After the Sarawak Law: evolutionary biology in Borneo since 1855.

In February 1855, while taking a rainy season break from his insect collecting at Rajah James Brooke's bungalow in Santubong, English naturalist Alfred Russel Wallace penned a short paper entitled "On the Law Which Has Regulated the Introduction of New Species." He sent the paper to the Annals and Magazine of Natural History, which published it in September of that same year.

In the ten-page article, Wallace elaborated on the phenomenon that related species are always found in close geographical proximity to each other and that species known as fossils usually have their closest relatives in the same geological layer. Drawing the logical conclusion, he proposed the biological law that "Every species has come into existence coincident both in space and time with a pre-existing closely allied species" (Wallace 1855).

The meaning of this "Sarawak Law," as is has become known, is that a new species appears either by the transmutation of an ancestral species, or by splitting off from an ancestral species (without the latter disappearing). Such a sequence of events clearly is supportive of evolution, not of divine creation. Therefore, the paper is generally considered as one of the key steps towards Darwin and Wallace's joint discovery and publication of the mechanism of evolution by natural selection, three years later (Slotten, 2004).

Yet, it would be a misunderstanding to think that his field work in Borneo was what convinced Wallace of the reality of evolution. The 1855 paper draws on a diversity of evidence, but most of it comes from the literature and from Wallace's travels in the Amazon and in Britain--it could have been written anywhere. Nevertheless, by writing his paper in Sarawak, Wallace firmly placed the cradle of evolutionary biology in Borneo. Moreover, his vast zoological collections from the island have been one of the bases upon which further taxonomic and evolutionary work in Borneo has been founded. Consequently, it is of more than passing interest to investigate how evolutionary studies have progressed in Borneo in the one and a half centuries since.

In this paper, I review the main events in Bornean evolutionary biology over the past 150 years. By necessity, this includes mostly research carried out by overseas researchers. Only very recently have evolutionary studies been based in universities and other research institutions on the island itself. I also make comparisons with the situation in parts of the world that are geographically comparable to Borneo. I conclude that, in spite of its auspicious beginnings and a number of beneficial factors, Borneo has played a relatively minor role in the development of evolutionary biology. However, if a shift in research policies were to take place, this situation could soon change for the better.

Background: Evolutionary Biology Worldwide 1855-2005

To place the developments in Bornean evolutionary biology in perspective, let me begin by sketching the main events in this field on a global scale. Darwin and Wallace (1858) and Darwin (1859, 1871) published the outlines of evolution by natural and sexual selection, which have survived essentially unchanged till the present time. However, a comprehensive research program only began to develop in the 1930s, after the broad acceptance of Mendelian genetics (Dobzhansy 1937), the mathematical development of population genetics (Fisher 1930), and the thinking of evolution in terms of populations (Mayr 1942). Later, this body of insights (collectively known as Neodarwinism) was complemented with the logical framework for reconstructing evolutionary trees (Hennig 1950). Before the 1930s, very few studies were undertaken with a distinct evolutionary focus. However, data were amassed in systematics and biogeography that have formed the foundation for later, evolutionary work. Among the major developments in evolutionary biology in the neodarwinian era, I would like to highlight the following:

(1) Phylogenetics. The Hennigian method of phylogenetic reconstruction using parsimony (i.e. reconstructing evolutionary trees on the principle that the trees that are most plausible require the least evolutionary changes to explain the distribution of characters among species) paved a way for reconstructing phylogenetic trees on a

sound philosophical basis. Initially, morphological characters were used for this, later to be taken over by DNA sequences. The latter, and increased computational power, allowed additional and better algorithms to be developed, such as the so-called maximum-likelihood and Bayesian methods, which are very popular today.

(2) Phylogeography. Building on the experience gained with phylogenetic reconstruction of groups of species, more refined genetic dissection and methods of analysis allowed, in the 1980s, the development of phylogeography (Avise et al. 1987). This field aims to elucidate, in detail, the histories of populations within species, including changes in population size, extinction, and migration.

