *L. colubrina* complex can serve as a model for the incipient stages of divergence of the three complexes. The other species in the *L. colubrina* complex have very restricted ranges (*L. guinea* in southern Papua; *L. saintgironsi* on New Caledonia; *L. frontalis* on Vanuatu) and probably have recently diverged from *L. colubrina*. These derived species are less variable than is *L. colubrina,* each in different ways but including condition of the nasal scale, number of colour patterns, range in size, degree of sexual dimorphism, and number of scale rows around the body. It seems that as they diverged from the parental *L. colubrina* stock, each fixed a portion of the ancestral genetic diversity and perhaps have become more narrowly adapted to the particular conditions obtaining in their restricted geographic range.

There are parallels in other taxa. For example, Wallace *et al*. (1991) reported that in the *Acropora selago* group of corals, the most primitive species were widespread with those having the most derived characters also having the greatest endemism to restricted areas.

8.1.3. Delimiting Type Locality

One of the taxonomic goals was to more precisely delimit the vague type locality of “East Indian Ocean” (see Appendix 1.2) for *Laticauda colubrina* so that in the event of further nomenclatural changes, the population that should retain the original name could be accurately designated. This attempt failed as the combination of characters of the type specimen allowed it to fit several widely dispersed locations (see Appendix 8.1).

The species was described in 1799 (Schneider, 1799) so the type must have been collected during, or prior to that year. Techniques are now available for extraction of DNA from specimens preserved for prolonged periods in alcohol. For example, Stuart and Fritz (2008) successfully sequenced mitochondrial DNA from a turtle that had been preserved in alcohol for since 1828 (179 years at the time of their study). Consequently, improvement of such techniques may make it possible to resolve this issue through the biochemical analyses now in progress.

Similarly, the questionable type locality for *Laticauda frontalis* could not be pinpointed with greater accuracy by the analyses of the present study (Appendix 8.1) and resolution of that problem also awaits analysis by biochemical techniques.

8.2 Sexual Dimorphism

Early studies recognized that females are larger in body size and have relatively shorter tails than do males, both in *L. colubrina* (Smith, 1926) and in the population now known as *L. saintgironsi* (Saint Girons, 1964, 1990), but failed to notice the extent of sexual dimorphism in a number of other characters. Pernetta (1977) studied two Fijian populations of *L. colubrina* and demonstrated sexual dimorphism in several additional characters, including body weight, thickness of the tail, number of gastrosteges, subcaudal scales, number of scale rows at mid-body, number of dark bands on the body, and the proportion of individuals with a black tip on the tail. He re-analyzed Smith's (1926) data on scutellation separately for males and females and compared them with his own measurements; he found them to be consistent with his interpretation of sexual dimorphism in those characters. Pernetta's data on numbers of gastrosteges and subcaudals, and of scale rows at midbody all fell within the range of Smith's data.

Guinea (1994, 2002) further extended the study of characters in Fijian *L. colubrina*, confirming various of the results of Smith and Pernetta, and extending the known range of subcaudals downward to 27 (in females); he added the number of scale rows at the vent as an additional sexually dimorphic character. Greer (1997) stated that the "degree of sexual dimorphism in sea kraits is almost unparalleled in other snakes" and reviewed the literature pertaining to it.

The present study found most of the variable characters to be sexually dimorphic, the dorsal widths of the dark and light bands being notable exceptions. In at least one character, number of dark bands on the body, sexual dimorphism varies geographically. Guinea (2002) concluded that there was little sexual dimorphism in the frequency of the azygous prefrontal scale in Fijian *L. colubrina*, as was true over all localities in the present study, but he noted that in some local populations this character did display sexual dimorphism.

For some characters the differences between the sexes, although consistent and significant, were of exceedingly small magnitude and thus sexual dimorphism may be subtle. For example, for particular localities, the mean number of scale rows around the body usually differed between the sexes by no more than 1-2 rows (Fig. 4.8) and the mean number of dark bands on the body by two or fewer (Appendix 4.13).

The variable quantitative characters of scutellation and colouration were compared between adult males and females and assessed as a means of searching for a character allowing accurate sexing of juveniles (Appendices 4.1-4.3). Most sexually dimorphic characters, however, still had sufficiently broad overlap between males and females as to be unsuitable for this purpose. Although male *Laticauda* have longer tails relative to body length than do females, the differences in relative tail length between the sexes is less pronounced in younger animals than in larger ones; tail length increases more rapidly with increasing snout-vent length in males than it does in females (Shine and Shetty, 2001b).

Scale numbers and type of colour pattern do not change throughout the life of sea kraits and the banded condition remains constant in *Laticauda*; thus, sexual dimorphism in such characters also applies to immature animals and may be more useful in sexing juveniles. A promising indicator of the gender of immature or otherwise problematic individuals was the number of subcaudal scales, but even this character showed some overlap between males and females. The number of scale rows around the body seems to be the best candidate (see Chapter 7).

The present study poses two questions about sexual dimorphism: Why do the sexes of *L. colubrina* differ in so many characters? Why do the different species of the complex differ in the extent to which they are sexually dimorphic?

Question 1: Why do the sexes in L. colubrina *differ so much in so many characters?*

Sexual dimorphism in size in marine snakes is common, with females being larger than males more often than the reverse (Heatwole, 1999). Sea kraits of the *L. colubrina* complex conform to this generalization in that there is sexual dimorphism in favour of larger females in *L. colubrina*, *L. guineai* and *L. saintgironsi* and the sexes are about equal in size in only one (*L. frontalis*). Such prevalence of sexual dimorphism in marine snakes suggests that it may have adaptive value, rather than merely occurring by chance.

Large females of *L. colubrina* produce more eggs than do smaller individuals (Gorman *et al*., 1981; Guinea, 1986). Thus, dimorphism could be driven by an advantage of greater fecundity to large females, but such is not necessarily the case, depending on energetic considerations and other aspects of life history (Shine, 1988, 1994; Bonnet *et al*., 2003). Also, larger females attract more intense courtship from males (Shetty, 2000; Shetty and Shine, 2002c) and hence sexual selection (mate choice) may be operative. There are a variety of other possible explanations for large female size.

Shine (1978, 1994) noted a correlation in snakes between combat among males and the occurrence of larger body size in males than in females. He attributed this to the competitive advantage in obtaining more frequent mating privileges by overpowering rival males. Again, sea kraits conform; male *L.*

colubrina do not engage in combat or other overt aggression and larger size in males does not increase mating opportunities (Shetty and Shine, 2002c); accordingly males have remained small.

Slatkin (1984) concluded that sexual dimorphism in size could originate either from sexual selection or purely from ecological differences between the sexes. Whatever the origin of a sexual difference in size, other ecological disparities may reinforce or perpetuate it. In an analysis of 114 species of snakes, including *L. colubrina*, Shine (1991a) concluded that males and females probably originally diverged in body size because of differences in reproductive biology, with the subsequent evolution of sexual dimorphism in feeding structures arising independently in the two sexes as adaptations for foraging. In *L. colubrina*, the two sexes are ecologically segregated. Sea kraits thermoregulate behaviorally (Saint Girons, 1964, 1990) and males maintain higher body temperatures throughout the day than do females (Shetty, 2000) and generally are more active (Shetty and Shine, 2002b). Speed of locomotion of males is faster than that of females, both in the sea and on land (Shine and Shetty, 2001a). Even among individuals of equivalent sizes, females have larger heads than do males, and their generally larger body-size enhances this effect. Accordingly, they can handle larger prey and more often have larger prey items in the stomach (usually single items of conger eels) than do males (usually multiple items of moray eels) (Shetty, 2000; Shetty and Shine, 2002a).

Boback (2003) concluded that body size of snake species was principally influenced by size of available prey. Shine *et al*. (2002a) suggested that size of available food might drive sexual dimorphism in snakes; they found that *L. colubrina* in Vanuatu generally contained smaller eels in their stomachs than in Fiji (Shetty and Shine, 2002a) and they suggested that a restricted range in prey size caused a decrease in sexual dimorphism in size. If the resource base were, in fact, narrower in Vanuatu there would be less amplitude there for sexual divergence in feeding habits, and the stimulus for sexual dimorphism in size would be expected to be relaxed. Other than a general impression from diving on the reef, however, there was no measure of the sizes of available prey, independent of the stomach contents themselves; until such an assessment can be made, the argument is circular but does constitute a plausible conjecture requiring testing. If the size-range of prey is so narrow as to curtail the extent of sexual dimorphism within *L. colubrina*, one needs to ask how it can be that *L. frontalis*, also a predator of eels, can also fit into the same resource base (see below). Voris and Moffett (1981) noted that in the beaked sea snake (*Enhydrina schistosa*) the maximum diameter of prey was 1-2 times the diameter of snakes' necks but nevertheless large snakes took a disproportionally high number of relatively small fish. Thus, large body size in snakes is permissive of larger items in the diet but may not be obligatory in this regard.

Dimorphism in body and/or head size may be related to differences in segregation of foraging sites. Some sea snakes, including sea kraits, seem unable to hunt successfully in the open but rather investigate crevices where they trap prey, such as eels (Cogger *et al*., 1987). The lesser size of males would enable them to enter small crevices, thereby gaining access to small eels unavailable to females too large to enter small crevices. On the other hand, the larger gape of females would allow access to eels too big for males to swallow. Thus, differences in body-size may restrict females to the upper size-range of prey through ecological limitations (restriction of available foraging sites) and males to the lower size-range of prey through morphological limitations (small gape size).

If different sizes of eels occupy different habitats or microhabitats one might expect spatial separation of foraging ranges of male and female *L. colubrina*. Pernetta (1977) found that in Fiji males ate smaller species from the shallow reef-flat whereas females fed on larger species adjacent to the reef. Shetty and Shine (2002a) confirmed this finding and noted the larger deep-water species favoured by females were conger eels (Family Congridae), while the shallow-water species eaten by males were moray eels (Family Muraenidae). Although most direct observations of the depth at which sea snakes dive are anecdotal and do not indicate the sex of the individual, these dietary data suggest that the sexes forage at different depths. Sea kraits are reputed to be less capable divers than are most hydrophiids, but there is one observation of a *L. colubrina* at 45 m that when disturbed descended deeper in an area where the bottom was at 60 m (see Heatwole and Guinea, 1993); Ineich and Laboute (2002) presented photographs of *L. saintgironsi* at depths of 8 m and of *L. laticaudata* at depths of 6 m, 6 m, and 33 m. The voluntary submergence time of undisturbed, inactive *L. colubrina* extends to about 30 minutes (Pickwell, 1972; Heatwole, 1975a, 1981b) and on average diving to the bottom and surfacing occurs at a rate of about one metre every three seconds (Heatwole *et al*., 1978). Thus, at a depth of 60 m, it would take about 6 minutes for a trip from a breathing bout on the surface to the bottom and back, leaving about 24 minutes bottom-time for foraging. Since activity increases oxygen consumption and reduces submergence time in sea snakes (Heatwole, 1975a,b), an actively foraging snake may be able to stay down an even shorter time. Pernetta (1977) reported a maximum of seven minutes for foraging *L. colubrina*. Unfortunately, neither Pernetta (1977) nor Heatwole (1975a, 1981) provided the sex of the individuals on which their observations were made and it is unknown whether males and females differ in voluntary submergence times. However, even at the longer submergence times, limitation of bottom-time, rather than scarcity of conger eels, might be the important constraint upon ability of female *L. colubrina* to obtain food. Where reefs drop off sharply into water too deep for female *L. colubrina* to engage in sustained foraging, large eels might be inaccessible compared either to areas where inter-reefal areas were shallower, or where descent into deep water was more gradual.

The location of terrestrial shelter sites relative to foraging grounds may be important. For selection to drive sexual dimorphism and ecological segregation of the sexes, such as observed in sea kraits, two different foraging habitats and kinds of prey would both need to be within effective range of the terrestrial habitat. If one or both sexes have to travel too far to forage, the extra expenditure of energy may offset the advantages of ecological segregation. If a cay is surrounded by an extensive shallow reef, males could forage in shallow water at close range, but females would have to travel long distances to reach deeper water and their preferred prey, compared to an island located near the edge of a drop-off.

Another aspect of sexual dimorphism is tail-size. Males have conspicuously longer and thicker tails relative to their body size than do females. One might expect that animals with tails of greater surface area would have more effective aquatic locomotion and thus be better able to escape predators at sea and show better survival. However, Shine and Shetty (2001b) found that in female *L. colubrina* relative tail length did not significantly affect speed of locomotion, either on land or in the water. In males, the crawling speed on land was not affected, but animals with intermediate values of relative tail size (close to average length) had higher swimming speeds than did those with longer tails. Perhaps tails that are too long are cumbersome and are less effective in aquatic locomotion.

Attributes other than speed of locomotion also are affected by tail-length. Males with average tail-length obtained more matings (in an arena) than did those that had longer tails; similarly, males with relatively shorter tails grew faster than did longer-tailed ones. In both sexes, animals with relatively shorter tails were more likely to be recaptured a year later than were relatively longer-tailed ones, i.e., shorter-tailed animals seemed to have better survival. This is clear from Shine's and Shetty's figure 2 and in their results section they accurately stated that "Shorter-tailed snakes were more likely to be recaptured in both sexes"; yet they contradicted their data and reversed this conclusion in other parts of their paper. In their discussion section they indicated that "*Shorter tails* enhanced swimming speeds and growth rates but *reduced survivorship*" and "male sea kraits appear to gain both *advantages* (*in survival* and mating success) as well as disadvantages….from having relatively *long tails*" and in their abstract they stated that "males with relatively *longer* tails grew more slowly, but were more *likely to survive*, than were shorter-tailed males" [all italics mine]. Thus, their claimed trade-off between growth and survival is not correct; growth and survival are both enhanced by relatively short tails in males.

In all the attributes studied by Shine and Shetty (2001b), male snakes with shorter tails, or of intermediate lengths, seemed to have an advantage over longer-tailed animals: they grew faster, swam faster, were more likely to mate, and survived better. Females, already with relatively short tails, did not display any significant difference in any of the above attributes except that survival was better in shorter-tailed animals even within the range of females' values. The most parsimonious hypothesis arising from that study would seem to be that the tail-length of females is optimum, or maybe even slightly too long, but that males suffer disadvantages in growth rate, swimming speed, frequency of mating, and survival as a consequence of tails that are too long. Some attribute, not yet specified, must exert a selective pressure that counteracts these disadvantages of being long-tailed. It may be as simple as the spatial requirements of housing the copulatory organs, the hemipenes, and their associated musculature. Another possibility (not applicable to *Laticauda*) is an advantage bestowed by longer tails in dislodging the hemipenes of rival males (Shine *et al*., 1999).

Shine and Shetty (2001b) compared the number of males that mated versus those that did not and referred to it as "mating success". What they measured was merely whether or not copulation occurred, not whether those matings were successful, i.e., whether fertilization took place. If the length of the hemipenes, and consequently the depth to which they can be inserted when everted, leads to more of the matings being successful (i.e., result in fertilization) or to a greater degree of success (greater number of ova fertilized), then one can visualize that a longer tail, with space for longer hemipenes, might bestow fitness that would counteract the disadvantages of a long tail. In general, snakes' hemipenes often have devices such as hooks or spines ("ornamentation") that reduce premature dislodgement during copulation; greater length might also assist in reducing loss of sperm.

In conclusion, sexual dimorphism likely reflects the facts that (1) certain characters improve fitness unequally between the two sexes, e.g., large females have better fitness because large size improves their fecundity, whereas since male-male combat does not occur in sea kraits, there is no advantage for males to be larger, and (2) ecological segregation of the sexes into econes based on body size and its correlated attributes allows partitioning of resources and hence maintenance of larger populations for a given area, with each sex optimally specialized for exploitation of a different portion of the spectrum of resources, e.g., bigger females with wider gapes eat larger taxa of eels but smaller males enter small crevices and exploit smaller taxa. Other dimorphisms may merely reflect multiple functions of some characters; females can develop optimal-sized tails in terms of locomotion, whereas locomotory advantages may need to be balanced by restrictions imposed by reproductive requirements related to housing the hemipenes in the tail.

Question 2: Why do the different species of the complex differ in the extent to which they are sexually dimorphic?

In some characters, the three species agreed in either all being dimorphic (bands on tail, subcaudals) or none being dimorphic (prefrontals, width of first dark band, width of first light band). In other characters the three species in the complex exhibit different degrees of sexual dimorphism. In body size *L. colubrina* is highly dimorphic, *L. saintgironsi* less so, and *L. frontalis* minimally, if at all. The present study did not detect sexual dimorphism in size in *L. frontalis* but Shine *et al*. (2002a) found it to a slight degree. The number of dark bands on the body showed sexual dimorphism in part of the geographic range of *L. colubrina* but not elsewhere, and not at all in the other two species. In the number of scale rows around the body, *L. colubrina* exhibited sexual dimorphism along the full length of the torso, whereas *L. saintgironsi* did so only at body-centre, and *L. frontalis* did so only toward the rear, and then doubtfully so, a result confirmed by the results of Shine *et al*. (2002a) for the mid-body region of *L. colubrina* and *L. frontalis* from Vanuatu. In number of gastrosteges, *L. colubrina* and *L. saintgironsi* were sexually dimorphic, but sexual differences in *L. frontalis* were not significant. Shine *et al*. (2002a) found that sexual dimorphism in relative head length was greater in *L. colubrina* than in *L. frontalis*.

L. colubrina, with the most extreme sexual dimorphism in body size, and *L. frontalis* with the least, are syntopic in Vanuatu, a locality where sexual dimorphism in size is reduced in *L. colubrina* compared to elsewhere in its geographic range (Shine *et al*., 2002a; Shine and Shetty, 2002a). *L. frontalis*, the smaller of the two species, overlaps broadly in diet with juvenile *L. colubrina* (Shine *et al*., 2002a). Adult *L. colubrina* eat larger eels, with the biggest prey of all taken by females, the largest sex. Shine *et al*. (2002a) proposed that the upper end of the size-range of eels in Vanuatu is truncated, with the result that females converge toward the males in size of prey taken and in body size, thereby reducing sexual dimorphism. *L. frontalis*, being restricted to the smaller eels, has such a narrow resource-base as to prohibit divergence of the sexes to any great extent, and accordingly, this species has slight, if any, sexual dimorphism in size. The critical test of this attractive hypothesis is to ascertain whether the impression of fewer large eels in Vanuatu is, in fact, true. It is likely that the situation is more complex than merely *L. frontalis* crowding into the lower end of the range of prey sizes, closer to the resource base of the male econe of *L. colubrina* than to the female one. Both econes of *L. colubrina* showed character displacement in the presence of *L. frontalis*, and indeed, the effect was more pronounced in female *L. colubrina* than in males (see section 5.2).

The above hypotheses do not address the reduced sexual dimorphism in *L. saintgironsi* in comparison to that of *L. colubrina*. If narrower size-ranges of prey restrict the extent of sexual dimorphism of these kraits, then the reduced sexual dimorphism of *L. saintgironsi* would lead one to predict that New Caledonia should have a restricted range of sizes of eels compared to that occurring throughout most of the range of *L. colubrina*.

There are only four specimens of *L. frontalis* known from the range of *L. saintgironsi* (one from New Caledonia and three from the Loyalty Islands). These are perhaps waifs, but if there is genuine overlap of these species, *L. frontalis* is extremely rare in the overlap zone. The theory of resource limitation would predict small eels in the size eaten by *L. frontalis* to be uncommon. Thus, a testable prediction is that in New Caledonia, the range in sizes of eels is narrow and truncated on both ends, not leaving resource space for the smaller species (*L. frontalis*) on the lower end, and not allowing for very much divergence between the sexes of the larger species (*L. saintgironsi*) on the upper end. The data from the snakes are available; what is needed for validating the hypothesis is quantitative comparison of the frequencies of sizes of eels on the reefs of New Caledonia (*L. saintgironsi* only or with rare *L. frontalis*), Vanuatu (*L. colubrina* and *L. frontalis*), and the many sites where *L. colubrina* is the only species of the three present.

An alternate hypothesis is that sexual dimorphism in size in the sea-krait clade might merely be an allometric effect, with the differences between the sexes increasing with increasing body length. Sexual dimorphism is most pronounced in *L. colubrina*, the largest species, less prominent in *L. saintgironsi*, which is intermediate in body length, and slight, if present at all, in *L. frontalis*, the smallest species. If the allometric hypothesis is true, then the advantages of ecological segregation through differences in body size between males and females would accrue only to larger species.

Sexual dimorphism in some other characters might be driven by sexual dimorphism in size. For example, a greater number of scale rows around the body may be more advantageous to a big snake eating large prey than to a smaller snake feeding on lesser prey. Hence, if sexual dimorphism in size arose, by whatever means, selection for an increased number of scale rows around the body of the larger sex would accrue. Alternatively, there could be pleiotropic effects between some sexually dimorphic character and one with neutral fitness. In either case, *L. frontalis*, lacking sexual dimorphism in size, would also lack sexual dimorphism in traits that are related to differences in body-size.

8.3. Ontogenetic Variation

If natural selection were intense for some character, it might be detectable by comparing the values of adults and juveniles. If juveniles were to either (1) show a greater range of characteristics than adults or (2) have significant mean differences from adults in some character, natural selection would be suggested. For example, Gritis and Voris (1990) found significant differences in the extent of fracturing of ventral scales and their relative size between juveniles and adults of *Lapemis curtus*. Cogger and Heatwole (2005) noted that in *L. frontalis* juveniles tend to have fewer of their dark bands on the body meeting below than do adults.

Differences between life history stages might be exacerbated if there were ecological differences between juveniles and adults. It is known that juvenile *L. colubrina* are more aquatic than the adults, and are restricted to the water and edge habitats, whereas the adults go farther inland and use the terrestrial habitat more extensively (Shetty and Shine, 2002b). Because of this habitat difference, juveniles and adults may be subjected to different selective pressures. The most extreme divergence of characters occurs in animals with more than one econe (Heatwole, 1989; also see Section 3.3.6). More subtle morphological differences in differentially adaptive characters might be expected in species, such as sea kraits, whose morphology must strike a compromise between the demands of two different media. The animals do not metamorphose when alternating between the two media, but the greater amount of time spent by adults on land might shift the selective value toward greater terrestrial adaptation than would be true for primarily aquatic juveniles. If this occurs, certain ranges of particular traits might be selected against as the aquatic juveniles become more terrestrial and there would be differential survival of those which strike a better morphological compromise between the two media.

Sexual dimorphism complicates interpretation of comparisons between juveniles and adults. Ideally one should compare juveniles and adults of the two sexes separately, but if, as in the present study, juveniles cannot be sexed reliably, this is not possible. Although one could compare all juveniles with both males and females, this could lead to spurious results arising from differences in the sex ratios in samples of juveniles. For example, Guinea (2002) found that various scutellation characters in some Fijian localities correlated with age-class, but upon further analysis he concluded that the apparent effect of age-class on these characters was an artifact of sexual dimorphism in scutellation and the relative numbers of males and females in each age-class. Comparisons of ranges of values would be even less precise.

Any characters that change ontogenetically are also inappropriate for assessing natural selection by comparison of juveniles and adults. Scutellation in snakes is not a problem in this regard as once the number and arrangements of scales have been determined developmentally they do not alter during the subsequent life of the animal except through injury. Wounds and scars are readily detected and specimens bearing them can be eliminated from the database. In some snakes, however, there is an ontogenetic change from a juvenile colour pattern to a different adult one, or polymorphic juvenile patterns may converge into a single adult one (e.g., Hadley and Gans, 1972). In other snakes, the colour pattern remains constant, other than fading or being obscured by increasing melanism with age (Camin and Ehrlich, 1958). *Laticauda* fits into the second cateory; juveniles and adults all have the banded pattern. Hence, differences in frequencies, either in colour pattern or scutellation, between juveniles and adults reflect differential mortality of individuals bearing different traits.

Because of the above difficulties, only those characters were used to assess differences between juveniles and adults that met the following criteria: (1) they were not sexually dimorphic, (2) they did not change within the life of an individual animal, and (3) juveniles and adults were both represented in a sample of more than trivial size (set in the present study as N=10 for both groups combined). Two characters, the number of scale rows in the dorsal width of dark bands and the number of prefrontals, met these criteria.

Width of Dark Bands: It was mentioned in Section 4.3.7 that juveniles had a greater number of scale rows in the dorsal width of the dark bands at all three levels of the torso than did adults at all localities but two. The two exceptions were Fiji and Tonga, for which it was the reverse. It is tempting to speculate that in the terrestrial environment over most of the range of *L. colubrina* there is greater selection for narrower dorsal bands and that juveniles with wide bands are selectively eliminated as they mature, thereby reducing mean values by the time they become adults, but that conditions favour the reverse in Fiji and Tonga. This hypothesis is especially attractive in view of the fact that mean band widths in adults are greater in Fiji and Tonga than in most other places tested (Appendix 4.3.7; Fig. 4.11). Thus, wide bands seem to be of greater selective advantage in the terrestrial environment of the far eastern part of the range of *L. colubrina* than for this species elsewhere. Narrow bands seem to be advantageous in the marine environment.

8.4. "Patchy" Distributions

Sea kraits are notoriously "patchy" in their distributions. They have patchy distributions on a broad scale in that they are associated with coral reefs that may be patchily distributed themselves, and hence sea kraits are found only in those geographic patches where corals occur (except for a lake-locked population in Lake Te-nggano, Solomon Islands). They also occur in patches of smaller scale. They seldom occur on the coasts of mainlands or even of the larger islands within their geographic range, but are mostly restricted to small offshore cays, possibly because of fewer terrestrial predators there, and a lesser disturbance by humans (see Chapter 3). Finally, they are patchy on a microscale. They are not evenly distributed around the periphery, even of small cays. Some of this unevenness in distribution may be associated with the structure of the habitat, such as suitable crevices in which to shelter or oviposit, or the availability of cover allowing thermoregulation (see Section 3.3.1). Even taking all of these sources of environmental heterogeneity into account the extremely patchy distribution of sea kraits remained enigmatic. Perhaps they are social and tend to aggregate with other members of their own species. This may be a partial answer, but recently, a new dimension to understanding of sea kraits' distribution was added by the research of Dr. Harvey Lillywhite and his colleagues. They found that sea kraits do not drink seawater, even when dehydrated, but need freshwater to survive. Accordingly, on Lanhyu (Orchid) Island, a small cay offshore of Taiwan, snakes were not distributed evenly around the coast, but rather were most abundant at sites where freshwater streams or springs were located (Lillywhite *et al*., 2008). Previous investigators had overlooked this possibility because it was assumed sea kraits were independent of freshwater because of their sublingual salt glands (see Chapter 1). Although these glands are important in osmoregulation, Lillywhite's work has shown that they are not adequate for freeing these snakes from requiring periodic access to freshwater. Consequently, sources of freshwater must be added to the list of environmental influences contributing to the patchiness of distribution of sea kraits.

