

## S23-1 The history of the biological species concept

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**Abstract** Populations of the same species are potentially capable of interbreeding and do not normally interbreed with populations of other species. The biological species concept (BSC) implies population thinking and models of speciation; it is process-driven, not pattern-driven. Several naturalists developed these views empirically during the course of the 19th century. The roots of these interpretations go back to the typological ideas of 18th and 17th century naturalists who stated that the constant succession of similar individuals constitutes the species, and cross-sterility preserves the distinctness of species, thus guaranteeing their permanence and fixity. A causal analysis of the BSC became possible only after the rise of population genetics during the 1930s. Several alternative species “concepts” proposed in recent years are basically guidelines for the delimitation of species taxa rather than different theoretical species concepts. The term “species” refers to the theoretical species concept, to the species category in taxonomy and to individual species taxa.

**Key words** Species, Biological species concept, Species taxa, Population genetics, Typology, Hybridization

### 1 Introduction

Ernst Mayr (1942: 120) defined biological species as “groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups”. The Biological Species Concept (BSC) is based on populations sharing a common gene pool, and reproductive isolation means genetic isolation from other species. Isolating mechanisms preserve the adaptive gene combinations of species. However, minor gene-flow between them from low-level interspecific hybridization does not affect the integrity of biological species. The BSC implies population thinking and models of speciation; it is a process driven concept. Although Ernst Mayr was not the originator of the BSC, as he himself emphasized repeatedly, his simple, concise definition and arguments led to its widespread acceptance from the mid 20th century on.

The previously applied species concept had been the typological species concept of most 18th and 19th century naturalists (Fig. 1). As Buffon (1749) had stated, “A species is a constant succession of similar individuals that can reproduce together” (Mayr, 1982). The type or essence of each species supposedly maintains their permanence and fixity. Under the typological species concept, variation is no more than the imperfect manifestation of the type and so-called “essential” characters distinguish the constant species.

### 2 Germ and growth of the biological species concept

The event which generated the paradigm shift from typological species based on the notion of essentialism to biological species based on the notion of evolution was the

appearance of Charles Darwin’s *Origin of Species* in 1859. The change-over was rapid and smooth in North America, but more hesitant and argumentative in Europe. Perceptions of the BSC developed slowly there over a long transitional period in the late 19th century (Mayr, 1957; Grant, 1994). “A solution to the problem of species diversification required an entirely new approach, and only the naturalists were in the position to find it. Leopold von Buch in the Canary Islands, Darwin in the Galapagos, Moritz Wagner in North Africa, and A. R. Wallace in Amazonia and the Malay Archipelago were the pioneers in this endeavor” (Mayr, 1991:19).

The first author to discuss briefly but accurately the nature and origin of biological species was Leopold von Buch (1819, 1825), one of the great naturalists of the first half of the 19th century. After Darwin returned from his expedition in 1836, he searched the literature on island biotas and read Von Buch’s “admirable discussion,” as he mentioned in one of his Transmutation Notebooks. He pointed out that speciation is achieved as soon as geographically separated populations reach reproductive isolation from their geographical representatives. During the late 1830s and 1840s Darwin came very close to the modern BSC, but from the 1850s he conceived species mostly by “degree of difference” rather than reproductive isolation. Even so, certain passages in the *Origin* (1859) indicate that he still appreciated the importance of biological criteria, including reproductive isolation (Kottler, 1978: 292–293).

The thread of genetic isolation reappeared elsewhere too. The Swiss malacologist Albert Mousson observed in 1849 that “If a peripheral variety does not interbreed with the basal form of the species ... then this constant variety would have to be elevated to the status of a separate



species". During the 1860s H. W. Bates and A. R. Wallace (1864: 158–159) were of the opinion that a new species would be produced "if a slight variety had become fixed as a local form, and afterwards been brought into contact with the parent species, with little or no intermixture of the two." The naturalist traveler Moriz Wagner (1868) became a vigorous advocate of the role of geographic isolation in taxonomic differentiation when he published his separation theory of evolution. He maintained that geographical isolation was necessary not only for speciation but also evolutionary change (Mayr, 1963: 485).

