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APPLICATION OF LINEAGE-BASED SPECIES CONCEPTS TO OCEANIC ISLAND FROG POPULATIONS: THE EFFECTS OF DIFFERING TAXONOMIC PHILOSOPHIES ON THE ESTIMATION OF PHILIPPINE BIODIVERSITY

RAFE M. BROWN AND ARVIN C. DIESMOS

"Despite the diversity of alternative species definitions, there is really only one general species concept in modern systematic and evolutionary biology — species are segments of population level evolutionary lineages."
de Queiroz (1998)

ABSTRACT

Appreciation of the magnitude of Philippine amphibian diversity has fluctuated over the past 150 years, with current estimates of diversity owing to progress during five distinct phases in Philippine herpetology. These include: (1) the early taxonomists' period, before the turn of the last century; (2) the career of E. Taylor in the 1920s; (3) the work by R. Inger in the 1950s; (4) the collaboration of A. Alcala and W. Brown between the 1960s and the 1990s; and (5), the current efforts to synthesize and comprehensively review Philippine amphibian diversity in the context of a lineage-based species framework for species recognition.

Until recently, taxonomic studies in the islands have all been conducted in the absence of an explicit species concept or within the context of the Polytypic Species Concept (a variant of the Biological Species Concept). In this paper, we argue that the latter should no longer be applied to Philippine vertebrates because it is a philosophical framework that is not necessarily consistent with evolutionary history. Rather, we suggest the adoption of lineage-based species concepts such as the Evolutionary Species Concept (Simpson, 1961; Wiley, 1978) or The General Lineage Concept (de Queiroz, 1998, 1999) because both of these approaches result in the recognition of taxa in a manner that is logically consistent with known evolutionary history. The geological history of the islands of the Philippines and the known common history of the vertebrates that occupy those landmasses are particularly amenable to interpretation within a lineage-based definition of the species.

Due to the unique geological history of the Philippines and the insular isolation postulated for many of its endemic amphibians, we argue that lineage-based species concepts are the most appropriate approaches for use in taxonomic studies of Philippine amphibians because populations on these islands possess known evolutionary histories and predictable evolutionary fates as deep-water island endemics. Thus, the identification of lineages is straight-forward and can be applied to species groups in a rigorous and repeat-

able fashion. Application of lineage-based species concepts also bolsters more realistic estimates of Philippine biodiversity and should further promote conservation efforts fueled by estimation of species numbers and percent endemicity.

In this paper we review several recent studies that have resulted in significant increases in estimated species numbers within Philippine Amphibia and discuss the historical significance of recent work. Finally, we note several as-of-yet unchallenged polytypic species complexes in the Philippines and suggest various taxonomic groups in need of comprehensive review within the context of lineage-based species concepts.

Introduction

Since the original description of the first species of endemic Philippine frog (Wiegmann, 1834; *Rana vittigera*), the history of amphibian biology of the country has been punctuated with significant incidental collections by early general collectors, and the targeted, dedicated careers of several pioneering herpetologists (see Inger [1954], Taylor [1975], and Duellman and Trueb [1986] for review). The history of Philippine herpetological diversity, like that of most countries, also is a history of disagreement between conservative taxonomists ("lumpers") versus more liberal proponents of species recognition ("splitters"). It is also the history of the discovery of remarkable biological diversity, coupled with the influence of a few charismatic personalities—and how the opinions of a few shaped the manner in which several generations viewed Philippine biodiversity.

Early collectors (Cuming, Everett, Jagor, Mearns, Moellendorff, Semper, and Thompson) sent preserved specimens to European and American museums; these specimens formed the basis of descriptions later published by Boettger, Boulenger, Günther, Mertens, Peters, and Stejneger (Inger, 1954). The age of discovery and description of some of the Philippines most interesting endemic amphibians (1860s through 1910) thus predated the arrival (in 1912) of the father of modern Philippine herpetology: Edward Harrison Taylor.

Taylor (1920–1928, see Literature Cited) recognized a total of 89 species of Philippine amphibians, 42 of which he described as new (one in collaboration with G. K. Noble). Inger (1954) later recognized 55 species of Philippine Amphibia (excluding the recently introduced cane toad, *Bufo marinus*), reducing the species level diversity of Philippine Amphibia by application of the Polytypic Species Concept and by careful re-appraisal of many of Taylor's taxa. Thus some species were relegated to the status of subspecies and others were considered invalid (submerged) and placed in the synonymy of wide-spread SE Asian species complexes (Inger, 1954).

Although recent years have witnessed the discovery of many new species of Philippine amphibians (summaries: Alcala and Brown, 1998, 1999), no systematic effort (e.g., Grismer, 1999) has been undertaken that would comprehensively address Philippine Amphibia in the context of recent philosophical syntheses of species concepts and reconsider the status of Inger's subspecies (Brown et al., 2000). Some investigators have conservatively followed Inger's polytypic taxonomy pending thorough review (e.g., Brown et al., 1996; Alviola et al., 1998; Alcala and Brown, 1998) and others have simply listed Inger's subspecies as full species without comment, justification, or accompanying data (Dubois, 1992; Duellman, 1993; Inger, 1999; Emerson et al., 2000; see comments by Inger, 1996 and Brown et al., 2000; review: Brown, Diesmos & Alcala, this volume.).