In Section 3.3.1 it was noted that sea kraits' broad-scale distribution did not seem to be related to general patterns of rainfall; snakes occurred in some areas where records from the nearest land-based weather stations showed relatively low registrations. By contrast, Lillywhite *et al.* (2008) found that in tropical Asia and Australasia the species richness of sea snakes correlated positively with annual precipitation. The resolution of these differences may lie in the semi-terrestrial nature of sea kraits. By being able to come to land, they can avail themselves or more permanent sources of water (streams, springs) and are not tied so strongly to rainfall *per se*, or to its seasonal distribution, as are oxyuranine sea snakes that never leave the water and have to rely on the film of freshwater briefly floating on the surface of the sea following rains.

There has been a marked decline in oxyuranine sea snakes on the Sahul Shelf of Australia, including the probable extinction of two species, at least in part attributable to elevated temperatures in seawater and the resulting bleaching of corals; the associated small rise in sea level by thermal expansion; and encroachment of sand and the smothering of corals (Guinea, 2007; Heatwole, personal observations).

Although sea kraits may be less vulnerable than oxyuranine sea snakes to climatic changes in precipitation because of sea kraits' ability to gain access to terrestrial sources of freshwater, they are not immune. Sea kraits have been found in nature in a dehydrated condition following droughts and the drying up of their streams and springs (Lillywhite, 2009). Thus, usually prolonged droughts could eliminate sea kraits from particular localities, that would then need to be recolonized by dispersal from other areas.

Because of their reliance on coral reefs, sea kraits would be expected to be as susceptible as other sea snakes to environmental changes, such as those affecting corals on the Sahul Shelf. It is likely that global climatic change will pose a threat to sea kraits and that some patches will be eliminated. Such an effect would likely be more serious for the species of the *L. colubrina* complex that have very limited distributions than the widespread nominate species.

8.5. Factors Affecting Patterns of Geographic Variation

One of the original intents of the research on which this dissertation is based was to relate the geographic distribution and patterns of variation of the *Laticauda colubrina* complex to tectonic, vicariant events and distinguish between an ancient Gondwanaland origin for the sea kraits and a more recent Asian one. During the course of the investigation, the question of the origin of the taxon was answered by other investigators (see Section 1.4) in favour of an Asian origin. The task of the present investigation then became the relating of the subsequent dispersal and speciation within the complex to palaeogeographic events and present-day influences.

Many of the factors affecting geographic distribution also affect geographic patterns of variation as both depend on the dispersal of animals from one place to another, resulting in range extensions in relation to the former, and to gene flow in relation to the latter. In this section, the most important of these factors are discussed as they apply specifically to geographic variation.

Not all variable attributes are interpretable in taxonomic or geographic terms. For example, McCarthy (1986) found that the presence of a vestigial left lung varied in *L. colubrina* but did not show any obvious geographic correlations. In the present study, a number of the characters differed somewhat in the way they varied geographically, but consistent patterns did emerge. In *Laticauda colubrina*, the geographic range resembled an inverted T with a north-south stem consisting of the Ryukyus, Taiwan, the Philippines and Sabah, and an east-west crosspiece comprising the Andaman and Nicobar Islands through Thailand, Peninsular Malaysia, Indonesia, Papua–New Guinea, and the eastern island-chain of the Solomon Islands, Vanuatu, Fiji and Tonga. In most characters there was a significant discontinuity between these two axes, in the west coinciding with the distributional gap in the species' range in the southern South China Sea, Kerimata Strait and western Java Sea. The only exceptions were (1) the subcaudal scales for which the differences between the Philippines and adjacent parts of Indonesia to the south were not significant (females) or for which Sabah did not differ significantly from Indonesia (males), and (2) the scale rows around the body of males and the number of gastrosteges for which Peninsular Malaysia grouped with the north-south axis rather than with the east-west one.

For some characters (scale rows around the body, width of first light band, head colour pattern, the north-south axis was homogeneous with no significant differences among the various island groups. However, for other characters this axis was subdivided into separate units. The most common discontinuity was between the Philippines and Taiwan (body bands, tail bands, female subcaudals, and gastrosteges), followed by one between the Philippines and Sabah (males' subcaudals, width of first dark band in males, ratio of dark and light band-width). There was only one character for which Taiwan and the Ryukyus diverged (females' subcaudals). Thus, all the island groups in the north-south axis seemed to be linked, but with the linkage weaker between two subgroups, Sabah–Philippines and Taiwan–Ryukyus; within these subgroups the affinity was greater in the latter than in the former.

There were no characters for which the entire east-west cross-piece was homogeneous. Rather, there were discontinuities for one or more characters between, and sometime within, each of the adjacent island groups. Such discontinuities were more common in the eastern chain of islands than elsewhere. For example, there were three characters for which the area from the Andaman Islands through the Solomon Islands tested as homogeneous (females' tail bands, males' subcaudals, females' scale rows) and two characters for which there were no identifiable discontinuities from the Andamans through Papua–New Guinea (males' and females' gastrosteges). There was only one significant discontinuity between the Andaman–Nicobar Islands and Sumatra (male tail bands), two between Sumatra and the rest of Indonesia (width of first dark band in males, ratio of dark and light bands), two within the rest of Indonesia (female body bands, head colour pattern). Thailand and Peninsular Malaysia/Singapore were homogeneous with a larger western area for most characters but Peninsular Malaysia/ Singapore was allied exclusively with the Andamans only in males' tail bands) and with the north-south axis in gastrosteges. In two characters, Peninsular Malaysia/Singapore was either an isolate (females' tail bands) or partial isolate (males' gastrosteges). Thailand was an isolate from all adjacent areas in head colour pattern. Myanmar is represented only by one specimen and its affinities cannot be evaluated.

In contrast to the relatively homogeneous nature of the western part of the east-west axis, in the east there were discontinuities between Indonesia and Papua–New Guinea in four characters (females' body bands, females' subcaudals, width of first light band, head colour pattern. Within Papua–New Guinea the situation was variable. Eastern Papua–New Guinea maintained continuity with the Solomon Islands in all characters except number of gastrosteges. However, there were some possible clines within Papua–New Guinea/Solomon Island archipelago and Rennell

Island was separated from the rest of this region in males’ tail bands, width of light bands and ratio of dark and light bands. In the latter character, Rennell was an isolate from all adjacent areas. In most characters, Vanuatu appeared as an isolate although it linked with the Solomon Island–New Guinean region in females’ subcaudals and males’ scale rows, with Rennell Island in males’ tail bands, with Fiji and/or Tonga in females’ tail bands, females’ scale rows, and males’ gastrosteges, and with both Rennell and Tonga in width of light band. Tonga and Fiji (in its entirety or in part) differed significantly in five characters, males’ body bands, males’ subcaudals, females’ scale rows, width of light bands, and ratio of dark and light bands. There were even discontinuities within Fiji itself in width of light bands) and ratio of dark and light bands.

Palau was somewhat enigmatic. It appeared as an isolate from all adjacent regions in number of body bands) and females’ gastrosteges, was allied with the combined north-south and east-west axes in females’ subcaudals, linked only with the north-south axis in females’ scale rows and only with the east-west axis in tail bands, males’ subcaudals, ratio of dark and light bands, males’ gastrosteges, and width of light bands; in the last character, however, there may have been a clinal connection with the north-south axis. In head colour pattern Palau and West Irian together formed a homogeneous unit isolated from all adjacent ones. In conclusion, Palau is allied primarily with the east-west axis, but does provide a link between the north-south and east-west axes, at the same time being somewhat isolated from both in some characters.

Clearly, the eastern part of the east-west axis is dissected more finely into relatively small, isolated units in comparison to the larger, more homogeneous western segment. Discontinuities occur over shorter intervening distances in the east than in the west. These observed patterns require explanatory hypotheses.

The influences affecting distribution also probably affect patterns of variation. Any barrier to dispersal, even if breached occasionally, would restrict gene flow and influence patterns of geographic variation. Thus, gaps in suitable habitat, whether caused by lack of coral reefs, absence of suitable predator-free terrestrial shelter, or other features, would be expected to demarcate boundaries between genetically differentiated populations.

Given that sea kraits forage mainly on or near coral reefs, and require land for reproductive and other activities, extremely deep water disrupts continuity of suitable habitat for feeding and shelter. This seems to be the case in the eastern chain of islands, where the Solomon Islands, Vanuatu, New Caledonia, and Fiji, and Tonga are all separated by water exceeding 2000 m (National Geographic Society, 1991; Defense Mapping Agency, 1996) more than an entire magnitude deeper than the maximum depth of diving of all sea snakes, not only sea kraits (Heatwole, 1999), and accordingly each of these regions shows considerable divergence in various characters from its neighbours. Geographic variation may be more sensitive to water depth than is geographic distribution. Expansion of the distribution of a species of sea krait from one island-group to another merely requires the dispersal of a few individuals, or even of one gravid female, whereas genetic continuity would necessitate gene flow via frequent exchange of individuals.

Deep water also occurs between islands within some of the eastern island groups. For example, between Rennell Island and the rest of the Solomon Islands water-depth exceeds 4000 m (National Geographic Society, 1991); this may explain why in at least one character (ratio of widths of dark and light bands) sea kraits at Rennell differ significantly from any neighbouring areas and in another (width of light bands) are more closely allied with Vanuatu than with the other Solomon Islands. There is also deep water between the eastern and western Solomon Islands (>200 m throughout and >2000 m for much of the length of the island chain); it was noted above that the eastern and western Solomons differ significantly in some characters and lack of continuous habitat may be the explanation. However, sample sizes are small for the Solomons and such a conclusion must be tentative. Similarly, there is deep water between New Caledonia and the Loyalty Islands (>2000 m; National Geographic Society, 1991).

The effect of deep-water barriers may be modified by their width as the probability of crossing a wide barrier by fortuitous means falls off sharply with distance (MacArthur and Wilson, 1967). The similarity of Fijian and Tongan populations in a number of characters, despite deep-water between the two groups, may reflect the short distance across that barrier. The deep-water gap between New Caledonia and the Loyalty Islands is short and the two areas differ significantly in one character (width of dark bands in male *L. saintgironsi*), but sample sizes are small for the Loyalty Islands. Gibbons and Clunie (1984) presented paleographic maps of the eastern island chain showing that sea level lowering resulted in the emergence of islands that are now submerged. These would likely have been surrounded by reefs and could have served as ‘‘stepping stones’’ affecting dispersal and gene flow of *Laticauda*. Note also, that in the past some of the islands were closer together than they are now (see Section 1.5). New Caledonia was much larger than at present and in The Solomon Islands, Vanuatu, Fiji and Tonga, not only were islands larger, but some coalesced. These changes shortened the distances separating populations of *Laticauda* and may have promoted genetic exchange. Offsetting this effect was the narrowing of suitable reefal habitat for *Laticauda* occasioned by the expansion of land closer to the permanent drop-off into deeper water.

Palau is both remote and separated from other areas inhabited by kraits by water exceeding 4000 m in depth, a combination of conditions that probably accounts for its distinctiveness in various characters.

The direction and strength of sea currents also may be important. Dispersal of a shallow-water marine animal across a wide barrier of deep water would be facilitated by a current flowing across the barrier than if the current were at right angles or in the opposite direction. Crossing a water-barrier would be faster and more likely to be successful if a favourable current were swift rather than slow. Perhaps one of the most important effects of water depth lies not in its present level, but in those of the past. Eustatic sea levels have fluctuated markedly in the past 250,000 years (Voris, 2000) and at lowered sea levels areas that once had a continuous coastline are now fragmented islands. Again, there is an important difference between the effect this has had on distribution as opposed to geographic variation. A rising sea level would fragment a continuous distribution of sea kraits along a coastline into patches around islands without reducing the breadth of the species’ range. Such fragmentation, however, would interpose gaps of open water not suitable to sea kraits and would establish barriers to gene flow. Geographic variation would seem to be more sensitive than distributional extent.

In conclusion, patterns of geographic variation in sea kraits probably depend upon the inter-related effects of (1) water depth, (2) distance, (3) paleogeography, (4) presence or absence of “stepping stones”, (5) continuity of coral habitat, and (6) directions of sea currents, through their causing gaps in suitable habitat and/or affecting gene flow across barriers to dispersal.

The most conspicuous feature of the geographic pattern of variation in the *Laticauda colubrina* complex is that ancient geological and palaegeographic events have impinged upon this complex only insofar as those events have influenced the present pattern of circulation of water and the present configuration of land and sea. The tectonic movements that formed the archipelagic landmasses encompassing the distribution of the complex had largely been completed by the time *Laticauda* came upon the scene. It is primarily the events of the past 30 million years that have had a more direct effect. The evidence for this comes not only from the biochemical data relating to the timing of the origin and dispersal of the group (see Chapter 1) but from the present distributional patterns of the species (see Chapter 3). There are populations that traverse areas of diverse ages, tectonic origins, and palaeogeographic histories and yet maintain a high degree of morphological homogeneity. For example the east-west axis includes elements from the abutment of the Indian and Asian plates (Andaman and Nicobar Islands), the Sunda Shelf of ancient mixed continental derivatives, a composite eastern Indonesia, a composite island of New Guinea and the Solomon Islands. The hierarchical analysis showed that a homogeneous series of demes straddle the transitional region between the Australian and Asian plates known as Wallesia or Malesia and demarcated by various biogeographic lines purporting to separate two distinctly different fauna (see Section 1.5). Clearly, more recent events than tectonic movements of these two ancient plates have shaped the present pattern of geographic variation in *L. colubrina*. A second relatively homogeneous series of populations, the north-south axis spans a wide range of latitude and environmental conditions and yet maintains its homogeneity as well as its distinctiveness from the east-west axis. A third region, contained the eastern islands; these were more similar to each other than to either of the above axes, but did show greater internal differences in some characters than was characteristic of the two axes. Palau shared some characteristics with the north-south axis and others with the east-west one.

This pattern was discovered by hierarchical analysis but was not obvious from trees based on phenetic data. Such trees make only direct comparisons among populations without taking account of possible morphological convergence among distant, but genetically distinct, populations. The hierarchical analysis assesses the extent of similarity or divergence among adjacent populations and thereby allows tracking of characteristics along a geographic continuum. If one or more characters are similar between two geographically distant populations that are connected along the spatial continuum by a series of populations containing sharp discontinuities at one or more points, it flags morphological convergence among the peripheral localities. There was a commonality of pattern among the location of such discontinuities between populations, lending confidence that they were based on barriers to gene flow. The Principal Components Analysis confirmed the pattern arising form hierarchical analysis and together they identified markedly different geographical isolates that were described as new species (*L. saintgironsi, L. guineai*) or resurrected from synonymy (*L. frontalis*) (Heatwole *et al*., 2005; Cogger and Heatwole, 2006) and the mapping of other cohesive, but infraspecific, units not given formal nomenclatural recognition (east-west axis, north-south axis, eastern islands, Palau).

The similarities and differences between these various populations can be explained by (1) facilitation of gene flow via waif dispersal by former and present-day directions of sea currents, and (2) by interruption and rejoining of land connections or habitat barriers (such as mangroves) among populations during Holocene changes in sea level.

8.5.1. Latitudinal and Developmental Effects

Geographically remote, peripheral populations of *L. colubrina* share characters or suites of characters that differ from those of intervening central populations (e.g., populations from the Andaman–Nicobar Islands in the far west, those from the Ryukyu Islands in the far north, and those from Fiji or Tonga in the extreme southeast have relatively low values in some characters compared to more central ones (Chapter 4) and that is perhaps why the trees based on phenotypes were not very conclusive. Such phenotypic characters as the details of the scutellation and colour pattern of snakes are subject to genetic, developmental and environmental influences. There are several possible explanations for peripheral/central geographic patterns of variation, depending on the relative importance of these categories of influences.

Developmental hypothesis: Earlier research suggested that the temperature at which snake embryos developed could influence meristic characters such as the number of vertebrae, scale rows, gastrosteges, supralabials, preoculars, postoculars, subcaudals, and lateral blotches (Fox, 1948; Fox *et al*., 1961; Osgood, 1978; Lordais *et al*., 2004). If this were true, the peripheral/central pattern could merely reflect the developmental effects of different physical (e.g., thermal) environments in peripheral areas compared to central ones and not be indicative of genetic affinities at all. Webster and Streten

(1972) showed a present-day gradient of isotherms of sea temperature from 22°–26° C (winter to summer) at New Caledonia to 26°–28° C just south of Java to 28°–29° C just north of New Guinea on the equator (see also Fig. 3.13 for greater detail). The gradient is in the reverse direction above the equator and thus the periphery has generally lower sea temperatures than the central core. Although there are some thermal data on sites where *L. colubrina* and *L. saintgironsi* occur in the water or shelter on land and on the level of temperatures at which they thermoregulate (Heatwole, 1981a; Guinea, 1986; Saint Girons, 1964, 1990; Shetty and Sivasundar, 1998), few data are available on the temperature of nest sites at different localities. Punay (1975) indicated temperatures as low as 15° C where he found *Laticauda* eggs (species unspecified).

Recent work by Arnold and Peterson (2002) on garter snakes cast doubt on the validity of the developmental hypothesis. They found that scale counts routinely used in snake systematics were buffered against thermal effects during development and concluded that geographic differences in meristic counts were caused by genetic drift and/or selection, rather than by direct environmental influences. They attributed the opposite conclusions of previous investigators to statistical artifacts and the use of inappropriate experimental temperatures.

Full assessment of the developmental hypothesis for sea kraits would require a combination of (1) detailed monitoring of the microenvironments experienced by developing eggs in different parts of the species' range and (2) experimental studies evaluating the developmental effects of appropriate environmental levels on relevant phenotypes.

Hypothesis of peripheral convergence: Ecological equivalents are species that resemble each other in appearance, ecology, physiology, and behaviour not because of close genetic relationship, but merely because they occupy similar environments that select for a similar suite of adaptive characters (e.g., see Heatwole, 1970). However, convergence need not be restricted to genetically distant taxa and the phenotypic similarity of widely separated peripheral populations of *L. colubrina* may be a case in point; the hierarchical method is uniquely suited to identify such possible cases. If the environments of peripheral locations are similar to each other but different from central ones, then all peripheral populations would be expected to adapt independently, but convergently, to those conditions, at the same time diverging from central populations experiencing a different selective environment. Under this scenario the central pattern would be the ancestral one (Darlington, 1963) with convergent adaptation occurring at the periphery as a taxon progressively extends its range centrifugally. Assessing this theory requires not only comparison of the peripheral and central environments impinging on this species, now and in the past, but an assessment of the genetic relatedness of peripheral populations to each other and to central ones, such as through a comparison of DNA.

Hypothesis of central divergence: This explanation is the antithesis of the previous one in that it postulates peripheral populations to be genetically similar and to exhibit the primitive condition (see Dunn, 1926). This implies that present peripheral environments most resemble the ones to which the species was historically subjected, but as conditions changed in central areas, the centrally located populations adaptively diverged from peripheral ones. Again, evaluation of past and present environments and the genetic relatedness of the various populations would allow assessment of this theory.

Rasmussen (1975) studied the geographic variation of the terrestrial snake, *Psammodynastes pulverulentus* on the southeastern Asian mainland, Taiwan, and the Indonesian and Philippine archipelagos. His results were similar to those of the present study in that various characters varied somewhat independently but there was similarity among peripheral populations in at least one character (number of small maxillary teeth between the anterior and rear fangs). He interpreted the high number of maxillary teeth in peripheral populations as the primitive condition and that the differentiation in other characters, such as colour and the number of gastrosteges and subcaudals, took place after the species had dispersed throughout the archipelago.

Interaction of factors: The above hypotheses are not mutually exclusive, and could operate either singly or in some combination. Furthermore, the validity of any of them may vary depending on the particular character under consideration. Dohm and Garland (1993) showed that not all meristic characters of scutellation in snakes have equal heritability (values ranged from 0 to 0.6) and that phenotypic correlations may be poor predictors of genetic correlations for scale counts. Ideally, one should know the heritability of the characters used and how much environmental or maternal influences modify genic expression. Furthermore, genes have pleiotropic effects, and different characters may be genetically linked in various ways. Thus, while one character may be subject to intense selection, others may follow passively in varying degrees. Clearly, all the relevant data required for testing these hypotheses are not at hand and would require considerable effort to assemble. The most critical approach, however, would be an analysis of DNA from selected localities.

8.6. Role of Palaeogeography and Paleoclimate in the Distribution and Phylogeny of Sea Kraits and their Derivatives

Sea kraits originated, diverged into different species complexes and species, and radiated geographically into morphologically identifiable, infraspecific demes in the past 30 million years (see Sections 1.4, 1.5) i.e., during a time of general global cooling and the formation of the Antarctic ice shelves (see Section 1.6). These large-scale thermal events, however, did not likely impinge directly upon the early phylogeny of sea kraits. Kent and Muttoni (2008) indicated that the equatorial humid belt, about 15°-20° wide and astride the equator but asymmetrical toward the north by several degrees, has probably been a relatively stable feature of global climate. It is precisely within that belt that the early phylogeny of *Laticauda* occurred; only later as individual species expanded their geographic range toward higher latitudes was temperature likely to have come into play.

It is uncertain how long sea kraits have been linked with coral, but the fact that species from all three complexes inhabit reefs suggests that the association may go back to near the inception of the genus *Laticauda*. If so, the history of coral reefs over the past 30 million years would be germane to any discussion of the radiation of sea kraits.

There was massive extinction of corals in the late Cretaceous and the few survivors began proliferating in the Palaeocene with diversity and reef development reaching an all time high in the late Oligocene and subdividing into the modern biogeographic provinces in the Miocene (Veron and Stafford-Smith, 2000; Veron, 2008). Thirty million years ago, when the sea-krait story began to unfold, the genera of corals that are still extant today occupied a geographic area (the so-called “coral triangle”) (Veron, 2008) practically identical to the present distributional range of the combined east-west and north-south axes of the *Laticauda colubrina* complex (compare Fig. 8.1 with any of Figs. 4.6, 4.8, 4.10-4.14). Thus, appropriate habitat was available for sea kraits from their inception and into their early dispersal stages. The only difference between the map of the coral triangle and the present distribution of sea kraits is that sea kraits now extend beyond the coral triangle, slightly in the northwest from Sumatra to the Andaman Islands, in the northeast from Taiwan to the Ryukyus and to the southeast from New Guinea down the eastern island chain. Those areas are now home both to corals and to sea kraits; probably as corals extended their range they created favourable habitat that the snakes later colonised. It well may be that a critical feature of the evolution of the genus *Laticauda* was its transition from a coastal, terrestrial form into a semi-aquatic one, thereby improving its capabilities for dispersal by sea and opening up the opportunity for radiating into the coral reef

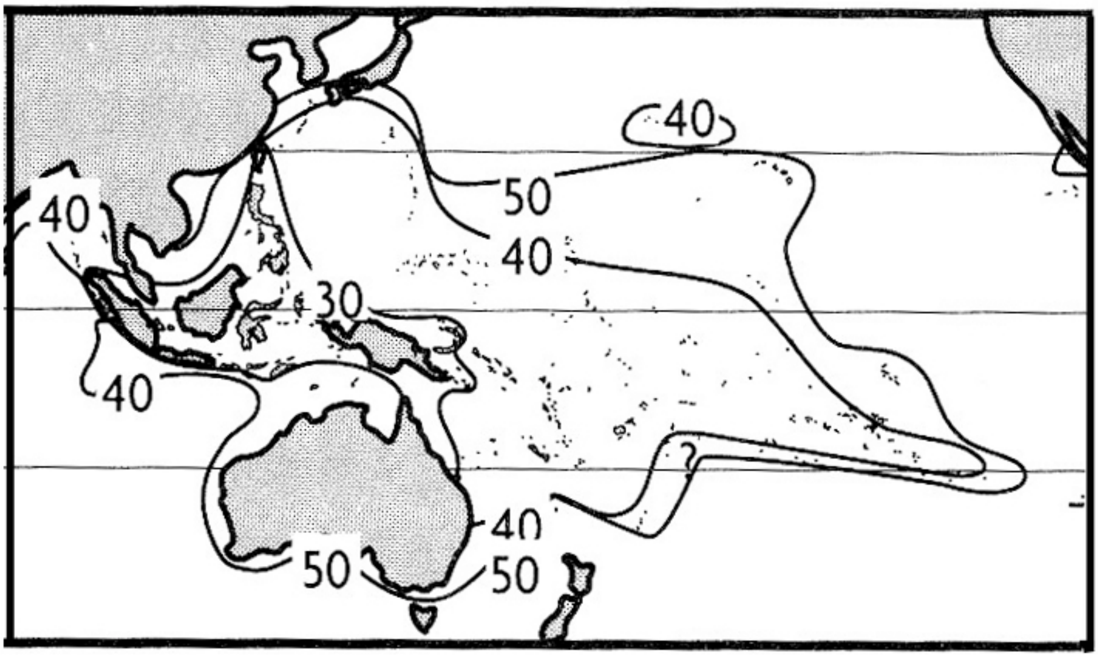


Figure 8.1. Contours showing the average age of extant reef coral genera (in million of years). The 30-million-year contour encloses the area where the most recent evolution of corals took place, i.e. the Indo-Pacific centre of coral diversity, or the “coral triangle”. Note that this area coincides closely with the combined east-west and north-south axes of the *Laticauda colubrina* complex. Modified from Veron (2008) with permission from J. E.N. Veron.

habitat and extending its geographic range accordingly.

The coral triangle, largely within the stable equatorial belt (see Section 1.6), probably served as a climatic refuge, not only for corals, but also for sea kraits. For example, Veron and Kelly (1988) noted that only 10% of corals at a New Guinean site went extinct during the ice ages. In this haven both taxa probably survived climatic extremes and radiated peripherally from there when conditions were generally more favourable. Consequently, there was probably not a single range extension, but rather a series of extensions and retreats as areas outside of the equatorial belt were influenced by the climatic oscillations of the Pliocene and Pleistocene.

Within the range of prevailing temperatures over most of its range, temperature has had minimal direct effect on patterns of geographic variation in *L. colubrina* as adding sea surface temperatures to the multivariate analysis, resulted in only a small increase in the amount of variation explained (see Chapter 7).

