

Primate Taxonomy: Inflation or Real?*

Colin P. Groves

Biological Anthropology, School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia; email: colin.groves@anu.edu.au

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Abstract

This article reviews changes in primate taxonomy, especially those pertaining to the meaning of the term species, since its inception two and a half centuries ago. Despite continuing discoveries and the involvement of competent practitioners, the adoption of the polytypic species concept, especially underpinned by the biological species concept, ensured that primate taxonomy was in a sorry state by the middle of the twentieth century. In the latter half of the twentieth century, a gradual rethinking of the nature of species took place, and many different species concepts were proposed. The phylogenetic species concept has been widely adopted over the past ~20 years, sustained by a gradual realization that species are evolutionary lineages. This review provides examples of how the old way of thinking about species hampered our understanding of primate biodiversity and of how the phylogenetic species concept (or the diagnosability criterion under the general lineage concept) has clarified matters, opening them up for discussion. The adoption of this evolutionary view of species has implications for conservation, particularly because it increases recognition of biodiversity.

Carl Linnaeus: an eighteenth-century botanist; the founder of biological taxonomy, including the binomial nomenclature of species

Subspecies: a geographic segment of a species that is distinguishable as a whole, but not absolutely, from other such geographic segments

Polytypic species concept: proposes that a species should incorporate, as subspecies, all taxa, even allopatric, that somewhat resemble each other

Karl Jordan: an eminent entomologist, the originator of the biological species concept. He nearly made his century (1861–1959)

Varieties: variants of a species. Jordan (q.v.) first argued the necessity to separate geographic varieties (subspecies) from varieties within populations (polymorphic variants)

Nominotypical subspecies: the subspecies that occurs at that species' type locality

INTRODUCTION

Primate taxonomy has been experiencing a revolution. The leading primatologists of the twentieth century, John and Prue Napier, in their 1967 compilation (Napier & Napier 1967), recognized 176 species of what we now regard as primates (exclusive of *Homo sapiens*; note that they also included the treeshrews, which we do not now regard as primates). The most recent compilation listed 376 species (Wilson & Reeder 2005). What has changed?

Carl Linnaeus, the founder of modern taxonomy and nomenclature in the seventeenth century, listed all the species then known to him, giving each of them a two-word name: The first word designated the genus (a group of apparently closely related species), and the second word designated the species itself. The practice of binomial nomenclature has persisted to the present day, but the understanding of the nature of species has gone through several stages. For Linnaeus, species were created by God in the beginning (Linnaeus 1736, p. 18). His successors removed the religious aspect from their understanding of species, mostly defining them by the simple principle of “like begets like” (see, for example, Cuvier 1812). Darwin has been accused of having a purely practical view of species: “[T]he opinion of naturalists having sound judgement and wide experience seems the only guide to follow” (Darwin 1859, p. 47), although in fact other passages clearly indicate that these naturalists were saying that species have no intermediates between them and that this was the crux of the problem (hence the title of his 1859 book, *The Origin of Species*). Having established the reality of evolution by natural selection, he concluded “that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected” (Darwin 1859, pp. 484–85).

THE POLYTYPIC SPECIES AND THE BIOLOGICAL SPECIES CONCEPT

The understanding that species are separated by gaps, whereas varieties are not, was refined in the latter half of the nineteenth century, initially by American ornithologists (as recounted by Groves 2001), and was fleshed out by Poulton (1904). The concept of subspecies—geographic varieties within species—followed from this notion almost as a corollary; the polytypic species concept (under which species are highly inclusive, most of them divided into subspecies) was rapidly adopted during the 1890s, but its detailed explication did not occur until a seminal paper by Karl Jordan (1905). Jordan argued in considerable detail that one must separate geographic from nongeographic varieties and why. Geographic varieties, designated subspecies, were clearly dignified as taxonomic entities, whereas nongeographic varieties were not of taxonomic significance. Subspecies were to be placed immediately subordinate to species and awarded their own status in nomenclature, the trinomial: Each of the subspecies within each species adds a third name after the binomial (one of them, occurring at the type locality of the species, is known as the nominotypical subspecies and simply repeats the species' name). But Jordan went further. In his paper, he discussed a group of African butterflies that exhibit intergradation between West and East African forms; because these were thus not separated by any morphological gap, he placed them as geographic varieties (his modification of Darwin's concept)—that is to say, subspecies within a single species. This practice was generally what the American ornithologists were also doing, but he went further: “Given that these two forms are part of a single species, it is self-evident that we should regard related forms, which differ in a similar fashion, as part of a single species whether there are intermediates between them or not” (Jordan 1905, p. 197; roughly translated from German). Thus we had subspecies (geographic varieties) that were not, contra Darwin and everyone else, connected by intermediate gradations. Thus were

sown the seeds of the downfall of the polytypic species concept, almost at the very moment of its birth.