The purpose of this paper is to report on the progress towards a case-by-case, lineage-based reconsideration of the diversity of Philippine Amphibia. Between the time that Inger published his review and the present, species concepts have followed the general growth of biological thought towards recognizing and explicitly addressing natural variation and the central theme that evolution plays in taxonomy, classification, and systematics. As such, the recognition of basal units of evolution has turned towards identifying (and naming as species) diagnosable lineage segments that possess recognizable evolutionary pasts and predictable evolutionary fates. In this paper, we attempt to show why this conceptual framework is particularly appropriate when considering the amphibians of the Philippines, largely because of the unique and reasonably well-known recent geological history of the archipelago.

Review of competing species concepts applied in the past to Philippine Amphibia.

Throughout the remainder of this paper we use the term "species concept" to refer to a guiding philosophy or a conceptual framework, and not a practical algorithm, recipe, or a set of rules (criteria for recognizing species). Thus, a species concept is a framework within which sits the notion of what constitutes a species, the basal unit of evolution. Because of the spectacular diversity of life and its history, exceptions to every species-recognition algorithm will exist; as such no recipe is fail-proof for the recognition of all the earth's units of life. Much heat and often very little light has been generated in the process of refutation of one kind of species definition in favor of another (see review in Otte and Endler, 1989; Ereshefsky, 1992; Howard and Berlocher, 1998; Wilson, 1999). Fortunately, recent advances in technology have afforded the taxonomist an expanding set of powerful tools that can be used in place of some of the past's guess work and application of personal opinion. Rather, taxonomy has in some circles become the practice of collection of real data that can be used to test the hypothesis of specificity in a sound and rigorous manner (see Wiens and Servidio, 2000). This technological advance has not arisen unguided. In fact, recent progress in the philosophy of science have advanced the scientific community's understanding of the species concept debate at the same time that several landmark synthesis papers have reviewed the common elements of disparate philosophical viewpoints. The result is a recent consensus in the

literature as to what constitutes and how to identify the units of evolution (review: de Queiroz 1998, 1999). It is our hope that species concept theoreticians can now turn to the task at hand and advance the progress of recognizing the diversity of life unencumbered by excessive philosophical baggage.

Early authors of Philippine amphibian descriptions (Boettger, Boulenger, Günther, Mertens, Peters, Stejneger) were trained at a time when typological philosophy (or "essentialism") dominated biological thought. This general philosophy can be traced to Aristotelian typology and the notion that species are embodied by *types* that are manifest in their truest essence as the "Creator" intended them—by a prototype individual (review: Mayr, 1982). Thus, it has become standard practice for each species to be assigned a holotype specimen. In the past, the holotype was presumed to be the specimen that best embodied what the "Creator" intended for the species. Today, designation of a holotype specimen is still useful for nomenclatural purposes. As a last resort, the holotype is the specimen to which each scientific name applies. In the Aristotelian world view, variation from the essence of a species (as embodied by the *type*) was considered unimportant and inconsequential. When an aberrant specimen that did not conform exactly to the type was inevitably discovered, it was dismissed as a "freak" or a mistake to be ignored, or even discarded (Mayr, 1982). No attempt was made to handle natural variation in species or populations; to an extent, natural variation was even considered troublesome. It was an annoying exception to Aristotelian typology, the philosophy of essentialism, and the notion that God created the perfect form of every species in a pure essence, or *type*.

Charles Darwin published the "Origin of Species" in 1859 but it took several years for the full implications of his and A. R. Wallace's revolution to reach the practitioners of every discipline of biology. Boettger, Boulenger, Günther, Mertens, Peters, Stejneger, and Taylor all published some or all of their descriptions of Philippine amphibians after the advent of the "Origin" (Fig. 1) but each of these workers essentially still followed the practice and unspoken underlying philosophy of typological taxonomy. Thus, many of their species were published on the basis of a single aberrant specimen, and many of those have now been recognized as part of a natural population of variation—possibly at one extreme of the range of that variation, but from within the overall pool of natural variation nonetheless. The slight exception to this trend are some of the later works of E. H. Taylor (1920–1925). Taylor appears to have had a unique and unparalleled understanding, or at least ability to appreciate the products of the evolution of Philippine species because of his personal field work in the country. There are exceptions to everything that can be said in retrospect about any historical character, but herpetologists in general now have an expanded admiration for Taylor's work in the Philippines (e.g., Duellman, 1978). Many of the species he described that were for a time submerged into the synonymy of "widespread" species are now being recognized as valid (e.g., Brown et al., 2000; Brown and Guttman, in press; McGuire and Kiew, 2001); he obviously was a talented field biologist with a sharp eye for variation

With the exception of his memoirs in 1975, Taylor published his last work on amphibians of the Philippines in 1928 and set the stage for the next chapter in Philippine herpetology, the arrival of Robert F. Inger. Inger's comprehensive treatment of Philippine amphibians (Fig. 1) was only the second of its kind ever attempted and his work was based on all previously collected specimens in major museum collections, and additional material gathered by the Philippine Zoological Expeditions of the Chicago Natural History Museum (now the Field Museum) in 1946 and 1947 (review: Hoogstral, 1951; Inger, 1954). His massive contribution took the form of a comprehensive review of Philippine Amphibia

within the framework of the Polytypic Species Concept (PSC). The PSC is a variant of Mayr's Biological Species Concept (BSC), emphasizing the idea that species are populations of interbreeding discrete and discontinuous organisms that often show within-species or interpopulational geographic variation (reviews: Mayr, 1969; 1982; Mayr and Ashlock, 1991). It was the first time that an investigator explicitly adopted a philosophical view of the nature of a species and then systematically applied it to all of Philippine Amphibia and it was the first time that acknowledgement of natural variation, "population thinking", and evolution were considered in the context of Philippine herpetology.