(3) Experimental studies of reproductive isolation (the inability to interbreed), hybridization, and adaptation. Since the early days of Neodarwinism, laboratory studies with Drosophila and other model organisms have played an important role in the understanding of evolutionary processes. Parts of the processes of speciation (the origin of new species) and/or adaptation have been replicated in the laboratory. Some of the more important outcomes of these studies are the realization that isolation alone does not drive speciation; that natural populations can quickly adapt to very subtle differences in environment; and that reproductive isolation often evolves as a byproduct of adaptation to different environments (Rice and Hostert 1994).

(4) Empirical studies of adaptation and speciation. Early field biologists tended simply to document species and communities, and their variability. This was followed by a period in which evolutionary research moved more and more to the laboratory environment. However, with the rise of scientific field ecology since the 1960s, studying evolution "in action" has represented an important revival of research on real organisms in their natural environment (Weiner 1995). Field observations and experimentation with groups like freshwater fish, birds, fruit flies, etc., have reinforced the notion of the relevance of adaptation and sexual selection in real populations.

Evolutionary Research in Borneo, 1855-1945

The period before the Second World War, essentially the colonial era, saw many naturalists visiting Borneo. Some of the more illustrious collectors, besides Wallace himself, were Italian botanist Oduardo Beccari, who worked with naturalist Giacomo Doria in Borneo in the 1860s, and zoologist John Whitehead, who explored Mount Kinabalu in the 1880s. While they did not analyze and describe their material themselves (and many did not), the specimens were traded, donated, and sold to collectors and museums throughout Europe and North America, usually eventually resulting in taxonomic notes and revisions. A few typical examples of the resulting fragmented literature from that era are Moser (1906) who described two new valgid beetle species from Sarawak, collected by Prof. Gillet; Gude (1918), who described a new species of Everettia land snail from "Borneo," received from "a natural history dealer as far back as 1904"; and Wallace (1865), who named after his host the new "Ornithoptera Brookeiana" which he discovered in Rajah Brooke's other resort, Peninjau.

However, several less haphazard scientific expeditions were also organized to Borneo (and elsewhere in the Malay Archipelago) during this period. For example, German phylogeneticist and embryologist Willy Kukenthal led a trip (1893-1894) that collected mostly marine organisms that were to form the basis of the collection of Jena University. The results were comprehensively described in a series of expedition reports (e.g., Kukenthal 1897). Doria and Beccari's mollusci collections from Borneo were published in full and authoritatively by Issel (1874) as Molluschi Borneensi. And Whitehead's zoological collections were described by himself and others in a series of papers on ornithology, herpetology, mammalogy, entomology, malacology, and ichthyology (Whitehead 1893 [1993]).

Yet, although very important from a taxonomic and biogeographic point of view, very few of these and other works from the same period can be considered as directly relevant to evolutionary biology. Only here and there, usually as an aside, are allusions made to evolutionary relationships. Whitehead (1893 [1993]), for example, says of the white-breasted wood-swallow (Artamus leucorhynchus), "This bird is called a Tree-Swallow from its habit of flying about after the manner of swallows, and frequently resting on the branches of dead trees; but I should think that, from its mode of nesting and its eggs, it is much more nearly allied to the Shrikes." DNA-DNA hybridization studies a century later proved him correct (Sibley and Monroe 1990). Mostly, though, authors of taxonomic papers of this era use vague terms such as "allied to," "close to," "intermediate between" and "having affinity with" to indicate species' phylogenetic relationships, without attempting any sort of explicit phylogenetic reconstructions.

Another evolutionary subject that was raised by some early authors is the evolution of mimicry and camouflage, so prominent among tropical insects. Like Wallace (1869), Whitehead (1893), while collecting in the Pitas peninsula of North Borneo, speculated on the selective pressures driving the evolution of crypsis in birds and insects (which he illustrates), writing that the "ever-waging war" of predators against prey will make sure that "unless a species has some special habit or peculiar form by which it escapes observation, ... it must soon cease to exist." Although falling short of what today we would consider evolutionary biology research, such observations do point out where the relevant questions lie and may have been important for directing later students to fruitful research subjects.

