

PERSPECTIVE ARTICLE

The Wettstein tesseract: A tool for conceptualising species-rank decisions and illustrating speciation trajectories

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Abstract Genealogy-based species-delimitation approaches resting upon multilocus sequence data aim at arranging organisms into species taxa (the “grouping” step in a classification procedure), but provide no criteria for the subsequent decision of whether these taxa should be acknowledged as species in the Linnaean classification system (the “ranking” step). By integration of genealogical, morphological, ecological, and geographical patterns as proposed by von Wettstein (1898), species-rank decisions can be conceptualised in a reproducible manner and comprehensibly depicted in a four-dimensional hypercube (the herewith introduced “Wettstein tesseract”). Additionally, the Wettstein tesseract provides a tool for illustrating and teaching components and properties of speciation pathways realised in nature.

Keywords ecology; genealogy; geography; morphology; species concepts; speciation; taxonomy

■ INTRODUCTION

Classification – as an integral part of taxonomy in particular and systematics in general – consists of two operational processes: grouping and ranking (Stuessy, 1979). Owing to the paramount role of the species rank in evolutionary, ecological and nature conservation studies, the delimitation of species is therefore an essential contribution of taxonomy to biodiversity research. Conceptualised species-delimitation approaches have gained tremendous importance since multilocus sequence data became widely available in the early 2000s and resulted in a broad array of species-delimitation software programs (Smith & Carstens, 2022). Ence & Carstens (2011) proposed that species-delimitation approaches can be broadly separated into two groups or sequential steps. The “species discovery” step may be considered as being a hypothesis-generating process that aims at the detection of genealogical, morphological, or ecological discontinuities and for which a broad array of methodological and statistical tools is available. It partitions samples into groups (species) without any a priori information regarding species membership. Conversely, the “species validation” step as a hypothesis-testing process incorporates models of variation expected at and below the species level and hence is based on assumptions that are deduced from an underlying species concept. The same is implicitly true even for some “species discovery” approaches; e.g., STRUCTURE (Pritchard & al., 2000) or fastSTRUCTURE (Raj & al., 2014) that both use a Bayesian cluster

approach to assign individuals to populations while assuming Hardy-Weinberg equilibrium in each population.

Species-discovery and species-validation approaches, however, do not coincide with Stuessy’s (1979) “grouping” and “ranking” processes. In analogy to that, Zachos & al. (2020) describe alpha taxonomy as having a twofold nature and distinguish between (a) grouping organisms into species taxa using both discovery and validation approaches and (b) the subjective decision of whether these taxa should be ranked as species under the Linnaean classification system. Though only some species-delimitation approaches used in the “grouping” step are based on assumptions deduced from species concepts (e.g., the above-mentioned Bayesian cluster approaches), the “ranking” step is completely dependent on adoption of a species concept because it constitutes “an executive decision that the species taxon warrants recognition at the species level” (Zachos & al., 2020: 3). The present contribution aims at providing a guideline for this important second, “ranking” step.

The failure of providing a single objective species concept that is applicable throughout the realm of organismic diversity is a consequence of the fact that speciation is a continuous process “over a timeframe that is too long to study from start to finish” (the “speciation continuum”; Stankowski & Ravinet, 2021) and that the temporal sequence and the relative importance of the different criteria stressed in the different species concepts is variable throughout the tree of life. Following the arguments of de Queiroz (2007) the properties

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(e.g., genealogy, morphology, ecology, reproductive isolation, geography, etc.) entertained by the plethora of species concepts are not helpful in species conceptualisation but can be used in species delimitation by applying a “unified species concept”: species are here considered hypotheses of independently evolving metapopulation lineages that receive support from indicators based on a multitude of properties.

This conjoint evaluation of species-indicating evidence revitalised the process-based “biosystematics” or “experimental taxonomy” approaches to species delimitation from the second half of the 20th century (Camp, 1951; Böcher, 1970; Merxmüller, 1970; Stebbins, 1970; Stace, 1980; Hagen, 1983; Stuessy, 2009) as a more pattern-based approach termed “integrative taxonomy” (Dayrat, 2005; Will & al., 2005). The latter was conceptualised either in form of procedural protocols (Doyen & Slobodchikoff, 1974; Schlick-Steiner & al., 2010; Padial & al., 2010) or as computational tools; e.g., Geneland (Guillot & al., 2012) for the joint analysis of morphology, genetics, and geography, “multivariate normal mixtures and tolerance regions” analysis (Zapata & Jiménez, 2012; Vázquez-Cruz & al., 2017) for morphology and geography, iBPP (Solís-Lemus & al., 2015) for genealogy and morphology, or regression analysis (Hausdorf & Hennig, 2020) for genetics and geography.