Polytypic species are species characterized by recognizable subspecies, usually in isolated pockets of a species range, or on islands (see comments by Shaffer and McKnight, 1996; Irschick and Shaffer, 1997). The term "subspecies" is thus synonymous with earlier investigators' use of the term "island races" (Inger, 1954) and later researchers' "pattern classes" (e.g. Grismer et al, 1994; Shaffer and McKnight, 1996; Irschick and Shaffer, 1997). Polytypic species in many ways are the result of the revolution of "population thinking." Mayr's BSC has at its heart the requirement of reproductive isolation as the key to recognizing species (Mayr, 1942, 1957, 1969, 1982). During this period most taxonomists conceived of species as widely distributed forms among which gene flow was expected to occur. In the absence of actual genetic studies of gene flow, morphological similarity was often used as a criterion for recognizing conspecific members of a biological species. Diagnosable isolated populations (island races) were assumed to have reduced gene flow with the main population, but by virtue of their similarity, would be expected to easily interbreed should they come in contact with mainland individuals (Mayr, 1982). As such, many island races were described as subspecies with trinomials indicating their status in the rank of hierarchical structure of biological organization.

Robert Inger never traveled to the Philippines himself, and lacked many critical data that are now available to taxonomists (color pattern, behavior, mating calls). His taxonomic decisions were based entirely on preserved museum specimens, many of which were old and poorly preserved (pre-WWII material). Nevertheless, his systematic hypotheses have prompted many later investigations of the amphibians of the Philippines and his 1954 monograph is a classic work of Philippine herpetology that should be considered required reading for students interested in SE Asian herpetology, the Philippines in particular, or biogeography and evolution in archipelagos.

In the mid-1950s, a team of biologists began a lifelong collaboration that continued to the present day. The contributions of Walter Brown and Angel Alcala number somewhere in the 70s and their influence has permeated all taxonomic groups in Philippine herpetology. During the same time, occasionally publishing in collaboration with Dioscoro Rabor and Alan Leviton, the pair systematically reviewed major lizard groups in the Philippines (Brown and Alcala, 1978; 1980, and later published landmark papers on development (Alcala, 1955, 1962; Alcala and Brown, 1955, 1956) reproductive biology (Alcala and Brown, 1982; Brown and Alcala, 1983), population biology (Alcala and Brown, 1967; Brown and Alcala, 1970a), ecology (Brown and Alcala, 1961) and biogeography (Brown and Alcala, 1970b) of Philippine amphibians. They also later published classic reviews on rhacophorid (Brown and Alcala, 1994) and ranid (Brown et al, 1997a, 1997b, 1997c, 1999, 2000; Alcala and Brown, 1998, 1999; Alcala et al., 1998) frog systematics as well (see review in Brown et al., this volume. Their descriptions of numerous subspecies of lizards (Brown and Alcala, 1978; 1980) demonstrate their continued use of the PSC as a general framework for the recognition of diversity, although papers from the last decade have for the most part recognized Philippine

diversity in the form of full species, thus implicitly recognizing species as evolutionary lineages (but see Brown et al., 1999; Alcala and Brown, 1998, 1999).

General concerns: the goals of recent taxonomic studies in the Philippines

In the past five years we have begun the process of attempting to identify and classify species-level lineages of Philippine Amphibia. Our intent is to clarify the status of Philippine amphibian species within the framework of a lineage-based species concept that emphasizes evolutionary history (Wiley, 1978; Frost and Hillis, 1990). The first form of a lineage-based species definition was Simpson's (1961) Evolutionary Species Concept (ESC; see Wiley, 1978, Wiens, 1993, and de Queiroz, 1998, 1999, for review). An evolutionary species is the largest single lineage (ancestor-descendant series of populations) that can be characterized as distinct from other such lineages and within which there is reproductive cohesion (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990). Although the meaning of what Wiley meant by "cohesion" eludes modern biologists to some degree (Frost and Hillis, 1990; L. Heaney, pers. comm.), the recognition of evolutionary species is the process of identifying (in the thin slice of time that biologists are afforded) the ancestor-descendant series of lineages that have a distinct evolutionary past and those that we expect to have an equally unique evolutionary future. Thus, lineages are any series of ancestor-descendant populations as depicted in a phylogenetic tree, while clades are all composed of all descendant lineages stemming from a single ancestor (Fig. 2).