Evolutionary Research in Borneo, 1945-2005

In the history of biology, the period directly after the Second World War is marked by an increase in work from an explicitly neodarwinistic vantage point. Although classical, descriptive work remained the staple of tropical biologists, studies with a distinct focus on testing evolutionary hypotheses began to appear at this time. Below, I give an overview of some of the more important or prominent studies that have been done in Borneo or on Bornean material over the past 60 years, differentiated into several fields. Although the paleoanthropological work in Niah (Cranbrook 2000) and the recent studies of genetics and linguistics (Gray and Jordan 2000) of the Austronesian peoples give Borneo an important position in the debates on human evolution, I will here refer the reader to Baer's (2005) recent review to cover anthropology, and limit myself to studies of non-human evolution.

(1) Paleontology. Where paleontological studies attempt to connect fossil forms from one stratum with those from other strata or with recent forms, they can be considered studies of evolution. Unfortunately, such a series of undisturbed sediment layers with relatively short intervals needed for this is rarely found (see, for a good example, Williamson's 1981 study on African freshwater molluscs), and no examples of this kind from Borneo are known, although some palynological (pollen) and marine diatom studies (mostly applied to paleoclimatology and paleoecology) could possibly be interpreted evolutionarily (see also below).

(2) Phylogenetics. With the advent of the phylogenetic method in the 1950s, its increase in popularity in the 1970s and subsequent further development of algorithms for phylogenetic reconstruction when molecular data became available in the 1980s, building evolutionary trees has become a standard extension of systematic work. Where earlier taxonomists would describe species and only allude to their evolutionary relationships haphazardly, modern taxonomic revisions often carry explicit phylogenetic hypotheses.

For the Borneo flora and fauna, some good examples of analyses for entire groups are Tanaka et al. (2001a, 2001b, 2003) and Suka and Tanaka (2005), who used mitochondrial DNA to elucidate the phylogeny of the Borneo honeybees (Borneo has five of the eight known honeybees), and Lam (2004), who used nuclear DNA for analyzing the evolutionary relationships between Bornean species of the ginger genus Boesenbergia. As the Borneo biota has close affinities with other regions within Sundaland, few comprehensive studies are done on Borneo endemics, as most groups of more or less vagile organisms are distributed over a wider area. Hence, e.g., there are studies of allozyme-based phylogeny of Sundaland shrews by Ruedi (1996), of the mtDNA-based phylogeny of Southeast-Asian flying lizards by McGuire and Kiew (2001), and of the mtDNA-based taxonomy of Malaysian fruit bats (Ryan et al. 2005), which all include many Bornean taxa as well. Phylogenetic studies that focus on clades that are restricted to Borneo are limited to taxa that are either very recent or have limited dispersal capabilities, or both, such as land snails (Schilthuizen et al. 2005).

Smaller studies, aimed at elucidating the phylogenetic position of particular, enigmatic species have also been published, such as Ahlquist et al.'s (1984) use of DNA-DNA hybridization to discover that two endemic birds, the Borneo Bristlehead (Pityriasis gymnocephala) and the Fruithunter (Chlamydochaera jefferyi), are related to Australo-

Papuan crows, and to the thrushes, respectively. Another example is the study of Fernando et al. (2003), who used mitochondrial DNA and microsatellites to finally prove that the Borneo "pygmy" elephant population is a distinct taxon, having branched off quite early from the Asian elephant tree, and not the result of feral domestic animals.

(3) Phylogeography. Perhaps more interesting from a Bornean perspective are studies that resolve evolutionary relationships within (endemic) species, as these may reveal patterns of population history within the island. This level of detail has only really been possible with the advent of DNA sequencing and consequently, studies are few, all very recent, and partly yet unpublished. In fact, just five years ago, Sheldon et al. (2001) wrote on a well-studied group like birds, "we do not have phylogenetic or population genetic data on any group of Bornean birds other than the Little Spiderhunter" (referring to Rahman [2000] for the latter). Since then, progress in this field has been considerable. For example, Moyle et al. (2005) used mitochondrial DNA to study the relationships among populations of the White-crowned Forktail (Enicurus leschenaulti) in Borneo. They found that the montane populations were genetically homogeneous and distinct from the lowland populations. The lowland populations separated into a western and a northern group, with the former having affinities with conspecific populations from Peninsular Malaysia and Sumatra. Similarly detailed phylogeographic scenarios have been constructed for other birds (Rahman 2001, Goh and Rahman 2005, Gawin and Rahman 2005), mammals (Zhi et al. 1996; Han 2000; Han et al. 2000; Warren et al. 2000, 2001; Abdullah et al. 2001; Abdullah 2003; Goossens et al. 2005), Fungi (Hibbett et al. 1995) and other taxa. Ongoing work of this kind will certainly allow generalizations on the paleoecological processes that have shaped evolution in Borneo species.