■ FROM PATTERNS TO RANKING

A by far much older and to the greatest possible extent unconsidered integration of genealogy, morphology, ecology, and geography in species-level taxonomy has been proposed by von Wettstein (1898) in his seminal *Grundzüge der geographisch-morphologischen Methode der Pflanzensystematik*. Here, a formalised procedure is described for deciding between species and subspecies rank for morphologically circumscribed entities that takes into account speciation processes in an impressively modern evolutionary line of reasoning. Allopatrically distributed, morphologically similar (i.e., closely related) units should be acknowledged at subspecies level, while species rank should be attributed to closely related, but sympatrically distributed entities; von Wettstein’s (1898) argument being that only in the latter case ecological and/or reproductive differentiation between the units is sufficiently advanced to prevent merging of these lineages via hybridisation. By interpreting observed patterns (morphological and ecological discontinuities, geographical distributions) by evolutionary processes (allopatric differentiation, ecological divergence, formation of reproductive barriers, disruptive selection in sympatry) the proposed concept integrates over a number of more sophisticated species concepts proposed

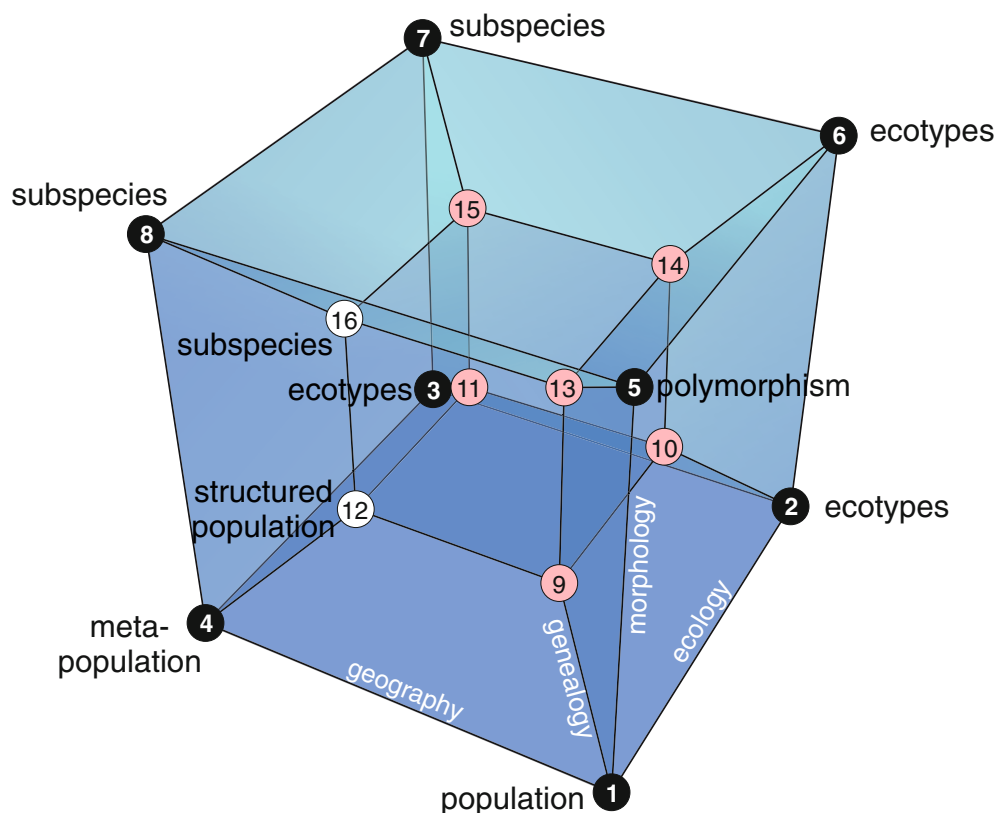


Fig. 1. The Wettstein tesseract – a four-dimensional hypercube for illustrating species delimitation and speciation trajectories, with the four dimensions representing geographical differentiation, ecological divergence, morphological difference, and genealogical independence, respectively, and species rank attributed to the vertices in red (while vertices in black and white indicate infraspecific diversification patterns without or with significant contribution of a genealogical factor, respectively).