For our purposes, we consider as distinct lineages segments that are (1) geographically isolated (as montane or insular endemics) and readily diagnosable (by morphology, biochemistry, bioacoustics, and/or ecology) and (2), sympatric, reliably diagnosable forms for which the hypothesis of conspecificity can be confidently rejected (Frost and Hillis, 1990; see also Wiens, 1993). Recently de Queiroz (1998, 1999) reviewed lineage-based species concepts and asserted that by considering speciation as a temporally-extended process one could arrive at a basis of understanding differences between species concepts and species criteria as well as differences between modern definitions of competing species concepts (Fig. 2). De Queiroz (1998, 1999) concluded that most modern species definitions are all aspects or properties of a single common entity and that differences between definitions were not as disparate as the variety of species concepts would suggest. He (de Queiroz, 1998, 1999) suggested the use of the General Lineage Concept (GLC) as the basis for a revised and conceptually unified terminology for resolving the species problem. We have adopted this approach in our recent work.

Lineage-based species concepts as applied to oceanic islands

The key to our understanding and application of the ESC and GLC has been our growing appreciation of the unique geological history of the Philippine Islands (Hall, 1996, 1998) coupled with an understanding of sea level fluctuations during the mid- to late Pleistocene (Heaney, 1985, 1986). It has become abundantly clear that events between the mid- to late Pleistocene have had an enormous impact on the distribution of life in the Philippines (Taylor, 1928; Inger, 1954; Leviton, 1963; Brown and Alcala, 1970; Heaney, 1985, 1986). It is now understood that five to seven major (and several minor) Philippine island groups (complexes of islands separated by shallow channels) intermittently formed much larger land mass amalgamations, the Philippine Pleistocene Aggregate Island Complexes (PAICs). Thus, at various times during the

mid- to late-Pleistocene sea water receded and shallow channel beds were exposed in the form of land bridges connecting smaller islands into larger land masses (Heaney, 1985, 1986; Fig. 3). It is presumed that these events allowed free exchange of fauna and flora via land–positive connections between the otherwise isolated islands of today. Each of the Philippine PAICs (Fig. 3) are now recognized by biogeographers as a kind of faunal subprovince (Taylor, 1928) due to the fact that each supports highly–celebrated suites of endemic taxa (Taylor, 1928; Leviton, 1963; Heaney, 1985, 1986, 1991, 2000; Dickinson, 1991; Peterson and Heaney, 1993; Alcala and Brown, 1998; Kennedy et al., 2000). Most significantly, since we know with certainty the age and history of isolation of amphibian populations on each PAIC, we can conclude with a degree of certainty that the evolutionary history of each lineage is known (e.g., The Palawan PAIC has been isolated from other such land masses and from the edge of the Sunda Shelf for ≥ 165,000 years before present).

Furthermore, since we can assume that for the foreseeable future Pleistocene aggregate island complexes in the Philippines will remain separated (e.g. we expect Palawan PAIC to maintain its isolation from Borneo to the south and Mindoro to the north), we can assert that the evolutionary fate of each lineage is predictable. Combined with careful examination of morphology, biochemistry, behavior, and ecology, it has been a straightforward task to diagnose evolutionary lineages from one another in a reliable fashion. In fact, in most cases, names already exist, as these same lineages have been recognized by typologists on the basis of morphology alone (Taylor, 1920, 1922a, 1922b, 1923, 1925). To date there have only been a few comprehensive reviews of the manner presented above; several others are currently underway (Diesmos, Brown, and Alcala, unpublished data). Application of lineage-based species concepts and expanded data sets to the *Rana signata* and *Rana everetti* species groups in the Philippines has increased Philippine biodiversity in these groups from two to twelve species in total (Brown, 1997; Brown et al., 2000; Brown and Guttman, in press; Table 1; Fig. 3).

The speciation process in the Philippines

While considering species concepts and their implications, it is also important to be explicit about the actual events and underlying evolutionary processes that give rise to current day amphibian diversity. We think of speciation as a process, not an event (de Queiroz, 1998, 1999; Fig. 2). We imagine that dispersal between islands and subsequent isolation, sea level vicariance, and habitat vicariance within islands (i.e., isolation and divergence of montane populations) have all contributed to the process of speciation within Philippine Amphibia (Inger, 1954; Leviton, 1963; Brown and Alcala, 1970; Brown, 1997; Brown et al., 2000). At present there is no evidence that geological vicariance (splitting, breaking apart, or rifting of islands) has occurred in the Philippines but there is evidence to suggest that formerly separate paleoislands have more recently fused together to form some of today's recognizable landmasses (Hall, 1996, 1998).

Due to our assumption that the process of speciation takes time and is not an instantaneous event, it is inevitable that biologists will discover species in the process of diverging. Such potential species may not be fully isolated or diverged from one another, they may show evidence of interbreeding, and as such they may not constitute individual evolutionary lineages. In cases such as this, judgment calls will have to be made; we espouse a conservative approach and caution readers from simply recognizing potential future species without evidence of lineage integrity, a history of isolation,

and the presumption of unique evolutionary fates (see also Frost and Hillis, 1990). Evidence of gene flow, or reticulation, between two potential species suggests to us that neither is a unique evolutionary lineage worthy of specific rank. While we generally do not favor the use of subspecies, the concept of a subspecies as a unique subpopulation (partially isolated from the remainder of the population but exchanging limited gene flow with the main population) is not inherently one to which we object . However, our own recognition of subspecies would have to be contingent upon the demonstration of limited but significant gene flow between a semi isolated deme and a main population of a given species. This would require actual genetic data of the type that is so far lacking in most systematic studies of Philippine frogs (but see Brown, 1997; Brown and Guttman, in press).

