DISSERTATION RESEARCH: BIOGEOGRAPHY OF SUMATRA AND THE MENTAWAI ISLANDS: PHYLOGEOGRAPHIC STUDIES OF SOUTHEAST ASIAN FLYING LIZARDS (AGAMIDAE: *Draco*)

I.   Introduction

Island systems have long held the interest of evolutionary biologists because they can provide independent, isolated natural experiments to test the diverse evolutionary processes that generate and maintain biodiversity. For example, studies of the flora and fauna of the Hawaiian and Galapagos Archipelagos have contributed tremendously to our understanding of evolutionary processes generally and in particular of mechanisms underlying speciation (e.g. Gillespie *et al*. 1994; Grant & Grant 2002; Jokiel 1987; Kizirian *et al*. 2004; McDowall 2003; Myers 1991; Petren *et al*. 1999). Islands are of special interest to biogeographers because the presence of geographical barriers separating island populations from neighboring mainland populations makes them ideal systems with which to study the roles of vicariance and dispersal in producing biodiversity. By combining traditional phylogeny-based biogeographic analysis with recently developed population genetic tools, biogeographers have the opportunity not only to elucidate historical patterns of occurrence, but also the recent and contemporary roles of migration (gene flow) in maintaining or altering those historical patterns.
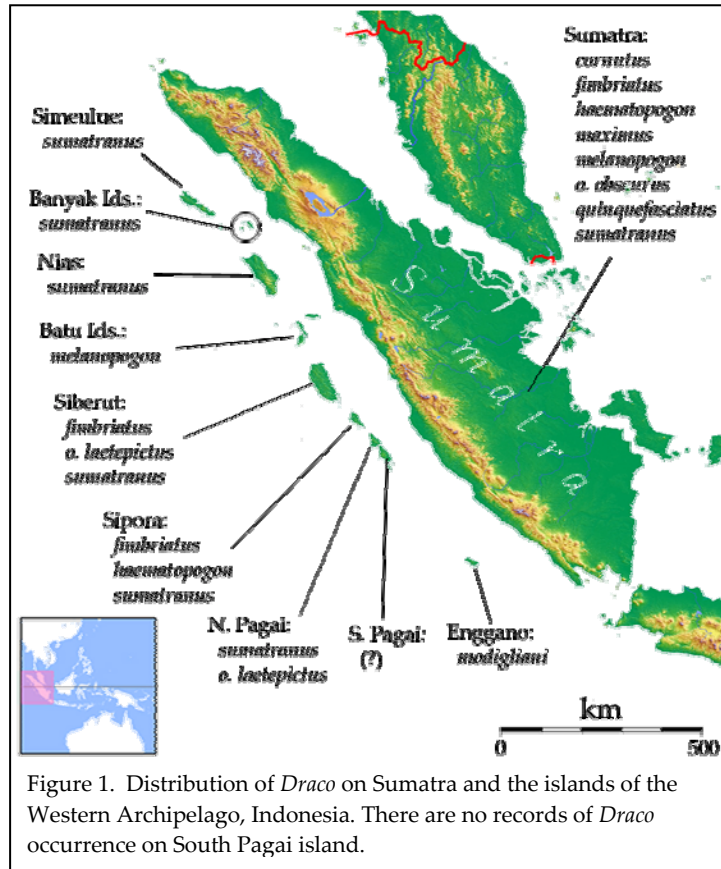
I propose to investigate the historical biogeographical relationships of the Indonesian mega-island of Sumatra and an archipelago of deep-water islands that lie off of its western margin (which I refer to as the Western Archipelago). This study, which will employ a diverse assemblage of flying lizards (genus *Draco*) as a model system, will apply a combination of phylogenetic and coalescent-based population genetic analyses to evaluate hypotheses regarding patterns of diversification, as well as levels of current and past genetic connectivity among islands and with mainland Sumatra.