Jordan's paper was written in German; even then the scientific world was predominantly English speaking, and his arguments would not likely have achieved the wide dissemination that they did but for his association with the Honorable Walter Rothschild. This eccentric young aristocrat had bought his own museum (at Tring, in the south of England) and hired a German ornithologist, Ernst Hartert, as director, and at the latter's urging he also hired Karl Jordan as curator. In 1894, the three of them founded a journal, *Novitates Zoologicae*, and in it they explicitly adopted the polytypic species concept (Rothschild et al. 1903), and throughout the journal's early years they lost no opportunity to promote it. Zoologists, including mammal specialists, eagerly and uncritically took it up, often, it would seem, largely as a way of reducing the number of species, if at the expense of recognizing a vast number of subspecies within many of their reduced number of species. Less than 20 years after Jordan's paper, we find the following in the introduction to a seminal work by Richard Lydekker on hoofed mammals: "To a great extent the principle of classing nearly related kinds of animals as races of a single species, rather than as distinct species, has been followed" (Lydekker 1913, p. vi), without even mentioning the question of intermediate gradations or even asking what "nearly related" means in this context.

Some 20 years after Lydekker's volumes came the evolutionary synthesis, which brought together geneticists and naturalists in a realization that evolution works on populations, not on individuals, and is the operation of natural selection on genetic mutations. And so population thinking entered biology, including taxonomy, bringing with it the proposal of the biological species concept (BSC) by Theodosius Dobzhansky and Ernst Mayr. Under this concept (see especially Mayr 1963), species are populations, or groups of populations, that do not interbreed under natural conditions with other such populations. In fact, this gelled rather well with the polytypic species, for which it can be regarded as a belated theoretical underpinning. The arguments for species versus subspecies under the BSC were almost identical to those of Jordan: "Allopatric populations that intergrade clinally with each other belong to the same species. . . . Geographically isolated allopatric populations may be either species or subspecies. . . . *It is preferable for various reasons to treat allopatric populations of doubtful rank as subspecies.* The use of trinomials conveys two important pieces of information: (1) closest relationship and (2) allopatry" (Mayr 1969, pp. 194, 197, italics in original). This is little advanced from the cavalier dictum of Lydekker (1913), this time specifying that species are testable only when sympatric—the species themselves being distinguished quite subjectively. Subjectivity rules OK.

In mammalogy, including primatology, the polytypic species concept held sway almost unchallenged through most of the twentieth century. Within a given species, compilations such as that of Ellerman & Morrison-Scott (1951) would characteristically list numerous subspecies, with their trinomials. These could be characterized (in the nomenclature of Groves & Grubb 2011, pp. 3–4) as the Good, the Bad, and the Ugly. There were good subspecies, 100% diagnosable; bad subspecies, merely points along the cline or differentiated at very-low-frequency levels; and ugly subspecies, differentiated at high frequencies but not 100% distinct. Because nontaxonomists would almost invariably cite only the species, ignoring subspecies altogether, the Good subspecies would be overlooked altogether in physiology, biochemistry, behavior, ecology, and conservation.

THE DEMISE OF THE BIOLOGICAL SPECIES CONCEPT

From the late 1960s on, however, objections to this conception of species were increasingly being raised. From the very start, there was disquiet about allopatric (geographically isolated) populations; they have no chance to interbreed so that whether they are different species or not is

Richard Lydekker:

a late-nineteenth-century/early-twentieth-century biologist who was, in effect, the mammalogist who brought the polytypic species concept into general use

Biological species concept (BSC):

proposes that the species is a population, or metapopulation, that does not interbreed under natural conditions with other such populations, or metapopulations

Ernst Mayr: eminent twentieth-century biologist, enlarged Jordan's ideas into the biological species concept. He made his century plus a bit (1904–2005)