Other than direct thermal effects, the indirect effect of global cooling likely had a great influence upon the geographic distribution of sea kraits. The locking of water into the polar ice lowered sea level to the extent that land connections occurred between some islands and between Australia and New Guinea, thereby providing continuous coast lines with shallow reefs along which sea kraits could extend their range, or alternatively such movements could be blocked by land

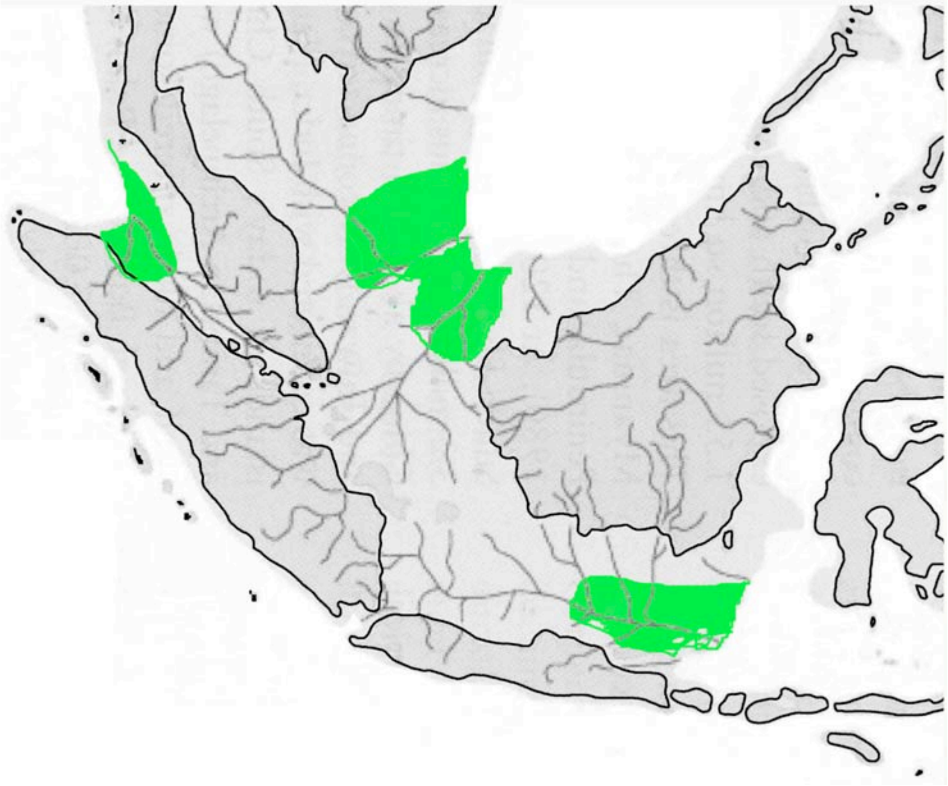


Figure 8.2. The configuration of land and sea and the distribution of mangrove swamps (in green) in Sundaland during the height of the last glaciation, 18,000-20,000 years ago and similar to that occurring during repeated cycles of sealevel-lowering during the late Pliocene and Pleistocene. Grey indicates the exposure of land at the lowest sea level; the present-day configuration of land is outlined in black. Modified from a combination of Voris (2000) and Tomascik *et al.* (1997) with permission from Harold Voris and Oxford University Press.

connections or unsuitable habitat such as mangroves (see Section3.3.2, 3.3.3; Fig. 8.2). There have been many cycles of alternating lower and higher sea levels than at present as the vagaries of the ice caps changed during the Pliocene and Pleistocene (Dowsett and Cronin, 1990; Voris 2000; Sathiamurthy and Voris, 2006; Hendy and Kamp, 2007) (see Fig. 8.2).

Although, until more accurate timing of the separation of particular species or demes is available through DNA analyses, particular events of sea-level lowering and divergences among sea krait populations cannot be precisely correlated, models can be produced that relate phylogeny to paleography in a general way. The timing of the older separations has been more thoroughly studied than have the more recent ones and consequently, the earlier stages of the following model inspire more confidence than do the more speculative later states.

After the elapids arose, they spread widely around the world and, although reaching Sundaland (Fig. 8.3, upper left, white arrow), did not directly penetrate

Australia as elapines, only as much later derivatives of that taxon. In coastal Sundaland a coastal species, possibly a semi-aquatic one, became established and was the stem taxon of the Laticaudinae (Fig. 8.3, upper right). It underwent overwater dispersal to some part of the Melanesian Arc that eventually became part of New Guinea) (Fig. 8.3, lower left, white arrow). Guinea's (2002) hypothesis that origin of the genus *Laticauda* was northern New Guinea seems the most plausible and parsimonious explanation. This occurred about 24-23 mya (end of Oligocene). The stem form was probably still terrestrial as it spawned a new lineage, the Oxyuraninae that first left primitive terrestrial representatives in Melanesia and then dispersed to Australia between 23 and 12 mya where it radiated into the Australian venomous terrestrial snakes which in turn, gave rise to the viviparous sea snakes (see Section 1.2) (Fig. 8.3, lower right, white arrow).

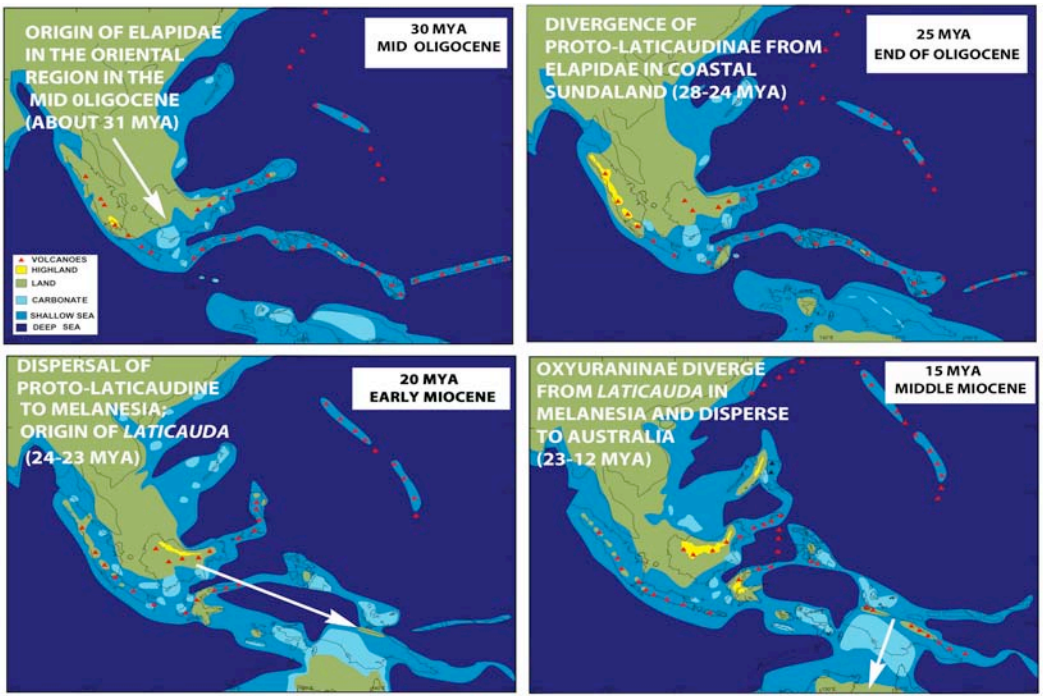


Figure 8.3. Palaeogeographic maps showing configuration of land and sea from 30 million years ago (mya) to 15 mya and the events in the history of *Laticauda* that are postulated to have occurred during that time. Arrows indicate direction of dispersal. See text for detailed explanation.

The stem stock remaining on New Guinea became independently marine and radiated into the coral habitat as the genus *Laticauda*. The paleomaps depicted in figure 8.4 show the configuration of land and sea of 10 mya and 5 mya and the dispersal events portrayed therein may have taken place then as they fit with the molecular data for the origin of *Laticauda* and it was a time when corals

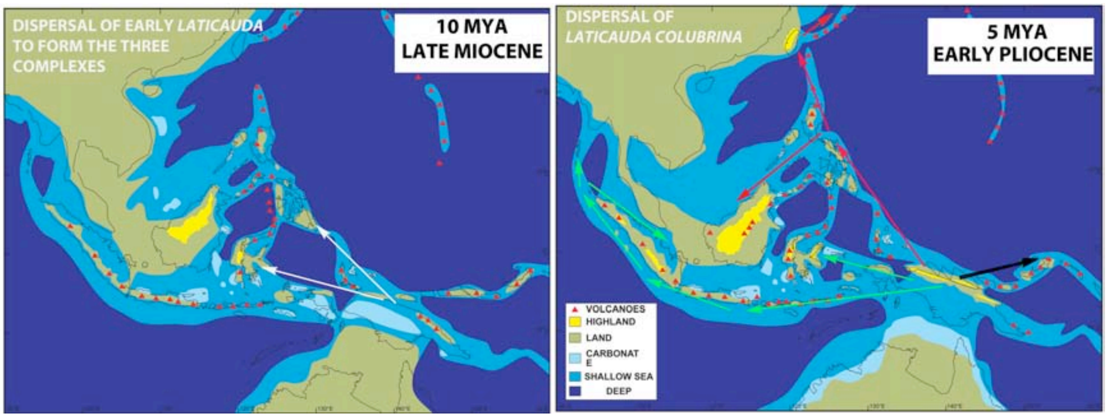
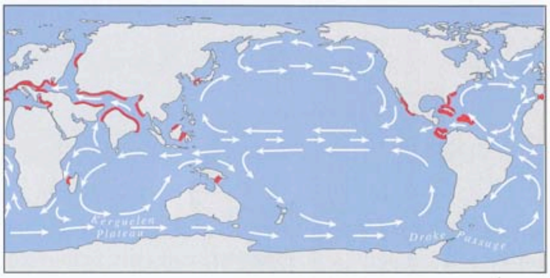
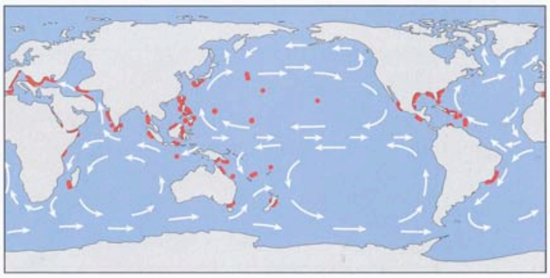


Figure 8.4. Palaeogeographic maps showing configuration of land and sea from 10 million years ago (mya) and 5 mya and the events in the history of *Laticauda* that are postulated to have occurred during that time or during similar configurations at a later time. Upper: arrows indicate dispersal of waifs to two different localities (may not necessarily have been the specific destinations indicated), one of these isolated populations radiated into the *Laticauda laticaudata* complex and the other into the *Laticauda semifasciata* complex. The *Laticauda colubrina* complex occurred at the place of origin (incipient northern New Guinea) and later (lower graph) dispersed from there, leading to establishment of the populations of the east-west axis (green arrows), north-south axis (red arrows) and eastern chain of islands (black arrow). See text for detailed explanation.



The Eocene world showing the distribution maximum of coral reefs and/or reef corals. The development of a circum-Antarctic circulation (through the opening of the Australian-Antarctic seaway, development of the Kerguelen Plateau and the opening of Drake Passage) is the key to Palaeogene climates. The most important feature of the tropical world remains the tropical circum-global ocean circulation through the Tethys Sea and the Central American Seaway. The slow blockage of this circulation underpins all Cenozoic tropical palaeobiogeography.



The Miocene world showing the distribution maximum of coral reefs and/or reef corals. The continents are close to their present positions. The Tethys Sea is reduced to a narrow band connecting the Indian Ocean with the proto-Mediterranean. Reef development globally is at a maximum for the Cenozoic.

Figure 8.5 Palaeocurrents (white arrows) and distribution of corals (red) in the Eocene before the origin and dispersal of *Laticauda* and in the Miocene when these events were postulated to have begun. Modified from Veron and Stafford-Smith (2000) with permission of J. E. N. Veron.

were widespread in the target area (Fig. 8.5). This dispersal may have taken place at some later time, however, when similar configurations occurred as eustatic changes in sea level took place during the Pliocene and especially in the Pleistocene. Burrett *et al*. (1991) described extensive vulcanism in the Sunda region in the Miocene and Pliocene, much of it submarine; some of the islands had not yet emerged and others were covered with thick ignimbritic sheets. They suggested that dispersal was not easy for terrestrial biota prior to 3 mya and coastal or shallow-water species, such as the emerging *Laticauda*, may have been similarly affected. Whatever the time, there must have been a northwestward migration of *L. colubrina* from the northern New Guinean part of Melanesia into at least two separate areas (as yet unspecified), where these isolates diverged from the parent population and from each other to form the founder species of the *Laticauda laticauda* and the *Laticauda semifasciata* complexes (Fig. 8.4, upper), leaving the parent population to give rise to the *Laticauda colubrina* complex. *Laticauda colubrina*, then itself dispersed in several directions, westward into what is now Indonesia, partly via long-distance overwater dispersal and partly probably by “island-hopping” and gradual extension along the coastal shallows of the Sunda Islands and Sumatra, eventually to reach the Andaman Islands and then in the reverse direction along the northern coast of Sumatra (Fig. 8.4, bottom, green arrows). This probably occurred gradually and may have been intermittent as eustatic changes in sea level cycled. This dispersal extended the species range to that of the present east-west axis.

At roughly the same time, there must have been an overwater island-hopping from Melanesia northward, again perhaps in stages, to what later became the Philippines and Taiwan and eventually to the Ryukyus and in a southwesterly direction from the Philippines to what was to become Sabah (Fig. 8.4, lower, red arrows). This range extension encompasses the area now inhabited by populations of the north-south axis.

A third prong of dispersal was eastward into various islands of Melanesia, eventually forming the northwestern end of the island chain (Fig. 8-4, bottom black arrow). During those times sea levels sometimes were higher than at present levels (Dowsett and Cronin, 1990) and sometimes lower.

Gibbons and Clunie (1984) presented paleographic maps of the eastern island chain showing that sea level lowering resulted in the emergence of islands that are now submerged. These would likely have been surrounded by reefs and could have served as "stepping stones" affecting dispersal and gene flow of *Laticauda*. New Caledonia was much larger than at present and in the Solomon Islands, Vanuatu, Fiji and Tonga, not only were islands larger, but some coalesced. These changes shortened the distances separating populations of *Laticauda* and may have promoted genetic exchange. Offsetting this effect was the narrowing of suitable reefal habitat for *Laticauda* occasioned by the expansion of land closer to the permanent drop-off into deeper water.

In areas peripheral to the coral triangle, expansion of the range of *L. colubrina* and its derivatives into the eastern island-chain probably occurred during periods of warmer sea water and at times of year when currents were favourable for waif transport in a southerly direction, whether in the Pliocene or later. Figure 8.6 shows the direction of currents at different times of year and during times of low water and of high water. The expansive phase would probably have taken place under warmer conditions resembling those of the present time, with *L. colubrina* extending progressively along the chain as far as Tonga (Fig. 8.6, blue arrow), leaving semi-isolated populations along the way. Some of these may have become extinguished during cooler periods resulting in a retraction of range to be followed again at the next climatic oscillation by a renewed expansion. Even during the warmer period in the Pliocene, there were parts of the southwestern Pacific with lower sea temperatures, probably because of local upwelling (Sabaa *et al*., 2004). New Caledonia is downstream of favourable currents for receiving dispersing waifs during part of the year during warmer high-water periods. With fewer stepping-stone islands intervening along the paths of currents and being more distant (Fig. 8.6, olive arrow), it probably received limited numbers of waifs from the mother population and over time its population became reproductively isolated and diverged into the New Caledonian endemic *L. saintgironsi*. In turn *L. saintgironsi* spawned the species *L. frontalis* now endemic on Vanuatu (Cogger and Heatwole, 2006). Currents are not favourable for waif transport from New Caledonia to Vanuatu and that dispersal (Fig. 8.6, orange arrow) must have taken place by some unusual, improbable means and must have

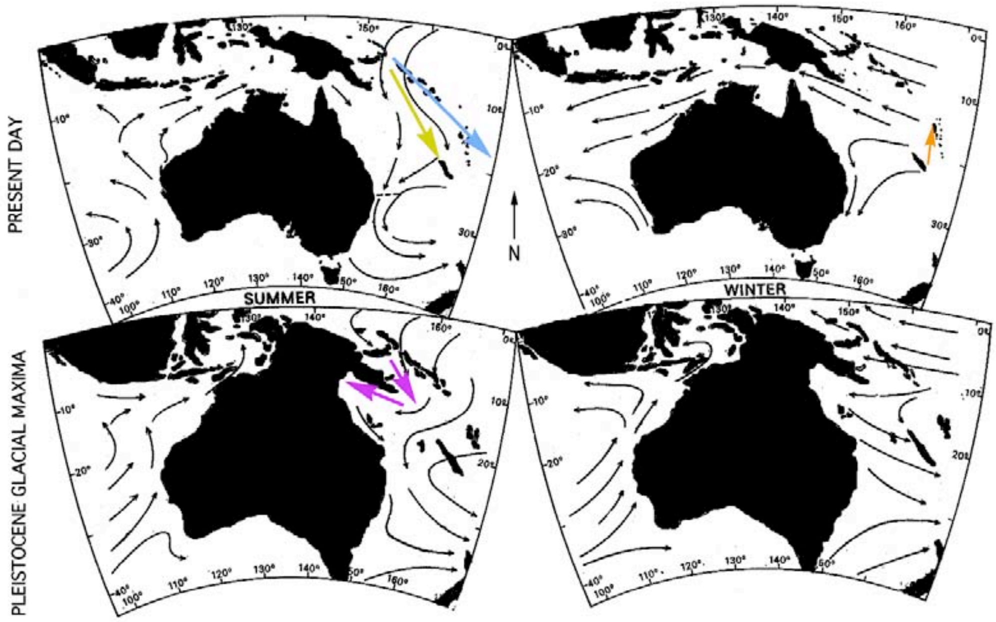


Figure 8.6. Patterns of Australasian sea currents in winter and summer at the present day and at maximal sea level lowering during glacial periods. Modified from Webster and Streten (1972).

been a single event, leading to isolation from further gene flow with the parent population and eventual speciation. Since the parental species, *L. saintgironsi*, was already reproductively isolated from *L. colubrina*, the founders of the Vanuatuan population would also have been distinct. With gene flow no longer possible either with *L. colubrina* with which it shared its new home, nor with its parental population of *L. saintgironsi*, it diverged into *L. frontalis*. Both in the cases of *L. saintgironsi* and *L. frontalis*, divergence from the mother species may have been enhanced by the effects of the founder principle and of genetic drift.

During periods of low water, expansion of *L. colubrina* along the southeastern Papuan coastline would have been blocked to the west by the land connection between Australia and Papua New Guinea (Doutch, 1972) (Fig. 8.6). Subsequently, it was isolated in the cul-de-sac of southern Papua by the easterly current through the Torres Straits in summer. In winter the currents reach that area from the eastern islands but because of the distance there would have been little gene flow from the small areas there. Accordingly, the southern Papuan populations differentiated into *L. guineai*.

In summary, a synthesis of the data on (1) the present distribution of sea kraits, (2) biochemical analyses of their phylogenetic relationships and the timing of divergence among taxa, (3) paleogeography, (4) paleoclimatology, and (5) directions of sea currents, produced a model for the 30-million-year history of the evolution of this taxon. The group originated from Asian elapids that dispersed over water to Melanesia (northern New Guinea) where they gave rise to a lineage leading to Australian venomous terrestrial snakes and their derivative the viviparous sea snakes. (Oxyuraninae). The stem group then adopted a marine habitat itself (*Laticauda*) and dispersed westward to form the east-west axis, northward to form the north-south axis, and eastward along the eastward island chain where several speciation events occurred, one (*L. guineai*) in southern Papua in a cul-de-sac cut off by land barriers at low water levels, another on New Caledonia (*L. saintgironsi*), which in turn gave rise to *L. frontalis* on Vanuatu.

8.6.1. Comparison with other Taxa of Reptiles

Other taxa of marine snakes show geographic patterns of variation parallel to those described here. For example, Gritis and Voris (1990) compared various localities of *Lapemis curtus* in terms of frequencies of various character states of the parietal scales and gastrosteges. Regions differed significantly in one or more character states, but the most striking result was that, considering the characters collectively (see their Figs. 5, 6; pp. 6, 8), the overall pattern showed similar affinities and divisions as in the present study. The Philippines and Sabah (corresponding to the north-south axis of the present study) were more similar to each other than to other localities and differed from five localities in peninsular Malaysia, all of which were similar to each other (corresponding to the western limb of the east-west axis). Finally, the southern Papuan population, as in the present study, differed from both of the above regions. There were also localities, extralimital to *L. colubrina*, that fit either into one of the above patterns (Gulf of Thailand, Australia) or formed a still different configuration of character states (Myanmar to the Persian Gulf).

Cerberus rynchops is an homolopsine snake whose extensive geographic range from India through the Australasian archipelago to Palau (Gyi, 1970) overlaps much of that *L. colubrina*. Karns *et al*. (2000) found that genetic divergence among its populations correlated more closely with interlocality distances, as measured along present shorelines and across minimal water gaps, than it did either to that measurement along paleo-shorelines at lower sea level, or to straight-line distances, suggesting the likelihood of recent gene exchange within the Sunda plate, but less frequent or older exchange with Australian populations. *Cerberus rynchops* and *L.*

colubrina both inhabit shallow coastal waters and their dispersal probably was similarly affected by changes in paleo-shorelines and sea levels. The slight differentiation among populations of *L. colubrina* over a wide area also bespeaks recent isolation, or frequent gene exchange.

Karns *et al*. (2000) suggested that in the patchy habitat along the coastlines of this region, *Cerberus* must encounter obstacles to dispersal. The same is likely true of *L. colubrina* but in an opposite fashion. The habitat requirements of these two species are nearly mutually exclusive, *C. rynchops* occupying mangrove swamps and mudflats and *L. colubrina* coral reefs. In the mosaic of muddy areas and reefs in this area, habitat serving as a refuge for one would pose a barrier to the other.

Even some non-marine reptiles show patterns of geographic variation reminiscent of that described here for the *Laticauda colubrina* complex. For example, agamid lizards of the *Trapelus agilis* complex in southwestern Asia are widespread, highly sexually dimorphic, and exhibit complicated patterns of geographic variation. Rastegar-Pouyani (2005) described operational taxonomic units (below the subspecific level) with degree of differentiation attributable to fragmentation of range by ecological and physiographic barriers and interruption or limitation of gene flow. These operational taxonomic units were further divided into demes.

8.7. General Conclusions

As described in Section 1.1, the objectives of this thesis were to (1) describe the distributions of sea kraits in the *Laticauda colubrina* complex and explain them in terms of historic and present biotic and abiotic influences (see Chapter 3), (2) analyse geographic patterns of morphological variation (see chapters 4-7), (3) assess the role of present geographic and ecological factors in affecting dispersal and gene flow among populations (Section 8.5), (4) interpret the role of palaeogeography and vicariant events in the evolutionary history of the taxa (Section 8.6), and (5) identify the most appropriate sources of molecular material to be used for further testing of evolutionary hypotheses (see Chapter 9).

These objectives have been achieved. The distribution of members of the complex depend on satisfaction of a number of requirements, including suitable marine habitat (coral reefs) in proximity to offshore islands with suitable cover and relatively free of terrestrial predators, year-round mean sea temperatures above about 20°C, and access to sources of freshwater.

In terms of geographic variation, the most important findings were that the *Laticauda colubrina* complex occurs in morphologically identifiable entities that have diverged in varying degrees from *L. colubrina*, the most primitive species of the complex. Those that have diverged the most were either described as new species (*L. guinea*, *L. saintgironsi*) or resurrected from synonymy (*L. frontalis*). Each of these derivative species have very limited distributions and represent different subsets of the morphological variation of the widespread and variable *L. colubrina*.

A hierarchical method was developed (Chapter 4) that was suited to analysing complex, archipelagic distributions such as that of *L. colubrina*. The pattern it revealed for a given character was one of a series of geographic entities that were each morphologically relatively homogeneous within themselves (sometimes with internal clines) but separated by sharp discontinuities from neighbouring entities. Congruence of pattern among a number of different characters of scutellation and colour pattern, allowed identification of regional groupings consistent with genetic cohesiveness. These are distinguishable from morphologically convergent populations by discontinuities between intervening populations. The major groupings recognized were an east-west axis from the Bay of Bengal eastward through the Malay Peninsula, Indonesia, and New Guinea to the Solomon islands, a north south axis from Sabah northward through the Philippines and Taiwan to the Ryukyu Islands, and the eastern islands of Vanuatu, Fiji and Tonga. Palau was allied both to the east-west and north-south axes but with some characteristics of its own. There were sub-groupings within these major ones, based on patterns of individual characters.

These patterns of speciation and geographic variation were supported by a Principal Components Analysis but a tree based on morphological phenotypes was inconclusive, possibly because, unlike the hierarchical analysis, it could not distinguish convergences. A multivariate analysis showed a strong latitudinal effect in the pattern of variation with a strong longitudinal warp. Inclusion of temperature of the sea surface and precipitation explained little additional variation.

A model portraying the history of sea kraits over the past 30 million years was developed in accordance with known information on their origin, phylogeny, and times of divergence, and with reference to the pattern of variation noted above and to the paleogeography of southeastern Asia and Australasia. This model depicts the dispersal of the precursor of the sea kraits from Sundaland to what is now New Guinea, where it gave rise a terrestrial lineage (that entered Australia and diversified into the Australian terrestrial snakes and their derivatives the oxyuranine sea snakes) as well as to the genus *Laticauda*. From northern New Guinea it radiated via a combination of overwater waif dispersal and lateral spread along shallow coast lines in three directions, westward into Indonesia, northward into the Philippines, and eastward into the islands of the southwestern Pacific. This occurred in several cycles, with dispersal taking place during periods of low water, and isolation and speciation occurring when high water increased distances between suitable habitat. The first cycle gave rise to the progenitors of the different complexes in the genus, and subsequent cycles to the species within each complex, and more recently to the morphological distinguishable infraspecific units of *L. colubrina*, denoted here as the east-west axis, north-south axis and eastern islands.

These events took place in the past 30 million years, well after the major tectonic and vicariant events that formed the region had taken place. Evidence of this comes from biochemical evidence of timing of divergences from the elapines, and from the fact that at present morphologically homogeneous populations of sea kraits spread from the Asian plate across the various biogeographic lines purported to separate Asian and Australian biogeographic realms, onto the Australian plate, and incorporating such geologically and palaeographicallly diverse land masses as New Guinea and the islands of Indonesia. Even the infraspecific taxon of the east-west axis spans these major geological boundaries, thereby attesting to the recency of the latest dispersal events. Thus, the patterns of geographic variation do not relate to the movement of continents or even their fragments, but do relate to patterns of sea currents and configuration of land and sea in the area only within the past 30 million years.

8.8. Recapitulation

- Two new species were discovered but described elsewhere: *Laticauda saintgironsi* and *Laticauda guineai*. One species, *Laticauda frontalis*, was resurrected from synonymy. Other morphologically and geographically distinct populations were identified but not given formal nomenclatural recognition.