II.   Background

Study system. On the western margin of Indonesia lies Sumatra, the 5th largest island in the world and a major component of Sundaland biodiversity hotspot (Conservation International online data). Along Sumatra's west coast sits an archipelago of comparatively smaller islands (although by no means small - Nias is 4048 km^2 in area) that I refer to here as the Western Archipelago. The Western Archipelago is composed of seven major islands, including from north to south Simeulue, Nias, Siberut, Sipora, Pagai Utara, Pagai Selatan, and Enggano. The Western Archipelago is situated approximately 85 – 150 km off the west coast of Sumatra, and is separated by a deep-water channel called the Mentawai Strait (Figure 1).

Geologically, the Western Archipelago formed by way of upward thrusting of oceanic plates in association with India's collision with mainland Asia approximately 60 million years ago (Whitten *et al*. 2001). Bathymetry studies show that the floor of the strait lies 200 – 500 m below current sea level except at two places where the water is shallower. These two points, which now exist as two clusters of small islands (the Batu Islands on the south and Banyak Islands on the north), indicate where the historical land bridge connections between Sumatra and the Western Archipelago may have occurred. These bathymetry readings combined with results from studies on Pleistocene sea level fluctuations suggest that Simeulue and Enggano have probably never had a land connection with mainland Sumatra, whereas the remaining islands were probably joined to the mainland between 250,000 and one million years ago (Dring *et al*. 1989; Voris 2000). The subsequent fragmentation sequence experienced by these islands remains unknown.

Having been separated from Sumatra for an extended period of time, the Western Archipelago harbors a wealth of endemic species. The Mentawai Archipelago, which is restricted to the four islands at the center of the chain (Siberut, Sipora, Pagai Utara & Pagai Selatan) has long been known for its four endemic primate species, which have received notable scientific attention with regards to their ecology, behavior, and phylogeny (e.g. Roos *et al*. 2003; Tilson 1977; Whittaker 2005). However, the remainder of the biota inhabiting the islands has been only poorly studied. These islands were mentioned in older records inventorying the herpetofauna of Sundaland and the Indo-Australian Archipelago (e.g. deRooj

Figure 1. Distribution of *Draco* on Sumatra and the islands of the Western Archipelago, Indonesia. There are no records of *Draco* occurrence on South Pagai island.

1915, 1917; vanKampen 1923), while more recent publications have updated lists of species occurrence and provided records of newly described species from the area (mostly on the basis of historical museum specimens rather than recent fieldwork; e.g. Das 2005; Das & Lim 2005; Dring *et al* 1989). I am not aware of any rigorous biogeographical or molecular analysis of the non-primate fauna inhabiting these islands.

Focal taxa. Flying lizards of the genus *Draco* (Reptilia: Agamidae) are a monophyletic assemblage with remarkable adaptations for arboreal life, including wing-like patagial membranes supported by modified, elongated thoracic ribs, which enable them to glide short distances between trees (McGuire 2003; McGuire & Alcala 2000; McGuire & Dudley 2005; McGuire & Kiew 2001; McGuire *et al* 2007). Their distribution ranges from India to southern China and insular South East Asia (Musters 1983). Flying lizards represent an ideal study system because at least nine species occur on Sumatra, and subsets of these species can be found on every major island in the Western Archipelago (Figure 1; Musters 1983, personal observation). Furthermore, a large unpublished phylogenetic data set comprised of three mitochondrial genes and three nuclear genes is already available, most of which have been sequenced for 742 individuals representing every described species of *Draco* as well as several undescribed species (see Figure 2 for summary). This data s*et al*ready includes sequences for 98 individuals that are directly relevant to the biogeographical study proposed here.