later-on, like the evolutionary species concept of Wiley (1978: 18), which considers species being “a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate”, or the ecological species concept of Van Valen (1976), which stresses the importance of ecological differentiation among species for their geographical co-existence as independent evolutionary lineages. By its stressing of reproductive isolation between sympatric lineages as a criterion for species rank it could be also viewed upon as an early version of Mayr’s biological species concept (Mayr, 1942).

Von Wettstein’s (1898) integrative reasoning on species delimitation can be nicely summarised and illustrated by a four-dimensional hypercube (a tesseract) that represents with its four dimensions the genealogical, morphological, geographical, and ecological layers involved (Fig. 1). If only non-significant (0) or significant (1) differences in these four dimensions are considered, the vertices of the tesseract represent the 16 possible combinations of differentiations that may occur in comparisons between two closely related units for which an adequate, traceable and reproducible taxonomic ranking is intended (Fig. 2). Owing to the fact that the temporal sequence of differentiation along the four axes of the tesseract is different in the various speciation modes and leads to dissimilar temporal sequences in the applicability of the diverse bunch of species concepts (the “Gray Zone” in de Queiroz’s [2007: 882] argumentation scheme

of speciation), the vertices of Fig. 2 could be traversed along different paths or edges. This also allows the illustration of deviating trajectories speciation may take in different organism groups (i.e., allopatric, peripatric, parapatric, or sympatric speciation processes; Fig. 3), especially when the four axes are interpreted as continuous variables (see last paragraph).

Genealogical patterns. — Genealogical differentiation between two hypothesised taxa (populations or population groups) is best inferred by species-delimitation approaches based on multilocus molecular data. These could be (among many others) coalescent-based like BPP (Yang & Rannala, 2014), SNAPP (Leaché & al., 2014; Leaché & Bouckaert, 2018), or DISSECT/STACEY (Jones & al., 2015; Jones, 2017a,b) or pattern-based machine-learning techniques like consensus *k*-means clustering (Monti & al., 2003; Wilkerson & Hayes, 2010; Wagner & al., 2020). Population-genetic approaches like fastSTRUCTURE (Raj & al., 2014) or simple pair-wise F_{ST} statistics will not provide indications of statistical significance for a species-delimitation hypothesis, but will give measures for the strength of differentiation between the compared entities or may point to the occurrence of genetically intermediate individuals (hybrids). More recent developments in species-delimitation programs allow for more complex models with quantification of gene flow between populations (e.g., PHRAPL, Jackson & al., 2017; BPP, Flouri & al., 2020; DELINEATE, Sukumaran & al., 2021) and will add to the correct estimation of genealogical differentiation.