- Some characters, previously believed to be stable and diagnostic of species or species complex were found to vary somewhat in *L. colubrina*.
- The primitive and widespread *Laticauda colubrina* was more variable than were the derived, more geographically restricted species.
- An attempt to restrict the vague type locality of *L. colubrina* was not successful.
- *Laticauda colubrina* and *L. guineai* were sexually dimorphic in size and in most morphological characters; *L. saintgironsi* was less dimorphic and *L. frontalis* showed the least sexual dimorphism. Possible advantages to sexual dimorphism in size is that (1) larger females have larger clutch sizes, and/or that (2) it allows for ecological segregation in diet, with the sexes feeding on different-sized prey, or that (3) larger males are more effective in fighting rivals for females. Numbers 1 and 2 could be operative in *L. colubrina* as females are larger, but not number 3 as males are not combative in this species, and in any case are smaller than females.
- In some ontogenetically stable characters, juveniles differed significantly from syntopic adults, suggesting that selection may be operating on those characters. In one character (width of dark bands) selection appeared to be in opposite directions in Fiji and Tonga than in other parts of the range.
- The “patchy” distribution of sea kraits on several scales was related to (1) the patchy distribution of its habitat (coral reefs) on a larger scale, to the need for seclusion on small offshore islands free of terrestrial predators, on an intermediate scale, and on dependence on suitable cover or sources of freshwater, on a smaller scale.
- Superficial resemblances among populations distant from each other, yet with disparate populations intervening between them geographically, can arise as a result of developmental responses to similar environments or as a result of convergent evolution. A major contribution of the hierarchical method is that it is especially suitable for identifying such patterns of variation.
- 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.

CHAPTER 9. FUTURE RESEARCH

Most research by answering some questions, raises others. This dissertation is no exception and in the text of various chapters, a number of areas in need of further investigation are foreshadowed:

(1) The intriguing possibility of a species of *Laticauda* existing in Central America should be explored. Localities from which *Laticauda colubrina* have been reported need to be searched with a view to obtaining specimens of this elusive taxon.

(2) Various characters need to be assessed as to whether their geographic patterns reflect adaptation to particular environments or are merely reflections of random, historic changes in partly isolated populations. For example, the adaptive nature of the banded colour pattern needs to be studied. Experiments should be conducted to ascertain the response of potential predators to this bold pattern, or alternatively, its effectiveness in camouflaging the snakes against particular naturally occurring backgrounds. Once a decision is made between these alternatives, or an interaction between them found, the geographic differences in number and width of dark bands should be evaluated in light of geographic differences in kinds and numbers of predators and/or in configuration of the visual background in various areas. Important questions are: Do the bands camouflage the snakes against a complexly-patterned coral reef? If so, do bands carry a disadvantage in terrestrial situations where such a pattern might be conspicuous? Is that related to why sea kraits usually come ashore at night and remain concealed under cover by day? Why does there seem to be selection for wider bands in juveniles but for more narrow ones in adults in most of the range of *L. colubrina*? Since juveniles are more marine than are adults, does this signify that wide bands are advantageous in the marine environment but narrower ones in the terrestrial one? If so, is the reversal of this pattern (narrower bands in juveniles than in adults) in Fiji and Tonga because of differences in the visual background of reefs there? In general, how does the visual properties of marine versus terrestrial predators relate to patterning of sea kraits? Or is banding not a camouflage, but rather an advertisement to potential predators of the venomous nature of these snakes? Alternatively, does a banded pattern confuse potential predators because of a flicker effect?

(3) The developmental plasticity of various characters requires further investigation. The convergence of some characters between peripheral areas on opposite sides of the equator suggests that those characters may either be developmentally labile or subject to convergent selection pressures. To test for the former, eggs from the same clutch should be incubated at, say, different temperatures and the scutellation compared. Biochemical techniques could be applied in conjunction with the morphological data from the present study (see next section) to test for the latter, thereby adding a new dimension to the understanding of geographic variation in sea kraits.

(4) The knowledge of the thermal biology of sea kraits should be expanded. Tolerance limits to cold should be measured and related to the temperature suggested by this thesis as limiting the northward distribution of *L. colubrina*. Heat-stress proteins should also be studied and related to the activity cycles and microhabitat selection of these snakes.

(5) More detailed and geographically extensive comparisons of the reproductive cycles of *L. colubrina* should be carried out to ascertain whether there is consistent geographic adjustment of breeding to coincide with the most favourable environmental conditions, i.e., avoidance of early development during the cooler months.

(6) The water balance and osmoregulation of sea kraits need further investigation. How will the changes in availability of freshwater, projected to occur in the face of global climatic change, affect marine snakes. Dr. Harvey Lilllywhite is now conducting such studies and I am a participant.

(7) Attempts should be made to extract DNA from the type specimen of *L. colubrina* and *L. frontalis* in order to restrict the type locality.

(8) Theories have been proposed regarding the evolution of sexual dimorphism in the *Laticauda colubrina* complex (see Section 8.2). So far, these are tantalizing conjectures that require empirical support in addition to that already presented. The reduction of sexual dimorphism in *L. colubrina* and the absence, or near absence, of it in *L. frontalis* in Vanuatu, where these two species are sympatric, have been postulated to be related to a narrower size-range of food resources there than elsewhere. To avoid circularity, one would need to demonstrate empirically that the range of eel-sizes is, in fact, truncated at the upper end in Vanuatu. Similarly, the fact that, in general, conger eels (favoured

by female *L. colubrina*) inhabit deeper waters off reefs, and moray eels (favoured by males) live in shallower waters on reefs led to the suggestion that the sexes probably forage at different depths. This hypothesis would be strengthened by demonstration that these eels are also segregated by depth in Vanuatu, and/or demonstration that depth of foraging, in fact does differ between male and female snakes. An interesting related topic is whether the sexes differ in the length of time they are capable of submergence while active. It is also critical to know the depth contours around the reefs in question and to obtain data on how far the two sexes travel to their foraging sites. The above types of information would allow assessment as to whether large (conger) eels are scarce in Vanuatu, or merely inaccessible because the water they inhabit is too deep or too distant from the snakes' terrestrial habitat for sustained foraging by females. Another possibility is that the greater nutritional demands of females when producing eggs might drive their dietary and foraging requirements. A tantalizing study by Ackman *et al*. (1991) in Papua, indicated that male and female *L. colubrina* did not differ either from each other or from sea turtles in the general composition of their depot fatty acids, but did differ in some constituents from the females' favoured prey, a conger eel (*Conger cinereus*). However, two fatty acids did reflect a specific dietary role for eel fat in females. The sample size was small and the fat of the males' favoured prey (*Echidne* eels) was not determined. It would be instructive to extend this study to compare the nutritional content of the species of eels preyed upon by male and female snakes, and whether any such differences might reflect the different energetic needs of the sexes. Operationally, it may not be easy to evaluate these theories. For example, quantitative sampling, even if accurate, may not reflect actual accessibility of prey to predators. Some species may be harder for a predator to find or to recognize than others. For example, Reed *et al*. (2002) found that humans collected 22 species of eels from Vanuatu and (presumably from the same habitats) sea kraits collected 18; only seven of the species were common to both lists. Clearly, humans and kraits have different accessibility to the eel fauna and sample it in different ways. Logistical difficulties, however, do not dispose of the empirical necessity to adequately test hypotheses.

The above are all side issues arising from the present thesis, however, and the main projection of my doctoral programme into the future is its use as the basis for a more complete elaboration of evolution within the genus *Laticauda* by amalgamating it with biochemical assessments now in progress and in which I am participating.

9.1. Relationship of Morphological and Biochemical Approaches

Application of biochemical techniques has made enormous strides in the understanding of the phylogeography of organisms from diverse taxa, including snakes (see Section 1.3). In morphological studies, pattern of phenetic variation is used as a surrogate for genetic relationships, and molecular-genetic studies can clarify the extent to which this is valid. In addition, analysis of DNA can uncover cryptic taxa that are not easily distinguished on the basis of morphological features alone.

Morphological and molecular data sometimes converge to produce common phylogenetic conclusions but such is not always the case and sometimes the two sources of information suggest quite different evolutionary and taxonomic scenarios. Such discrepancies have a high heuristic content as they lead to intensified investigation in order to resolve apparent paradoxes. That is how science progresses. If one were able to explain why morphologically based schemes differ from biochemically based ones, a fuller understanding of the processes and course of evolution would be achieved than could be gained by either approach alone. Consequently, it is important to pursue both avenues. Zaher *et al*. (2009) noted that although a number of recent, molecularly-based studies addressed the classification of caenophidian snakes, few of them attempted to integrate morphological data into the resulting classification, a procedure they regarded as a deficiency.

The present study provides a firm base from which to launch effective, meaningful, and detailed biochemical and genetic studies leading to a more comprehensive understanding of evolution within the genus *Laticauda*. The pattern of morphological variation that has unfolded allows a more rigorous approach to planned biochemical analyses. Morphological data provide detail, relate directly to data from previous literature, and expand sample size to include specimens collected over the centuries. The development of hierarchical analysis during the present research has added a new dimension to morphological studies in that it allows identifying populations that are morphologically similar but geographically distant and, because of sharp discontinuities between intervening populations, are probably also genetically different. Biochemical approaches can clarify the genetic bases of such differences and in conjunction with morphological studies can definitively distinguish between convergence and developmental lability.

Often localities for collection of tissue samples for molecular studies ("taxon sampling") are haphazard or opportunistic with little guidance for the most effective selection of material. Accordingly, they have suffered from inadequate understanding of the breadth of morphological variation within a taxon and, especially at higher taxonomic levels, a few ill-chosen individuals have been used to represent an entire lineage.

Without the base of the present study, random, or even gridded collection of tissue samples almost certainly would have missed localities critical for a complete understanding of the evolution of sea kraits, as some morphologically distinctive entities are very restricted in their distribution and thus easily overlooked. For example, significant collections of *L. guineai* and *L. saintgironsi* were known and had been studied over extended periods of time by various investigators. Yet, both had been considered to be populations of *L. colubrina*, partly because investigators were concerned with local populations and few studies were geographically comprehensive. The detailed morphological analysis of the present study revealed them to be quite distinct and any biochemical approach pretending to inclusiveness would need to include tissue samples from these populations, a requirement likely to have been overlooked previously. On the other hand if one were to circumvent such a mistake by uncritically sampling tissues as widely as possible over the whole area, a great deal of time and money could be wasted. From the morphological data it is now clear that the *mininum* requirement for sampling this complex would include tissue not only from each of the described species, but also from *Laticauda colubrina* from the north-south axis, the east-west axis, Palau, and various of the eastern islands. Within each of the axes, internal patterns similarly provide a guide to a more intelligent selection of sub-sites. Differences between the eastern and western Solomon Islands were suggested by the present data (albeit on the basis of small samples from some areas) and populations from both these areas need to be subjected to biochemical analysis to ascertain the reality of these putative differences. Populations in Palau were identified as possibly receiving gene flow from two separate sources, the east-west axis and the north-south axis, and inclusion of tissue samples from that locality is essential.

A start has already been made in preparation for such a planned molecular extension of the present dissertation. Dr. Ulrich Kuch has underway a biochemical analysis of the genus *Laticauda*, including all three complexes, and has assembled the available bank of tissue samples from various sources. This involves a number of collaborators from around the world. He now has samples of *L. colubrina* from northern New Guinea, the Solomon Islands, Vanuatu and Tonga and of *L. frontalis* from Vanuatu contributed by Dr. Harold Cogger, from Palau made available by Dr. Ronald Crombie, and from Thailand contributed by Dr. Bryan Stuart and me. I made a special trip to Papua to obtain tissue samples of *L. guineai* and to Biak, West Irian, for samples of *L. colubrina*. The last locality was important because Endermann (1970) considered populations there as possibly distinct. Although that suggestion was not supported by the present study, it needs to be assessed by biochemical techniques. I understand that the late Joseph Slowinski collected some samples from islands off Myanmar and the possibility of using these is being pursued. My recent discovery of *L. colubrina* on Futuna should be supplemented by tissue samples, as this is a significant range extension and the most peripheral locality to the east. Thus, resources have been, and are being, assembled to carry the study of the phylogeography of the genus *Laticauda* to the next level and to further test some of the hypotheses posed by the present investigation.

9.2. Widening the Scope of Morphological Studies

Another area of potentially fruitful research suggested by the present investigation is a comparative morphological study of the other complexes of the genus *Laticauda*. Like the *L. colubrina* complex, each of these has one widespread species and derivative ones of very restricted distribution. Each widespread species occupies a similar, albeit somewhat less extensive, distribution as that of *L. colubrina*. Thus, there are three replicates with similar biogeography and evolution. It would be fascinating to ascertain whether the other widespread species show geographic patterns of morphological variation similar to that of *L. colubrina*. Questions that need to be asked are: Is the geographic pattern of morphological variation the same in all three, e.g., is there a north-south and an east-west axis in all of them? Are there parallels in particular characters, e.g., are high numbers of gastrosteges for one species matched in the same area by high numbers in the other species, and low numbers matched with low numbers? If so, it would suggest parallel adaptation among species to similar habitats. Do the derived species with restricted ranges in the other complexes also show reduced phenotypic diversity compared to the parental species? Do primitive species retain greater genetic diversity than derived forms, based on molecular and genetic evidence? What was the chronological order in the timing of dispersal and range expansion in the three complexes? Since *L. colubrina* is putatively the most primitive member of the genus, did it give rise to the other two complexes and later all three disperse from slightly different centres but at the same time and under similar influences, or did range expansion occur sequentially in the three complexes? Comparative biochemical and genetic analyses may answer this question. Answers to all these questions would provide insight into the process of evolution and speciation and, with combinations of morphological and biochemical analyses of geographic variation would place *Laticauda* among the best understood genera of snakes.

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Appendix 1.1. Synonymy of the species of the *Laticauda colubrina* complex

The synonymies of the species of the *Laticauda colubrina* complex are listed below; only the first usage of a particular name is given; all references were seen by the authors in the original, not merely taken from previously published synonymies. Errors in the spelling of the generic name have occurred in the literature (see Williams and Wallach [1989] for a listing); these are not included in the synonymy below.

***Laticauda colubrina* (Schneider, 1799)**

Coluber laticaudatus (in part) (Linnaeus, 1758). Linnaeus (1754) described the species now known as *Laticauda colubrina* under the name *Coluber laticaudatus*. This name was based on two specimens, each of a different species. One specimen (Catalog # 88 in the Museum Regis Adolphi Friderici) (see Plate 1) is the present *Laticauda colubrina* and the other (Catalog # 87) is now known as *Laticauda laticaudata* (Andersson, 1899). In the tenth edition of Systema Naturae (Linnaeus, 1758), the beginning of officially accepted zoological nomenclature, Linnaeus' original designation remained unchanged, and thus *Coluber laticaudatus* was a composite name referring to both *L. colubrina* and *L. laticaudata*. Linnaeus' (1754) written description and scale counts (220 gastrosteges; 42 subcaudals) could have applied to either species but the published drawing (his Figure 1 in Plate 16) was of *Laticauda laticaudata*. Subsequent designation (see Stejneger [1907, 1936] and Williams and Wallach [1989]) restricted the name *laticaudata* to the type species of the genus *Laticauda* erected by Laurenti (1768). *Laticauda colubrina* was first described as a separate entity by Schneider (1799; see below).

Anguis Platura (Lacépède, 1790). Count de La Cépède provided this name, probably for a composite of species including *Laticauda colubrina* and attributed the name to "Linn. Amphib. Serpents" with no date given.

Hydrus colubrinus. Schneider (1799) provided the type description for the species *colubrinus* and named it, thereby separating it from *laticaudata*. The original description is: "*Scutis ventralibus integris caudalibus divisis colubrum refert plumbeus, fasciis brunneis corpus cingentibus*." [Ventral scales complete; caudal scales divided; snake characterized by gray, dark bands encompassing the body---translated by H. Heatwole]. The data recorded for the type specimen (Museum für Naturkunde der Humboldt-Universität zu Berlin, catalog number 9078) indicated the locality as “Ost Ind Meer” (East Indian Ocean) and the collector as “Lampe” but without a date of collection.

Platurus fasciatus Latreille (1801)

Platurus colubrinus (Wagler, 1830)

Coluber platycaudatus (Oken, 1836)

Hydrophis colubrina (Schlegel, 1837a, b): Note that Schlegel's (1837b) Plate 10, purported to be *L. colubrina*, is not that species, but rather appears to be *L. semifasciata.*

Laticauda scutata (Cantor, 1847). Not *L. scutata* of Laurenti (1768) (see Stejneger [1907] and Cogger *et al.* [1983]).

Platurus fasciatus var. *colubrina* (Fischer, 1856)
Platurus laticaudatus var. B. (in part) (Günther, 1858)
Platurus scutatus (Günther, 1864); not the *Laticauda scutata* of Laurenti (1768)
Platurus laticaudatus var. *colubrinus* (Peters and Doria, 1878)
Platurus laticaudatus var. *colubrina* (Böttger, 1885)
Laticauda colubrina Stejneger, 1907

Laticauda frontalis **(De Vis, 1905)**

Platurus frontalis (De Vis, 1905)
Laticauda frontalis Cogger and Heatwole, 2006

Laticauda saintgironsi **Cogger and Heatwole, 2006**

Laticauda colubrina (in part) (Schneider, 1799)
Platurus laticaudatus var. B. (in part; a specimen from the "Island of Pines") (Günther, 1858)
Platurus colubrinus (in part; specimens from Isle of Pines, New Caledonia) (Boulenger, 1896; p. 309)
Laticauda saintgironsi Cogger and Heatwole, 2006

Laticauda guineai **Heatwole, Busack, and Cogger, 2005**

Laticauda colubrina was the name formerly used for this species in various papers referring to the populations of southern Papua-New Guinea either individually or collectively for *L. colubrina* (*sensu lato*) inclusive of *L. guineai*.

Appendix 2.1. Glossary

This being a dissertation in earth sciences, the following glossary is provided for the convenience of geographers and geologists who may not be familiar with some of the technical biological and herpetological terms used in the text.

Azygous: Unpaired and lying singly in a median position.

Clad: any group of organisms defined by characters exclusive to all its members and that distinguish the group from all others.

Cline (adjectival form: **clinal)**: a gradual geographic change in the frequency of a particular characteristic within a species, as opposed to sharp boundaries between populations with markedly different characteristics.

Congeneric (noun: **congener)**---refers to members of the same genus.

Conspecific: refers to members of the same species.

Crypsis (adjective: **cryptic)**: the property of being hidden or camouflaged.

Diphyletic: a taxon containing two lineages of separate origin.

Econe: A species or some component of a species (such as a life history stage, age class, morph or sex), whose members share common patterns of resource utilization and niche characteristics, but differ from other such components or species.

Ectopterygoids: certain bones found in the roof of the mouth in snakes.

Eurytopic: refers to species with generally broad tolerances to a variety of environmental conditions.

Gastrosteges: the strap-shaped scales (often called “ventrals”) stretching across the underside of a snake and which imparts traction with the substrate. These are large in terrestrial snakes, greatly reduced in size in many sea snakes, but intermediate in size in sea kraits. Illustrated in Figure 2.8.

Halophilous: “salt-loving”; refers to plants that grow in areas of high salt.

Hemipenis (plural: **hemipenes)**: refers to the pair of intromittent organs of lizards and snakes. These are spine-covered organs lying in lateral sacs posterior to the vent, and which are everted dduring mating. Only one is used in any particular mating.

Intercalary: literally means “inserted” but in anatomy means a small structure wedged into an unusual location between larger structures. In this thesis refers to rare occurrence of small scales between larger scales.

Gastrosteges: the strap-shaped scales (often called “ventrals”) stretching across the

underside of a snake and which imparts traction with the substrate. These are large in terrestrial snakes, greatly reduced in size in many sea snakes, but intermediate in size in sea kraits. Illustrated in Figure 2.8.

Lepidosauria: the lineage of reptiles containing lizards, snakes, and the tuatara.

Melanotic: refers to a species that is much darkened by the presence of the pigment melanin.

Nasal scale: refers to a scale that borders upon, or encloses, the nostril in snakes and lizards (illustrated in Figure 2.8).

Osteology: the study of bones.

Oviparous (noun: **oviparity)**: refers to an animal that lays eggs, as opposed to giving birth.

Oviposition: the act of laying eggs.

Oxyuraninae (adject **oxyuranine**): a subfamily diverging from the terrestrial land snakes and containing the completely marine sea snakes, as compared to the Laticaudinae which contains the sea kraits.

Paraphyletic: refers to a taxon composed of two or more species and their common ancestor, but not all of their descendents.

Phenotype: the physical characteristics of an organism, as opposed to its genetic make-up.

Prefrontal scales: scales in snakes and lizards located on the dorsal anterior region of the head (illustrated if Figure 2.8).

Proteroglyphous: refers to the condition in venomous snakes of having fixed fangs ion the front of the mouth. A **proteroglyph** is a species of snake with this condition.

Rostral scale: scale in snakes located at the tip of the snout in lizards and snakes (illustrated in Figure 2.8).

Scutellation: the number and arrangement of scales on reptiles.

Sexual dimorphism: refers to the condition in which females and males differ in characteristics other than those related to reproduction.

Subcaudal scales: scales located in a double row along the lower margin of the tail of snakes.

Submental scale: a scale beneath the chin.

Supralabial scales: scales located on the upper lips of snakes and lizards (illustrated in Figure 2.8).

Sympatric: refers to species that occupy the same geographic regions.

Synonymy: a listing in chronological order of the various scientific names that have been used for a particular. Each name is accompanied by the name of the person that used it as well as the date of use.

Syntopic: refers to species that occupy the same habitat in the same geographic area.

Temporal scales: scales in snakes and lizards located on the posterior lateral region of the head (illustrated in Figure 2.8).

Venter: the underside of an animal.

Viviparous (noun: **viviparitiy**): "live-bearer"; refers to an animal that gives birth, as opposed to laying eggs.

Waif: an organism transported involuntarily (as opposed to intentional migration) by natural forces such as wind or sea currents (as opposed to transport by humans).

Appendix 2.2. Numbers[1] of specimens of the *Laticauda colubrina* complex examined from different countries.

SPECIES/Locality	**MALES**	**FEMALES**	**JUVENILES**	**INDETERMNATE**	**TOTAL**
LATICAUDA COLUBRINA					
Andaman & Nicobar Islan	5	11	3	1	20
Australia	3	1	4	0	8
Fiji	88	73	33	4	198
Futuna	1	0	0	0	1
Guatemala	0	0	1	0	1
Indonesia	44	39	58	3	144
Malaysia	149	86	26	25	286
Myanmar	1	0	0	0	1
New Guinea	28	24	33	5	90
Pacific	2	1	7	1	11
Palau	21	13	7	7	48
Philippines	30	22	32	5	89
Ryukyu Islands	6	19	2	0	27
Singapore	11	13	8	1	33
Solomon Islands	31	22	24	4	81
Taiwan	13	18	4	0	35
Thailand	6	2	2	0	10
Tonga	16	14	13	0	43
Vanuatu	36	32	2	3	73
New Zealand	1	1	0	0	2
Uncertain*	6	8	12	6	32
Total *L. colubrina*	498	399	271	65	1,233
LATICAUDA GUINEAI					
Southern Papua	25	24	11	1	61
LATICAUDA SAINTGIRONSI					
Caroline Islands	0	1	0	0	1
Loyalty Islands	2	1	2	0	5
New Caledonia	84	66	32	3	185
New Zealand	1	0	0	0	1
Total *L. saintgironsi*	87	69	34	3	192
LATICAUDA FRONTALIS					
Loyalty Islands	1	1	1	0	3
New Caledonia	0	0	1	0	1
New Guinea	0	2	0	0	2
Vanuatu	14	5	3	0	22
Uncertain*	0	0	1	0	1
Total *L. frontalis*	15	7	6	0	28
TOTAL all species	625	499	322	69	1,514

[1] Note that N for specific characters may be lower (see text).

* includes specimens (1) that had only a general region (e.g., Indian Ocean) listed as the locality, (2) that lacked locality data altogether, or (3) were found to have been mislabeled or whose provenance was doubtful.

Appendix 4.1. Range of values of measurements and meristic characters in *Laticauda colubrina*, all localities combined. M = males; F = females; J = juveniles; All = all adults including males, females and those for which gender could not be determined. P values In **boldface** indicate differences are significant at the 5% rejection level as determined by a t-test.

	RANGE				P VALUES OF t-TESTS OF:		
CHARACTER	**M**	**F**	**J**	**All**	**M vs F**	**M vs J**	**F vs J**
Prefrontal scales	1-4	2-4	2-3	1-4	P_{565}=0.072	P_{545}=0.106	P_{526}=0.862
Supralabial scales							
Left	6-9	6-9	6-8	6-9	P_{533}<**0.0001**	P_{516}=0.207	P_{499}=**0.0012**
Right	3-9	3-9	6-9	3-9	P_{536}=**0.007**	P_{520}=**0.0012**	P_{498}=0.127
Snout-vent length	305-1270	295-1655	210-760	210-1655	P_{658}<**0.0001**	P_{589}<**0.0001**	P_{559}<**0.0001**
Tail length	32-301	32-301	32-139	32-301	**P_{659}=0.020**	P_{588}<**0.0001**	P_{561}<**0.0001**
Dark bands on body	23-62	22-61	24-58	24-58	P_{688}=0.391	P_{626}=0.242	P_{592}=0.762
Dark bands on tail	3-7	1-6	2-6	1-7	P_{680}<**0.0001**	P_{618}<**0.0001**	P_{590}<**0.0001**
Gastrosteges	213-242	218-249	207-247	207-249	P_{662}<**0.0001**	P_{579}=**0.013**	P_{547}<**0.0001**
Subcaudal scales	30-48	26-47	28-49	26-49	P_{664}<**0.0001**	P_{587}<**0.0001**	P_{559}<**0.0001**
Scale rows around body:							
at first gastrostege	19-25	18-25	19-24	18-25	P_{536}<**0.0001**	P_{514}=**0.0002**	P_{504}=0.102
at 20th gastrostege	19-25	19-25	19-25	19-25	P_{666}<**0.0001**	P_{594}=0.177	P_{560}<**0.0001**
at 50th gastrostege	20-25	20-27	19-25	19-27	P_{661}<**0.0001**	P_{591}<**0.0001**	P_{558}<**0.0001**
at 100th gastrostege	21-25	20-25	19-26	19-27	P_{656}<**0.0001**	P_{590}<**0.0001**	P_{556}<**0.0001**
at 150th gastrostege	20-27	21-28	16-25	16-28	P_{651}<**0.0001**	P_{582}=0.134	P_{551}<**0.0001**
at 200th gastrostege	17-25	19-25	15-24	15-25	P_{651}<**0.0001**	P_{573}<**0.0001**	P_{546}<**0.0001**
at last gastrostege	12-28	11-23	11-24	11-28	P_{531}<**0.0001**	P_{509}=**0.009**	P_{490}<**0.0001**
Scale rows in band width:							
1st dorsal dark band	2-10	3-11	3-11	2-11	P_{595}=0.566	P_{522}=0.670	P_{525}=0.324
10th dorsal dark band	3-10	3-10	2-10	2-10	P_{615}=0.304	P_{581}=0.179	P_{552}=0.760
25th dorsal dark band	3-12	2.14	0-12	0*-14	P_{578}=0.412	P_{543}=0.401	P_{513}=0.999
1st dorsal light band	1-11	2-11	2-11	1-11	P_{594}=0.865	P_{551}=0.356	P_{523}=0.463
10th dorsal light band	1-11	4-12	4-14	1-14	P_{613}=0.091	P_{579}=0.887	P_{552}=0.092
25th dorsal light band	1-14	2-13	2-1**	1-14	P_{578}=0.952	P_{542}=0.706	---
1st ventral dark band	0-5	0-8	0-7	0-8	P_{577}=**0.0009**	P_{534}=**0.018**	P_{515}=0.408
10th ventral dark band	0-7	0-7	0-5	0-7	P_{601}=**0.024**	P_{554}=0.337	P_{541}=0.275
25th ventral dark band	0-7	0-8	0-7	0-8	P_{569}=**0.016**	P_{524}=0.406	P_{505}=0.168
1st ventral light band	2-1**	2-1**	2-1**	2-1**	---	---	---
10th ventral light band	2-1**	2-1**	2-1**	2-1**	---	---	---
25th ventral light band	2-1**	2-1**	2-1**	2-1**	---	---	---

** I = indefinite; black bands did not meet below, so width of black bands on the venter was zero; accordingly, the width of the white bands extended indefinitely. Dashes indicate “not applicable”.