Practical considerations and types of data

There has been much discussion of the types of data suitable for the recognition of species (reviews: Otte and Endler, 1989; Ereshefsky, 1992; Howard and Berlocher, 1998). All early investigators and most recent workers have utilized data from external morphology in the form of morphological character and color pattern differences between species (Taylor, 1920; Inger, 1954; Brown et al., 2000), differences in ratios or body proportions (Brown and Alcala, 1994; Brown et al., 1997a-c; Brown et al, 1999, 2000), variation in absolute body size (Alcala and Brown, 1998) and even osteology and live color (Brown et al., 2000). Recent systematic studies have also used information from allozymes (Brown, 1997; Brown and Guttman, in press), biogeography, ecology (Brown et al., 2000), and advertisement calls (Brown et al, 1997b-c, 1999, 2000; Alcala et al., 1998; Brown and Guttman, in press), and molecular sequence data (McGuire and Alcala, 2000; McGuire and Kiew, 2001; Brown, unpublished data).

We are of the opinion that no one type of characters is inherently "better" than any others for species level distinctions and the task of diagnosing lineage-based species. Thus, while some types of studies are better suited (more easily applied, less expensive, more accessible in the Philippines, generally available to all students) to certain studies, there is nothing inherently better about an allozyme, morphological, or color pattern character difference for distinguishing species. Each of these types of data, hopefully reflect evolution, indicate a history of isolation, and serve as convenient or reliably discernable diagnostic characters for the biologist. One fixed character difference between two species is just as good as any other fixed character difference between two species, whether it take the form of an allelic variant on a gel, the presence or absence of asperities on the skin, color pattern differences, the presence or absence of various skeletal elements, dominant frequency of the advertisement call, or microhabitat preferences.

The impact of the application of lineage-based species concepts on the estimated diversity of Philippine Amphibia and a note of caution

As mentioned above, limited use of lineage-based species concepts in our review of Philippine Amphibia has increased species diversity in selected frog groups from two to twelve species in total (Brown, 1997; Brown et al., 2000; Brown and Guttman, in press; Table 1; Fig. 4). For the most part, this exercise has been one of elevating the subspecies of earlier studies to the status of full species in recognition of their status of full, reliably-diagnosable evolutionary lineages with unique pasts and fates. We expect that cautious and conservative application of these principles to Philippine Amphibia will increase the frog fauna of the country by another 20 species at least (Brown, Diesmos and Alcala, unpublished data). Selected species complexes in need of reconsideration (and possible revision) are summarized in Table 2. Even though the practice of reviewing species groups within the context of the GLC has, for the most part, resulted in the simple elevation of the subspecies of earlier studies, we caution the reader from concluding that one could save time and energy simply by systematically elevating all of Inger's (1954) subspecies to full species and arrive at a realistic estimate of Philippine amphibian diversity (e.g., Dubois, 1992; Duellman, 1993; see comments by Inger, 1996; Brown et al., 2000).

First, there has been a major technological advancement of tools for the systematist in the last 48 years, and many data are now available that were not available to Inger at the time of his review. Second, many more specimens are now housed in museum collections than were available at the time of Inger's (1954) review. These specimens represent a wealth of data that must be collected before taxonomic changes should again be made. Third, the past 10 years has seen the discovery of many new species of frogs in the Philippines. Simply elevating Inger's subspecies without careful consideration would not be a realistic way to characterize evolutionary lineages. Fourth, several cases are now apparent to us (Brown and Diesmos, unpublished data) where Inger's subspecies do not correspond to full evolutionary lineages. In these instances, we have concluded that two or more species may actually be contained within a single Inger subspecies and in some cases subspecies will have to be submerged as they correspond to no biologically relevant entity that we are able to detect now that larger samples are available for study (Brown and Diesmos, unpublished data). It is only through careful consideration of all available data on a case-by-case basis (Table 2) that we will be able to arrive at a realistic estimate of the diversity of evolutionary lineages within Philippine Amphibia—and only when this effort is conducted in concert with continued field survey work by trained herpetologists. At present, we recommend the continued use of some of Inger's subspecific taxonomic arrangements until comprehensive reviews are forthcoming. In cases where subspecies have been shown to correspond to distinct evolutionary lineages (e.g., the *Rana signata* and *Rana everetti* complexes), we have elevated these to full species (see Brown, 1997; Brown et al., 2000; Brown and Guttman, in press).