Analytical approach. For the past two decades, mitochondrial DNA has been the workhorse for most phylogeographical studies (Avise1998, 2000; Hare 2001). However, as more sophisticated analytical tools have become available – particularly those in the realm of statistical phylogeography (Edwards & Beerli 2000; Knowles 2004; Knowles & Maddison 2002) – it has become necessary to base our studies on data sets comprised of multiple independent genetic loci (Bermingham & Moritz 1998; Hare 2001). In the recent past, most phylogeographic analyses were based on traditional phylogenetic analysis. While this presented few analytical difficulties for analyses based on mitochondrial markers, application of standard phylogenetic techniques to nuclear loci has proven more challenging because these markers tend to have longer coalescence times (leading to greater degree of incomplete lineage sorting), as well as recombination. With recently developed computational techniques based on the coalescent such as Isolation with Migration (Hey & Nielsen 2004), Bayesian Estimation of Species Trees (Edwards *et al*. 2007; Liu & Pearl 2007), and approximate Bayesian computation (ABC; Hickerson *et al*. 2007), we can now account for these confounding factors. Indeed, a counterintuitive realization based on coalescent theory is that analysis of a combination of completely and incompletely sorted genetic loci actually enhances our ability to estimate phylogenetic relationships and divergence timing relative to data sets comprised only of completely sorted loci (Degnan & Rosenberg 2006).

My goal is to employ a suite of markers from mitochondrial and nuclear DNA to understand the patterns and processes that have shaped the *Draco* assemblages of Sumatra and the Western Archipelago. I will test alternative biogeographic scenarios and patterns of inter-island connectivity using a combination of phylogenetic analysis and statistical phylogeographic methods.

III. Hypotheses, Predictions & Approach

The major goals of this study are to elucidate the extent to which the species assemblage found on the Western Archipelago was influenced by a common set of vicariance events, and to test hypotheses regarding levels of connectivity between the several islands, and with mainland Sumatra.

Hypothesis 1 – The assembly of *Draco* species on the Western Archipelago.

With nine islands and/or island groups comprising the chain, all of which are approximately equidistant from Sumatra, there are numerous scenarios involving dispersal that can be proposed as hypotheses. Here I present two opposing hypotheses that represent the two extremes of the possible histories. These two hypotheses are most easily testable because they lead to predicted analytical outcomes that are clearly differentiable.

Null hypothesis: Simultaneous vicariance. I hypothesize that the Western Archipelago was once a continuous landmass connected to Sumatra by a land bridge. As a result, the Western Archipelago was colonized via overland dispersal by all or most of the Sumatran *Draco* fauna. Subsequent marine inundation or subsidence of this land bridge simultaneously separated the Sumatran and Western Archipelago populations of at least five and possibly all nine modern Sumatran species. Most of these species later went extinct on some of the islands as the archipelago became further fragmented, resulting in current Western Archipelago species assemblages comprised of 0 – 3 species per island.

Alternative hypothesis: Independent over-water dispersal. All of the *Draco* species populated the Western Archipelago through independent colonization of individual islands by dispersing over the Mentawai Strait.

Predictions: Under the null hypothesis, I would expect that: (1) Each *Draco* species in the Western Archipelago should form a monophyletic assemblage relative to its closest relatives on the Sumatran mainland. Such a comparison is most informative for species known to occur on multiple Western Archipelago islands such as *D. obscurus laetepictus*, *D. fimbriatus*, and *D. sumatranus*. (2) The signature of simultaneous divergence for these species will be detected using ABC (approximate Bayesian computation; Hickerson *et al*. 2006) analysis comparing Sumatran and Western Archipelago populations of all 5 species.

Hypothesis 2 – Connectivity of the islands of the Western Archipelago.

Regardless of the mechanism by which the Western Archipelago became populated with *Draco*, sea level fluctuations may have reconnected some of the islands in the more recent past. Bathymetric data suggest that sea level fluctuations driven by glacial cycles should have produced subaerial connections between the Mentawai Islands (Siberut, Sipora, Pagai Utara, Pagai Selatan), whereas Simeulue, Nias, and Enggano should have remained isolated during these periods (Sathiamurthy & Voris 2006).

Null hypothesis: There has been recent gene flow among the islands of the Mentawai group, but the other islands in the Western Archipelago have remained isolated.

