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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 Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references if given.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 16^{th} 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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