Allopatric: of two taxa or populations, found in different areas and not coming into contact

Nuclear swamping:

the effective replacement of one species by another, leaving only the mitochondrial DNA of the replaced species

Evolutionary species concept (ESC):

the concept of species first proposed by Simpson, that a species is simply an individuated evolutionary lineage

Phylogenetic species concept (PSC):

proposes that a species is simply a population, or metapopulation, that is diagnosably different from other such populations, or metapopulations

General lineage concept:

a recent reworking of the evolutionary species concept that emphasizes that every lineage is a species

inherently untestable, Mayr's (1969) words notwithstanding. How would one tell? "Degree of difference," much the same criterion as had been appealed to by the polytypic species adherents of the early twentieth century, was an anomaly: a phenotypic concept in an evolutionary world.

With the "molecular revolution" in the mid-1980s came evidence that species very often do, in fact, interbreed, even when sympatric. First came the discovery that two consistently different species of North American deer, the white-tailed deer (*Odocoileus virginianus*) and the mule deer (*O. hemionus*), had historically been interbreeding in areas where their ranges overlap. This finding was deduced by the presence of one species' mitochondrial DNA in populations of the other species (Carr et al. 1986), which indicated that interbreeding had occurred, followed by what is called "nuclear swamping": Males of species A interbred with females of species B and then with successive hybrid generations until the nuclear DNA of B had been all but replaced, leaving just the mitochondrial DNA (which is purely matrilineally inherited) of B to document that species B had once existed there. Because the BSC purported that different species should not interbreed in the wild, this finding was sensational. Abundant evidence of former, and sometimes continuing, interbreeding has since emerged in large mammals.

As described by Mayden (1997) and Groves (2001), different species concepts sprang up from the 1970s onward, some to rectify perceived deficiencies in the BSC and others to put forward a different point of view altogether: the cladistic, phenetic, and evolutionary species concepts, species as fuzzy sets, species as individuals, and the ecological, phylogenetic, recognition, cohesion, autapomorphic, composite, and genetic species concepts. The view of the evolutionary species concept (ESC) (Simpson 1961) is completely different from that of the BSC: A species is "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson 1961, p. 153). The ESC was mostly ignored or overlooked in favor of the BSC until it was revived, discussed, and modified by Wiley (1978); but since then, everyone who has listed species concepts and compared them has focused on the ESC as being the very essence of what a species is: an evolutionary lineage. But how can we put this into operation? How can we make it testable?

This is where the phylogenetic species concept (PSC) comes into play. The PSC depends on the diagnosability of candidates for species recognition: "A species is the smallest population or aggregation of populations which has fixed heritable differences from other such populations or aggregations" (Groves & Grubb 2011, p. 1). This species concept is eminently testable:

- First, a species is a population (or aggregation of populations). This assertion is testable, if ideally by field observations, although for museum or laboratory workers it is commonly assumed until shown otherwise.
- Second, the differences between species are heritable. This is testable, if ideally by breeding experiments. Again, for museum or laboratory workers it is commonly assumed as the default condition.
- Third, the differences between species are fixed (i.e., 100%). This is, in all cases, testable. If further research uncovers new specimens showing that the distinguishing characteristics of two putative species actually overlap, then the idea that they are distinct species is refuted.

A series of key papers by Kevin de Queiroz placed the PSC and the other species concepts in the framework of the ESC, which he modified as the "general lineage concept of species," arguing that, if species are evolutionary lineages, then there must be some point at which they become recognizable as such. The properties on which different species concepts rely (interbreeding, specific mate recognition systems, ecological niches, cohesion, diagnosability, genetic distances, etc.) are acquired by evolutionary lineages, as they continue to diverge, at different times; they are all actually trying to define evolutionary lineages. The general lineage concept is, then, offering

TAXONOMIC INFLATION

Taxonomic inflation is the idea that the phylogenetic species concept (q.v.) has caused alarm and despondency by raising former subspecies to full species rank, thereby doubling (or more) the number of species that have to be accounted for (whether in conservation reckoning or simply as a feat of memory).

reconciliation between all the various species concepts, which, as a consequence, are not actually species concepts but rather methods of delimiting species, and all in their own way are relevant: Any one of such properties is evidence that an evolutionary lineage has individuated (separated from its sister lineage), although its absence is certainly not evidence that it has not achieved individuation. One may argue, and de Queiroz inferentially does so, that the earliest definitive evidence that a lineage has become separate is that it is diagnosable (has fixed heritable differences from other lineages). The PSC (or, better, in de Queiroz's clarification, the phylogenetic or diagnosability criterion for species delimitation) is thus primary.