(4) Empirical studies of adaptation, speciation, and hybridization. Very few studies have been carried out that aim to study the processes of evolution directly, either by experimental or by empirical means. Schilthuizen et al. (2006) studied the evolution of shell shape in isolated snail populations and found effects of both neutral genetic divergence and adaptation to local predators. And, although primarily ecological in focus, several studies have addressed the evolution of ant-plant (Treseder et al. 1995, Fiala et al. 1999, Feldhaar et al. 2003) and fig-wasp (Harrison 2000) mutualisms in Borneo, as well as the evolution of mast-fruiting as an adaptation to seed-predation (Curran and Leighton 2000, Curran and Webb 2000).

The Relevance of Borneo as a Testing Ground for Evolutionary Biology

Overall, Borneo appears to have (or have had) several characteristics that, in comparison with many regions elsewhere in the tropics, would appear to make it an ideal place for tropical evolutionary biologists to work. First of all, it has been politically stable. With the exception of the Second World War (1941-1945) and perhaps the period of the Malaysian-Indonesian "Confrontation" (1962-1966), there have been no political upheavals that could have seriously frustrated scientific work. Second, Borneo is rich in elevational and edaphic (soil) gradients that produce a patchwork of vegetation types and corresponding changes in fauna. This would make the island extra-attractive for students of adaptation and endemism. Third, Borneo has remained environmentally almost untouched until the mid-1950s, and even today most montane forests still are in good shape. Finally, Sabah, Sarawak, Brunei and Kalimantan have all been under the influence of two colonial powers, Britain and the Netherlands, both of which have academic institutions with active and long-lasting research programs in evolutionary biology. Research stations like the Danum Valley Field Centre in Sabah and Wanariset in Kalimantan continue to operate with academic and financial support from the UK and the Netherlands, respectively.

Consequently, one would expect Borneo to figure prominently in the evolutionary literature. However, somewhat surprisingly, this does not seem to be the case. When we peruse conspicuous milestones in the evolutionary biology literature, we find very little usage of Bornean examples. Darwin's On the Origin of Species mentions Borneo only once (in Chapter 11, on representatives of otherwise Australian plant taxa endemic to Borneo's mountains). Reference to Bornean organisms is completely absent from Dobzhansky's (1937) Genetics and the Origin of Species, Mayr's (1963)Animal Species and Evolution, and Coyne and Orr's (2004) Speciation. Ridley's (1997) selection of classic texts on evolution contains several studies of tropical organisms, but none are from Borneo (instead, papers on Hawaiian Drosophila, Amazonian birds, and Galapagos finches are highlighted). And even when one eschews these standard textbooks, studies that first come to mind when one thinks of influential tropical evolutionary biology are, for example, the work on African cichlids (e.g., Meyer 1993, Schliewen et al. 1994, Seehausen and Schuter 2004), and the above-mentioned work on Galapagos finches. My personal collection of journal reprints (about 4,000 entries), which is of course biased towards Southeast Asian work, contains less than ten Borneo-based papers on evolutionary biology. It does, however, contain large numbers of Borneo-based work in forest ecology.

This suggests that, in spite of the work reviewed above, Borneo has not played an important role in the development of tropical evolutionary biology. One can think of several reasons why this may have been so. First of all, Borneo is quite far removed from all important centers of evolutionary biology. At least until about 25 years ago, when air travel became more easily available, this may have discouraged researchers from working here. North American evolutionary biologists have tended to work in Central and South America. European ones may have preferred Africa, whereas Australian evolutionary biologists have mostly focused on tropical Queensland. Japan has only recently developed centers for evolutionary biology, and indeed this may increase the amount of Japanese scientists working in Borneo. A second reason may be that Borneo is part of Sundaland, and has been connected with Sumatra, Java and Peninsular Malaysia for much of its geological past. Consequently, it has low levels of endemism. Since endemism has been a feature that has attracted tropical biologists to such areas as Lake Victoria, Madagascar and the Pacific islands, this may be an additional reason why Borneo has been neglected.

