SUBSPECIES, SEMISPECIES, SUPERSPECIES

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DISTINCT POPULATIONS THAT REPLACE EACH OTHER GEOGRAPHICALLY were recognized either as full species or as lower-level "varieties" or "forms" under the original Linnean taxonomy. A practical resolution of this ambiguity took place in zoology largely between about 1880 and 1920, with the recognition of an additional taxon, the geographic subspecies. Since the 1980s, the fashion has changed once more. Some systematists are again recognizing geographical replacement forms as full species, even when they blend together at their boundaries.

I. A brief history of subspecific taxonomy

A. Variation below the level of species

Since the invention of binomial nomenclature by Linnaeus, there has been a conflict between "splitters" who named more or less well-defined local populations as separate species, and "lumpers" who ignored geographic variation, and united local variants into a single species. The problem was compounded by early systematists' belief that species had an Aristotelian "essence", each fundamentally different from similar essences underlying other species. To Linnaeus' followers, it seemed important to decide which level of variation was fundamental. The term "genus" and "species" both result from Aristotelian philosophy, and although Linnaeus is usually credited with establishing the species as the basal taxonomic unit, he confused matters, after recognizing that some plant species were of hybrid origin, by suggesting that genera were a more important taxonomic level (i.e. a separately created kind) than species.

Once evolution was accepted, it became clear that variation at all levels in the taxonomic hierarchy was due to more or less similar causes; the only difference between variation above the level of genus or species and below was one of degree. Darwin realized that species could evolve from intraspecific varieties. Darwin used the term "species" in a new and non-essentialist sense: "... the complete absence, in a well-investigated region, of varieties linking together two closely-allied forms, is probably the most important of all the criterions of their specific distinctness... Geographical distribution is often brought into play unconsciously and sometimes consciously; so that forms living in two widely separated areas, in which most of the other inhabitants are specifically distinct, are themselves usually looked at as distinct; but in truth this affords no aid in distinguishing geographical races from so-called good or true species" (Darwin 1874). Darwin showed convincingly that there was no essential difference between species and "varieties"; species were simply varieties which had diverged more. However, with his term "varieties" Darwin did not clearly distinguish between polymorphic variants within populations and the identifiable geographic populations normally today considered geographic "races" or "subspecies". To Darwin the distinction was unimportant, because polymorphic variants, clinal variation, geographic races or subspecies, and "good" species formed a continuum. Darwin demonstrated that this continuum was excellent evidence for an evolutionary origin of the taxa we call species.

B. The trinomial revolution

Many systematists wished to preserve the purity of the simple genus - species binomial nomenclature, but by the 1850s, there were enormous stresses. It began to be realized that many clearly identifiable geographic replacement forms were an important intermediate stage between insignificant local variants and "good" species. Some lumped these replacement forms as varieties within species, while others continued describing these replacement forms as separate species: practices varied widely, leading to considerable confusion. Although

some Europeans had long advocated naming geographic forms as subspecies, the accumulation of major North American museum collections during the great push of colonization and railway construction westwards was probably the most important catalyst of a revolutionary new systematics. In this new approach, nomenclature consisted of a trinomial: genus - species - subspecies, which still is the dominant taxonomic practice today. The maxim was: "intergradation [at the boundary between two geographic replacement forms] is the touchstone of trinomialism". Examples from commonly observed birds which intergrade are, in North America, the eastern rufous-sided towhee (*Pipilo erythrophthalmus erythrophthalmus*) replaced in the west by the spotted towhee (*Pipilo erythrophthalmus maculatus*), and in Europe the carrion crow (*Corvus corone corone*) found in the south and west, replaced by the hooded crow (*Corvus corone cornix*) in the north and east. Among ornithologists responsible for this revolution in North America were Elliott Coues, who published a catalog of American birds in 1872 incorporating an early version of this trinomial nomenclature, in which subspecies were prefixed by "var.", and Robert Ridgway, who finally dropped the "var." in his own 1881 summary of North American bird nomenclature.