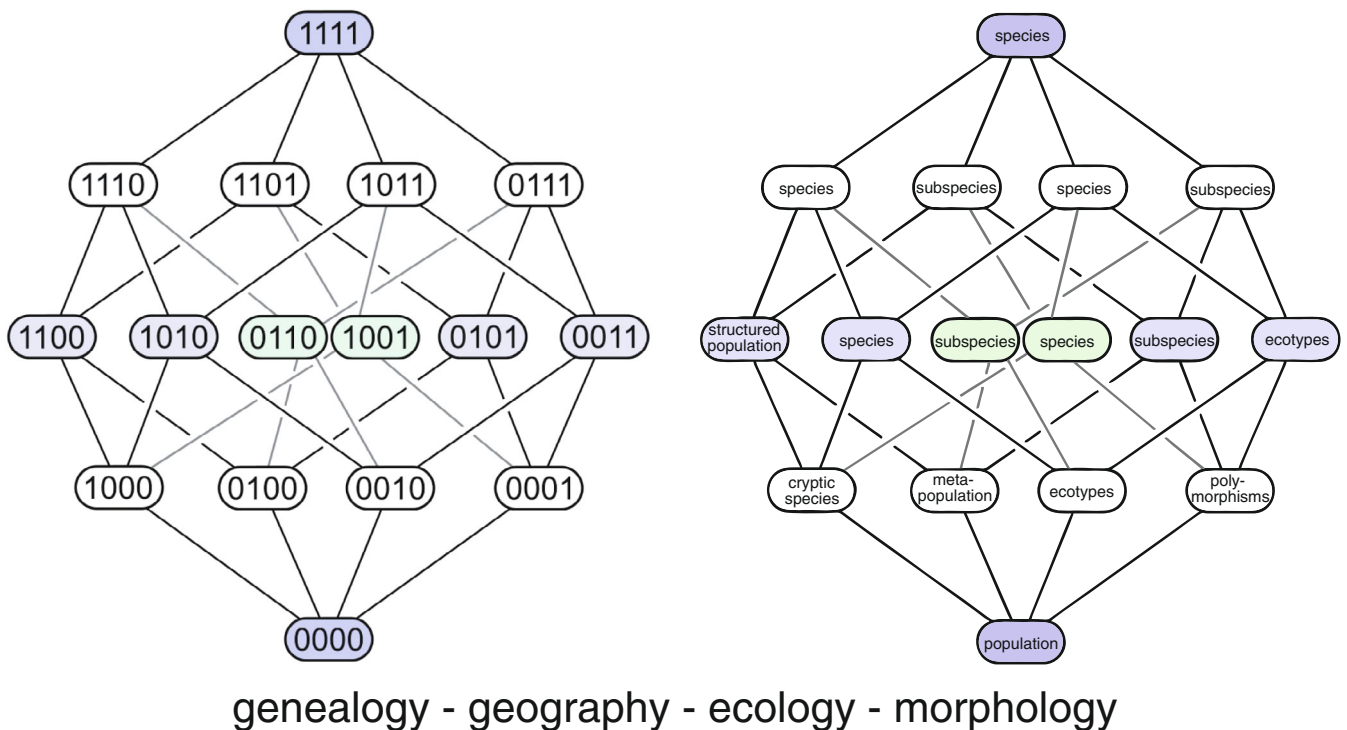


Fig. 2. The Wettstein tesseract unfolded, with vertices representing binary-coded (statistically significant) genealogical, geographical, ecological, and morphological differences between two sister-taxa under study (left) and their taxonomical counterparts (right). Colours of vertices are just for clarity of the illustration and have no semantic implication.

Morphological patterns. — Phenotypic discontinuity between taxa is best inferred by multivariate-statistic techniques like principal component analysis (PCA) or principal coordinate analysis (PCoA) and could be tested for statistical significance by multivariate permutation tests (e.g., npMANOVA, Anderson, 2001; Ott & al., 2022). Morphological differentiation in terms of both neutral traits and traits under selection may parallel genealogical differentiation among taxa. This is the rationale behind approaches using both layers together in species-delimitation analyses (as in iBPP, Solís-Lemus & al., 2015). Treating the two data types as independent dimensions of the “Wettstein tesseract” will allow specification of cases of cryptic species (genealogical discontinuity without morphological distinctness) or polymorphisms (morphological distinctness without genealogical discontinuity).

Geographical patterns. — The degree of overlap of distribution ranges of two taxa plays an important role in the argumentation scheme on species rank in von Wettstein (1898), who considers geographically motivated (allopatric, peripatric, or parapatric) differentiation as the prevailing speciation mode in plants. Gradual speciation leading to finally sympatric species via “geographical races” and allopatrically distributed “semispecies” is also considered as being an important (albeit not the only) possible pathway of speciation for Grant (1971: 48, 110). Sympatric speciation is here considered being either caused by strong disruptive selection or chromosomal rearrangements (homoploid or polyploid speciation) leading to the fast or instantaneous formation of reproductive isolation between the diverging entities, respectively. Barraclough & Vogler’s (2000) method for inferring the biogeography of speciation of a plant or animal group is in the same line of this argumentation when plotting range overlap between two sister-species against the age of their divergence to discriminate between allopatric and sympatric speciation as the prevailing speciation mode in an organism group.