The theoretical views of most North American ornithologists of the late 19th century were fully in accord with the theory of evolution and they called geographical subspecies somewhat simplistically as "nascent species." Henry Seebohm (1881: X) in Britain was the first ornithologist to emphasize geographical isolation as a precondition for speciation in birds. He observed that two forms "become so far separated, that should their areas of distribution again overlap they will nevertheless not interbreed and the two species may be considered to be completely segregated." Then came Karl Jordan (1905) with the next conceptual step, the coexistence of distinct natural populations at a single locality at the same time: "The living inhabitants of a region are not a chaotic mass of intergrading groups of individuals, but ... are composed of a finite number of distinct units which are sharply delimited against each other and each of which forms a closed unit ... The units, of which the fauna of an area is composed, are separated from each other by gaps which at this point are not bridged by anything. This is a fact which can be tested by any observer."

The main ideas embodied in the biological species and of speciation had been established empirically by naturalists during the course of the 19th century (Haffer, 1992). Their causal analysis became possible, however, only after the rise of population genetics during the 1930s. Dobzhansky's endorsement of the BSC (1935, 1937) contributed to its increasing popularity; and then through Ernst Mayr's publications of 1942 and 1963, as well as those of Stebbins (1950) and Grant (1971), the BSC became one of the central tenets of the modern synthetic theory of evolution. David Lack (1944, 1949) added important ecological explanants of species and the speciation process.

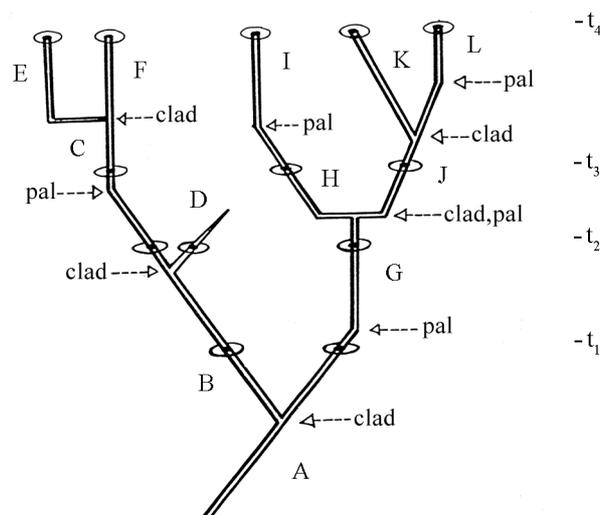
### 3 Theoretical considerations

The "horizontal" perception of biological species, as shown in Fig. 2, refers to genetically isolated reproductive communities at a particular time, whether present or past. The "vertical" life or the "duration" of a species is a matter of convention and, in most cases, determined by the incompleteness of the fossil record. Phyletic lineages through time are not involved in the processes of evolution and should not be designated as species. Phyletic evolution and speciation take place in living species populations (Bock, 1986; Szalay and Bock, 1991).

The theoretical BSC is nondimensional and can be

applied directly only to sympatric or parapatric populations of bisexual organisms. It is the multidimensional species notion in taxonomy, with its extensions over space and time, that applies to the real units observed in nature (Fig. 3) and which is subject to all the difficulties of any pragmatic application of a theoretical concept (Mayr, 1963, 1982; Bock, 1986). The distinctiveness of species becomes increasingly vague as one progresses geographically and/or chronologically farther and farther away from an area where two species occur in sympatry or parapatry. Within continents, intergradation of contiguous populations or their geographical exclusion along their contact zone (without or with restricted hybridization) determines their rank as subspecies and paraspecies, respectively. Allopatric populations are assigned subspecies or species status by inference (Mayr, 1969: 197; Mayr and Ashlock, 1991: 104–105; Helbig et al., 2002). Several alternative species concepts proposed in recent years are merely guidelines for the delimitation of species taxa rather than different theoretical species concepts.