Predictions: Under this null hypothesis, I expect the Mentawai Islands populations to be genetically homogeneous, whereas Simeulue, Nias, and Enggano will exhibit unique genetic structure distinguishing these populations from Sumatra and the other islands in the Western Archipelago.

Approach. The hypothesis of a single common vicariance history will be tested by taking into account branching patterns and timing of population splitting events in all taxa being examined. This will

be accomplished by first generating a multi-locus phylogeny for each of the species to be examined for pattern congruence. If the species had been fragmented from the mainland population by rising sea levels, their phylogenies should reveal a pattern in which the island populations form monophyletic clades relative to Sumatran populations. Furthermore, these divergence events must occur simultaneously, indicating a common underlying mechanism. Alternatively, the populations found on the islands may have been established via independent over-water dispersal. This is most likely if our phylogenetic analyses indicate that populations on the individual Western Archipelago islands are paraphyletic with respect to Sumatran populations, or if I find significantly distinct dates of divergence between the populations of different species that occur on the same island.

There are other scenarios that can be proposed that include a combination of vicariance and dispersal, but the number of possible permutations dissuaded me from laying out all the possibilities in an explicit hypothesis-testing framework. Rather, I will examine individual demographic histories of each species utilizing coalescence-based methods to estimate parameters such as migration rates between islands and their divergence times (i.e., using IM; Hey & Nielsen 2004). This approach involves simulating coalescence under specific migration rates (e.g. $m_{12} = m_{21} = 0$ for population divergence event) and divergence times and then comparing the observed values of the data against posterior distributions derived from the simulations (Hey & Nielsen 2004; Knowles 2001; Rannala & Yang 2003). By estimating demographic parameters, I can infer levels of connectivity among the islands of the Western Archipelago, and between these islands and Sumatra as proposed in Hypothesis 2.

Dates of divergence will be estimated using Bayesian inference methods and their simultaneity will be examined by direct comparison as well as testing for simultaneous divergence between pairs of sister clades using Approximate Bayesian Computation (ABC; Hickerson *et al*. 2006). Because there is no known fossil record for *Draco*, selection of an appropriate nucleotide substitution rate for IM analyses is a significant challenge. I will estimate this rate by first conducting a comprehensive BEAST analysis including all *Draco* species plus additional agamid taxa with known divergence date estimates based on fossil calibrations (see Hugall & Lee 2004; Hugall *et al*. 2007). Because calibration is a major assumption of this and all molecular clock methods, I will also perform uncalibrated analyses to estimate relative timing of divergence across multiple comparisons. This requires the realistic assumption that rates of molecular evolution for homologous loci are similar across our *Draco* focal species.

Biogeography of Sumatra. Sumatra itself provides a compelling setting for biogeographical inquiry. The few Sumatran phylogeographic studies, although based on very few samples, have nevertheless found substantial genetic substructuring occurring on the island. However, the geographic patterns recovered in these studies are highly dissimilar. For example, two species of blood python (*Python curtus* and *P. brongersmai*) occur on Sumatra, and they appear to be separated into eastern and western species by the Bukit Barisan mountain range which runs length-wise down the spine of the island (Keogh *et al*. 2001). In contrast, a study of Sundaland forest frogs (the *Rana chalconota* group) revealed a deep north/south genetic break on the island occurring between Pagaralam and Padang (Inger & Stuart, in press). At this time, Sumatran phylogeography is essentially *terra incognita* – so little is known at this stage that it is difficult to establish a priori hypotheses. I propose to remedy this situation by applying traditional phylogeographic analysis of *Draco* mitochondrial data. I anticipate that these analyses will allow us to establish a set of hypotheses that can be further evaluated using multilocus nuclear data and the same analytical tools available for our coalescent-based investigations of the Western Archipelago.