Conclusions

We have argued that lineage-based species concepts are the most appropriate conceptual frameworks for application to Philippine herpetological diversity. We believe that this approach is particularly useful for evaluating specific rank of Philippine Amphibia because of the well known geological history of the Philippines. The isolation of amphibian populations on the separate Pleistocene aggregate island complexes suggests a uniquely recognizable evolutionary past and presumably predictable evolutionary fate. This fact renders taxonomic decisions straightforward and conveniently consistent with evolutionary processes when fixed character states can be found to define and diagnose evolutionary lineage segments (species). Although we demonstrate that expanded appreciation of Philippine

biodiversity can result from application of lineage-based species concepts, we caution the reader from considering elevation of all subspecies to be a fail-proof algorithm for recognizing biodiversity. This is because many exceptions to the patterns of distribution discussed here are known and continue to be uncovered. Only careful, case-by-case evaluation of polytypic species complexes will result in a taxonomy reflective of the evolutionary process of speciation. Only when such an approach is conducted in concert with continued data collection (exploration and field surveys) will the necessary information be gathered. And only in this manner can we recognize and appreciate the full magnitude and unique evolutionary history of the diversity of the amphibians of the Philippines.

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Table 1. Summary of results of recent taxonomic reviews or systematic analyses bearing on taxonomy of Philippine Amphibia within the context of lineage-based species concepts (e.g., ESC, GLC).

Polytypic species	Subspecies	Current species recognized (range in parentheses)
Limnonectes magnus[1]	*L. magnus magnus*	*L. magnus* (Mindanao PAIC)
	L. magnus acanthi	*L. acanthi* (Palawan + Mindoro PAICs)
	L. magnus macrocephalus	*L. macrocephalus* (Luzon PAIC)
	L. magnus visayanus[1]	*L. visayanus* (Visayan PAIC)
Rana signata[2]	*R. signata similis*	*R similis* (Luzon PAIC)
		Rana sp. (Mindoro PAIC)
	R. signata moellendorffi	*Rana moellendorffi* (Palawan PAIC)
	R. signata grandocula	*R. grandocula* (Mindanao PAIC)
	R. signata signata	*R. signata* (Borneo + Malay peninsula)
		R. picturata (Borneo)
Rana everetti[3]	*Rana everetti everetti*	*R. everetti* (Mindanao PAIC)
	Rana everetti albotuberculata	*R. albotuberculata* (Mindanao PAIC)
	Rana everetti luzonensis	*R. luzonensis* (Luzon PAIC)
		R. igorota (Luzon PAIC, Central Cordillera)
		R. tipanan (Luzon PAIC, Sierra Madres)
		Rana sp. (uncertain)

[1] Philippine populations treated by Emerson and Berrigan (1993) and Emerson et al. (2000) as full species. Other Philippine species in this group include Limnonectes diwatus and Limnonectes new species (unpublished data). The status of L. acanthi on both the Mindoro and Palawan PAICs is suspect and in need of review.
[2] Philippine populations last reviewed by Brown (1997) Brown and Guttman (in review). This species complex also contains Rana melanomenta (type specimens destroyed) and Rana siberu (Mentawi islands, Indonesia).
[3] Philippine populations last reviewed by Brown et al., 2000

Table 2. Selected Philippine polytypic species in need of review, and the major Pleistocene Aggregate Island Complexes (PAICs), constituting their geographical distribution.

Polytypic species	Subspecies	Range in the Philippines
Bufo biporcatus[1]	*B. b. philippinicus*	Palawan PAIC
Megophrys monticola[1]	*M. m. stejnegeri, M. m. ligayae*	Mindanao PAIC; Palawan PAIC
Occidozyga laevis[1]	*O. l. laevis*	throughout the Philippines
Rana cancrivora[1]	*R. c. cancrivora*	throughout the Philippines
Rana limnocharis[1]	*R. l. vittigera*	throughout the Philippines
Limnonectes microdiscus[1]	*L. m. leytensis*[2], *L. m. palawanensis*	Mindanao + Visayan PAIC; Palawan PAIC
Rana nicobariensis[1]	*R. n. nicobariensis*	Palawan PAIC
Nyctixalus pictus[3]	*N. p. pictus*	Palawan PAIC
Polypedates leucomystax[3]	*P. l. leucomystax*	throughout the Philippines
Rhacophorus everetti[3]	*R. e. everetti*	Palawan PAIC
Kaloula conjuncta[1]	*K. c. conjuncta, K. c. negrosensis,*	Luzon + Mindoro PAICs; Visayan PAIC;
	K. c. meridionalis, K. c. stickeli	Mindanao PAIC; Mindanao PAIC

[1] Philippine populations last reviewed by Inger (1954)
[2] See also Emerson et al. (2000)
[3] Philippine populations last reviewed by Brown and Alcala (1994)

Fig. 1.— The relationship between the cumulative total of recognized Philippine Amphibia and the year of each species (lineage's) description. Only currently recognized species were included in this figure.