The adoption of the diagnosability criterion for primates by Groves (2001) and others has caused dismay in some circles, and the phrase “taxonomic inflation” has been uttered (Isaac et al. 2004; see sidebar, Taxonomic Inflation). The implication, sometimes made explicit as a kind of accusation, is that subspecies under the PSC (diagnosability criterion) are simply raised to species level without further study. This is simply not so. A little history of primate taxonomy in the twentieth century is in order.

PRIMATE TAXONOMY FINDS ITS FEET

A three-volume work, *Review of the Primates*, purporting to be a complete taxonomic revision of the order Primates, was published early in the twentieth century (Elliot 1913). The work may be characterized as part breakthrough, part chaos: breakthrough, because the order's taxonomy and nomenclature are considered in full historical context, with such essentials as type species for each genus (often designated for the first time); and chaos, because Elliot, although he did take pains to examine type specimens, appears to have examined little else, giving no idea of the variation within each species or subspecies. Elliot's lack of interest in variation by age and sex led him into error several times and even led him to describe, in the third volume, a new genus of great ape, *Pseudogorilla*, based on a perfectly normal young adult male and adult female western gorilla. Overall, one could do very little with such a false start to primate taxonomy for the new century, and any subsequent author who aspired to make a taxonomic statement on primates would have little option but to start afresh.

Overwhelmingly, that subsequent author was Ernst Schwarz. In a series of terse, succinct papers, Schwarz (1928a,b,c, 1929, 1931a,b,c, 1934) reclassified most of the primates of Africa and Madagascar; essentially, only the baboons among African primates escaped his attentions. So terse and so succinct were most of these papers that it is often difficult to work out on what basis he had made various taxonomic decisions. Yet Schwarz was clearly a first-rate taxonomist of his day, making a few silly mistakes but overall being competent and sometimes even insightful, and it is no wonder that the gist of his revisions survived until late in the twentieth century. But it must be remembered that he was indeed “of his day”—deeply embedded in the polytypic species concept. Indeed, he went further than most of his contemporaries; for him, it was necessary only that subspecies approximately replaced each other geographically, and quite large-range overlaps between subspecies were permitted. A particularly glaring example of this was his revision of

Diagnosability criterion (of the general lineage concept of species):

indicates that an evolutionary species is most convincingly recognizable if it is diagnosably different from other species

Ernst Schwarz:

mammalian taxonomist in the first half of the twentieth century; responsible for wide dissemination of the polytypic species concept (q.v.)

black-and-white colobus monkeys. These he lumped into a single species, *Colobus polykomos*. The real *Colobus polykomos* lives in the far west of Africa (mainly Sierra Leone and Liberia), but he extended his concept of this species to black-and-white colobus all over the forests of West, Central, and East Africa. He did this despite being aware of large areas of overlap between two of its subspecies (*uellensis* and *cottoni*) in the northeastern Congo and between two others (*satanas* and *occidentalis*) in west-central Africa (Schwarz 1929). The real *Colobus polykomos* he regarded as merely the species' nominotypical subspecies, which by the rules of nomenclature would take the name *Colobus polykomos polykomos*.

Colobus polykomos, sensu Schwarz (1929), is now split into at least five different species (Groves 2001), although a proper taxonomic revision may well increase this number yet again. But the legacy of Schwarz's taxonomic arrangement was long-lasting. More than 40 years later, Ohwaki et al. (1974) studied microbial fermentation in a population of leaf-eating black-and-white colobus, which they designated *Colobus polykomos*—but their specimens were from Mount Kenya and therefore belong to the species which by this time most primatologists were recognizing as *Colobus guereza*. The real *Colobus polykomos*, at the opposite end of Africa, turns out to be more of a seed eater. Literature databases have presumably nonetheless been listing the species studied by Ohwaki et al. (1974) under the name *C. polykomos*, the species they thought they were studying, and one can envisage a variety of resulting confusions [for example, other physiologists scratching their heads uncomprehendingly at discrepancies between their own findings on the real *C. polykomos* and those reported by Ohwaki et al. (1974)]. Taxonomic lumping, in such a case, has the potential to seriously mislead nonspecialists.