Appendix 4.2. Range of values of meristic characters in *Laticauda saintgironsi and Laticauda guineai,* all localities combined. For sample sizes, see Appendix 2.2. M=males; F=females; J=juveniles; All=all adults including males, females and those for which gender could not be determined. P values in **boldface** indicate differences are significant at the 5% rejection level as determined by a t-test.

	RANGE				**P VALUES OF t-TESTS OF:**		
SPECIES/CHARACTER	**M**	**F**	**J**	**All**	**M vs F**	**M vs J**	**F vs J**
LATICAUDA SAINTGIRONSI							
Prefrontal scales	2-3	2-3	2-4	2-4	P_{103}=0.849	P_{82}=0.582	P_{69}=0.534
Supralabial scales							
Left	7	7	7	7	All values identical		
Right	6-7	7	7	6-7	P_{98}=0.459	P_{89}=0.501	Identical
Snout-vent length	374-1064	335-1210	276-623	276-1210	P_{140}**<0.0001**	P_{110}**<0.0001**	P_{88}**<0.0001**
Tail length	47-125	40-135	32-83	32-135	P_{141}**<0.0002**	P_{110}**<0.0001**	P_{89}**<0.0001**
Dark bands on body	22-32	21-34	22-31	21-34	P_{139}=0.619	P_{108}=0.421	P_{87}=0.309
Dark bands on tail	2-4	2-3	2-4	2-4	P_{142}**<0.0001**	P_{110}**<0005**	P_{80}**<0.0001**
Gastrosteges	210-225	212-238	210-231	210-238	P_{140}**<0.0001**	P_{109}=**0.045**	P_{87}**<0.0001**
Subcaudal scales	30-45	26-39	26-42	26-45	P_{141}**<0.0001**	P_{108}**<0.0001**	P_{89}**<0.0001**
Scale rows around body							
at first gastrostege	18-23	18-21	19-22	18-23	P_{98}=0.958	P_{88}=0.495	P_{60}=0.444
at 20th gastrostege	19-23	20-23	19-22	19-23	P_{147}=0.133	P_{117}=0.976	P_{88}=0.229
at 50th gastrostege	19-23	20-25	19-22	19-25	P_{147}=0.145	P_{117}=0.967	P_{88}=0.326
at 100th gastrostege	20-23	21-25	19-24	19-25	P_{145}**=0.006**	P_{115}=0.253	P_{86}=0.175
at 150th gastrostege	18-23	20-24	19-24	18-24	P_{145}=0.063	P_{115}=0.458	P_{86}=0.073
at 200th gastrostege	17-21	19-23	17-21	17-23	P_{145}**<0.0001**	P_{115}=0.010	P_{86}**<0.0001**
at last gastrostege	16-21	16-22	16-20	16-22	P_{98}=0.262	P_{89}=0.745	P_{61}=0.200
Scale rows in band width							
1st dorsal dark band	6-15	7-13	6-13	6-15	P_{140}=0.053	P_{111}=0.348	P_{87}=0.622
10th dorsal dark band	6-14	6-12	6-13	6-14	P_{141}=0.927	P_{111}=0.848	P_{88}=0.788
25th dorsal dark band	4-16	6-19	6-15	4-19	P_{117}=0.111	P_{93}=0.946	P_{74}=0.206
1st dorsal light band	5-9	4-8	5-9	4-9	P_{141}=0.260	P_{111}=0.755	P_{88}=0.574
10th dorsal light band	4-9	3-9	4-9	3-9	P_{141}=0.518	P_{111}=0.255	P_{88}=0.575
25th dorsal light band	4-11	3-10	5-10	3-11	P_{117}=0.924	P_{93}=0.784	P_{74}=0.715
1st ventral dark band	0-7	0-7	0-7	0-7	P_{139}=**0.007**	P_{110}=0.988	P_{87}=0.063
10th ventral dark band	0-11	2-7	1-7	0-11	P_{138}=0.462	P_{110}=0.662	P_{86}=0.272
25th dark ventral band	0-8	0-10	1-9	0-10	P_{114}=0.200	P_{89}=0.852	P_{71}=0.256
1st light ventral band	2-1**	2-1**	2-1**	2-1**	---	---	---
10th ventral light band	2-1**	2-6	2-7	2.1**	---	---	---
25th ventral light band	2-1**	1-1**	1-6	1.1**	---	---	---
LATICAUDA GUINEAI							
Prefrontal scales	2-3	3	2-3	34-58	P_{37}=0.210	P_{29}=0.594	P_{26}=0.185
Supralabial scales							
Left	7	7-8	7	7-8	P_{38}=**0.011**	---	P_{27}=0.079
Right	7	7-8	7	7-8	P_{38}=**0.027**	---	P_{27}=0.127
Snout-vent length	420-1006	895-1621	280-562	280-1621	P_{41}**<0.0001**	P_{32}**<0.0001**	P_{29}**<0.0001**
Tail length	65-193	90-160	33-69	33-193	P_{41}=0.780	P_{32}**<0.0001**	P_{29}**<0.0001**
Dark bands on body	48-58	46-58	34-58	34-58	P_{41}=0.210	P_{32}=**0.005**	P_{29}=0.306
Dark bands on tail	4-7	4-5	4-6	4-7	P_{41}**<0.0001**	P_{32}**<0.0001**	P_{29}**<0.025**
Gastrosteges	223-241	224-245	214-236	214-245	P_{40}=**0.0008**	P_{31}=0.115	P_{29}=**0.0003**
Subcaudal scales	36-45	27-36	32-44	27-45	P_{40}<**0.0001**	P_{31}=**0.002**	P_{29}=**0.0004**
Scale rows around body							
at first gastrostege	21-23	19-24	21-23	19-24	P_{36}=0.531	$P_{27=}$0.521	P_{27}=0.972
at 20th gastrostege	21-23	19-23	21-23	19-23	P_{40}=0.199	P_{31}=0.399	P_{29}=0.768
at 50th gastrostege	21-23	20-24	21-24	20-24	P_{40}=0.279	P_{31}=0.324	P_{29}=0.973
at 100th gastrostege	22-24	22-25	23-25	22-25	P_{40}=0.080	P_{31}=0.142	P_{29}=0.937
at 150th gastrostege	21-23	22-23	21-23	21-23	P_{40}=**0.016**	P_{31}=0.306	P_{29}=0.319
at 200th gastrostege	19-23	21-23	19-22	19-23	P_{40}=**0.017**	$P3_{31}$=0.456	P_{29}**<0.008**
at last gastrostege	16-20	18-21	17-20	16-21	P_{38}=0.064	P_{29}=0.313	P_{27}=0.610
Scale rows in band width							
1st dorsal dark band	2-5	3-6	3-6	2-6	P_{40}=0.409	P_{30}=0.290	P_{28}=0.683
10th dorsal dark band	3-4	3-5	2-6	2-6	P_{41}=0.819	P_{31}=0.350	P_{28}=0.486
25th dorsal dark band	3-4	2-5	3-5	2-5	P_{41}=0.417	P_{31}=**0.004**	P_{28}=0.062
1st dorsal light band	4-7	3-7	2-6	2-7	P_{40}=0.485	P_{30}=0.172	P_{28}=0.436
10th dorsal light band	4-7	4-7	5-10	4-10	P_{41}=**0.048**	P_{31}=0.078	P_{28}=0.571

Appendix 4.2 continued							
SPECIES/CHARACTER	**M**	**F**	**J**	**All**	**M vs F**	**M vs J**	**F vs J**
LATICAUDA GUINEAI							
1st dorsal light band	4-7	3-7	2-6	2-7	P_{40}=0.485	P_{30}=0.172	P_{28}=0.436
10th dorsal light band	4-7	4-7	5-10	4-10	P_{41}=**0.048**	P_{31}=0.078	P_{28}=0.571
25th dorsal light band	4-6	4-7	4-8	4-8	P_{41}=0.266	P_{31}=0.716	P_{28}=0.685
1st ventral dark band	1-2	0-3	0-2	0-3	P_{41}=0.819	P_{30}=0.731	P_{27}=0.903
10th ventral dark band	1-2	1-3	1-2	1-3	P_{41}=0.540	P_{30}=0.507	P_{27}=0.895
25th dark ventral band	1-2	1-2	1-2	1-2	P_{41}=0.148	P_{31}=0.912	P_{28}=0.300
1st light ventral band	2-4	2-4	2-4	2-1**	P_{40}=0.860	P_{29}=0.979	P_{25}=0.929
10th ventral light band	2-3	2-4	2-6	2-6	P_{41}=0.339	P_{30}=0.248	P_{27}=0.609
25th ventral light band	2-4	2-4	2-6	2-6	P_{41}=0.785	P_{31}=0.051	P_{28}=0.104

* Values of 890 mm for males and 1120 for females were obtained by Bauer and Sadlier (2000).

** I=indefinite; black bands did not meet below, so width of black bands on the venter was zero; accordingly, the width of the white bands extended indefinitely. Dashes indicate “not applicable”.

Appendix 4.3. Range of values of measurements and meristic characters in *Laticauda frontalis*, all localities combined, but juveniles and animals of unidentified sex excluded.

	N		RANGE	
CHARACTER	**MALES**	**FEMALES**	**MALES**	**FEMALES**
Prefrontal scales	8	2	All values identical (3)	
Supralabial scales				
Left	7	3	All values identical (7)	
Right	7	3	All values identical (7)	
Snout-vent length (mm)	15	7	487-582	293-717[1]
Tail length (mm)	14	7	66-88	34-81[1]
Dark bands on body	13	6	28-36	29-34
Dark bands on tail *	13	6	3-4	3-4
Gastrosteges*	13	6	193-210	199-208
Subcaudal scales*	13	6	35-40	31-34
Scale rows around body				
at first Gastrostege	6	2	19-22[2]	20-21
at 20th gastrostege	15	7	20-21	21
at 50th gastrostege	15	7	All values identical (21)[3]	
at 100th gastrostege	15	7	All values identical (21)	
at 150th gastrostege	15	7	19-22	21
at 200th gastrostege	7**	4**	16-19[4]	19[4]
at last gastrostege	6	2	15-18	18-19[5]
Scale rows in band width				
1st dorsal dark band	15	6	5-8[6]	5-8[6]
10th dorsal dark band	15	6	5-7[7]	5-7[7]
25th dorsal dark band	15	6	4-7[8]	4-6[8]
1st dorsal light band	15	6	6-8	6-8
10th dorsal light and	15	6	6-9	6-9
25th dorsal light band	14	6	7-10	6-8
1st ventral dark band	2	0	0[9]	---[9]
10th ventral dark band	4	0	0-2[10]	---[10]
25 ventral dark band	6	3	0-2[11]	---[11]
1st ventral light band	2	0	Indef.[12]	---
10 ventral light band	4	0	4-7 (-indef.[12])	---
25th ventral light band	6	2	1-2[13] (-indef.[12])	1[13]

* Males and females significantly different as determined by t-tests (P values 0.002 for dark bands on tail, 0.001 for gastrosteges, and <0.001 for subcaudal scales); all other tested differences between the sexes not significant (P values ranged from 0.143-0.954). Dashes indicate “not applicable”. When the combined N for both sexes was less than ten, no test was performed. The failure of black bands to meet below reduced the sample sizes of the ventral white bands below testable levels. The degrees of freedom in each case=$N\text{-}1_{males} + N\text{-}1_{females}$.

** Sample size reduced because not all specimens had 200 gastrosteges

[1] No juveniles found smaller than minimum female value

[2] Juveniles extend the range to 17

[3] Juveniles extend the range to 20

[4] Juveniles extend the range to 15

[5] Juveniles extend the range to 21

[6] Juveniles extend the range to 4-10

[7] Juveniles extend the range to 4-9

[8] Juveniles extend the range to 9

[9] Juveniles extend the range to 5

[10] Juveniles extend the range to 4

[11] Juveniles extend the range to 6

[12] Indef. indicates that the width of the white band is not measurable because the adjacent black bands do not meet below. i.e., width of white band is indefinite

[13] Juveniles extend the range to 4

Appendix 4.4. Mean and maximum snout-vent lengths (mm) of male and female sea kraits of the *Laticauda colubrina* complex from various localities in which the N for both sexes combined was ten or greater.

LOCALITY	**N**	**MEAN**	**MAXIMUM**
LATICAUDA COLUBRINA			
ANDAMAN & NICOBAR ISLANDS	2	871	1002
Male	12	1005	1290
Females			
MALAYSIA			
SABAH			
Males	10	764	927
Females	9	1256	1558
ALL LOCALITIES*			
Males	14	778	927
Females	9	1256	1558
SINGAPORE			
Males	10	799	954
Females	13	1023	1239
INDONESIA			
BIAK			
Males	10	649	790
Females	17	766	1166
ALL LOCALITIES			
Males	30	644	904
Females	28	768	1328
PAPUA-NEW GUINEA			
ADMMIRALTY ISLANDS			
Males	15	726	799
Females	9	1035	1200
ALL LOCALITIES			
Males	51	737	1006
Females	46	1104	1621
SOLOMON ISLANDS			
NEW GEORGIA			
Males	9	680	725
Females	3	753	818
ISABEL			
Males	5	669	725
Females	6	1007	1130
RENNELL ISLAND			
Males	7	579	710
Females	7	859	1360
ALL LOCALITIES*			
Males	30	649	956
Females	22	939	1360
VANUATU			
EFATE			
Males	28	649	785
Females	22	765	1443
ALL LOCALITIES			
Males	35	706	859
Females	32	894	1443
FIJI			
BUIBA			
Male	20	612	875
Females	8	770	1270
LABASA			
Males	10	754	825
Females	14	996	1240
SUVA			
Males	8	585	780
Females	4	726	986
KIA			
Males	6	783	850
Females	6	1075	1300
TAVARUA			
Males	12	757	1080
Females	10	897	1200

APPENDIX 4.4, CONTINUED			
LOCALITY	**N**	**MEAN**	**MAXIMUM**
LATICAUDA COLUBRINA			
BIRD			
Males	8	735	830
Females	3	1185	1260
ALL LOCALITIES			
Males	88	708	1080
Females	71	933	1404
TONGA			
VELITOA			
Males	7	886	985
Females	4	1075	1230
ALL LOCALITIES			
Males	16	821	985
Females	16	898	1315
PHILIPPINES			
JAGULIAO			
Males	10	778	855
Females	9	1116	1190
GIGANTE			
Males	9	849	920
Females	2	1198	1210
ALL LOCALITIES			
Males	30	789	1001
Females	21	1028	1655
PALAU			
Males	19	728	846
Females	10	1009	1242
TAIWAN			
HENG CHUN			
Males	3	731	826
Females	12	947	1302
ALL LOCALITIES			
Males	12	632	841
Females	17	912	1302
***LATICAUDA COLUBRINA* FROM ALL LOCALITIES**			
Males	24	799	1140
Females	20	1266	1621
LATICAUDA GUINEAI			
ALL LOCALITIES			
Males	24	799	1140
Females	20	1266	1621
LATICAUDA SAINTGIRONSI			
NEW CALEDONIA			
NOUMEA AND VICINITY			
Males	21	656	775
Females	9	841	948
PORC EPIC ISLAND			
Males	6	716	765
Females	11	862	1074
ATIRA			
Males	8	702	742
Females	3	893	1210
REDIKA			
Males	11	717	948
Females	5	848	948
ALL LOCALITIES			
Males	87	683	1064
Females	59	823	1210
LATICAUDA FRONTALIS**			
ALL LOCALITIES			
Males	15	542	582
Females	7	544	717

* Collectively including the specific localities treated in this table plus those from the region that were not treated individually because of sample sizes below ten. Therefore N may be greater than the total N for individual localities.

** Difference between the sexes not significant (t=-0.058; P=0.954).

Appendix 4.5. Results of an ANOVA testing for differences among the various major localities (countries) for all characters used in this study, separately by gender for *Laticauda colubrina*. Values in **boldface** indicate significant differences at the 5% rejection level. % Loc. Sig. = Percentage of the individual localities within a country that show significant differences between males and females. Subscripts to P values indicate degrees of freedom for the F test.

CHARACTER	MALES			FEMALES		
	F	P	%LOC. SIG.	F	P	% LOC. SIG.
PREFRONTALS	2.07	**$P_{18,312}<0.0063$**	8.8	2.85	**$P_{17,292}=0.0003$**	12.4
SUPRALABIAL SCALES						
Left	1.32	$P_{18,295}=0.169$	6.6	4.10	**$P_{17,278}=<0.0001$**	36.2
Right	0.17	$P_{18,299}>0.999$	0	2.20	**$P_{17,277}=0.0048$**	27.6
DARK BANDS						
Body	19.21	**$P_{18,384}<0.0001$**	49.3	44.00	**$P_{17,349}<0.0001$**	69.5
Tail	43.40	**$P_{18,377}<0.0001$**	43.4	6.12	**$P_{17,348}<0.0001$**	46.7
GASTROSTEGES	11.81	**$P_{18,367}<0.0001$**	41.9	15.54	**$P_{17,333}<0.0001$**	54.3
SUBCAUDAL SCALES	3.15	**$P_{18,368}<0.0001$**	18.4	2.02	**$P_{17,339}=0.012$**	11.4
SCALE ROWS AROUND BODY						
at 1st gastrostege	3.04	**$P_{18.292}<0.0001$**	29.4	2.86	**$P_{17,283}=0.0002$**	26.7
at 20th gastrostege	1.63	**$P_{18,372}=0.048$**	7.4	3.38	**$P_{17,33}<0.0001$**	24.8
at 50th gastrostege	1.03	$P_{18,369}=0.427$	5.9	8.93	**$P_{17,335}<0.0001$**	43.8
at 100th gastrostege	1.64	**$P_{18,367}=0.046$**	11.8	11.44	**$P_{17,332}<0.0001$**	38.9
at 150th gastrostege	1.61	$P_{18,363}=0.052$	16.9	15.50	**$P_{17,331}<0.0001$**	52.4
at 200th gastrostege	3.18	**$P_{18,361}<0.0001$**	25.7	9.64	**$P_{17,331}<0.0001$**	42.9
at last gastrostege	2.32	**$P_{18,294}=0.002$**	18.4	3.24	**$P_{17,273}<0.0001$**	24.7
SCALE ROWS IN BAND WIDTH						
1st dorsal dark band	25.03	**$P_{18,333}<0.0001$**	4.4	26.05	**$P_{17,305}<0.0001$**	45.7
10th dorsal dark band	26.86	**$P_{18,345}<0.0001$**	42.7	26.18	**$P_{17,315}<0.0001$**	50.5
25th dorsal dark band	33.56	**$P_{18,329}<0.0001$**	44.1	33.00	**$P_{17,295}<0.0001$**	60.0
1st dorsal light band	10.70	**$P_{18,333}<0.0001$**	33.8	14.53	**$P_{17,314}<0.0001$**	46.7
10th dorsal light band	14.44	**$P_{18,343}<0.0001$**	45.0	23.56	**$P_{17,314}<0.0001$**	54.3
25th dorsal light band	16.50	**$P_{18,327}<0.0001$**	42.7	21.67	**$P_{14,295}<0.0001$**	66.7
1st ventral dark band	4.04	**$P_{18,321}<0.0001$**	21.3	4.34	**$P_{17,299}<0.0001$**	44.8
10th ventral dark band	4.00	**$P_{18,330}<0.0001$**	25.8	4.46	**$P_{17,314}<0.0001$**	41.0
25th ventral dark band	10.47	**$P_{18,317}<0.0001$**	39.0	89.27	**$P_{17,295}<0.0001$**	45.7

Appendix 4.6. Geographic variation in the temporal scales of *Laticauda saintgironsi*, *Laticauda frontalis* and *Laticauda colubrina*. Where the two sides of the head were different, a score of one-half was given to the pattern of each side. Specimens with only generalized locality (e.g., Indian Ocean) or of uncertain locality are excluded. **Boldface** indicates prevalent values.

	PER CENT OF INDIVIDUALS WITH				
SPECIES/LOCALITY	1+2	1+3	2+2	Other	PER CENT ASYMMETRIES
LATICAUDA COLUBRINA					
ANDAMAN & NICOBAR ISLAND	**100**	0	0	0	0
MYANMAR (BURMA)	**100**	0	0	0	0
THAILAND	**87.5**	0	12.5	0	0
PENINSULAR MALAYSIA	**80.0**	0	20.0	0	0
SINGAPORE & SAMBU	**70.6**	0	29.4	0	0
SABAH	**93.8**	0	6.3	0	0
INDONESIA	**79.1**	2.1	17.3	1.6[1]	6.2
PAPUA NEW GUINEA & SOLOMON ISLAND (see Appendix 4.7)					
VANUATU	**80.0**	3.3	16.7		6.7
FIJI	**68.4**	0.4	29.7	1.5 [2,3]	8.3
TONGA & FUTUNA	**46.5**	9.3	32.6	11.7[4]	23.8
CAROLINES-PACIFIC	**80.0**	0	20.0	0	0
PALAU	**47.9**	1.0	42.7	8.3[2]	14.6
PHILIPPINES	26.4	0	**73.6**	0	1.1
TAIWAN	**69.7**	0	27.3	3.0[2,5]	12.1
RYUKYUS	**91.3**	2.2	6.5	0	8.7
UNCERTAIN*	**83.3**	0	11.1	5.6[7]	5.6
LATICAUDA GUINEAI (see Table 4.2)					
LATICAUDA SAINTGIRONSI	**78.1**	0.4	20.3	1.2[6]	6.6
LATICAUDA FRONTALIS	**100.0**	0	0	0	0

* includes specimens (1) that had only a general region (e.g., Indian Ocean) listed as the locality, (2) that lacked locality data altogether, or (3) were found to have been mislabeled or whose provenance was doubtful.

In the following, values not enclosed in parentheses refer to counts that are symmetrical on both sides of the heads; parentheses enclose asymmetrical combinations.

[1] (1+2, 2+2); [2] 2+3; [3] 1+1 with what would have been the upper posterior temporal fused with the parietal; [4] (1+2, 1+3), (1+2, 2+2), 1+3, (1+3, 1+4), (1+3, 2+2), (1+4, 2+2), 2+3, 3+2; [5] 3+2;
[6] (1+1, 1+2), (1+1, 1+3), (1+2, 2+2); [7] (1+3, 1+2)

Appendix 4.7. Geographic variation in the temporal scales in *Laticauda colubrina* and *Laticauda guineai* in Papua-New Guinea and the Solomon Islands. When the two sides of the head were different, a score of one-half was given to the pattern of each side. Specimens of uncertain locality are excluded. Prevalent values are in **boldface**. Blank spaces indicate values of zero.

SPECIES/LOCALITY	N	NUMBER (%) OF INDIVIDUALS WITH:				ASYMMETRIES: NO. (%)
		1+2	1+3	2+2	Other	
LATICAUDA COLUBRINA						
PAPUA-NEW GUINEA						
NE New Guinea (Madang/Karkar Islanc	4	**3**		1		
Bismarck Archipelago						
Manus Island	26	**24**		1	1[1]	
Mussau Island	2	**2**				
New Hanover/Kavieng/New Irelanc	10	**8.5**		1.5		1
New Britain	11	**10.5**		0.5		1
Nissan	2	**1.5**	0.5			1
Milne, Samarai, Panaeti Isl., Misima Isl.	5	1.5	0.5	**3**		1
Buka	3			**3**		
Bougainville	6	2		**4**		
TOTAL	69	**53.0 (76.8)**	1.0 (1.5)	14.0 (20.3)	1.0 (1.5)	4.0 (5.8)
SOLOMON ISLANDS						
San Cristobal	1			**1**		
Choiseul	1			**1**		
Santa Cruz	1			**1**		
Rubiana	2			**2**		
Guadalcanal	2			**2**		
Isabel	15	1		**14**		
Shortlands	7			**7**		
Florida	3	1		**2**		
Rennell	14	**11.5**	2.5			
New Georgia	4	**4**				
Malaita	2	**2**				
TOTAL	52	19.5 (37.5)	2.5 (4.8)	**30 (57.7)**		
LATICAUDA GUINEAI						
SOUTHERN PAPUA-NEW GUINEA	50	13.5 (27.0)	0.5 (1.0)	**33.5 (67.0)**	2.5[2] (5.0)	2 (4.0)

[1] 1+1

[2] 2+3

Appendix 4.8. Geographic variation in the number of supralabials in species of the *Laticauda colubrina* complex. When the number differed on the two sides of the head, each side was give a score of 0.5.