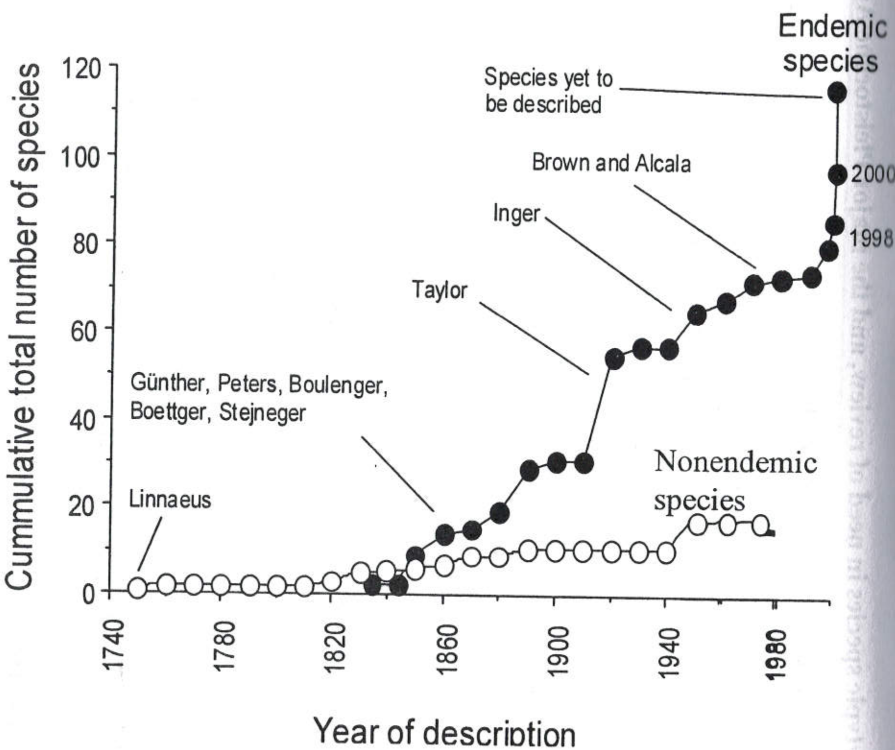


Fig. 2.—Clades versus lineages and the speciation process. The nine branching diagrams (A and B) represent the same phylogeny, with various clades emphasized in part A and some of the possible lineages emphasized in part B. Speciation and criteria for the recognition of species (C): the set of events constituting the process of speciation may be considered by different workers as the basis of recognizing the two species at various levels of divergence, isolation, or accumulation of diagnostic or apomorphic characters. Adapted from de Queiroz (1998), with permission.

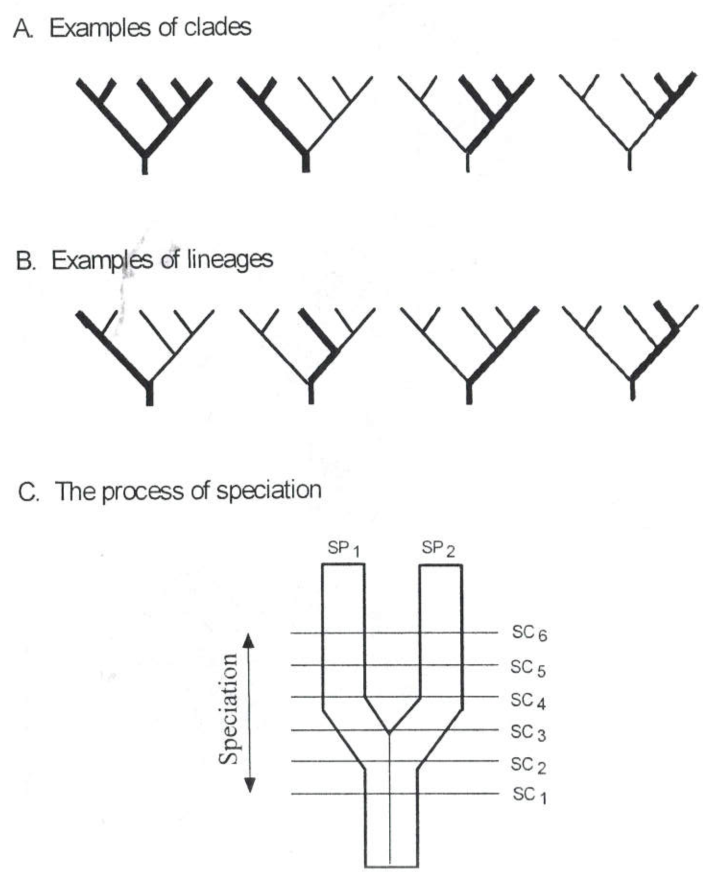


Fig. 3.— Zoogeographical classification of the Philippines into major Pleistocene Aggregate Island Complexes (PAICs) in recognition of the 120 underwater bathymetric contour and known mid- to late-Pleistocene sea level reductions (following Heaney, 1985, 1986).