In this case, Schwarz's overlumping was unusual even at the time. In other cases, where his overlumping was not so extreme, errors nonetheless resulted. His taxonomic revision of Malagasy lemurs (Schwarz 1931c) yielded a total of 21 species (more than 100 are now recognized). Among the Malagasy lemurs, he recognized just two species of the genus *Propithecus*, the large jumping, bouncing animals known as Sifakas. The two species he recognized were *Propithecus verreauxi* in western Madagascar and *P. diadema* on the eastern side. Each of these in Schwarz's arrangement had several subspecies, and this classification persisted in most quarters right up to the turn of the present century. We now know that it is quite wrong. There are at least nine species; one of these, classified by Schwarz as *Propithecus verreauxi coquereli*, is now known to be not even sister to the other presumed subspecies of *P. verreauxi*, but to belong to a different clade within the genus (Mayor et al. 2004).

To recapitulate, in the case of the African and Madagascan primates, no taxonomic revisions had been done subsequent to 1934, and these early revisions were lumped to the extent of concealing genuine biodiversity and even misrepresenting affinities. Yet they held sway (with, in some cases, a little tinkering at the edges) virtually throughout the remainder of the twentieth century, even forming the basis for conservationists' species lists, constituting a spurious taxonomic stability. If the PSC (or diagnosability criterion of the general lineage concept) demanded a reexamination of the evidence, how can this possibly be "taxonomic inflation"?

For New World primates (platyrrhines), the situation is a little better because the leading authority, Philip Hershkovitz, began to change his orientation throughout his long working life. Earlier, he recognized just three species in the genus *Callicebus*, known as titi monkeys (Hershkovitz 1963); nearly 30 years later, in what he still called a "preliminary" revision, he recognized 13 species (Hershkovitz 1990). At no time, however, did he actually define his own concept of a species. The paradigm shift in the case of the New World monkeys, unlike the cases of the African and Madagascan primates, can be traced to a single publication, a monograph on marmosets by Brazilian taxonomist Mario De Vivo (1991); after this, the platyrrhine specialists, almost with one accord, and many other primatologists, dropped any pretense of following the BSC/polytypic

species concept and became diagnosability junkies (Jolly 2014; Louis & Lei 2014 and elsewhere; Rylands & Mittermeier 2014; Zinner & Roos 2014 and elsewhere; for one notable exception, see Rosenberger 2012, 2014). How interesting it was that the turnabout was due to a habitat-country primatologist.

BUT ARE THEY REAL?

Field studies on primates have blossomed in the present century, but surprisingly few have been comparative in nature. Therefore, much of the analysis of potential species differences in ecology and behavior, or in physiology for that matter, must be pieced together from different reports. I have recently tried to do this in a small way for some of the Malagasy lemurs and for the red colobus, an Old World Monkey group that has been split, by the new view of species, into many different species where there used to be just one (Groves 2014). The differences turn out to be very real. Different lemur species have different diets and, in some cases, different physiological responses to such things as seasons. Different red colobus species also have different diets, and their social organizations differ. Dry-forest species differ in group size and composition not only from rainforest species, which one might maintain could be purely behavioral plasticity, but from each other as well, which could not be.

We are finding, then, that recognition of species under the PSC (also known as the diagnosability criterion of the general lineage concept) is having a positive effect on our understanding of primates (and other mammals, at the very least). By insisting on simply identifying the units of biodiversity, it avoids spurious prejudgments of interrelationships. By splitting to the smallest diagnosable units, it avoids hiding what may be strong biological differences. And ultimately, in insisting on testability/falsifiability, it brings species recognition into the scientific fold in the Popperian sense (see below).

Much more remains to be done in the reexamination of primate taxonomy. A number of spurious species, which actually consist of two or more different species, likely still remain, presumably in different (perhaps adjoining) geographic regions. If field studies are performed on such over-lumped species, when proper taxonomic assessments are completed, our successors will have the difficult challenge of determining which of the proper, evolutionary species was or were actually intended in the old field studies.