		% OF SPECIMENS WITH THE FOLLOWING NUMBER OF SUPRALABIALS:			% OF SPECIMENS WITH THE SUPRALABIALS ENTERING THE ORBIT:	
LOCALITY	% ASYMMETRIES	7	8	Other	3+4	Other
LATICAUDA COLUBRINA						
Andaman & Nicobar Islands	0	100	0	0	100	0
Myanmar (Burma)	0	100	0	0	100	0
Thailand	0	100	0	0	100	0
Malaysia	0	98.5	1.5	0	100	0
Singapore	3.2	100	0	0	98.4	1.6[1]
Indonesia	4.3	96.4	2.2	1.4	98.3	1.7[4]
Papua-New Guinea	3.9	89.4	10.6	0	98.5	1.6[3]
Solomon Islands	13.2	83.0	16.0	1.9	98.1	1.9[1, 2]
Vanuatu	10.0	75.0	25.0	0	100	0
Fiji	9.2	80.9	16.4	1.7	98.9	1.1[1]
Tonga	16.3	83.7	16.3	0	98.8	1.2[4]
Futuna	0	100	0	0	100	0
Carolines-Pacific	0	88.9	11.1	0	100	0
Palau	0	100	0	0	100	0
Philippines	1.1	97.2	2.8	0	98.9	1.1[4]
Taiwan	3.0	98.5	1.5	0	100	0
Ryukyus	0	100	0	0	100	0
Uncertain*	1.7	96.4	2.2	1.4	100	0
All localities	6.7	90.6	8.5	0.8	98.9	1.1
LATICAUDA SAINTGIRONSI	0.8	99.6	0.4	0	100	0
LATICAUDA FRONTALIS	0	100	0	0	100	0
LATICAUDA GUINEAI	13.9	93.1	3.5	0	100	0

* includes specimens (1) that had only a general region (e.g., Indian Ocean) listed as the locality, (2) that lacked locality data altogether, or (3) were found to have been mislabeled or whose provenance was doubtful.

[1] =4 only; [2] =4 + 5; [3] =3 + 5; [4] =3 only (several fused)

Appendix 4.9. Sexual dimorphism in the position of the midpoint of the yolk-sac scar of species in the *Laticauda colubrina complex* (number of gastrosteges anterior to the vent). M=males; F=females; df=degrees of freedom.

SPECIES/LOCALITY	N (df) Males, Females	MEAN MIDPOINT		t	P
		Males	Females		
LATICAUDA COLUBRINA					
Indonesia	20, 13 (31)	20.4 ± 0.36	21.0 ± 0.79	-8.26	0.450
Fiji	16, 17 (31)	19.5 ± 0.63	21.1 ±-1.94	-1.94	0.061
Philippines	9, 3 (10)	20.9 ± 0.63	23.8 ± 0.17	-2.52	**0.028***
Taiwan	4, 5	20.6	21.5	---	---
Palau	6, 3	19.9	22.5	---	---
Papua New Guinea	5, 1	19.5	20.5	---	---
Peninsular Malaysia And Singapore	2, 3	22.8	24.0	---	---
Tonga	2, 3	20.0	22.8	---	---
Vanuatu	3, 2	19.2	22.8	---	---
Australia (waifs)	2, 1	19.5	24.5	---	---
Andaman & Nicobar Islands	0, 1	---	22.5	---	---
Thailand	1, 0	22.0	---	---	---
Futuna	1, 0	18.0	---	---	---
Ryukyu Islands	0, 1	---	23.0	---	---
TOTAL**	82, 64 (144)	20.0 ± 0.23	21.8 ± 0.29	-4.78	**<0.0001***
LATICAUDA GUINEAI	6, 6 (10)	20.0 ± 0.56	20.6 ± 1.26	-0.42	0.682
LATICAUDA SAINTGIRONSI	33, 16 (47)	19.3 ± 0.34	20.9 ± 0.31	-2.94	**0.005***
LATICAUDA FRONTALIS	4, 2	17.8	19.3	---	---

* Significant at the 5% rejection level

** Includes all specimens of *L. colubrina* in the table plus those with only general locality data.

Dashes indicate “not applicable”.

Appendix 4.10. Proportions of individuals with different numbers of prefrontal scales in species of the *Laticauda colubrina* complex. Values in ordinary type arose from a small number of prefrontal counts; those in **boldface** represent sample sizes greater than 30.

		Percent of individuals with the following number of prefrontals:		
REGION	N	3	2	Other
LATICAUDA COLUBRINA				
Andaman and Nicobar Islands	20	100	0	0
Myanmar	1	100	0	0
Thailand	9	100	0	0
Peninsular Malaysia	11	90.9	9.1	0
Singapore	**32**	**65.6**	**34.4**	**0**
Sabah	**62**	**100**	**0**	**0**
Indonesia	**104**	**87.5**	**12.5**	**0**
Australia (waifs)	8	75.0	12.5	12.5[1]
Papua New Guinea	**134**	**90.3**	**9.0**	**0.8**[2]
Solomon Islands	**66**	**89.4**	**10.6**	**0**
Vanuatu	**31**	**87.1**	**9.7**	**3.2**[2]
Fiji	**130**	**94.6**	**4.6**	**0**
Tonga	**38**	**86.8**	**2.6**	**10.5**[2]
Futuna	1	100	0	0
Philippines	**88**	**94.3**	**5.7**	**0**
Palau	**44**	**93.2**	**6.8**	**0**
Pacific (waifs)	10	90.0	10.0	0
Guatemala	1	100	0	0
Taiwan	**33**	**90.9**	**6.1**	**3.0**[1]
Ryukyu Islands	23	91.3	8.7	0
“Indian Ocean”	3	100	0	0
Other	19	94.7	5.3	0
All Localities	**850**	**90.9**	**8.1**	**0.9**[1,2]
LATICAUDA GUINEAI				
Papua New Guinea	**50**	**96.0**	**4.0**	**0**
LATICAUDA SAINTGIRONSI				
New Caledonia	**137**	**91.2**	**5.8**	**2.9**[2,3,4]
Loyalty Islands	7	100	0	0
New Zealand (waif)	1	100	0	0
Caroline Islands	1	100	0	0
All Localities	**146**	**91.8**	**5.5**	**2.7**[2,3,4]
LATICAUDA FRONTALIS				
All localities	13	100	0	0

[1] One prefrontal (all fused into a single scale).

[2] Four prefrontals (central one divided into an upper scale and a lower scale).

[3] Three prefrontals but with the central one fused with the frontal.

[4] Two prefrontals with one of them fused laterally with the internasal.

Appendix 4.11. Comparison of the number of prefrontals in males and females of species in the *Laticauda colubrina* complex.

	N		MEAN NO. OF PREFRONTALS		
LOCALITY	MALES	FEMALES	MALES	FEMALES	P
LATICAUDA COLUBRINA					
ANDAMAN AND N ICOBAR ISLANDS	4	12	3.00	3.00	**
MALAYSIA					
Labuan	10	12	3.00	3.00	**
All localities*	23	18	3.00	3.00	**
SINGAPORE	10	14	2.80	2.5	$P_{22}=0.147$
INDONESIA					
Biak	10	17	2.90	2.94	$P_{25}=0.707$
All localities*	31	37	2.87	2.97	$P_{68}=0.112$
PAPUA NEW GUINEA					
Admiralty islands	15	10	2.67	2.90	$P_{23}=0.196$
All localities*	24	21	2.75	2.91	$P_{43}=0.245$
SOLOMON ISLANDS					
New Georgia	7	3	2.71	3.00	$P_{8}=0.356$
Rennell Island	5	7	2.80	3.00	$P_{10}=0.255$
All localities*	25	17	2.80	3.00	$P_{42}=0.051$
VANUATU	17	12	2.88	3.00	$P_{27}=0.339$
FIJI					
Suva	8	5	2.88	3.00	$P_{11}=0.453$
Kia	6	6	3.00	2.83	$P_{10}=0.341$
Tavarua	12	10	2.91	3.00	$P_{20}=0.374$
Bird	8	3	3.00	3.00	**
All localities*	51	45	2.90	2.98	$P_{94}=0.183$
TONGA					
Velitoa Island	7	4	3.43***	3.00	$P_{9}=0.391$
All localities*	13	15	3.31***	2.93	$P_{26}=0.054$
PHILIPPINES					
Jaguliao	10	9	2.70	3.00	$P_{17}=0.081$
Gigantes	9	2	3.00	3.00	**
All localities*	29	22	2.90	3.00	$P_{49}=0.083$
PALAU	18	10	2.89	2.90	$P_{26}=0.076$
TAIWAN					
Heng Chun	3	12	3.00	2.83	$P_{13}=0.484$
All localities*	12	17	3.08***	2.88	$P_{27}=0.341$
RYUKYU ISLANDS					
Iriomote	2	9	3.00	3.00	**
All localities*	3	17	3.00	3.00	**
ALL L. COLUBRINA****	293	274	2.90	2.95	$P_{565}=0.075$
LATICAUDA GUINEAI	21	18	2.92	3.00	$P_{37}=0.362$
LATICAUDA SAINTGIRONSI					
Atira Island	8	3	3.00	3.00	**
All New Caledonia	59	39	2.93	2.92	$P_{96}=0.865$
LATICAUDA FRONTALIS	6	2	3.00	3.00	**

* Collectively including the specific localities treated in this table plus those from the region that were not treated individually because of sample sizes below ten. Therefore N may be greater than the total N for the individual localities listed.

** Statistical test not performed as all values were identical.

*** Four prefrontals occurred in some specimens at this locality.

**** All specimens, including not only those in this table, but also waifs, those of uncertain provenance or from countries with too few specimens to be included in this table, and those from general localities (e.g., Indian Ocean).

Appendix 4.12. Comparison of the number of prefrontals in juveniles and adults of the species in the *Laticauda colubrina* complex, for which there were both adults and juveniles in the same samples and the combined sample size was 10 or greater.

LOCALITY	N		MEAN NO. OF PREFRONTALS		P
	JUVENILES	ADULTS	JUVENILES	ADULTS	
LATICAUDA COLUBRINA					
MALAYSIA					
Kecil	10	19	3.0	3.0	**
All Labuan	19	22	3.0	3.0	**
All Sabah	21	40	3.0	3.0	**
SINGAPORE	7	24	2.7	2.6	$P_{29}=0.677$
INDONESIA					
Biak	4	28	3.0	2.9	$P_{30}=0.595$
All localities*	38	63	2.9	2.8	$P_{99}=0.501$
NEW GUINEA					
Admiralty Islands	2	25	3.0	2.8	$P_{25}=0.452$
All localities*	37	26	2.8	3.0	$P_{61}=0.123$
SOLOMON ISLANDS					
New Georgia	2	10	3.0	2.8	$P_{10}=0.533$
Isabel	3	9	3.0	2.9	$P_{10}=0.588$
Rennell Island	7	12	2.7	2.9	$P_{17}=0.268$
All localities*	21	42	2.9	2.9	**
FIJI					
Suva	17	13	3.0	2.9	$P_{28}=0.260$
Bird	2	11	3.0	3.0	**
All localities*	31	97	3.0	2.9	$P_{126}=0.781$
PALAU	6	28	3.0	2.9	$P_{32}=0.417$
RYUKYU ISLANDS					
Iriomote	1	11	3.0	3.0	**
LATICAUDA SAINTGIRONSI					
Noumea	17	7	3.0	2.9	$P_{22}=0.387$
All New Caledonia	22	90	2.9	3.0	$P_{110}=0.246$
All localities*	23	94	2.9	3.0	$P_{115}=0.246$
LATICAUDA GUINEAI	9	43	2.9	3.0	$P_{50}=0.221$
LATICAUDA FRONTALIS	3	7	3.0	3.0	**

* Collectively including the specific localities treated in this table plus those from the region that were not treated individually because of sample sizes below ten. Therefore N may be greater than the total N for the individual localities listed.

Appendix 4.13. Sexual dimorphism and regional differences in the number of dark bands on the body in adults of the *Laticauda colubrina* complex. Comparisons between sexes include only localities in which the combined number of males and females equals ten or more. "All localities" includes in addition to the precise localities specifically listed in the table, the snakes from all localities with fewer than ten snakes as well as those with only a general regional designation rather than precise locality data; consequently Ns may be larger than the sum of the localities individually listed in the table. Comparisons between the sexes or between two localities was by two-tailed t-test. Comparisons among three or more localities was by analyses of variance (ANOVA) with comparisons between each possible pair of component localities tested by Fisher PLSD tests. **Boldface** indicates significance at a rejection level of 5%.

	N			**DARK BANDS ON BODY (Mean ± SE)**			
LOCALITY	**MALES**	**FEMALES**	**ALL**	**MALES**	**FEMALES**	**ALL**	**P (M VSF)**
LATICAUDA COLUBRINA							
ANDAMAN & NICOBAR ISLANDS	4	12	19	35.5 ± 0.96	35.3 ± 0.83	34.7 ± 0.61	P_{21}=0.258
The two localities, Andaman Islands and Nicobar Islands, did not have sufficient specimens to test differences between the sexes separately by locality. However, there were enough females for such a test and the difference between the two island groups (Andaman: N=7, mean= 36.9 ± 1.03; Nicobar: N= 5, mean=33.2 ± 0.58) was significant (t=2.748; **P_{10}=0.021**). Also, because there was no sexual dimorphism, males, females and juveniles could be combined for a test; the two island groups were again significantly different (Andaman: N=10, mean=36.0 ± 0.92; Nicobar: N=9, mean=33.2 ± 0.47; t=2.61, **P_{17}=0.019**). **Conclusions**: There is no sexual dimorphism in body bands in the Andaman & Nicobar Islands, but snakes have a significantly greater number of bands in the Andamans than in the Nicobars.							
MALAYSIA-SINGPORE							
Labuan (two small cays)	10	12	41	44.4 ± 0.69	46.9 ± 0.99	45.2 ± 0.41	P_{20}=0.069
All Sabah	26	21	---	44.6 ± 0.82	47.5 ± 0.76	---	**P_{45}=0.004**
Singapore	21	17	43	36.8 ± 0.62	36.8 ± 0.63	36.8 ± 0.44	P_{36}=0.988
All Peninsular Malaysia+Singapore	27	18	45	36.4 ± 0.57	37.0 ± 0.62	36.7 ± 0.42	P_{43}=0.524
All localities: Males F=11.23, **$P_{7, 30}$=0.0001**; Females F=19.20, **$P_{4, 28}$=0.0001** Localities within Sabah: Males F=2.11, $P_{5, 17}$=0.106; Females F=0.74, $P_{3, 16}$=0.580 Localities within Peninsular Malaysia + Singapore: Males F=2.15, $P_{1, 12}$=0.109; Females all from one locality. Sabah versus Peninsular Malaysia + Singapore: Males t=8.54, **P_{51}=0.0001;** Females t=10.53, **P_{37}=0.0001** **Conclusions**: There may be sexual dimorphism in some localities; Localities within Sabah and within Peninsular Malaysia + Singapore do not differ, but Sabah and Peninsular Malaysia + Singapore are different.							
INDONESIA							
Biak	10	16	29	39.5 ± 1.59	40.7 ± 2.68	40.0 ± 0.68	P_{24}=0.769
All localities	39	29	111	37.1 ± 0.96	37.8 ± 0.93	37.9 ± 0.51	P_{66}=0.608
Localities within Indonesia: All snakes F=4.26, $P_{32, 110}$ **<0.0001** **Conclusions**: There are no significant differences between the sexes but there are significant differences among localities in Indonesia.							
NEW GUINEA							
Admiralty Islands	15	9	26	35.1 ± 0.42	34.7 ± 0.69	35.0 ± 0.42	P_{22}=0.172
All localities	23	18	61	36.3 ± 0.76	35.3 ± 0.82	35.5 ± 0.52	P_{39}=0.368
Localities within New Guinea: All snakes F=6.38, **$P_{18, 60}$<0.001** New Hanover, New Ireland, New Britain, Bougainville: All snakes F=13.49, **$P_{3, 31}$<0.001** **Conclusions**: The sexes do not differ significantly; the only significant differences among localities may be artifacts of outliers of small sample size (see text).							
SOLOMON ISLANDS							
Isabel	8	8	---	37.06± 1.80	42.1 ± 0.81	---	**P_{14}=0.039**
New Georgia	9	7	16	36.1 ± 0.66	36.0 ± 0.69	36.1 ± 0.46	P_{14}=0.910
Rennmell	11	10	21	34.1 ± 0.96	35.8 ± 1.53	34.9 ± 0.88	P_{19}=0.345
Eastern Solomons[1]	10	9	19	40.3 ± 2.81	42.4 ± 0.78	41.3 ± 1.51	P_{17}=0.493
Western Solomons[2]	27	24	52	35.6 ± 0.53	36.0 ± 0.94	35.9 ± 0.42	P_{49}=0.985
BOUGAINVILLE[3]	2	8	---	39.5 ± 0.50	35.8 ± 0.53	---	**P_{8}=0.010**
Localities within the Solomon Islands + Bougainville: Males F=6.96, **$P_{10, 22}$=0.0001**; Females F=3.46, **$P_{7, 15}$=0.003** Eastern Solomons, Western Solomons, Bougainville: Males F=3.53, **$P_{2, 32}$=0.040**; Females F=18.05, **$P_{2, 22}$=0.0001** Eastern Solomons vs Western Solomons: Males Fisher PLSD: **P_{35}=0.003**; Females FisherPLSD: **P_{31}=0.001** Eastern Solomons vs Bougainville: Males Fisher PLSD, P_{10}=0.100; Females Fisher PLSD: P_{15}=0.200 Western Solomons vs Bougainville: Males Fisher PLSD: P_{27}=0.683; Females Fisher PLSD: P_{30}=0.170 **Conclusions:** There may be sexual dimorphism in some populations. The eastern islands differ significantly from the western ones, but neither group differs significantly from Bougainville.							
VANUATU							
Efate	22	19	45	33.1 ± 0.43	33.0 ± 0.43	33.1 ± 0.28	P_{39}=0.252
All localities	35	32	72	32.9 ± 0.38	32.8 ± 0.28	32.8 ± .023	---
Localities within Vanuatu: All snakes F=3.53, $P_{3, 48}$=0.627 **Conclusions:** There are no significant differences between the sexes and no significant differences among localities.							

APPENDIX 4.13, CONTINUED

	N			DARK BANDS ON BODY (Mean ± SE)			
LOCALITY	**MALES**	**FEMALES**	**ALL**	**MALES**	**FEMALES**	**ALL**	**P (M VSF)**
FIJI							
Kia	5	6	12	26.8 ± 0.74	27.3 ± 0.42	27.1 ± 0.36	$P_{9}=0.729$
Labasa	21	23	44	27.1 ± 0.55	26.7 ± 0.43	26.9 ± 0.34	$P_{42}=0.387$
Tavarua	12	6	---	29.3 ± 0.65	27.3 ± 0.42	---	**$P_{16}=0.016$**
Suva	9	6	30	29.2 ± 1.33	25.7 ± 0.99	27.3 ± 0.54	$P_{13}=0.130$
Buiba	19	8	28	27.8 ± 0.43	27.9 ± 0.52	27.8 ± 0.32	$P_{25}=0.783$
Bird	8	3	---	29.1 ± 0.58	27.0 ± 1.00	---	**$P_{9}=0.038$**
All localities	88	72	---	27.9 ± 0.27	26.7 ± 0.22	---	**$P_{158}<0.001$**
Localities within Fiji: Males F=2.28, $P_{7, 76}=0.057$; Females F=1.04, $P_{12, 62}=0.406$ **Conclusions**: There may be sexual dimorphism in some populations. Localities within Fiji do not differ significantly from each other.							
TONGA							
Velitoa	7	4	11	29.4 ± 0.69	27.6 ± 0.85	28.8 ± 0.57	$P_{9}=0.564$
All localities	24	17	---	28.8 ± 0.38	27.1 ± 0.63	---	**$P_{39}=0.014$**
Localities within Tonga: Males F=2.58, $P_{3\ 13}=0.100$; Females F=2.38, $P_{5, 10}=0.110$ **Conclusion:** Males and females may differ, but there are no significant differences among localities.							
PHILIPPINES							
Gigantes	10	2	15	44.1 ± 0.78	47.5 ±1.50	45.3 ± 0.76	$P_{10}=0.500$
Jaguliao	10	8	18	45.5 ± 1.19	48.6 ± 0.99	46.9 ± 0.86	$P_{16}=0.217$
All localities	30	21	---	43.5 ± 0.80	47.0 ± 0.67	---	**$P_{49}=0.024$**
Localities within the Philippines: Males F=1.14, $P_{8, 27}=0.382$; Females F=2.32; $P_{6, 19}=0.092$ **Conclusions**: There may be significant differences between the sexes in at least some localities. Neither among males, nor among females, are there significant differences among localities within the Philippines.							
PALAU	21	13	---	33.6 ± 0.36	34.9 ± 0.71	---	**$P_{32}=0.003$**
Conclusion: There are significant differences between the sexes.							
TAIWAN							
Heng Chun	3	9	12	38.7 ± 2.03	39.7 ± 0.55	39.4 ± 0.61	$P_{10}=0.478$
All localities	12	17	33	39.3 ± 0.63	39.7 ± 0.37	39.7 ± 0.37	$P_{39}=0.716$
Conclusions: There are no significant differences between the sexes.							
RYUKYUS							
Iriomote	2	9	12	40.5 ± 1.50	40.4 ± 0.99	40.5 ± 0.75	$P_{9}=0.981$
All Localities	3	16	20	40.7 ± 0.88	40.9 ± 0.71	40.9 ± 0.57	$P_{17}=0.469$
Localities within the Ryukyus: All snakes with data for specific locality were from Iriomote. **Conclusions**: There are no significant differences between the sexes, and no significant differences among localities within the Ryukyus							
LATICAUDA SAINTGIRONSI							
Porc Epic	7	11	18	25.5 ± 0.72	25.9 ± 0.61	25.8 ± 0.46	$P_{16}=0.622$
Atira	7	3	10	27.0 ± 0.49	25.7 ± 0.67	26.6 ± 0.43	$P_{8}=0.163$
Redika	11	5	17	26.4 ± 0.58	27.0 ± 0.84	26.5 ± 0.45	$P_{14}=0.545$
All localities	78	57	192	26.6 ± 0.20	26.3 ± 0.27	26.7 ± 0.16	$P_{133}=0.341$
Localities within New Caledonia: All snakes F=1.01, $P_{18, 162}=0.449$ **Conclusions**: There are no significant differences between males and females, nor are there significant differences among localities within New Caledonia.							
LATICAUDA GUINEAI							
All localities	24	22	55	52.7 ± 0.60	52.0 ± 0.87	51.6 ± 0.63	$P_{44}=0.516$
Localities within southern Papua: All snakes, F=0.81, $P_{3, 54}=0.453$ **Conclusions:** There are no differences between the sexes and there are no significant differences among localities.							
LATICAUDA FRONTALIS							
Ngoriki Islet	9	4	13	31.6 ± 0.63	32.0 ± 0.12	31.7 ± 0.55	$P_{11}=0.725$
All localities	15	7	28	31.7 ± 0.44	32.3 ± 0.92	31.7 ± 0.39	$P_{20}=0.498$
Localities within entire range (including waifs): All snakes, F=2.20, $P_{8, 27}=0.076$ **Conclusions**: There are no differences between the sexes and there are no significant differences among localities.							

[1] Isabel, Malaita, Choiseul; [2] all other Solomon islands, including Buka and Nissan[3]

Dashes indicate “not applicable”.

Appendix 4.14. Sexual dimorphism and regional differences in the number of dark tail bands in adults of the *Laticauda colubrina* complex. Comparisons between sexes for individual localities include only those localities in which the combined number of males and females equals ten or more. “All localities”collectively includes the above localities as well as those localities for which there were smaller sample sizes as specimens with only the country name listed as he locality; consequently Ns may be larger than the sum of the localities individually listed in the table. Comparisons between the sexes or between two localities was by two-tailed t-test for large samples and by Mann Whitney U test for small ones. Comparisons among three or more localities was by analyses of variance (ANOVA). **Boldface** indicates statistical significance with a rejection level of 5%. M = males; F= females.

	N		DARK BANDS ON TAIL (MEAN ± SE)		
LOCALITY	**MALES**	**FEMALES**	**MALES**	**FEMALES**	**P (M vs F)**
LATICAUDA COLUBRINA					
ANDAMAN & NICOBAR ISLANDS	6	12	4.5 ± 0.22	3.8 ± 0.18	**P_{16}=0.024**
Localities within the Andaman & Nicobar Island (Andamans vs Nicobars): Sample size was too small for males for testing parametrically, but a Man Whitney U test suggested no difference between the Andaman and Nicobar Islands (Z=-1.73; P=0.083); Females: t=0.69; P_{11}=0.506. **Conclusions**: There is sexual dimorphism in number of dark tail bands in the Andaman & Nicobar Islands, but in neither sex does there seem to be any significant difference between the Andamans and the Nicobars.					
MALAYSIA-SINGAPORE					
Labuan (two small cays)	10	12	5.2 ± 0.13	4.1 ± 0.15	**P_{20}<0.0001**
All Sabah	21	20	5.3 ± 0.10	4.2 ± 0.14	**P_{39}<0.0001**
Singapore	11	13	4.3 ± 0.20	3.2 ± 0.17	**P_{22}=0.0005**
All Peninsular Malaysia + Singapore	14	13	4.4 ± 0.17	3.2 ± 0.17	**P_{25}<0.0001**
All localities: Males F=3.64; **$P_{2,41}$=0.009**; Females F=4.76, **$P_{2,57}$=0.005** Localities within Sabah: Males F=0.70, $P_{5,12}$=0.637; Females F=0.72; $P_{3,13}$=0.558 Localities within Peninsular Malaysia + Singapore: Males F=2.36, $P_{1,11}$=0.153; Too few localities with females to test. Sabah vs Peninsular Malaysia + Singapore: Males t=4.58, **P_{34}<0.0001**; Females t=4.47; **P_{31}<0.0001** **Conclusions**: There is sexual dimorphism in all localities tested; For a given sex, localities within Sabah do not differ, nor do those within Peninsular Malaysia + Singapore, but in both sexes Sabah and Peninsular Malaysia + Singapore differ significantly from each other.					
INDONESIA					
Biak	9	18	4.9 ± 0.20	4.1 ± 0.16	**P_{25}=0.007**
All localities	37	28	4.8 ± 0.12	3.7 ± 0.15	**P_{63}<0.0001**
Localities within Indonesia: Males: F=1.08; $P_{16,27}$=0.459: Females: F=1.49; $P_{9,23}$=0.203 after omitting an outlier (see text). **Conclusions**: There are significant differences between the sexes, and for a given sex there are no significant differences among localities within Indonesia.					
NEW GUINEA					
Admiralty (Bismarck)	15	10	4.7 ± 0.12	3.6 ± 0.16	**P_{23}<0.0001**
All localities	23	19	4.8 ± 0.11	3.6 ± 0.12	**P_{40}<0.0001**
Localities within New Guinea: Males F=1.23; $P_{8,22}$=0.352: Females F=0.98; $P_{7,10}$=0.497 **Conclusions**: The sexes differ significantly, but neither sex shows significant differences among localities.					
SOLOMON ISLANDS					
Isabel	5	6	5.2 ± 0.20	4.0 ± 0.26	**0.006**
New Georgia	9	3	4.6 ± 0.18	3.7 ± 0.33	**P_{10}=0.033**
Rennell	8	7	4.0 ± 0	3.4 ± 0.43	P_{13}=0.174
Eastern Solomons^1	6	6	5.2 ± 0.17	4.0 ± 0.26	**P_{10}=0.004**
Western Solomons^2	23	14	4.4 ± 0.12	3.6 ± 0.23	**P_{35}=0.0009**
Localities within the Solomon Islands: Males F=3.05; **$P_{7,22}$=0.021**: Females F=0.36; $P_{5,14}$=.087 **Conclusions:** There is sexual dimorphism in all but one of the localities tested, and in that locality, adults and juveniles did not differ significantly. There are significant differences among populations for males (see text for details), but not for females.					
VANUATU					
Efate	2	19	4.5 ± 0.50	3.3 ± 0.11	**P_{19}<0.0001**
All localities	33	32	4.2 ± 0.11	3.3 ± 0.08	**P_{63}<0.0001**
Localities within Vanuatu: Males F=2.12; $P_{2,23}$=0.160: Females F=0.47; $P_{2,18}$=0.632 **Conclusions:** There are significant differences between the sexes but neither sex exhibited significant differences among localities.					
FIJI					
Kia	5	5	3.4 ± 0.25	3.6 ± 0.25	0.580
Lambasa	21	23	3.7 ± 0.11	3.1 ± 0.16	**P_{42}=0.008**
Tavarua	11	8	3.9 ± 0.09	3.2 ± 0.23	**P_{17}=0.002**
Suva	8	6	3.6 ± 0.18	3.0 ± 0	**P_{12}=0.017**
Buiba	19	7	3.6 ± 0.14	3.7 ± 0.18	P_{24}=0.746
Bird	9	3	3.7 ± 0.17	3.7 ± 0.33	identical
All localities	86	70	3.7 ± 0.05	3.3 ± 0.08	**P_{154}<0.0001**
Localities within Fiji: Males F=0.67; P=0.700: Females F=1.54; $P_{11,48}$=0.145 **Conclusions**: Sexual dimorphism was demonstrated for some populations, but not for others. For the one testable locality that was not dimorphic juveniles and adults did not differ significantly. Localities do not differ significantly from each other.					