Irrespective of their theoretical views of species, field naturalists of the 19th and 20th centuries in practice delimited species taxa narrowly, intermediately or widely according to the particular species category which they applied (Table 1). The narrow Linnaean species taxon of many 19th century ornithologists comprised only one morphologically-defined taxon, such as a subspecies of a polytypic species or a monotypic species in modern terminology. Often their reference points were only one or two specimens which supposedly represented the Platonic type of the species. Intermediates were dismissed as accidental variants or hy-



**Fig. 2** "Species" limits under the cladistic concept (clad) and the paleontological concept (pal) applied schematically to several imaginary phyletic lineages

Groups of populations representing the various lineages at particular time levels (e.g.,  $t_1 - t_4$ ) are different biological species (oval circles). Present time is level  $t_4$ . Vertical scale = geological time; horizontal scale = morphological and other biological change. A – L represent paleontological "species", except "species" C and F, which together form two cladistic "species" in one paleontological "species".

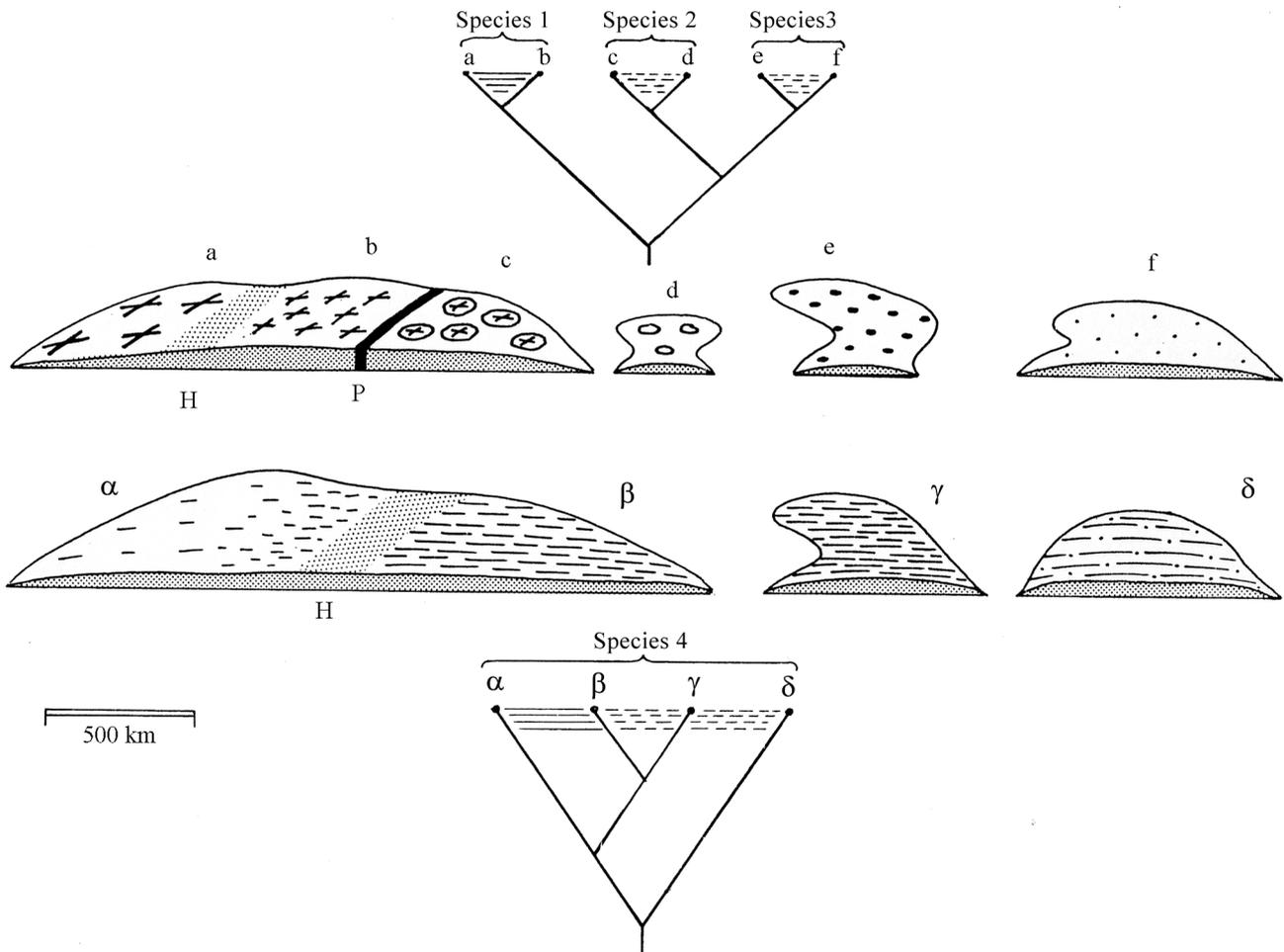
birds with no more significance than any abnormality. Such were the species of many museum workers, e.g. C. J. Temminck, L. P. Vieillot, R. P. Lesson, N. A. Vigors, C. L. Bonaparte, G. R. Gray, J. Gould, J. Verreaux, G. Hartlaub, P. L. Sclater, R. B. Sharpe, E. Dresser, H. E. Oustalet, J. Cabanis, T. Salvadori, and A. Reichenow.