IV. Methods & Current Progress
a. Field work

This project relies on thorough sampling of *Draco* species from the Western Archipelago and across Sumatra. I plan to visit nine islands/island groups in the chain (i.e. each of the major islands and two representative of the smaller islands) as well as several locations on the west coast of Sumatra (estimated

number of Sumatran localities = 10). For each of these locations, I will capture 10 – 20 individuals of *Draco* spp. found in the area (estimated total number of individuals = 300 – 400). Liver tissue will be preserved in RNALater to serve as a source of genetic material, and information on sex, morphometric measurements, geographical position, ecology and natural history as observed at the time of capture will be recorded for each specimen. The animals will be fixed in formalin as voucher specimens and deposited at the Museum Zoologicum Bogoriense, Indonesia.

b. Molecular work

DNA Extraction & sequencing. Extraction of genomic DNA and total RNA will be carried out using Qiagen extraction kits following protocols provided by the manufacturer. Markers will be subsequently PCR-amplified (see below for marker identification), and primers will be removed from PCR products using ExoSAP (Exonuclease 1 and Shrimp Alkaline Phospatase). Cycle sequencing will be done using ABI Big Dye version 3.1 and and run on ABI 3730 Capillary automated sequencer.

Identification of anonymous nuclear loci. I am in the process of developing anonymous nuclear loci for *Draco* as part of another NSF funded project investigating the comparative biogeography of Sulawesi. I describe the protocol here, but note that I anticipate that the loci developed for that other project will be directly applicable here. I am generating the anonymous locus library and will consequently be well-prepared to apply the resulting loci to the present study. Anonymous nuclear loci will be developed by first generating a genomic library from one of the species, followed by steps in the following protocol: (1) hydroshear high quality genomic DNA; (2) blunt-end the sheared fragments; (3) ligate sheared fragments into vector; (4) transform the ligation product into electrocompetent cells using electroporation; (5) grow the cells in SOC media on agar plates; (6) pick 192 (equal to two sequencing plates) colonies that contain inserts; (7) plasmid prep each colony; (8) sequence each plasmid prep using primers designed from vector's nucleotide sequence; (9) BLAST-search sequenced inserts to determine whether they are from known genes or gene families; (10) design new primers that are specific to each inserts using Primer3 software; (11) amplify the anonymous locus in a 12-sample mini-panel; (12) sequence mini-panel amplicons and screen for loci that exhibit sufficient variation.

Identification of nuclear introns. I am also in the process of developing nuclear introns for *Draco* as part of the comparative biogeography of Sulawesi study. Again, I describe the protocol here, while noting that I anticipate that the loci developed for the other project will be directly applicable here. I am also directly involved in generating the nuclear intron primer sets. Nuclear introns will be developed by first generating complementary DNA (cDNA) library from samples preserved in RNAlater by following this protocol: (1) reverse-transcribe high-quality total RNA into cDNA; (2) run PCR products on agarose gel and size select cDNA centered around 1 kb; (3) TA-clone cDNA; (4) pick colonies with inserts; (5) plasmid-prep and sequence colonies using nucleotide sequences from the vector; (6) design new primers specific to inserts using Primer3 software; (7) amplify and run on agarose gel to screen for introns (occurrence of introns will be present as larger fragments that travel slower through the gel); (8) amplify loci in a 12-sample mini-panel; (9) sequence those that amplify consistently across the mini-panel samples; (10) assess degree of variability to determine if the locus has sufficient variation to be used in this study.

I am planning to incorporate 10 – 20 nuclear markers into the analyses to minimize the stochastic effect introduced by using gene trees to infer population history (see Edwards & Jennings 2005). Six of these markers are already identified in conjunction with another NSF-funded project that studies the comparative biogeography of *Draco* and other taxa that occur on Sulawesi as mentioned above (see also "Feasibility & Timeline" section).

c. Data analyses

Sequences alignment & phylogenetic analyses. Alignment of nucleotide sequences will be carried out using MUSCLE (Edgar 2004) and continued with manual editing using the software MacClade 4.07