APPENDIX 4.14, CONTINUED					
	N		**DARK BANDS ON TAIL (MEAN ± SE)**		
LOCALITY	**MALES**	**FEMALES**	**MALES**	**FEMALES**	**P (M vs F)**
TONGA					
Velitoa	6	3	4.0 ± 0	3.3 ± 0.33	**0.019**
All localities	14	13	3.9 ± 0.10	3.0 ± 0.11	**P_{25}<0.001**
Localities within Tonga: Males F=0.005, P not calculated as all values for a given locality were identical and were either 3 or 4 for all localities: Females F=0.571; $P_{3,6}$=0.725 **Conclusion:** Males and females differ significantly, but in neither sex are there significant differences among localities.					
PHILIPPINES					
Gigantes	10	2	5.3 ± 0.15	3.5 ± 0.50	**P_{10}=0.001**
Jaguliao	9	9	5.3 ± 0.17	4.2 ± 0.15	**P_{16}=0.0001**
All localities	30	22	5.3 ± 0.11	4.0 ± 0.09	**P_{50}<0.0001**
Localities within the Philippines: Males F=1.81; $P_{8,27}$=0.137: Females F=1.49; $P_{7,11}$=0.267 **Conclusions**: There are significant differences between the sexes but neither sex exhibited significant differences among localities.					
PALAU	19	13	4.7 ± 0.13	3.6 ± 0.14	**P_{30}<0.0001**
Localities within Palau: Males F= 3.40; $P_{5,14}$=0.131: Females F=1.47; $P_{4,4}$=0.320 **Conclusions**: There are significant differences between the sexes, but neither sex shows significant differences among localities.					
TAIWAN					
Heng Chun	3	13	4.7 ± 0.67	3.5 ± 0.14	**P_{14}=0.017**
All localities	11	18	4.6 ± 0.20	3.5 ± 0.12	**P_{27}<0.0001**
Localities within Taiwan: There were too few males with specific locality data for parametric testing, but a Kruskal Wallis test was not significant (z=0.24; P=0.814): Females F=0.93 $P_{2,12}$=0.420 **Conclusions**: There is significant sexual dimorphism, but neither sex exhibited significant differences among localities.					
RYUKYUS					
Iriomote	2	9	5.0 ± 0	3.4 ± 0.18	**0.003**
All localities	3	16	5.0 ± 0	3.5 ± 0.13	**P_{17}=0.0001**
Localities within the Ryukyus: Only one locality with specific locality data. **Conclusions**: There is significant sexual dimorphism.					
LATICAUDA SAINTGIRONSI					
Porc Epic Island	7	11	3.0 ± 0	2.1 ± 0.16	**P_{16}=0.0004**
Atira Island	8	3	3.4 ± 0.18	2.0 ± 0	**0.002**
Redika Island	11	5	3.3 ± 0.14	2.4 ± 0.25	**P_{14}=0.005**
All localities	80	58	3.3 ± 0.06	2.3 ± 0.07	**P_{136}<0.0001**
Localities within New Caledonia: Males F=0.52; $P_{13,48}$=0.913: Females F=1.56; $P_{13,29}$=0.134 New Caledonia versus the Loyalty Islands: Males t=-0.71; P_{62}=0.480: Females t=-3.11; **P_{43}=0.003** **Conclusions**: There are significant differences between males and females, but in neither sex are there significant differences among localities within New Caledonia. There is a significant difference between New Caledonia and the Loyalty Islands in females but not in males.					
LATICAUDA GUINEAI	21	21	6.1 ± 0.16	4.3 ± 0.13	**P_{40}<0.0001**
Localities within southern Papua: Males F=0.61; $P_{1,20}$=0.444: Females F=1.15; $P_{1,18}$=0.299 **Conclusions**: There are significant differences between males and females, but neither sex exhibits significant differences among localities.					
LATICAUDA FRONTALIS					
Ngoriki Islet	9	4	3.8 ± 0.15	3.3 ± 0.25	**P_{11}=0.081**
All localities	14	5	3.8 ± 0.11	3.2 ± 0.20	**P_{17}=0.018**
Localities within Vanuatu (all adults and juveniles; see text): F=0.20, $P_{8,19}$=0.893 **Conclusions:** There is no sexual dimorphism in dark tail bands. There are no significant differences among localities within Vanuatu.					

[1] Isabel, Malaita, Choiseul; [2] all other Solomon islands; **[3]** including Buka and Nissan

Appendix 4.15. Sexual dimorphism and regional differences in the number of subcaudal scales in adults of the *Laticauda colubrina* complex. Comparisons between sexes for individual localities include only those localities in which the combined number of males and females equals ten or more. "All localities"collectively includes the above localities as well as those localities for which there were smaller sample sizes as specimens with only the country name listed as he locality; consequently Ns may be larger than the sum of the localities individually listed in the table. Comparisons between the sexes or between two localities was by two-tailed t-test for large samples and by Mann Whitney U test for small ones. Comparisons among three or more localities was by analyses of variance (ANOVA). **Boldface** indicates statistical significance with a rejection level of 5%. M = males; F = females.

	N		**NO. OF SUBCAUDALS (MEAN ± SE)**		**P**
LOCALITY	**M**	**F**	**M**	**F**	**M vs F**
LATICAUDA COLUBRINA					
ANDAMAN & NICOBAR ISLANDS	3	12	42.0 ± 0.58	33.6 ± 0.98	**0.001**
Localities within the Andaman & Nicobar Island (Andamans vs Nicobars): Sample size was too small for males for testing parametrically, but a Man Whitney U test suggested no difference between the Andaman and Nicobar Islands (Z=-1.23; P=0.221); Females F=0.36; P=0.827 **Conclusions**: There is sexual dimorphism, but no significant difference among localities for either sex.					
MALAYSIA-SINGAPORE					
All Sabah	11	10	43.0 ± 0.41	35.0 ± 1.14	**<0.0001**
Singapore	11	13	42.4 ± 1.02	33.5 ± 1.02	**<0.0001**
All localities	25	25	42.8 ± 0.49	34.2 ± 0.76	**<0.0001**
All localities: Males F=0.25; P=0.936: Females F=0.69; P=0.571 **Conclusions**: There is sexual dimorphism, but neither sex shows significant variation among localities.					
INDONESIA					
Biak	9	18	41.4 ± 0.80	35.5 ± 0.95	**0.0004**
All localities	37	28	42.2 ± 0.42	34.6 ± 0.73	**<0.0001**
Localities within Indonesia: Males: F=1.02; P=0.501: Females F=0.71; P=0.678 **Conclusions**: There is sexual dimorphism. Neither sex shows significant variation among localities.					
NEW GUINEA					
Bismarck Archipelago	15	10	42.7 ± 0.37	33.1 ± 0.35	**<0.0001**
All localities	23	20	42.6 ± 0.30	32.9 ± 0.33	**<0.0001**
Localities within New Guinea: Males F=0.93; P=0.520: Females F=0.65; P=0.706 **Conclusions**: There is sexual dimorphism, but neither sex shows significant variation among localities.					
SOLOMON ISLANDS					
Isabel	5	6	42.6 ± 1.03	34.3 ± 1.05	**0.0004**
New Georgia	9	3	42.8 ± 0.70	34.0 ± 1.16	**<0.0001**
Rennell	8	7	41.3 ± 1.16	33.3 ± 0.42	**<0.0001**
All localities	31	22	41.6 ± 0.52	33.9 ± 0.40	**<0.0001**
Localities within the Solomon Islands: Males F=1.19; P=0.348: Females F=0.74; P=0.609 **Conclusions:** There is sexual dimorphism. Neither sex shows significant variation among localities.					
VANUATU					
Efate	20	19	43.6 ± 0.26	34.5 ± 0.23	**<0.0001**
All localities	33	32	43.7 ± 0.26	34.2 ± 0.21	**<0.0001**
Localities within Vanuatu: Males F=0.25; P=0.781: Females F=5.55; **P=0.013** **Conclusions:** There is sexual dimorphism. Females, but not males showed significant variation among localities (but see text).					
FIJI					
Kia	5	6	36.0 ± 1.70	38.8 ± 1.91	0.305
Lambasa	20	22	39.1 ± 0.96	35.2 ± 0.76	**0.003**
Tavarua	11	10	41.6 ± 1.07	36.4 ± 1.52	**0.011**
Suva	8	6	38.4 ± 1.30	34.2 ± 1.64	0.064
Buiba	19	7	39.5 ± 1.10	38.7 ± 1.87	0.708
Bird	9	3	39.6 ± 1.22	40.0 ± 1.00	0.846
All localities	85	71	39.4 ± 0.46	36.3 ± 0.52	**<0.0001**
Localities within Fiji: Males F=0.87; P=0.544: Females F=1.51; P=0.153 **Conclusions**: There is sexual dimorphism at some localities, but it was not demonstrated at others. For the latter, no significant differences between adults and juveniles were found. Neither sex showed significant variation among localities.					
TONGA					
Veltoa	7	4	43.3 ± 0.64	37.8 ± 2.46	**0.021**
All localities	14	13	42.9 ± 0.50	35.5 ± 1.08	**<0.0001**
Localities within Tonga: Males F=1.33; P=0.323: Females F=1.54; P=0.325 **Conclusion:** There is sexual dimorphism. Neither sex shows significant variation among localities.					
PHILIPPINES					
Gigantes	10	1	44.3 ± 0.80 44.6 ±	39.0 ± ---	0.149
Jaguliao	9	9	0.53	35.9 0.61	**<0.0001**
All localities	30	21	44.6 ± 0.37	36.2 ± 0.39	**<0.0001**
Localities within the Philippines: Males F=0.60; P=0.765: Females F=1.34; P=0.326 **Conclusions**: There are significant differences between the sexes except for one locality with a small sample for females. Neither sex shows significant variation among localities.					

TABLE 4.15, CONTINUED					
PALAU	19	12	42.8 ± 0.39	34.8 ± 0.51	**<0.0001**
Localities within Palau: Males F= 0.54; P=0.743: Females F= 0.50; P=0.710 **Conclusions:** There are significant differences between the sexes, but neither sex shows significant variation among localities.					
	N		**NO. OF SUBCAUDALS (MEAN ± SE)**		**P**
LOCALITY	**M**	**F**	**M**	**F**	**M vs F**
TAIWAN					
Heng Chun	3	13	43.7 ± 1.20	34.0 ± 0.45	**<0.0001**
All localities	11	18	43.7 ± 0.43	34.2 ± 0.37	**<0.0001**
Localities within Taiwan: Males F=0.20; P=0.678: Females F=0.70; P=0.516 **Conclusions**: There is significant sexual dimorphism. Neither sex shows significant variation among localities.					
RYUKYUS					
Iriomote	2	9	46.5 ± 0.50	34.7 ± 0.29	**<0.0001**
All localities	3	17	45.0 ± 1.53	35.1 ± 0.32	**<0.0001**
Localities within the Ryukyus: Only one locality with specific locality data. **Conclusion**: There is significant sexual dimorphism.					
LATICAUDA SAINTGIRONSI					
NEW CALEDONIA					
Porc Epic Island	7	11	39.0 ± 0.22	31.7 ± 0.49	**<0.0001**
Atira Island	8	3	37.0 ± 1.09	30.3 ± 0.33	**0.006**
Redika Island	11	5	39.9 ± 0.50	31.4 ± 1.50	**<0.0001**
All localities	78	59	38.6 ± 0.25	30.9 ± 0.33	**<0.0001**
LOYALTY ISLANDS	2	2	37.0		**---**
Localities within New Caledonia (excluding Loyalty Islands): Males F=2.12; **P=0.031**: Females F=1.37; P=0.251 **Conclusions**: There is significant sexual dimorphism. There are significant among localities in New Caledonia in males but not in females.					
LATICAUDA GUINEAI	21	21	42.0 ± 0.50	33.0 ± 0.45	**<0.0001**
Localities within southern Papua: Males F=0.85; P=0.369: Females F=0.13; P=0.727 **Conclusions**: The number of subcaudal scales are significantly different between males and females but there are no significant differences among localities in either sex.					
LATICAUDA FRONTALIS					
Ngoriki Islet	8	4	37.8 ± 0.45	32.8 ± 0.75	**0.0001**
All localities	13	5	37.6 ± 0.42	32.4 ± 0.68	**<0.0001**
Localities within Vanuatu: Males F=0.36; P=0.783: Females F=1.09; P=0.373 **Conclusions:** Number of subcaudal scales is sexually dimorphic.					

Appendix 4.16. Probability values arising from t-tests or Mann-Whitney U tests for sexual dimorphism in number of scale rows around the body at different points along the torso in species of *Laticauda colubrina* complex for all localities in which N of the two sexes combined equaled or exceeded 10. Note that Malaysia is deleted from this analysis as the only large sample (Labuan) included many live animals for which scale rows were not counted, with a remaining N of only 2. For parametric tests the degrees of freedom are $N_{(males\ )} + N_{(females)} - 2$.

	N		NO. OF SCALE ROWS AROUND BODY AT GASTROSTEGE NUMBER:						
LOCALITY	MALES	FEMALES	1	20	50	100	150	200	LAST
LATICAUDA COLUBRINA									
ANDAMAN AND NICOBAR ISLANDS	3-4	11-12	0.009*	0.334	0.590	0.042*	0.029*	0.008*	0.094
SINGAPORE	10	12-14	0.646	0.666	0.165	0.010*	0.046*	0.129	0.193
INDONESIA									
Biak	9	16	0.038*	0.096	0.076	0.041*	0.100	0.009*	0.718
PAPUA NEW GUINEA									
Admiralty	15	9-10	0.187	0.105	0.775	0.021*	0.272	0.069	0.076
SOLOMON ISLANDS									
New Georgia	9	3	---	0.588	0.588	0.082	0.418	0.027*	---
Isabel	5	6	---	0.024*	0.226	0.389	0.214	0.189	---
Rennell	7	7	---	0.147	0.337	0.787	0.070	1.000	---
VANUATU									
Efate	28	19-21	---	0.022*	0.000*	0.0001*	0.0005*	0.0008*	---
FIJI									
Buiba	20	8	---	0.204	0.502	0.050	0.126	0.001*	---
Labasa	9	14	---	0.070	0.026*	0.003*	0.072	0.0001*	---
Suva	8	4-5	0.363	0.453	0.039*	0.348	0.167	0.023*	0.044*
Kia	6	6	0.145	0.341	0.341	0.341	0.341	0.296	0.270
Tavarua	11-12	10	0.0003*	0.0006*	0.022*	0.051*	0.003*	0.0008*	0.081
Bird	8	3	0.033*	0.568	0.237	0.006*	0.568	0.016	0.309
PHILIPPINES									
Jaguliao	9-10	8-9	0.434	0.927	0.003*	0.004*	0.001*	0.081	0.083
Gigantes	9	1-2	0.875	0.567	---	0.0003*	0.001*	0.0001*	0.067
PALAU	16-19	10	0.422	---	0.0004*	0.0001*	0.015*	0.0009*	0.655
TAIWAN									
Heng Chun	3	12	0.030*	0.173	0.004*	0.004*	0.0008*	0.008*	0.643
RYUKYUS									
Iriomote	2	9	0.662	0.118	0.052	0.001*	---	0.024*	0.202
PERCENT OF TESTS SIGNIFICANT	---	---	**40**	**15**	**35**	**67**	**45**	**67**	**20**
LATICAUDA GUINEAI	21-22	19-22	0.117	0.335	0.171	0.019*	0.002*	0.020*	0.024*
LATICAUDA SAINTGIRONSI									
NEW CALEDONIA									
Noumea	21	9	---	0.278	0.522	0.064	0.522	0.0001*	---
Porc Epic	6	11	---	0.236	1.000	0.478	1.000	0.010*	---
Atira	8	2	0.645	0.836	0.286	1.000	0.645	0.645	0.713
PERCENT OF TESTS SIGNIFICANT	---	---	**0**	**0**	**0**	**0**	**67**	**0**	**0**

* Statistical significant at a rejection level of 5%.
** Values were identical; no statistical test conducted.
--- Insufficient data.
Dashes indicate “not applicable”.

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 *Laticauda colubrina* as tested by ANOVA. Values in **boldface** are significant at the 5% rejection level. Note that some specimens only had a general locality and for this reason N values for regions may be higher from those for specific localities. NA indicates that specific localities were not grouped into regions for that country. Dashes indicate that because of small sample size for this character, or because of lack of data on specific locality, the test could not be performed. A number of countries were excluded because both sexes had too small a sample size of this character to be treated.

	SPECIFIC LOCALITIES						**REGIONS**					
	MALES			**FEMALES**			**MALES**			**FEMALES**		
COUNTRY	**N**	**F**	**P**	**N**	**F**	**P**	**N**	**F**	**P**	**N**	**F**	**P**
Andaman & Nicobar Isls.	---	---	---	9	0.53	$P_{3, 4}$=0.723	3	---	---	11	0.61*	P_{8}=0.557
Malaysia-Singapore	21	0.18	$P_{5, 15}$=0.967	20	2.90	$P_{3, 16}$=0.067	24	0.06	$P_{1, 21}$=0.813	22	5.92	$P_{1, 20}$=**0.010**
Indonesia	33	2.49	**$P_{15, 12}$=0.039**	26	3.40	**$P=_{8, 17}$=0.016**	34	1.66	$P_{4, 23}$=0.179	26	5.39	$P_{5, 20}$=**0.002**
Papua-New Guinea	47	3.64	**$P_{8, 15}$=0.002**	41	2.35	**$P_{6, 10}$=0.038**	47	1.75	$P_{3, 20}$=0.171	42	1.45	$P_{5, 12}$=0.223
Solomon Islands	30	2.00	$P_{7, 22}$=0.102	20	0.53	$P_{5, 14}$=0.752	30	0.56	$P_{1, 28}$=0.463	20	1.21	$P_{1, 18}$=0.286
Vanuatu	---	---	---	---	---	---	23	0.04	$P_{1, 21}$=0.867	20	3.74	**$P_{2, 17}$=0.045**
Fiji	79	0.94	$P_{7, 68}$=0.490	62	0.41	$P_{12, 48}$=0.953	79	0.96	$P_{3, 72}$=0.416	61	0.59	$P_{3, 56}$=0.622
Tonga	14	0.36	$P_{3, 10}$=0.787	11	1.24	$P_{5, 5}$=0.409	16	0.82	$P_{1, 14}$=0.381	11	0.41	$P_{3, 7}$=0.124
Philippine Islands	27	3.56	**$P_{8, 19}$=0.012**	16	0.84	$P_{5, 10}$=0.551	28	2.08	$P_{7, 21}$=0.095	17	0.45	$P_{5, 11}$=0.802
Taiwan	---	---	---	14	**0.02**	$P_{2, 11}$=0.978	---	---	---	NA	NA	NA

* indicates a value of t, rather than of F, as there were only two categories and they were compared by a t-test rather than by an analysis of variance. Dashes indicate insufficient data.

Appendix 4.18. Comparisons along the torso and from dorsum to venter of the widths of the dark and light-coloured bands in *Laticauda colubrina* and *Laticauda guineai*. P = probability values arising from Wilcoxon Matched-Pairs Signed-Ranks tests; those in **boldface** indicate significance at the 5% rejection level. N= number of paired values. Values were paired by specimen.

		% OF RANKS IN WHICH:			
COMPARISON	N	A=B	A>B	A<B	P
LATICAUDA COLUBRINA					
DARK BANDS					
DORSAL WIDTHS					
1st (A) vs. 10th (B)	623	44.8	26.3	28.9	0.726
1st (A) vs. 25th (B)	608	40.5	31.3	28.3	0.876
10th (A) vs. 25th (B)	607	44.0	30.6	25.4	0.913
VENTRAL WIDTHS					
1st (A) vs. 10th (B)	594	59.8	25.1	15.2	**0.0006**
1st (A) vs. 25th (B)	579	53.4	17.4	29.2	**<0.0001**
10th (A) vs. 25th (B)	586	58.0	12.6	29.4	**<0.0001**
LIGHT BANDS					
DORSAL WIDTHS					
1st (A) vs. 10th (B)	622	33.9	22.0	44.1	**<0.0001**
1st (A) vs. 25th (B)	608	31.7	21.6	46.7	**<0.0001**
10th (A) vs. 25th (B)	606	36.1	30.2	33.7	**0.040**
VENTRAL WIDTHS*					
1st (A) vs. 10th (B)	557	47.6	13.5	39.0	**<0.0001**
1st (A) vs. 25th (B)	541	50.1	19.2	30.7	**<0.0001**
10th (A) vs. 25th (B)	556	53.2	28.6	18.2	**<0.0001**
DARK (A) VS. LIGHT (B) BANDS					
DORSAL					
1st	626	21.1	12.1	66.8	**<0.0001**
10th	622	16.9	7.7	75.4	**<0.0001**
25th	608	14.6	8.6	76.8	**<0.0001**
VENTRAL*					
1st	577	5.4	1.7	92.9	**<0.0001**
10th	587	4.8	1.4	93.9	**<0.0001**
25th	571	7.0	1.6	91.4	**<0.0001**
LATICAUDA GUINEAI					
DARK BANDS					
DORSAL WIDTHS					
1st	626	21.1	12.1	66.8	**<0.0001**
10th	622	16.9	7.7	75.4	**<0.0001**
25th	608	14.6	8.6	76.8	**<0.0001**
VENTRAL WIDTHS					
1st (A) vs. 10th (B)	52	73.1	13.5	13.5	>0.999
1st (A) vs. 25th (B)	52	69.2	7.7	23.1	0.108
10th (A) vs. 25th (B)	52	63.5	25.0	11.5	0.108
LIGHT BANDS					
DORSAL WILDTHS					
1st (A) vs. 10th (B)	53	34.0	26.4	39.6	0.187
1st (A) vs. 25th (B)	53	35.9	34	30.2	0.834
10th (A) vs. 25th (B)	53	39.6	39.6	20.8	0.051
VENTRAL WIDTHS*					
1st (A) vs. 10th (B)	50	62.0	14.0	24.0	>0.251
1st (A) vs. 25th (B)	50	16.0	84.0	0	**<0.0001**
10th (A) vs. 25th (B)	52	67.3	15.4	17.3	0.808
DARK (A) VS. LIGHT (B) BANDS					
DORSAL					
1st	53	13.2	3.8	83.0	**<0.0001**
10th	53	5.7	0	94.3	**<0.0001**
25th	53	7.6	0	92.5	**<0.0001**
VENTRAL*					
1st	50	16.0	0	84.0	**<0.0001**
10th	52	15.4	0	84.6	**<0.0001**
25th	53	7.6	0	92.5	**<0.0001**

*Omits cases in which dark bands did not meet below, i.e., ventral width of dark bands = 0 and width of light bands incalculable (see Appendix 4.1).

Appendix 4.19. Comparisons of dorsal widths of the dark and light bands along the torso in *Laticauda frontalis*. P = probability values arising from Wilcoxon Matched-Pairs Signed-Ranks tests; those in **boldface** indicate significance at the 5% rejection level. N= number of paired values. Values were paired by specimen.

		PERCENT OF RANKS IN WHICH:			
COMPARISON	N	A=B	A>B	A<B	P
DARK BANDS					
1st (A) vs. 10th (B)	22	31.8	40.9	27.3	0.293
1st (A) vs. 25th (B)	22	13.6	59.1	27.2	0.083
10th (A) vs. 25th (B)	23	43.5	34.8	21.7	0.244
LIGHT BANDS					
1st (A) vs. 10th (B)	23	26.1	8.7	65.2	**0.007**
1st (A) vs. 25th (B)	23	34.8	8.7	56.5	**0.015**
10th (A) vs. 25th (B)	23	47.8	30.4	21.7	0.869
DARK (A) VS. LIGHT (B) BANDS					
1st	22	31.8	22.7	45.5	0.199
10th	23	8.7	4.4	87.0	**0.0007**
25th	23	8.7	4.4	87.0	**0.0002**

Appendix 4.20. Comparisons along the torso and from dorsum to venter of the widths of the dark and light-coloured bands in *Laticauda saintgironsi*. P = probability values arising from Wilcoxon Matched-Pairs Signed-Ranks tests; those in **boldface** indicate significance at the 5% rejection level. N= number of paired values. Values were paired by specimen.

