


A paradigm shift in our view of species drives current trends in biological classification

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ABSTRACT

Discontent about changes in species classifications has grown in recent years. Many of these changes are seen as arbitrary, stemming from unjustified conceptual and methodological grounds, or leading to species that are less distinct than those recognised in the past. We argue that current trends in species classification are the result of a paradigm shift toward which systematics and population genetics have converged and that regards species as the phylogenetic lineages that form the branches of the Tree of Life. Species delimitation now consists of determining which populations belong to which individual phylogenetic lineage. This requires inferences on the process of lineage splitting and divergence, a process to which we have only partial access through incidental evidence and assumptions that are themselves subject to refutation. This approach is not free of problems, as horizontal gene transfer, introgression, hybridisation, incorrect assumptions, sampling and methodological biases can mislead inferences of phylogenetic lineages. Increasing precision is demanded through the identification of both sister relationships and processes blurring or mimicking phylogeny, which has triggered, on the one hand, the development of methods that explicitly address such processes and, on the other hand, an increase in geographical and character data sampling necessary to infer/test such processes. Although our resolving power has increased, our knowledge of sister relationships – what we designate as species resolution – remains poor for many taxa and areas, which biases species limits and perceptions about how divergent species are or ought to be. We attribute to this conceptual shift the demise of trinomial nomenclature we are witnessing with the rise of subspecies to species or their rejection altogether; subspecies are raised to species if they are found to correspond to phylogenetic lineages, while they are rejected as fabricated taxa if they reflect arbitrary partitions of continuous or non-hereditary variation. Conservation strategies, if based on taxa, should emphasise species and reduce the use of subspecies to avoid preserving arbitrary partitions of continuous variation; local variation is best preserved by focusing on biological processes generating ecosystem resilience and diversity rather than by formally naming diagnosable units of any kind. Since many binomials still designate complexes of species rather than individual species, many species have been discovered but not named, geographical sampling is sparse, gene lineages have been mistaken for species, plenty of species limits remain untested, and many groups and areas lack adequate species resolution, we cannot avoid frequent changes to classifications as we address these problems. Changes will not only affect neglected taxa or areas, but also popular ones and regions where taxonomic research remained dormant for decades and old classifications were taken for granted.

Key words: anthropocene, conservation, species concept, species delimitation, species resolution, phylogeny, subspecies, taxonomy, tokogeny, tree-thinking

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I. INTRODUCTION

“Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation.” (Darwin, 1859, p. 486).

Biological classification – the system of names that represents our understanding of Earth’s past and present species diversity and their affinities – provides a communication infrastructure that facilitates connections across scientific disciplines and serves broader societal goals such as conservation and regulation of trading in natural resources. Familiar classifications have experienced considerable change in recent times as taxonomists and other biologists addressed particular problems, and although changes in names and the content of taxa are not the purpose, they are indispensable for precise communication about our understanding of species diversity and their relationships. Changes are therefore generally trusted and reflected in major biodiversity repositories such as the IUCN *Red List*, GenBank or the Global Biodiversity Information Facility (GBIF), but because of their disruptive effects at the user end, they give rise to intermittent complaints and disputes between taxonomists and users of classifications (e.g. Isaac, Mallet & Mace, 2004; Köhler *et al.*, 2005; Padial & De la Riva, 2006; Sangster, 2009, 2014; Heller *et al.*, 2013; Cotterill *et al.*, 2014). To take one recent example, Garnett & Christidis (2017) argued that taxonomy has gone off course and called for the control of classification through rules and regulatory committees overseen by the International Union of Biological Sciences (IUBS), triggering a heated debate (e.g. Buckeridge, 2017; Cotterill, Groves & Taylor, 2017; Dijkstra, 2017; Hollingsworth, 2017; Jackson, Scherz & Zona, 2017; Lambertz, 2017; Takeda, 2017; Thomson *et al.*, 2018; Zachos, 2018; Taylor, Denys & Cotterill, 2019; Zachos, Christidis & Garnett, 2019; Garnett *et al.*, 2020).