The American Ornithologists' Union soon adopted this policy, and the idea then spread to Europe, particularly England where Walter Rothschild began amassing his vast collection of birds and butterflies, and had hired excellent and productive staff, the ornithologist Ernst Hartert and the entomologist Karl Jordan, to curate and describe and the new material. Jordan was particularly important in spreading the idea of trinomial nomenclature to entomologists, and was regarded by the Rothschilds as the "clever" member of the staff. He published important papers on the theory of systematics, justifying trinomial nomenclature and the recognition of the "subspecies" as a valid, identifiable taxon in its own right. Both Jordan and Hartert were Germans who contributed to and read German as well as English journals, and in Germany a similar revolution was taking place. Thus, these systematic ideas were able to spread to the rest of Europe in a time when science was often highly parochial. The standard trinomial nomenclature for subspecies soon became established in the International Code for Zoological Nomenclature, and has remained there ever since.

C. Theories of divergence

It is hard to imagine the diversity of ideas by which the systematists of 100 years ago explained geographic variation. At that time, evolution by natural selection was far from generally accepted, in fact many believed it had been disproved. One of the most influential ornithologists of the time was Otto Kleinschmidt, who believed that all species suddenly came into being long ago, and since then had remained completely separate. Replacement forms or subspecies developed via natural selection from the main species but, in Kleinschmidt's view, subspecies could never evolve into new species as the Darwinians supposed. To distinguish his new species concept from the older one in which geographical replacements might be named as separate species, Kleinschmidt called his theory of variation the *Formenkreis* (ring of forms) theory. The *Formenkreis* theory fitted neatly with, and indeed promoted the new practices of naming subspecies and trinomial nomenclature.

In those times there were many somewhat peculiar competing explanations for geographic variation and speciation, including Kleinschmidt's non-speciation theory, J.P. Lotsy's hybridization theory, mutationism, inheritance of acquired characters, as well as natural selection. In Britain, Jordan and Rothschild argued eloquently and influentially against any new terminology (including *Formenkreis*) that had theoretical implications, and proposed incorporating as little evolutionary theory into taxonomy as possible, in view of the lack of agreement among scientists at the time. Although Rothschild and Jordan (e.g. 1895, 1903), supported by Hartert, agreed both with the nomenclatural practice of naming subspecies, and also that subspecies were valid real taxa, they argued that the Linnean term "species" should be retained for the whole group of races, and that the geographic forms were not true species, they were simply "subspecies" or incipient species.

But others felt that the term species was too emotive to be used in the new, multiple-subspecies sense. Some scientists continued following the *Formenkreis* doctrine, and had begun to name quite distinct taxa, which did not intergrade at their boundaries, as subspecies. This situation led in the 1920s and 1930s to the neoDarwinian ornithologist Bernhard Rensch scrapping the term *Formenkreis* because of its theoretical limitations, and instead substituting two new terms, *Rassenkreis* (circle of races) and *Artenkreis* (circle of species). *Rassenkreise* were again considered to be equivalent to species, composed of races or subspecies. However, now there was an additional layer in the taxonomy, of groups of *Rassenkreise* that replaced one other geographically, the *Artenkreise*. Thus an *Artenkreis* could consist of multiple *Rassenkreise*. Rensch and many others believed that the subspecies was an incipient species, of which the geographic replacement species, *Artenkreise* were a further development, until finally divergence was sufficient to allow complete geographic overlap, whereupon new *Rassenkreise* could again form.

These terms did not catch on, and most people came to the conclusion that the *Rassenkreise* were equivalent to the species referred to by Linnaeus and by Darwin. Probably a major reason that we do not use these multiple taxonomic terms is due to the prolific work published in English by another German, Ernst Mayr. Mayr had worked for Walter Rothschild, and knew Hartert. After Walter Rothschild was blackmailed by a lover, his enormous bird collection of 280,000 skins was sold in 1932 to the American Museum of Natural History, where Mayr was hired as curator. Mayr's experience of ornithology, contact with the European literature, and friendship with the geneticist Theodosius Dobzhansky (who helped to convince him of the lack of evidence for inheritance of acquired characters), lent a unique opportunity to influence the course of systematics and evolutionary biology. Mayr did not waste this opportunity. Mayr used the ideas underlying Rensch's new terms, but renamed them in English. The *Rassenkreis* became simply the true species or "polytypic" species, with its geographic races being subspecies, while the *Artenkreis* became the "superspecies", and its component parts "semispecies", i.e. not very divergent true species. Mayr successfully blended the local species concept of Poulton and Dobzhansky based on interbreeding with the geographic *Rassenkreis* idea of species, and renamed this combination of ideas "the biological species concept" (see also SPECIES, CONCEPTS OF), a term which has since remained strongly associated with Mayr's name. His many influential articles and books promoted a new program of species study, a science of the species which is with us to this day. Central to Mayr's system was the belief that discrete taxa such as species or subspecies would normally diverge in "allopatry", i.e. in complete geographic isolation (see SPECIATION).