(Maddison & Maddison 2000). Phylogenetic relationships will be estimated using Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian approaches to allow for detection of biases that may be introduced when relying on only one criterion. MP and ML analyses will be carried out using PAUP 4.0 software (Swofford 2003) and support for branches will be evaluated using nonparametric bootstrapping method. Standard Bayesian estimation of phylogenies will be performed using MrBayes (v. 3.1; Huelsenbeck & Ronquist 2001) and BEAST (Drummond & Rambaut 2006). Selection of nucleotide substitution models to be used in ML and Bayesian analyses will be performed using the Akaike Information Criterion (AIC; Posada & Buckley 2004) as implemented in the software ModelTest (Posada & Crandall 1998). Ultimately, I will analyze our multilocus data using the program BEST (Edwards *et al*. 2007; Liu & Pearl 2007), which evaluates a set of independent gene trees in a coalescent framework to infer the underlying species tree.

      Population genetic analyses. Before performing population genetic analyses, I will first determine the gametic phase of the samples and perform tests on the markers to detect recombination. Gametic phase will be determined analytically using the program Phase 2.1.1 (Stephens *et al*. 2001; Stephens & Donnelly 2003), or by cloning and sequencing when analytical approach fails to resolve phase. Tests for recombination will be performed using the four-gamete test (Hudson & Kaplan 1985). Loci that exhibit evidence of recombination will be partitioned into blocks of sequences that do not show recombination (Hey & Nielsen 2004). I will also test for linkage by looking for nonrandom association of alleles at different loci using an exact test of linkage disequilibrium as implemented in Arlequin 3.0 (Excoffier *et al*. 2005). Estimation of population parameters will be performed using coalescence approach as implemented in the software Isolation with Migration (IM; Hey & Nielsen 2004). Specifically, IM applies a Markov chain Monte Carlo method to estimate the posterior probability distributions of model parameters from multiple unlinked loci. Up to six parameters can be estimated using IM: migration rates (m_{12}, m_{21}), divergence time (T), and levels of population diversities (θ_A, θ_1, θ_2; $\theta = 4N\mu$).

      Divergence dating and tests for simultaneous divergence. Estimates of timing of divergence will be carried out using a Bayesian inference as implemented in the software package BEAST (Drummond & Rambaut 2006). Test for simultaneous divergence will be performed using Approximate Bayesian Computation as implemented in the software package msBayes (Hickerson & Takebayashi 2006).

d. Preliminary data

      This past summer, I (the co-PI) led an expedition to the Western Archipelago and adjacent Sumatra. The primary focus of this trip was to establish a working relationship with the relevant agencies in Indonesia and to scout field-collecting sites, but I was able to collect 47 *Draco* specimens representing three of our focal species despite uncooperative weather.

      Our preliminary phylogenetic analyses of these samples indicate that the biogeographical relationships between populations on the Western Archipelago, Sumatra, and the remainder of the Sunda Shelf are both interesting and complex (Figure 2). I highlighted some of the findings, as follow:

(1) All of the island populations exhibit high levels of divergence with respect to the Sumatran and/or broader Sundaland populations.

(2) In the case of *D. sumatranus*, individuals from the island populations emerged as sister taxa not to the neighboring West Sumatra population (uncorrected patristic sequence divergence $p = 10 - 11\%$), but to individuals collected from Borneo and North Sumatra (uncorrected $p = 5.8 - 6.3\%$).

(3) *D. obscurus laetepictus*, which is endemic to the Mentawai Archipelago, emerged as the sister clade not of its putative sister taxon *D. o. obscurus* (uncorrected $p = 8.5 - 8.9\%$), but to a clade comprised of *D. formosus* and *D. taeniopterus* (uncorrected $p = 7.8 - 9.7\%$).

(4) Individuals of *D. fimbriatus* collected from the Western Archipelago exhibit different levels of divergence when compared to individuals from the Malay Peninsula (uncorrected $p = 3.5 - 3.9\%$) and Borneo (uncorrected $p = 6.8 - 7\%$; no samples are available from Sumatra).