Taxonomists are in general not fond of taxonomic changes themselves, and measures to increase stability of taxon names or attenuate the effect of changes fill nomenclatural codes and are promoted by taxonomists every time the practice of classification finds itself in a state of flux. For example, taxonomists have consistently cautioned about the proliferation of subspecies driven by the arbitrary partitioning of continuous geographical variation (e.g. Huxley, 1942; Burt, 1954; Gillham, 1956; Frost & Hillis, 1990; Zink, 2004; Hillis, 2019) and, early on, Wilson & Brown (1953)

encouraged substituting subspecies for vernacular names to refer to local variation instead of endowing each variant form of unknown nature with implications and expectations associated with Linnaean trinomials. When DNA barcoding raised concerns about the proliferation of changes to species taxonomy that the use of a single short fragment of a rapidly evolving mitochondrial gene could promote by conflating the histories of mitochondrial lineages with those of species, taxonomists contended that rigorous inference of species limits requires concerted evidential support from the evolutionary histories of various genomic and phenotypic traits (e.g. Dayrat, 2005; DeSalle, Egan & Siddall, 2005; Padial *et al.*, 2010; Padial & De la Riva, 2010; Schlick-Steiner *et al.*, 2010; Hillis, 2020). In the same spirit, the surge of phylogenetic hypotheses challenging many long-standing supra-specific classifications stimulated proposals to increase the stability and content of taxon names (e.g. Wiley, 1979; De Queiroz & Gauthier, 1992; Vences *et al.*, 2013).

All such proposals agree on the need to avoid unnecessary change, but are mindful about the empirical nature of classification and are conscious of the often unfinished work concealed under the worn-out carpet of stable names. They acknowledge that classification is susceptible to assumptions as well as to the testing and re-testing of new and old evidence about the limits and affinities of species – evidence that is not only limited but also subject to methodological and conceptual biases and which requires constant monitoring.

Our purpose is to explain how our current understanding of the nature of species affects changes in the classification of species and subspecies, as these are the categories for which higher stability is demanded. We contend that changes do not stem from taxonomy going astray, but are driven by a paradigm shift in evolutionary biology that compels us to conceive species as the phylogenetic lineages that form the branches of the Tree of Life, coupled with unprecedented access to evidence and new analytical tools to infer the origin and limits of these lineages.

It is undeniable that taxonomic changes can be the result of bad practice and that social factors – the rush to publish, the desire to attach one’s own name to the names of taxa or to release a new classification for everyone to cite it – sometimes lead to pointless taxonomic changes, unnecessary or inadequate, that could have waited for better evidence or be avoided altogether. There are also unintentional biases in the handling of evidence, assumptions and methods, associated with the immature stages of a paradigm shift. But, as we will contend, we should look at current trends with hope,

for even if far from perfect, correspondences between species names and species limits should become increasingly consistent with theory about species, speciation, and the nature of trait variation. Another positive aspect of this conceptual shift is that classification is now decreasingly authoritative and increasingly empirical, with species limits being tested by taxonomists and other biologists alike, thus providing a fair and rigorous framework for research and conservation.

Note that we will use the term ‘phylogeny’ to refer to the general process of species cleavage that results in a genealogy of species — the branches of the Tree of Life (Hennig, 1950, 1966, 1975). This notation is similar to the original definition of speciation as “the origination or multiplication of species by subdivision” (Cook, 1906, p. 506), but we use speciation in its modern sense as the set of biological processes and external factors that promote the formation of each particular species. Phylogeny as a process should not be conflated with tree-like representations such as cladograms or phylogenetic trees (colloquially referred to as ‘a phylogeny’ or ‘phylogenies’). Although the process of phylogeny is represented by trees and cladograms, not all tree-like diagrams represent phylogeny because not all lineages are species (e.g. gene lineages, cell lineages, colonies, families, etc.). Only a hypothetical tree of species represents phylogeny while phylogenetic trees built on multiple genes and/or phenotypic traits constitute empirical approximations to the species tree.