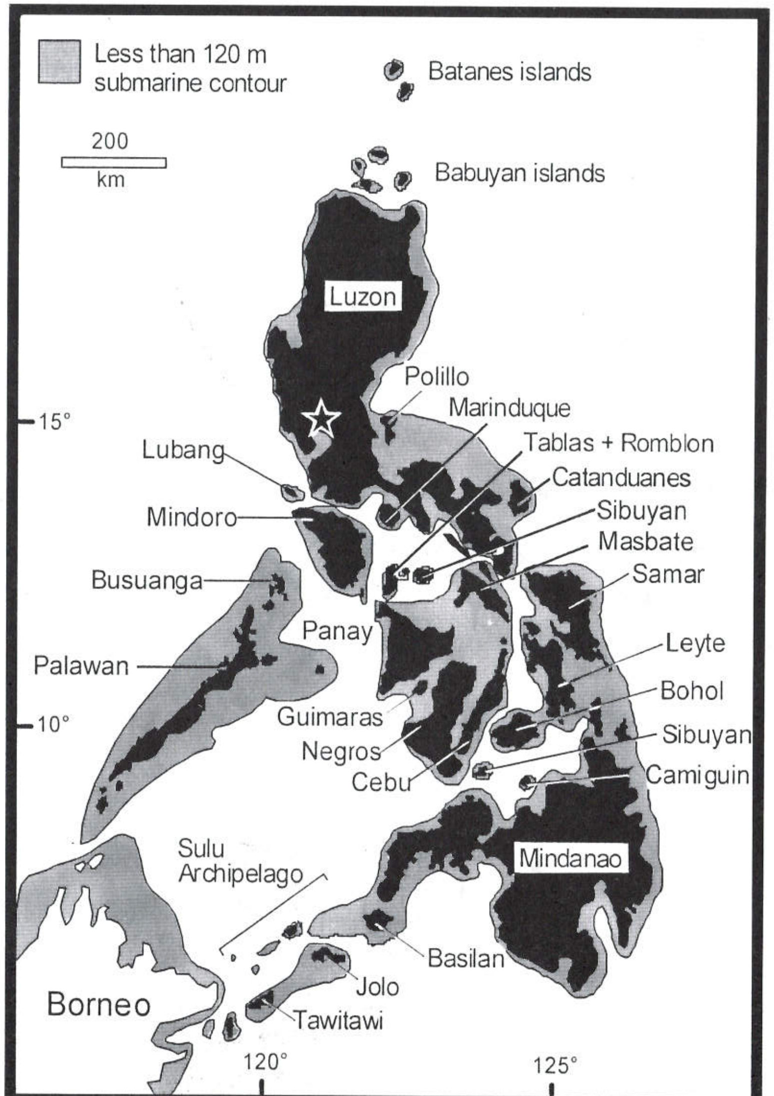


Fig. 4.— Representative Philippine species of the *Rana everetti* and *Rana signata* species complexes. See Brown (1997; Brown and Guttman, in press) and Brown et al. (2000) for review.

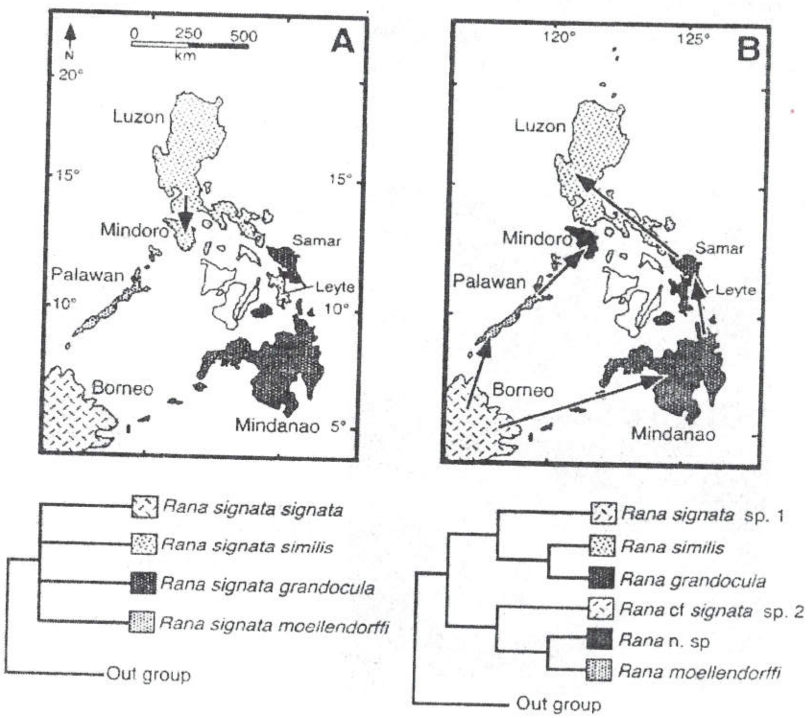
Rana grandocula
(photo: R. Brown)

Rana moellendorffi
(photo: R. Brown)

Rana luzonensis
(photo: R. Brown)

Rana tipanan
(photo: J. McGuire)

Fig. 5 -- Alternative interpretations of the *Rana signata* complex and its distribution in Borneo and the Philippines. Previous taxonomic interpretations (A; Inger, 1954) considered each insular lineage in the Philippines to be subspecies of the widely distributed polytypic *R. signata* (this taxonomy provided no phylogenetic resolution of relationships) and the Mindoro and Leyte populations were considered conspecific with the Luzon subspecies (*R. signtata similis*). In contrast, morphology, acoustical analyses of advertisement calls, biogeography and geological information, and the phylogeny for the group suggests that all Philippine populations previously considered subspecies should be recognized as full species in accordance with their status as independent evolutionary lineages (Brown and Guttman, in press). These six lineages are divided into two major clades, consistent with the hypothesis of two invasions of the Philippines from Sundaic sources. Thus the common ancestor of the *R. signata* clade may have given rise to *R. grandocula* and *R. similis* by faunal exchange eastward into the Sulus-Mindanao-Leyte-Samar-Luzon arc while the ancestor of the *R.* cf *signata* sp. 2 clade may have given rise to *R. moellendorffi* and *R. mangyanum* by faunal exchange along the Palawan-Busuanga-Mindoro arc (note arrows, B).



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