These findings suggest that the entire Sundaland region needs to be taken into consideration in order to account for the biogeographical history of the genus *Draco*. Fortunately, representative sampling for the remainder of the region is already available and my field efforts associated with this study will focus only on the biogeographical relationship of the Western Archipelago to its neighboring island Sumatra.

V. Feasibility & Timeline

Feasibility. Being a native Indonesian citizen enrolled as a graduate student at the University of California, Berkeley, I am at an advantage and in a very good position to undertake this project. My citizenship and ethnic heritage will benefit the field work needed for this study because they will facilitate permit-related processes that may otherwise hamper foreign researchers, and my knowledge
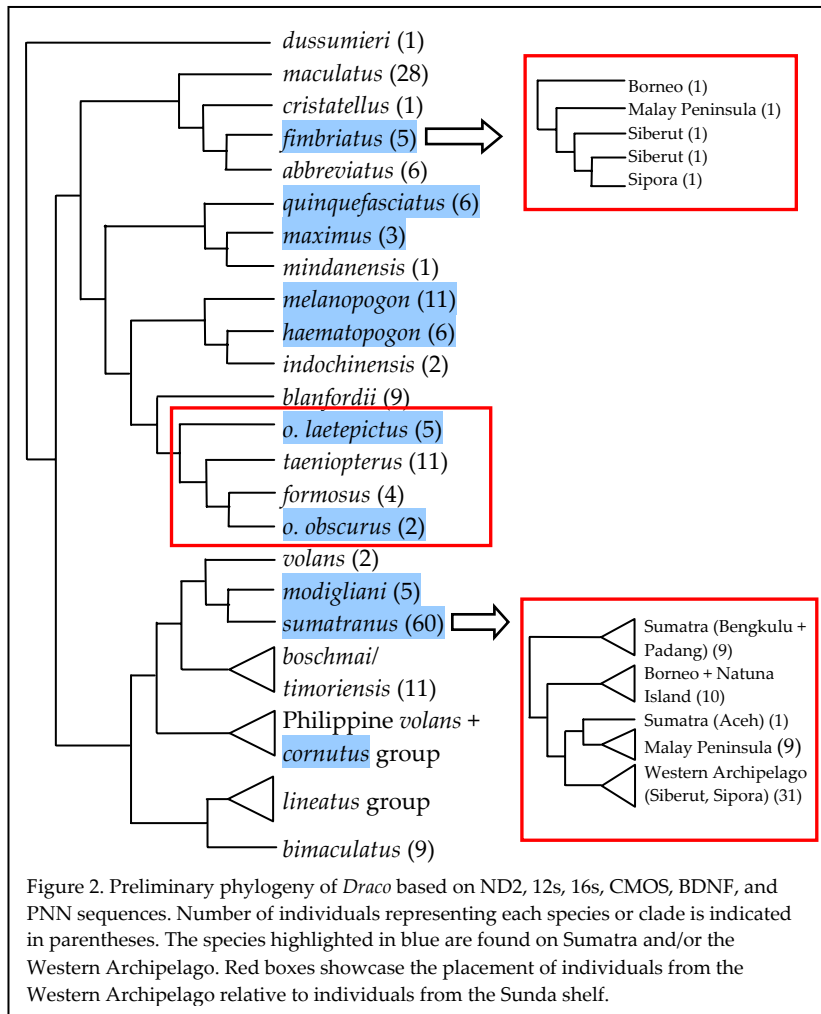

Figure 2. Preliminary phylogeny of *Draco* based on ND2, 12s, 16s, CMOS, BDNF, and PNN sequences. Number of individuals representing each species or clade is indicated in parentheses. The species highlighted in blue are found on Sumatra and/or the Western Archipelago. Red boxes showcase the placement of individuals from the Western Archipelago relative to individuals from the Sunda shelf.

of the Indonesian language as my mother tongue ensures that there will be relatively minor language barriers between myself and local inhabitants. Also, since I have conducted a scouting/preliminary field trip in the Mentawai Islands, I am optimistic that I can plan my subsequent trips effectively and efficiently. Furthermore, my status as a graduate student at UC Berkeley and my affiliation with the Museum of Vertebrate Zoology grant me invaluable access to many resources, including but not limited to a wealth of scientific literature, a modern fully-equipped laboratory, and the invaluable guidance and advise from Berkeley's excellent community of faculty, postdocs, and graduate students.