Geographical population differences within a variable species, however, had been mentioned in the literature since the time of Linnaeus, Esper (the coiner of “subspecies” in 1781), G. L. Buffon, I. Kant, E. A. W. Zimmermann and P. S. Pallas (Mayr, 1963, 1982). Thus many early naturalists delimited species taxa rather widely, but without making clear whether geographical forms of species should be merely described or named formally with trinomina. As Table 1 illustrates, systematists adhering to the same theoretical species concept may delimit species taxa quite differently and systematists adhering to different theoretical species

concepts may delimit species taxa similarly.

The narrowly-defined species category in taxonomy resulted in high numbers of species taxa, mainly through the influence of the authoritative *Catalogue of the Birds in the Collection of the British Museum* (27 volumes, 1874 – 1898). Within the next 20 years, the situation changed entirely. Numerous Linnaean morphospecies were reinterpreted as subspecies and combined in more widely conceived biological species taxa. The result was a precipitous decline in the number of species recognized (Fig. 4). Several authors went too far in “lumping” geographically allopatric forms into species units. This trend was eventually halted, especially by Rensch’s (1928, 1929) emphasis on the existence of closely related allopatric or parapatric species that together form a superspecies.

A period of moderate stability for species numbers followed during the late 1930s and early 1940s, when Mayr