And what are the consequences for the conservation of these species? Biology is science; conservation is (unfortunately) politically driven. It has been maintained that the consequences of the PSC for conservation are dire: “If threatened species are incorrectly split into several units and managed as such, for example in captive breeding or meta-population management, there could be unnecessary loss of genetic variation and an increased risk of extinction” (Zachos et al. 2013b, p. 35). No concrete examples of this notion were cited, and the opposite viewpoint has been put eloquently: “Modern integrative approaches have shown that [overlumping] has hidden an incommensurable number of distinctive species from conservation efforts” (Gutiérrez & Helgen 2013, p. 315). These latter authors did give a source for their claim: an often-overlooked paper by Morrison et al. (2009), which investigated cases of taxonomic change, including splitting, and found, if anything, a positive effect. Rylands & Mittermeier (2014) have also argued against the claims of a baleful influence of the PSC on conservation.

The gray-cheeked mangabeys were formerly classified in a single species, *Lophocebus albigena*. Groves (2007) reinvestigated the taxonomy and found that the “species,” in fact, consists of four distinct, allopatric species, one of them, *L. ugandae*, being almost confined to Uganda, a near-endemic of that country. This case has been featured in the Uganda press, reporting a push to strengthen the protection of Mabira Forest, the area of the species’ type locality (Ssebuyira 2013).

OBJECTIONS TO THIS VIEW OF SPECIES

This is not to say that there have not been objections, on what has been claimed to be a scientific basis as well as a political one (see above). The most elaborated paper opposing the diagnosability criterion appeared early in 2013 and was headed by a noted molecular phylogenetics practitioner (see above): “To automatically interpret diagnosable populations with no phenetic overlap in the characters studied as distinct species results in an unwarranted explosion of species numbers because even the tiniest fragments of a species can be made diagnosable if the markers have enough resolution power” (Zachos et al. 2013a, p. 3). There appears to be a misunderstanding here: As described above, the population thinking ushered in by the evolutionary synthesis of the 1930s specified that species are populations, or metapopulations, yet reference to “the tiniest fragments of a species” suggests that the authors think that, under the diagnosability criterion, species will be carved out of segments of populations (and note that the second half of the sentence is in contradiction to the first, where it is acknowledged that species are indeed populations). The authors continue: “How many ‘species’ would exist, if this rationale were applied to, say, domestic dogs or even humans? Domestic forms are particularly revealing as many races are completely different morphologically (100% diagnosability!), and yet they readily and freely interbreed” (Zachos et al. 2013a, p. 3).

Whether there are different species of modern humans was long and earnestly discussed by anthropologists, with or without specific metaphorical axes to grind, from the 1820s to the 1930s, and one might have hoped that the question had been decently buried long ago. Now it seems that we have to disinter the corpse to explain yet again that humanity forms a global population continuum; different as the extremes of the spectrum may appear to be, they form a genetic continuum, and there are no points at which this continuum can be broken into diagnosable segments, nor can it be maintained that there ever were such breakpoints, across the whole of the Late Pleistocene and Holocene history of our species. The observation that “there are differences” (see, for example, Woodley 2010), although correct, is not relevant: The diagnosability of populations, not the amount of difference, is the crux.

I cannot count the number of times that I have heard people—even anthropologists—asking whether the dog is a different species from the wolf. The conundrum of the taxonomy and consequent nomenclature of domestic animals has been abundantly discussed in the literature: “Domestic animals do not fall into a recognised and consistent system of taxonomy” (Gentry et al. 2004, p. 646), and this latter source gives references to publications where this proposition has been argued. Domestic “species” are not the products of natural selection, unlike wild species, and they are not, in any meaningful sense, species, nor are their breeds.

And that is all that the detractors can manage: exhumation of one old, long-settled argument and raising of another, more recently settled. At no point are alternative definitions of species offered, even by Zachos et al. (2013a), in their critique. Although they do mention de Queiroz’s papers on the general lineage concept, they do not cite his remarks on how lineages are delimited (see above). Nor, at any time, do they recognize that species are scientific propositions and, as such, must be testable/refutable/falsifiable, the *sine qua non* of science, and the way it is to be distinguished from pseudoscience and from metaphysical concepts, as Popper (1963 and elsewhere) argued at length. Popper, too, had his detractors, but his basic principle remains: Science must above all be testable.

Indeed taxonomy is, or should be, part of science, specifically biological science; how curious it is, therefore, that it took so long for biological taxonomists to realize that species recognitions must be scientific propositions—and how even more curious that there is such resistance to it among some biologists (none of them actually taxonomists, as far as I know).

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