The number of nuclear markers that I propose to incorporate in my analysis (i.e. 10 – 20) may seem daunting, but the development of these markers, both anonymous loci and introns, is already well underway as a part of an NSF-funded project investigating the comparative biogeography of *Draco* and other taxa on Sulawesi Island. I have been directly involved with the development of these markers and at the time of writing have managed to identify six anonymous loci. Given this experience, I do not anticipate crippling difficulties in developing the rest of the desired number of loci.

Timeline of completion (based on a June 2008 award):
- Development of anonymous and intron nuclear loci: March 2008.
- Field work: June 2008 (pending support from another source).
- Screening, amplification, and sequencing: December 2008.
- Phylogenetic and population genetic analyses: December 2008 – April 2009.
- Manuscript preparation – August 2009.

VI. Intellectual Merit & Broader Impacts

Intellectual merit. For the Western Archipelago and parts of Sumatra, little is known about the distribution of *Draco*. Furthermore, there are very few specimens and possibly no tissue samples available for scientific investigation. My sampling on Sumatra and the Western Archipelago will remedy this situation by providing a dense sampling throughout area, resulting in a comprehensive collection not only of *Draco* occurrence but also other reptiles and amphibians that are previously unavailable. Given the long standing isolation of the Western Archipelago from Sumatra, I anticipate this study to reveal the discovery of new and cryptic species (as already suggested by our preliminary result on *D. o. laetepictus*), thus highlighting the previously under-documented levels of biodiversity and endemism on this archipelago. This research will also be the first study to employ a suite of mitochondrial and nuclear markers to tackle questions on historical biogeography for this island system using explicit hypothesis-testing framework.

Broader impacts. As many as 44% of all species of vascular plants and 35% of the species in four vertebrate groups are confined to 25 hotspots that comprise a mere 1.4% of the Earth's land surface (Myers *et al*. 2000). Indonesia is one of the world's biodiversity hotspots, but unfortunately it being a third world country means that lack of capacity, funding, and infrastructure may hinder biodiversity research and exploration. Therefore, this research will be highly beneficial for the exploration and study of Indonesia's biodiversity in general and in particular for the conservation of the Western Archipelago flora and fauna.

Having grown up in Indonesia, I realize that there is little appreciation among the general public for basic sciences such as Biology. I view my research as a good opportunity to illuminate the fact that science can have many beneficial impacts through its application. I earned my B.S. degree from the University of Indonesia and have maintained strong ties with its faculty members and students, and I plan to present my research there. I am hoping that this will motivate students to pursue a career in biological sciences and/or conservation. I also plan to collaborate with the University of Indonesia to help conduct the field part of this project. On my last field trip I had the assistance of Jarot Arisona, a faculty member of the University of Indonesia, to help me with sample collection. I plan to involve undergraduate students as my field assistants in future trips, thus providing them with learning opportunities and field experience. I will also employ the help of field assistants from the local communities living around the field sites, hence providing them with capacity building opportunities. The lab portion of this project will be assisted by undergraduates from the University of California, Berkeley, providing them with laboratory skills and experience and an opportunity to be directly involved in a scientific research.

The training that I will receive through this project will have broader impacts than just my own edification. I intend to return to Indonesia upon earning my degree to apply the skills and knowledge that I have gained through my graduate education and dissertation research. I am hoping to be able to make conservation recommendations to policy makers based on rigorous scientific findings. Perhaps even more importantly, my education and research experience will have their broadest impacts through my plan on joining the academic world in Indonesia, which I see as a good way to promote scientific awareness as well as to reach out and recruit young scientists to be directly involved in research generally and in conservation particularly.