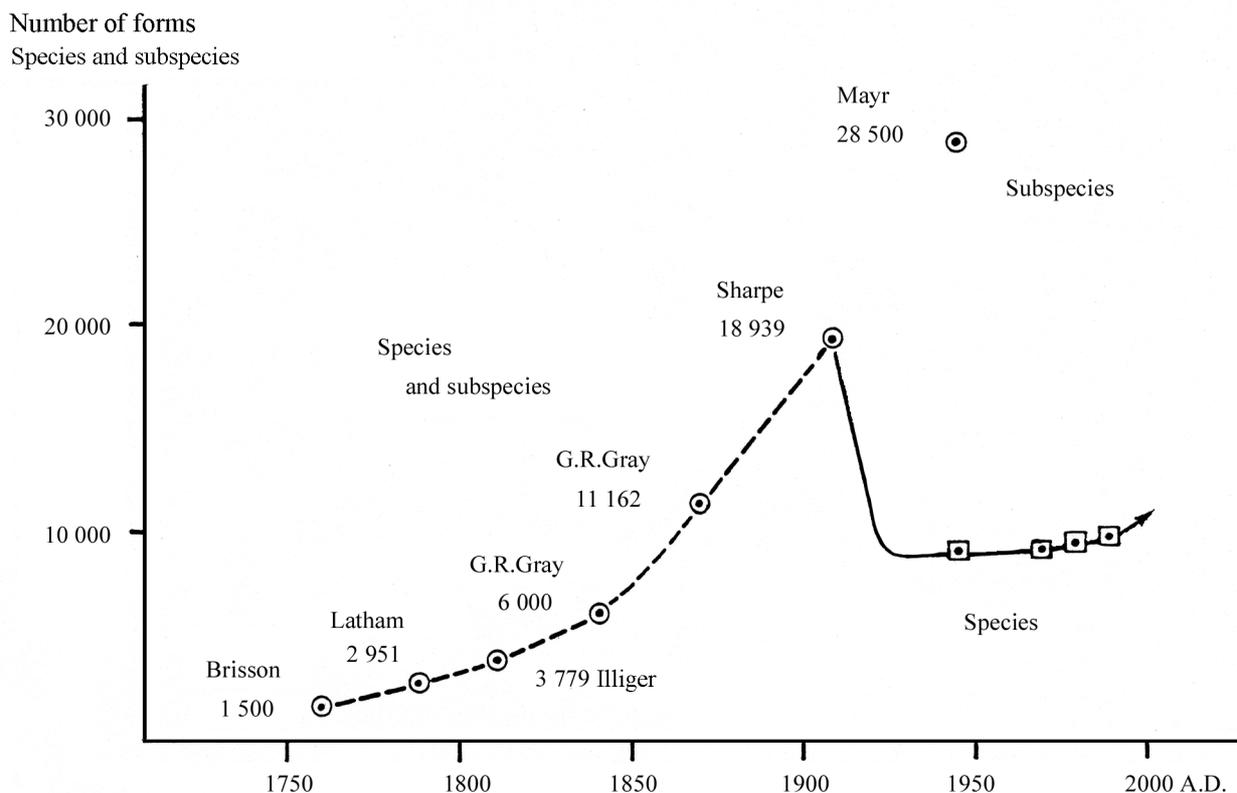


**Fig. 3** Schema of two sets of species and subspecies taxa forming one large continental unit (left) and several geographically isolated populations (right), with respective hypothetical cladogram

H = hybrid zone between subspecies, P = parapatric contact zone between species. In the cladograms, hatching indicates known intergradation (hybridization) and dashes indicate presumed hybridization. In all areas, the respective sympatric populations of these two entities are specifically distinct with respect to each other (biological species). In the upper unit, forms a and b hybridize and together represent species 1 which does not hybridize with species 2 (subspecies c and d). The taxonomic status of island populations d – f is judged by inference. Because, in the lower unit, forms  $\alpha$  and  $\beta$  hybridize freely where they meet, forms  $\gamma$  and  $\delta$  are also assumed to hybridize were they to establish contact; so all four taxa are considered subspecies of one polytypic species. Species 1 to 4 are all monophyletic.

**Table 1 Theoretical species concepts (horizontal) and species limits under different taxonomic species categories (vertical), as applied during the 19th and 20th centuries (Simplified from Haffer, 1992)**

Species category	Species concept	
	Typological	Biological
Wide	Gloger Middendorff Kleinschmidt	Hellmayr 1920s Stresemann 1919–1927
Intermediate	Brehm Schlegel Blasius	Hartert Stresemann Chapman Mayr
Narrow	Temminck Vieillot Sclater Sharpe	Stepanyan



**Fig. 4 Increases in the number of species and subspecies of birds recognized during the last 250 years**  
 Delimitation of polytypic species taxa (under the BSC) shortly after the end of the 19th century resulted in a precipitous fall, a trend halted during the late 1920s when geographically representative biospecies were recognized. From Haffer (1992).

(1946: 68) estimated the total number of known bird species to be 8 616. From the late 1940s on, many geographically isolated forms were reinterpreted as species and combined in superspecies. This “quiet revolution” (Mayr, 1980) at the microtaxonomic level led to a continuous increase in the number of bird species, only slightly boosted by the discovery of genuine new biospecies. Bock and Farrand (1980) recognized a world total of 9 021, and Sibley and Monroe (1990) 9 672. In the latter, superspecies are indicated to add an estimate of global ecological units of geographical replacement forms.

The world total of species would rise dramatically to about 20 000 bird species were species taxa to be delimited narrowly, ranking thousands of subspecies as taxonomic species. Almost all recent ornithological textbooks and all regional handbooks, however, have preferred the now traditional BSC and an intermediate delimitation of species taxa to reflect the global diversity of birds (Sibley and Monroe, 1990; del Hoyo et al., 1992; Dickinson, 2003) or of single continents (Cramp and Simmons, 1977; Brown et al., 1982; Ridgely and Tudor, 1989; Marchant and Higgins, 1990).

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