II. The subspecies today

A. Modern views of subspecies, semispecies, and superspecies

The view of Darwin, Wallace, Rensch and Mayr that geographic replacement forms, subspecies, semispecies, which form a continuum with species, were in fact incipient species, has few critics today. Most geographic replacement species or "semispecies" which do not intergrade when they meet must indeed have evolved from previously interbreeding subspecies. Modern genetic data has done nothing to cast doubt on this idea.

However, taxonomists were now required to describe subspecies, which has never been seen as a particularly honourable or worthwhile activity in comparison with describing species, especially recently. A strong attack on the subspecies was mounted by Wilson & Brown (1953). Both were systematists working on ants, a group particularly riddled with poorly conceived trinomials at the time. Wilson and Brown argued that subspecies rarely, if ever, could be justified on the basis of multiple characters, and that therefore they were not "real taxa". The only "real taxa" were species, which in a sense were self-defining because interbreeding prevented divergent genes from flowing from one species to another. Subspecies which interbred at their boundaries, on the other hand, were not so endowed, so that genes and morphological characters could flow between them. Good examples were put forward of subspecies which undoubtedly would be hard to justify on multiple character grounds. This single paper was enormously influential on systematics in the USA, and generations of systematists trained at Harvard and Cornell, where Wilson and Brown worked, and their own many intellectual descendants, and their students' students in turn, have eschewed the practice of naming subspecies.

Through genetic studies we now know, however, that many subspecies separated by hybrid zones differ at multiple morphological, behavioural, and genetic characters (Barton & Hewitt 1985). For instance, the toad *Bombina bombina* meets its relative *Bombina variegata* across a broad front in Europe, and differs strongly in call, morphology, skin thickness, the sizes of water bodies used, and egg size, as well as in mitochondrial DNA and protein sequence. Their levels of differentiation suggest that the *Bombina* have evolved separately for many millions of years. (The two forms hybridize freely in the contact zone – although the hybrids can be shown to suffer some inviability – and so should be classified as members of the same polytypic species under the polytypic or biological species concept, but it has always seemed natural to place such well-defined forms in separate species in spite of the fact they have not truly "speciated"). This situation of multiple character changes has now been shown to be true across very many examples of hybrid zones, and gene flow can be shown to be almost completely blocked by hybrid zones such as these, in spite of abundant hybridization. Thus, while many named subspecies undoubtedly merited Wilson & Brown's scorn, genetic evidence shows that there are plenty of local replacement forms which hybridize at their boundaries but which do form "real" identifiable taxa, and are valid subspecies under the Wilson & Brown criteria.

B. Subspecies, species and conservation

This opposition among modern taxonomists to the subspecies can be traced as an influence on the recent "diagnostic" version of the phylogenetic species concept (see SPECIES, CONCEPTS OF). The adherents of this

view of species, led by the ornithologist Cracraft (1989), proposed a radical species concept so that even a single fixed character difference may define a geographic form as a separate species; multiple character justification is not considered necessary by them even at the species level. The practical result of this new concept is that many local forms are again being recognized as species. In birds and butterflies, which often have many morphologically or genetically distinct subspecies, this could easily result in a 2-10 fold increase in the number of species, or even more in some groups.

It is probable that the revision of geographic forms upwards to the level of species is being driven not only by theoretical considerations, but also by existing legislation, which proposes that "endangered species" are the valuable units to be conserved. If an area contains a taxon recognized as a species rather than just a local race, it may be seen as more valuable for conservation purposes. The potential consequences for biodiversity and conservation of the continued instability of the term "species" are detailed elsewhere (see SPECIES, CONCEPTS OF). Here I will only mention that today's conservationists are reducing emphasis on species conservation, and are becoming increasingly aware of biodiversity at all the levels of the hierarchy of life, including well-marked subspecies. Thus, the legislative need for differentiating local races as species may ultimately become less of an impetus provided that future legislation falls more into line with prevailing biological thought.

III. Further reading

Much of the historical overview in this article is covered by the excellent reviews of Stresemann (1936, 1975), Mayr (1982), Rothschild (1983), as well as by other sources already cited.

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