Ecological patterns. — With regard to the following fourth – the ecological – dimension of the Wettstein tesseract discussed below, it is important to stress the essential difference between the terms “sympatric” and “allopatric” on the one hand and “syntopic” and “allotopic” on the other as suggested by Rivas (1964): while sympatry/allopatry refers to overall geographic distributions, syntopy/allotopy refers to what Rivas (1964) calls “ecologic distributions”. Two sympatric species may either share the same habitat (syntopy) or may not occupy the same habitat (allotopy) due to different abiotic or biotic requirements as part of their ecological niche. In both cases, however, the two entities will not interbreed at all (in the syntopic case) or only in ecotonic regions (hybrid zone formations in the allotopic case) and will evolve as independent lineages (species) due to the effectiveness of pre- and/or post-zygotic isolation mechanisms and selection-dispersal equilibria. As a consequence, in the argumentation scheme of the Wettstein tesseract, we strictly discriminate between a geographical dimension (the third axis) that could be inferred from distribution (grid) maps and an ecological one (the fourth axis) that describes the ecological niches of the two lineages for which a taxonomical ranking is pursued.

The ecology axis in the Wettstein tesseract either measures the overlap of ecological niches of two taxa (in a quantitative approach) or asks for the realisation of a statistically significant difference between the two (in a binary approach). Owing to the multi-faceted concept of an “ecological niche”, this dimension may represent both abiotic (e.g., climatological, edaphic, etc.) and intrinsic (e.g., annual or diurnal flowering times, etc.) or extrinsic biotic factors (e.g., pollinators, herbivores, etc.) that govern the co-occurrence in the same habitat (syntopy) and the reproductive isolation between the two entities under study. While similar ecological niches of two allopatrically distributed taxa may indicate the potential for interbreeding (and genealogical merging) of the two entities after

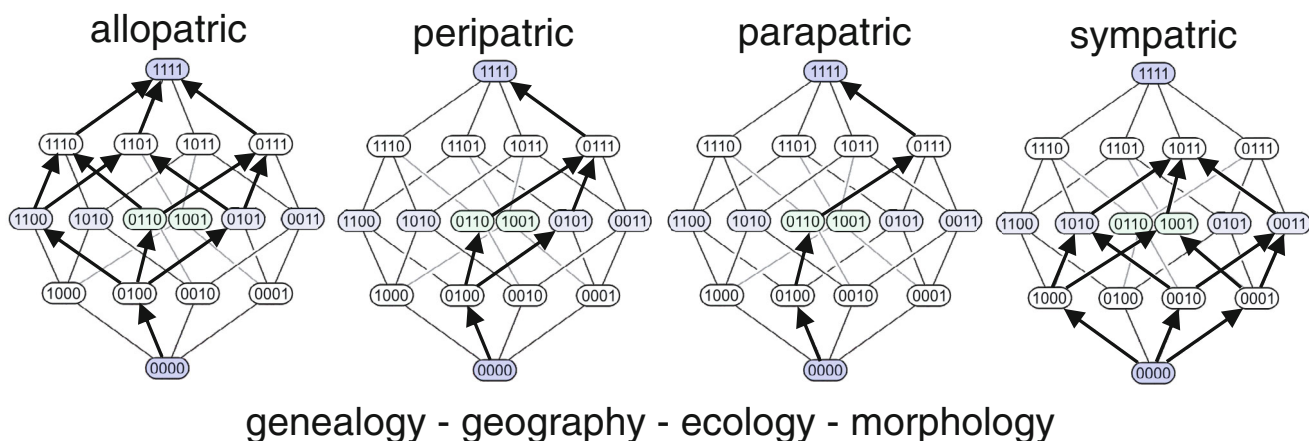


Fig. 3. The Wettstein tesseract as a tool for illustrating geographical (allopatric, peripatric, parapatric) or non-geographical (sympatric) pathways of speciation. Arrows indicate different paths through the tesseract from a coherent population to final stage of two evolutionary independent entities (species). Note that these paths end whenever species rank is achieved; subsequent changes of biogeographical patterns (allopatrically, peripatrically, or parapatrically formed species becoming sympatric and sympatrically formed species becoming allopatric) are not illustrated.

establishment of sympatry (and hence syntopy), significantly different ecological niches will allow sympatric co-existence of the two as independently evolving lineages (species). Therefore, the ecological species concept of Van Valen (1976) is equally accounted for here as is the “potential to interbreed” (and not the actual interbreeding) in some versions of the biological species concept of Mayr (1942: 120). The ecological axis of the Wettstein tesseract, therefore, may not only comprise ecological aspects but also genetic and genomic aspects of reproductive isolation and could be experimentally approached with a diverse toolkit as exemplified by Ramsey & al. (2003) or Husband & Sabra (2004).