On-line bibliographic data bases allow a more quantitive analysis of the impact of Bornean work in evolutionary biology. At the time of writing, the Institute for Scientific Information's Web of Science contained 22.7 million scientific papers from the period 1980-2005. I searched these literature databases using the Boolean search string "(Borneo OR Kalimantan OR Sabah OR Sarawak OR Brunei) AND Evol*." I then excluded all papers on non-organic (i.e. social or tectonic) "evolution." The result was a total of 78 papers. The database also provides the number of times each paper was cited elsewhere, and this allowed me to calculate an average "impact" of 8.7 citations per title. To place these numbers in perspective, I repeated the same procedure for three other geographical regions in the humid tropics, with size roughly equal to Borneo, i.e. Venezuela, Cameroon, and Sumatra. The results are summarized in Table 1.

The results show an interesting pattern. As expected from the general observations above, Borneo scores low on total number of papers, which have on average a moderate impact. The results for Sumatra are very similar, suggesting that it is a consequence of regional biases. In contrast, Venezuela and Cameroon both generate more papers, but their impact is either much higher (Cameroon) or much lower (Venezuela). Although the survey in Table 1 is nowhere near a proper evaluation of the literature, I feel that it is warranted to state that the progress of evolutionary biology in Borneo has been somewhat disappointing and full use of the potential of the island has not been made. Below, I will provide some thoughts on how this situation might be improved in the near future.

The Future

Closer inspection of the data upon which Table 1 is based reveals an interesting pattern. Of the four regions compared, the one with the highest number of papers is Venezuela. Among these papers, a relatively large fraction was produced within the country itself. For Borneo, this is not the case: the vast majority of papers were written by foreign (mostly European, American and Japanese) researchers, though sometimes with local co-authors. This suggests that productivity might be increased if more work is carried out fully (that is, field work, laboratory work, data analysis and manuscript preparation, rather than just the former activity) in Borneo itself. Opportunities for this, hardly available previously, have been put in place over the past decade. Several modern universities with state-of-the-art facilities have been built in, for example, Brunei, Sabah, and Sarawak. In fact, many of the papers on DNA-phylogeography in vertebrates reviewed above were conceived and carried out solely by local researchers from Universiti Malaysia Sarawak, a situation that is unique in the history of evolutionary biology in Borneo. In the future, more and more work may originate from local research institutions, rather than foreign ones.

There may be a second reason for this. The regulations put in place under the Convention for International Trade in Endangered Species (CITES) as well as the national biodiversity legislations (e.g., the Sarawak and Sabah Biodiversity Enactments) prevent indiscriminate collecting and exporting of biological specimens by overseas scientists. Though these legislations are often rightly considered too restrictive and hampering research, they may have as a positive side-effect that overseas researchers will more and more do their laboratory work in research institutions in Borneo itself, reinforcing collaborations with local evolutionary biologists.

Another way for enhancing evolutionary biology would be to make better use of valuable but underused research systems. Mount Kinabalu, for example, is an evolutionary biologist's paradise, with large numbers of well-described endemic species that have adapted along elevational and edaphic gradients. Yet until today, virtually no students of speciation and adaptation have capitalized on this rich biogeographic and taxonomic knowledge base. Other underexploited systems are cave and shallow marine deposits, often already studied by geologists, that presumably contain the undisturbed layers of sediments well-suited for time-series studies of evolutionary change in e.g., land snails and diatoms, respectively.

Consequently, the future for evolutionary research in Borneo looks promising. However, it will partly depend on socio-political developments in the countries of Malaysia, Brunei and Indonesia. As mentioned above, biodiversity legislation, if not conceived and enforced appropriately, will hinder, rather than regulate, much valuable research (see also Ng 2000). Another cause for concern is the rapid rise of Islamic creationism, an offshoot of Christian creationism, which may tend to make universities wary of installing professorships and research programs in evolution.

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Table 1
Impact of Evolutionary Biological Literature for the Period 1980-2005 in Borneo and Three Humid-Tropical Regions of Comparable Size

Region	Papers	Average Citations
Borneo	78	8.7
Venezuela	167	5.3
Cameroon	91	12.0
Sumatra	50	8.6