		PERCENT OF RANKS IN WHICH:			
COMPARISON	N	A=B	A>B	A<B	P
BLACK BANDS					
DORSAL WIDTHS					
1st (A) vs. 10th (B)	172	33.7	33.7	32.6	0.960
1st (A) vs. 25th (B)	145	19.3	60.7	20.0	**<0.001**
10th (A) vs. 25th (B)	145	15.9	66.9	17.2	**<0.001**
VENTRAL WIDTHS					
1st (A) vs. 10th (B)	170	45.3	17.7	37.1	**<0.001**
1st (A) vs. 25th (B)	140	28.6	65.7	5.7	**<0.001**
10th (A) vs. 25th (B)	140	18.6	77.9	3.6	**<0.001**
LIGHT BANDS					
DORSAL WIDTHS					
1st (A) vs. 10th (B)	173	38.2	23.7	38.2	**0.010**
1st (A) vs. 25th (B)	145	27.6	53.1	19.3	**<0.001**
10th (A) vs. 25th (B)	145	24.1	59.3	16.6	**<0.001**
VENTRAL WIDTHS*					
1st (A) vs. 10th (B)	168	51.2	36.9	11.9	**<0.001**
1st (A) vs. 25th (B)	140	52.1	14.3	33.6	**<0.001**
10th (A) vs. 25th (B)	137	40.2	45.3	14.6	**<0.001**
DARK (A) VS. LIGHT (B) BANDS					
DORSAL					
1st	172	5.8	1.7	92.4	**<0.001**
10th	173	4.6	5.2	90.2	**<0.001**
25th	145	2.8	9.0	88.3	**<0.001**
VENTRAL					
1st	169	17.2	13.1	69.8	**<0.001**
10th	168	24.4	19.1	56.6	**<0.001**
25th	137	2.2	10.2	87.6	**<0.001**

* Omits cases in which dark bands did not meet below, i.e., ventral width of dark bands = 0 and width of light bands incalculable (see Table 21).

Appendix 4.21. Comparison between males and females of the dorsal width of the first dark band for all localities for which there were data from 10 or more adult specimens. P = probability value arising from either a t-test or a Mann-Whitney test (*) comparing the sexes. SE = standard error of the mean.

	N		MEAN ± SE		
COUNTRY/LOCALITY	MALES	FEMALES	MALES	FEMALES	P
LATICAUDA COLUBRINA					
ANDAMAN & NICOBAR ISLANDS	4	10	4.8 ± 0.48	5.2 ± 0.39	P_{12}=0.527
MALAYSIA					
Sabah	10	10	4.2 ± 0.25	3.9 ± 0.18	P_{18}=0.342
SINGAPORE	11	13	5.3 ± 0.24	5.5 ± 0.29	P_{22}=0.497
INDONESIA					
Biak	10	18	4.7 ± 0.15	4.7 ± 0.14	P_{26}=0.918
VANUATU					
Efate	15	12	5.7 ± 0.19	5.9 ± 0.19	P_{25}=0.365
FIJI					
Buiba	15	7	7.9 ± 0.23	7.9 ± 0.26	P_{14}=0.981
Lambasa	12	13	8.3 ± 0.28	8.1 ± 0.35	P_{23}=0.705
Suva	8	6	7.8 ± 0.41	8.3 ± 0.42	P^{12}=0.351
Kia	5	6	8.6 ± 0.25	8.3 ± 0.33	P_{9}=0.550
Tavarua	12	9	7.3 ± 0.41	7.8 ± 0.36	P_{19}=0.449
Bird	9	3	7.6 ± 0.29	8.0 ± 0.58	P_{10}=0.479
PHILIPPINES					
Jaguliao	8	8	4.9 ± 0.23	4.9 ± 0.13	0.958*
Gigantes	8	2	4.8 ± 0.25	4.5 ± 0.50	P_{10}=0.667
PALAU	21	13	6.1 ± 0.17	6.1 ± 0.24	P_{32}=0.949
TAIWAN					
Heng Chun	3	11	4.7 ± 0.33	4.5 ± 0.21	P_{12}=0.636
RYUKYUS					
Iriomote	2	9	4.5 ± 0.50	5.4 ± 0.24	P_{9}=0.130
LATICAUDA GUINEAI					
NEW GUINEA					
Port Moresby	24	21	4.0 ± 0.24	3.8 ± 0.19	P_{43}=0.640
LATICAUDA SAINTGIRONSI					
NEW CALEDONIA					
Porc Epic	7	11	10.7 ± 0.78	10.6 ± 0.41	P_{16}=0.836
Atira	8	3	8.8 ± 0.31	9.3 ± 0.33	P_{9}-=0.325
Redika	11	5	9.9 ± 0.42	10.4 ± 0.25	P_{14}=0.460
LATICAUDA FRONTALIS					
VANUATU					
Ngoriki Islet	9	4	6.7 ± 0.24	7.0 ± 0.58	P_{11}-0.529

Appendix 4.22. Comparison between juveniles and adults (males and females combined) of the number of scale rows in the dorsal widths of black bands for individual localities in which the number of specimens in the two categories combined was ten or greater. Animals of uncertain maturity excluded. J=juveniles; A=adults; SE = standard error of the mean; P = probability value arising from a t-test or a Mann Whitney U test (*). *Laticauda frontalis* and some localities for other species could not be tested because of lack of juveniles in the samples. Probability values in **boldface** indicates a significant difference at the 5% rejection level.

	N	MEAN ± SE		
BAND/SPECIES/LOCALITY	J, A	JUV.	ADULTS	P
FIRST DARK BAND				
LATICAUDA COLUBRINA				
ANDAMAN AND NICOBAR ISLANDS	1, 14	6.0	5.1 ± 0.31	P0.418*
MALAYSIA				
Sabah	6, 23	5.3 ± 0.33	4.1 ± 0.15	**P_{27}=0.001**
SINGAPORE	8, 24	5.9 ± 0.48	5.4 ± 0.19	P_{30}=0.291
INDONESIA				
Biak	4, 28	5.5 ± 0.29	4.7 ± 0.10	**P_{30}=0.011**
SOLOMON ISLANDS				
Rennell	7, 9	5.4 ± 0.30	5.3 ± 0.17	P_{14}=0.772
Isabel	4,9	5.8 ± 0.48	4.6 ± 0.18	**P_{11}=0.013**
VANUATU				
Efate	1, 27	6.0	5.8 ± 0.13	0.757*
FIJI				
Suva	16, 14	7.5 ± 0.43	8.0 ± 0.30	P_{28}=0.359
Tavarua	2, 22	7.5 ± 0.50	7.6 ± 0.28	P_{22}=0.924
Bird	1, 12	7.0	7.7 ± 0.26	0.423*
TONGA				
Niaou'fou	6, 4	8.2 ± 0.65	8.3 ± 0.25	P_{8}=0.924
PALAU	7, 34	7.0 ± 0.54	6.1 ± 0.14	**P_{39}=0.021**
LATICAUDA GUINEAI				
PAPUA NEW GUINEA				
Port Moresby	8, 40	4.1 ± 0.40	3.7 ± 0.13	P_{46}=0.255
LATICAUDA SAINTGIRONSI				
NEW CALEDONIA				
Noumea	17, 8	10.0 ± 0.35	10.6 ± 0.60	P_{23}=0.351
Isle de Pines	1, 9	9.0	9.2 ± 0.52	0.728*
TENTH DARK BAND				
LATICAUDA COLUBRINA				
ANDAMAN AND NICOBAR ISLANDS	1, 14	6.0	5.4 ± 0.23	0.386*
MALAYSIA				
Sabah	22, 41	4.7 ± 0.15	4.4 ± 0.11	P_{61}=0.098
SINGAPORE	7. 24	6.0 ± 0.49	5.6 ± 0.19	P_{29}=0.347
INDONESIA				
Biak	4, 28	6.0 ± 0.41	4.8 ± 0.13	**P_{30}=0.003**
SOLOMON ISLANDS				
Rennell	7, 9	5.6 ± 0.48	5.4 ± 0.24	P_{14}=0.804
Isabel	4, 9	6.0 ± 0.71	5.2 ± 0.15	P_{11}=0.147
VANUATU				
Efate	1, 27	7.0	5.8 ± 0.15	0.144*
FIJI				
Suva	16, 15	7.7 ± 0.41	7.9 ± 0.29	P_{29}=0.725
Tavarua	1, 21	9.0	7.8 ± 0.29	0.370
BIrd	1, 12	8.0	7.5 ± 0.26	0.475
TONGA				
Niaou'fou	13, 30	7.9 ± 0.35	8.1 ± 0.14	P_{41}=0.505
PALAU	8, 33	6.8 ± 0.41	6.3 ± 0.14	P_{39}=0.176
LATICAUDA GUINEAI				
PAPUA NEW GUINEA				
Port Moresby	10, 43	4.1 ± 0.41	3.7 ± 0.09	P_{51}=0.141
LATICAUDA SAINTGIRONSI				
NEW CALEDONIA			1	
Noumea	17, 14	10.1 ± 0.35	0.2 ± 0.40	P_{29}=0.769
Isle de Pines	1, 9	10	9.9 ± 0.48	>0.999*

APPENDIX 4.22, CONTINUED				
TWENTY-FIFTH DARK BAND				
LATICAUDA COLUBRINA				
ANDAMAN AND NICOBAR ISLANDS	1, 14	4.0	4.7 ± 0.22	0.373*
MALAYSIA				
Sabah	4, 21	4.8 ± 0.25	3.9 ± 0.14	**P_{23}=0.018**
SINGAPORE	7, 23	5.6 ± 0.37	5.2 ± 0.18	P_{28}=0.359
INDONESIA				
Biak	4, 27	4.8 ± 0.63	4.4 ± 0.13	P_{29}=0.468
SOLOMON ISLANDS				
Rennell	7, 9	5.7 ± 0.42	5.3 ± 0.17	P_{14}=0.373
Isabel	4.9	5.3 ± 0.95	4.3 ± 0.17	0.184
VANUATU				
Efate	1, 27	7.0	5.7 0.16	0.127*
FIJI				
Suva	16, 13	8.1 ± 0.63	8.2 ± 0.32	P_{27}=0.836
Tavarua	1, 21	8.0	8.6 ± 0.31	P_{20}=0.686
BIrd	1, 21	7.0	8.4 ± 0.45	P_{20}=0.273
TONGA				
Niaou'fou	12, 27	7.9 ± 0.36	8.5 ± 0.27	P_{37}=0.214
PALAU	8, 33	7.0 ± 0.33	6.1± 0.13	**P_{39}=0.004**
LATICAUDA GUINEAI				
PAPUA NEW GUINEA				
Port Moresby	10, 43	4.1 ± 0.23	3.4 ± 0.09	**P_{51}=0.003**
LATICAUDA SAINTGIRONSI				
NEW CALEDONIA				
Noumea	15, 10	10.3 ± 0.59	10.6 ± 0.37	P_{23}=0.676
Isle de Pines (Insufficiend Data)				

Appendix 4.23. Variation among specific localities within countries in the dorsal width of first dark band of adult *Laticauda colubrina*. Values in **boldface** are significant at the 5% rejection level. “Percent Significant” is the percent of the paired combinations that were significant at the 5% rejection level. Countries not listed had insufficient data for testing.

COUNTRY	F	P	PERCENT SIGNIFICANT
Malaysia/Singapore	4.04	**$P_{7,37}$=0.0032**	19.1
Indonesia	2.79	**$P_{18,59}$=0.0025**	11.1
Papua New Guinea	4.45	**$P_{9,26}$=0.001**	36.0
Solomon Islands	1.20	**$P_{8,23}$=0.0062**	22.2
Vanuatu	0.21	$P_{3,27}$=0.954	0
Fiji	1.99	**$P_{12,102}$=0.033**	24.4
Tonga	0.21	$P_{5,19}$=0.954	0
Philippines	1.34	$P_{12,33}$=0.242	0
Palau	0.25	$P_{7,16}$=0.963	0
Taiwan	2.52	$P_{2,18}$=0.108	0

Appendix 4.24. Comparison between males and females of the dorsal width of the first light band for all localities for which there were data from 10 or more adult specimens. P = probability value arising from either a t-test or a Mann-Whitney test (*) comparing the sexes. SE = standard error of the mean.

	N		MEAN ± SE		
COUNTRY/LOCALITY	MALES	FEMALES	MALES	FEMALES	P
LATICAUDA COLUBRINA					
ANDAMAN & NICOBAR ISLANDS	4	10	6.8 ± 0.25	6.9 ± 0.99	P_{12}=0.782
MALAYSIA					
Sabah	11	10	6.1 ± 0.21	5.7 ± 0.26	P_{19}=0.254
SINGAPORE	11	13	7.6 ± 0.41	7.2 ± 0.34	P_{22}=0.465
INDONESIA					
Biak	10	18	7.1 ± 0.35	6.6 ± 0.22	P_{22}=0.174
VANUATU					
Efate	15	12	7.5 ± 0.17	8.1 ± 0.23	P_{25}=0.057
FIJI					
Buiba	15	7	7.8 ± 0.20	7.5 ± 0.20	P_{20}=0.491
Lambasa	12	13	8.3 ± 0.31	7.9 ± 0.27	P_{23}=0.370
Suva	8	6	8.1 ± 0.23	8.3 ± 0.42	P_{12}=0.649
Kia	5	6	8.2 ± 0.20	8.3 ± 0.62	P_{9}=0.854
Tavarua	12	9	7.8 ± 0.27	8.2 ± 0.28	P_{19}=0.337
Bird	9	3	8.1 ± 0.31	8.0 ± 0.58	P_{10}=0.863
PHILIPPINES					
Jaguliao	9	9	5.9 ± 0.26	5.8 ± 0.22	P_{16}=0.750
Gigantes	8	2	5.9 ± 0.30	7.0	P_{8}=0.106
PALAU	21	13	6.6 ± 0.26	6.5 ± 0.31	P_{32}=0.937
TAIWAN					
Heng Chun	3	11	6.0	6.6 ± 0.24	P_{12}=0.211
RYUKYUS					
Iriomote	2	9	5.5 ± 0.50	6.4 ± 0.29	P_{9}=0.196
LATICAUDA GUINEAI					
PAPUA NEW GUINEA					
Port Moresby	21	21	5.1 ± 0.32	5.0 ± 0.25	P_{40}=0.647
LATICAUDA SAINTGIRONSI					
NEW CALEDONIA					
Porc Epic	7	11	6.4 ± 0.37	6.6 ± 0.28	P_{16}=0.655
Atira	8	3	5.9 ± 0.40	6.3 ± 0.33	P_{9}=0.528
Redika	11	5	6.7 ± 0.33	7.2 ± 0.37	P_{14}=0.411
LATICAUDA FRONTALIS					
VANUATU	4	9	7.3 ± 0.48	6.6 ± 0.24	P_{11}=0.175
Ngoriki Islet					

Appendix 4.25. Comparison of the number of scale rows in the dorsal width of the first light band between juveniles and adults (males and females combined) for individual localities in which the number of specimens in the two categories combined was 10 or greater. Animals of uncertain maturity excluded. J=juveniles; A=adults; SE = standard error of the mean. P = probability value arising from a t-test or a Mann Whitney U test (*). *Laticauda frontalis* and some localities for other species could not be tested because of lack of juveniles in the samples. Probability values in **boldface** indicates a significant difference at the 5% rejection level.

SPECIES/LOCALITY	N	MEAN ± SE		P
	J, A	JUVENILES	ADULTS	
LATICAUDA COLUBRINA				
ANDAMAN AND NICOBAR ISLANDS	1, 14	7.0	6.9 ± 0.23	0.700*
MALAYSIA				
Sabah	3, 21	6.3 ± 0.67	5.9 ± 0.17	P_{13}=0.401
SINGAPORE	8, 24	6.3 ± 0.37	7.3 ± 0.26	**P_{30}=0.038**
INDONESIA				
Biak	4, 28	7.0 ± 0.41	6.8 ± 0.19	P_{30}=0.639
SOLOMON ISLANDS				
Rennell	7, 9	7.0 ± 0.38	7.8 ± 0.22	P_{14}=0.083
Isabel	4, 9	6.3 ± 0.75	6.6 ± 0.24	P_{11}=0.621
VANUATU				
Efate	1, 27	8.0	7.8 ± 0.15	0.688*
FIJI				
Suva	16, 14	7.5 ± 0.30	8.4 ± 0.23	**P_{28}=0.024**
Tavarua	1, 21	8.0	8.0 ± 0.20	>0.999*
Bird	1, 12	8.0	8.1 ± 0.26	0.887*
TONGA				
Niaou’fou	6, 4	8.8 ± 0.54	9.3 ± 0.25	P_{8}=0.572
PALAU	7, 34	6.3 ± 0.29	6.6 ± 0.20	P_{39}=0.556
LATICAUDA GUINEAI				
PAPUA NEW GUINEA				
Port Moresby	8, 42	4.9 ± 0.52	5.1 ± 0.20	P48=0.741
LATICAUDA SAINTGIRONSI				
Noumea	16, 7	6.4 ± 0.29	6.3 ± 0.36	P_{21}=0.764
Isle de Pines	1,9	7.0	7.0 ± 0.24	>0.999*

Appendix 4.26. Variation among specific localities within countries in the dorsal width of first light band of adult *Laticauda colubrina*. Values in **boldface** are significant at the 5% rejection level. “Percent Significant” is the percent of the paired combinations that were significant at the 5% rejection level. Countries not listed had insufficient data for testing.

COUNTRY	F	P	PERCENT SIGNIFICANT
Malaysia/Singapore	2.63	**$P_{7,34}$=0.033**	9.1
Indonesia	1.46	$P_{19,48}$=0.149	0
Papua New Guinea	14.80	**$P_{9,26}$=0.073**	0
Solomon Islands	3.27	**$P_{8,23}$=0.012**	22.2
Vanuatu	0.32	$P_{3,27}$=0.749	0
Fiji	2.23	**$P_{12,103}$=0.016**	21.8
Tonga	1.17	$P_{5,19}$=0.358	0
Philippines	1.72	$P_{11,33}$=0.112	0
Palau	1.59	$P_{7,16}$=0.208	0
Taiwan	0.20	$P_{2,18}$=0.825	0

Appendix 4.27. Geographic variation in the colour pattern of the cephalic shield, body bands, and tip of the tail in species of the *Laticauda colubrina* complex.

	% WITH LIGHT SPOT IN CENTER OF HEAD	% WITH LIGHT VENTRAL MARK IN CENTER OF DARK BAND	% OF SPECIMENS IN WHICH DARK BANDS:			% OF TIPS OF TAIL:	
				DON’T ALL MEET:			
SPECIES/REGION			ENCIRCLE	ABOVE	BELOW	LIGHT	DARK
LATICAUDA COLUBRINA							
Andaman and Nicobar Islands	0	0	95.0	5.0	0	89.5	10.5
Thailand	0	0	100.0	0	0	66.7	33.3
Peninsular Malaysia/Singapore	0	0	100.0	0	0	97.8	2.2
Sabah	0.4	0	100.0	0	0	89.8	10.2
Indonesia	3.7	0	86.2	0	13.8	93.2	6.8
Papua New Guinea	6.2	0	92.3	0	7.7	86.6	13.4
Australia*	0	0	100.0	0	0	100.0	0
Solomon Islands	2.7	0	67.5	2.7	29.8	83.0	17.0
Vanuatu	0	0	90.3	0	9.7	90.0	10.0
Fiji	2.3	0	100.0	0	0	91.0	8.9
Tonga	18.6	0	69.8	0	30.2	95.3	4.7
Philippines	2.3	0	86.5	1.1	12.4	96.7	3.3
Palau	0	0	100.00	0	0	96.3	3.7
Taiwan	0	0	97.0	0	3.0	93.9	6.1
Ryukyu Islands	0	0	100.0	0	0	95.0	5.0
LATICAUDA GUINEAI	9.6	1.9	96.2	0	3.8	57.1	42.9
LATICAUDA SAINTGIRONSI							
News Caledonia and Loyalty Islands	1.6	98.5	98.5	0	1.5	100.0	0
LATICAUDA FRONTALIS							
Vanuatu	0	---	0	0	100.0	100.0	0

*=-waifs

Appendix 4.28. Incidence (%) of incomplete dark bands at different levels along the torso in species of the *Laticauda colubrina* complex. N=number of specimens for band 1, 10 and 25 respectively.

		BAND NUMBER:		
SPECIES	N	ONE	TEN	TWENTY-FIVE
Laticauda colubrina	850, 877, 821	4.0	3.4	0.01
Laticauda guineai	53, 53, 54	3.8	0	0
Laticauda saintgironsi	172, 171, 140	2.3	1.2	1.4
Laticauda frontalis	6, 8, 13	66.7	50.0	30.8

Appendix 4.29. Comparison between males and females of the number of gastrosteges for all localities for which there were data from 10 or more adult specimens. P = probability value arising from either a t-test comparing the sexes. SE = standard error of the mean.

	N		**MEAN ± SE**		
COUNTRY/LOCALITY	**MALES**	**FEMALES**	**MALES**	**FEMALES**	**P**
LATICAUDA COLUBRINA					
ANDAMAN AND NICOBAR ISLANDS	3	12	224.7 ± 0.88	231 ± 2.50	P_{13}=0.241
MALAYSIA					
Sabah	9	10	233.4 ± 1.97	239.4 ± 1.58	**P_{17}=0.029**
SINGAPORE	11	12	233.7 ± 0.88	239.3 ± 1.83	**P_{21}=0.015**
INDONESIA					
Biak	10	18	228.9 ± 1.29	230.2 ± 1.26	P_{26}=0.505
SOLOMON ISLANDS					
New Georgia	9	3	217.6 ± 0.71	224.7 ± 1.76	**P_{10}=0.0011**
Rennell Island	7	7	222.3 ± 1.99	223.1 ± 1.83	P_{12}=0.708
VANUATU					
Efate	22	19	224.7 ± 0.58	232.1 ± 0.74	**P_{39}=<0.0001**
FIJI					
Buiba	19	7	225.1 ± 1.04	225.9 ± 2.10	P_{24}=0.727
Lambasa	21	22	226.4 ± 1.00	227.0 ± 0.78	P_{41}=0.672
Suva	6	5	220.7 ± 1.52	227.8 ± 1.93	P_{9}=0.164
Kia	5	6	227.8 ± 2.27	226.3 ± 1.12	P_{9}=0.555
Tavarua	12	9	225.1 ± 0.99	228.8 ± 0.88	**P_{19}=0.015**
Bird	19	7	225.1 ± 1.04	225.9 ± 2.10	P_{24}=0.727
PHILIPPINES					
Jaguliao	16	12	226.3 ± 2.07	237.3 ± 2.03	**P_{26}=0.0009**
Gigantes	17	5	226.5 ± 1.97	235.0 ± 4.07	P_{20}=0.057
PALAU	21	13	217.0 ± 0.65	226.0 ± 1.19	**P_{32}=<0.0001**
TAIWAN					
Heng Chun	3	11	231.7 ± 2.33	235.7 ± 0.91	P_{12}=0.075
RYUKYU ISLANDS					
Iriomote	2	9	229.0 ± 2.00	238.2 ± 1.43	**P_{9}=0.020**
LATICAUDA GUINEAI					
PAPUA NEW GUINEA					
Port Moresby	19	18	232.4 ± 1.03	237.1 ± 1.23	**P_{35}=0.0064**
LATICAUDA SAINTGIRONSI					
NEW CALEDONIA					
Porc Epic	7	10	217.7 ± 1.60	223.3 ± 1.17	**P_{15}=0.031**
Atira	8	3	217.1 ± 1.09	221.0 ± 2.08	P_{9}=0.109
Redika	11	5	217.1 ± 0.96	225.0 ± 1.48	**P_{14}=0.0004**
LATICAUDA FRONTALIS					
VANUATU					
Ngoriki Islet	9	4	198.0 ± 1.19	202.3 ± 1.49	P_{11}=0.063

Appendix 4.30. Colour pattern on the heads of male and female *Laticauda colubrina* and *Laticauda saintgironsi* from regions for which there were 100 or more adults of known gender. **Boldface** indicates statistical significance at the 5% rejection level. Blanks indicate “not applicable”.

LOCALITY/SEX	N	INCIDENCE (%) OF COLOUR PATTERN					CHI-SQUARE	P
LATICAUDA COLUBRINA								
SABAH		**A**	**C**	**D**	**Other**		5.02	P_4=0.20>P>0.10
Males	144	79.2	13.2	3.8	3.9			
Females	81	66.2	22.2	6.8	4.8			
FIJI		**D**	**I**	**Other**			0.79	P_3>0.90
Males	71	83.1	7.0	9.9				
Females	59	82.2	8.5	9.3				
LATICAUDA SAINTGIRONSI								
NEW CALEDONIA		**D**	**I**	**H**	**Q**	**Other**	12.92	**P_5=0.02>P>0.01**
Males	79	10.8	70.3	7.6	7.0	4.4		
Females	55	0	70.9	11.8	10.9	6.3		

Appendix 4.31. Statistical comparison of head colour patterns of species in the *Laticauda colubrina* complex among adjacent geographic regions. **Boldface** identifies the dominant colour pattern for each region. Numbers in *italics* indicates statistical significance at the 5% rejection level. The *Laticauda guineai*, *Laticauda saintgironsi* and *Laticauda frontalis* databases include specimens from all localities. Blanks indicate "not applicable".

SPECIES/LOCALITY	**N**	**PATTERN AND PERCENT OCCURRENCE**				**CHI^2**	**P**	**PERCENT ASYMMETRY**
		D	**H+Q**	**I**	**Other**			
Laticauda saintgironsi (males)	82	11.6	15.2	**68.9**	4.2^1			4.9
Laticauda saintgironsi (females)	58	0	25.0	**68.1**	6.9^1			3.5
Males: *L. saintgironsi* vs. *L. frontalis*						133.80	P_4*<0.001*	
Females: *L. saintgironsi* vs. *L. frontalis**						107.00	P_2*<0.001*	
Laticauda frontalis	28	0	**96.5**	3.6	0			0
versus						200.10	P_2*<<0.001*	
Laticauda colubrina (Vanuatu)	57	**92.1**	0	0	7.9^2			1.8
versus *L. saintgironsi* males						147.74	P_2*<<0.001*	
versus *L. saintgironsi* females						185.26	P_2*<<0.001*	
LATICAUDA COLUBRINA								
Tonga	43	**81.4**	9.3	8.1	1.2^3			2.3
versus						0.72	>0.800	
Fiji	162	**85.5**	7.7	6.2	0.6^4			3.1
versus						20.40	P_2*<0.001*	
Vanuatu	57	**92.1**	0	0	7.9^2			1.8
		A	**C**	**D**	**Other**			
Vanuatu	57	6.1	1.8	**92.1**	0			
versus						41.88	P_2*<0.001*	
Solomon Islands	39	25.6	20.5	**51.3**	2.6^5			
versus						23.92	P_3*<0.001*	
Papua New Guinea	62	2.4	25.8	**63.7**	8.0^6			7.9
versus						95.4	P_3<<0.001	
LATICAUDA GUINEAI (Papua New Guinea)	57	**42.1**	17.0	9.7	34.3^6			

* Test of *L. saintgironsi* females versus *L. frontalis* involved only three categories: H+Q, I and Other.

[1] Males: A, G. Females: C, G, J, X, a

[2] A, C

[3] J

[4] A

[5] P

[6] B, E, L, M, N, P, W, b