With regard to the Wettstein tesseract as a taxonomic tool, the present proposal contributes to the conceptual discussions on species and infraspecific ranks in botanical systematics given by Stuessy (2009, 2014), who provides a comprehensive historical treatment of the topic and gives some recommendations that are considerably overlapping with the present one. Following this author and common botanical-taxonomic practice, the categories “subspecies”, “variety”, and “form” are considered sufficient to capture infraspecific variation in a formal classification scheme. However, the present approach differs somewhat from the criteria for distinguishing these categories given by Stuessy (2009: 158, table 12.1; 2014: 305, table 20.1). While both classification and ranking schemes stress the importance of geographical patterns, the morphological distinctness of taxa is considered less pivotal in the present approach. On the other hand, genetic divergence and genealogical independence is nowadays much easier to infer than decades ago and should be given a more pronounced role in taxonomic decisions. While following Stuessy (2009, 2014) in attributing subspecific rank to geographically cohesive, allopatrically or peripatrically distributed population groups within species, the ranks of “variety” and “form” are considered here for morphologically and/or ecologically distinct taxa being geographically non-cohesive (i.e., sympatric in terms of overlap of outlines of distribution ranges and therefore termed “polymorphisms” or “ecotypes” in the Wettstein tesseract). A distinction between the latter two taxonomic ranks could be drawn with regard to either the homogeneity of local populations in a morphological and/or ecological feature (variety) or the sporadic appearance of deviating individuals within polymorphic or ecologically diverse populations (form).

■ ILLUSTRATING SPECIATION PROCESSES

Besides supporting pattern-based conceptual clarification and argumentation schemes with regard to species delimitation and taxonomic decisions on species and infraspecific ranks, the here-presented Wettstein tesseract could be also helpful for illustrating the different speciation trajectories realised in different organism groups in a process-based manner (Fig. 3). In geographically motivated speciation modes (allopatric, peripatric, parapatric speciation), an initial phase as a

metapopulation system is followed by a genealogical (structured population system), ecological (ecotype, subspecies), and/or morphological (subspecies) differentiation phase, that culminates in first allopatrically and later-on (partly) sympatrically distributed species. In the peripatric case, genetic drift in the small founder population and strong selection pressures due to the novel environment encountered leads to even accelerated morphological and ecological divergence from the source population in addition to its gain of genealogical independence. Conversely, in the highly problematic case of parapatric speciation (see Coyne & Orr [2004: 111ff.] for a discussion on the challenging proof of this speciation mode in reality), the ecological differentiation along clinally varying environmental conditions will predate any morphological divergence. Finally, sympatric speciation may follow a pathway via cryptic species (e.g., in the case of autopolyploid species formation, where the instant emergence of reproductive isolation is not paralleled by immediate morphological or ecological divergence) or via divergent selection in ecologically and/or morphologically polymorphic populations (ecological speciation; Nosil, 2012).

Speciation pathways in the Wettstein tesseract become more realistic when along all four dimensions differentiation of two taxonomic units is allowed to take intermediate values, treating them as continuous and not binary characters. Differentiation trajectories will then pass through the four-dimensional hypercube as a string of dots with time being the fifth dimension comparable to populations in De Finetti plots and adaptive landscapes in population genetics (Hamilton, 2009). Additionally, the vertices representing the taxonomic ranks of species, subspecies, or varieties/forms will then expand into the four dimensions as regular or irregular volumes, whose borders will be debatable and different from organism group to organism group and from taxonomist to taxonomist. However, when feeding the Wettstein tesseract with expert knowledge from many settled taxonomies in diverse organism groups following a machine-learning logic, one may hope for a steady growth of objectivity in taxonomic decisions. Yet, even if this appears overly optimistic to those who have given up hope for objectivity in taxonomy and have grown fatigued with the metaphysics of species concepts, the Wettstein tesseract may at least help as an auxiliary tool or conceptual rail in species-rank decisions and as a visual aid in teaching and illustrating speciation processes.

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