II. THE ORDER OF THINGS

“As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications.” (Darwin, 1859, p. 130).

Biological classifications are powerful abstract tools that communicate our understanding of the diversity of life. Every culture develops more or less complex classifications to denote the living beings with which it coexists (folk taxonomies), which suggests a universal cognitive ability to construct and reinforce language categories that capture not only what is similar and what is different among the objects of our experience, but their abstract relations as well (Atran & Medin, 2008). These categories in turn shape the way we see things by, for example, reinforcing our perception of similarity among objects in a category and exaggerating differences between those in different ones (Goldstone & Hendrickson, 2010). Thus, by thinking about what we see in terms of how we see it, and seeing it in terms of how we think about it, we develop and reinforce common-sense ideas about the identity of the objects of our experience that are not necessarily objective (Atran, 1985, 1993). This is best exemplified by the notion of species (from the Latin term *specere*, to look, which refers to appearance or form), which is

widely used across cultures in a field-guide fashion (‘these things are different from those in such and such way’) with varying levels of detail.

Our biological classifications also reflect our perceptions of nature as a whole and our position in it, mirroring the dominant ideologies of our time. During the Enlightenment, for example, when scientific biological classification began to take shape, the study of similarity and difference, of essential and superfluous traits, sought to describe and support an observable natural order envisaged as a hierarchical, continuous and progressive *Scala Naturae* (Great Chain of Being) that led inexorably to the human – the pinnacle of creation (e.g. Bonnet, 1745; Lamarck, 1809; see Lovejoy, 1936; Foucault, 1994; Stevens, 1994; Müller-Wille, 2015) (Fig. 1). It was within this ideological climate that Linnaeus developed his *Systema Naturae*, a system of classification that triumphed over all others because of its ability to convey in language and representation the observed hierarchical structure of the living and inanimate world. It was the order assumed by the *Scala Naturae* that dictated the purpose and goal of classification: to disclose the continuous nature of affinities between organisms revealed through the number, shape, proportion, and situation of their most essential parts (Bremekamp, 1953; Larson, 1967; Atran, 1993; Stevens, 1994). Classification merely reflected a given order of things. Traits observable in their bodies provided the necessary clues; as Linnaeus wrote in his *Systema Naturae*, the naturalist merely “distinguishes the parts of the natural bodies with his eyes, describes them appropriately according to their number, form, position, and proportion, and he names them.” (quoted in Foucault, 1994, p. 215). The ideas of Buffon and Lamarck, with natural processes and time as central presumptions of the observed patterns, did not question the logic of the Great Chain of Being (Lamarck, 1809; Sloan, 1979; Foucault, 1994; Stevens, 1994; Müller-Wille, 2015), it was Darwin’s (1859) metaphor of a budding tree that finally pushed naturalists to reconsider the causes and shape of the apparent order of life.

The quotation above from Darwin (1859, p. 130) shows the dawn of the paradigm shift that is slowly replacing both common sense notions of species and higher groups and the abstract ideas of levels and progress that dominated biological classification in the time of Linnaeus. With Darwin, species started to be thought of as the lines of descent of an ever-branching and erratic genealogy of life (Fig. 2). During the 20th century the view of species as either fixed or as convenient partitions of continuous organismal diversity were replaced with the notion of species as discrete entities, reproductive communities discoverable through empirical evidence (e.g. De Vries, 1904; Dobzhansky, 1937; Mayr, 1942), which, extended back in time, formed branching evolving lineages of organisms connected by descent (Hennig, 1950, 1966; Simpson, 1951; Wiley, 1978; Frost & Hillis, 1990; Frost & Kluge, 1994; Mayden, 1997; De Queiroz, 1998), entities with large spatiotemporal dimensions and shifting limits, of which we can observe only a tiny fraction of the organisms that comprise them. Take for

IDEE D'UNE ECHELLE
DES ETRES NATURELS.

L'HOMME.
Orang-Outang.
Singe.
QUADRUPÈDES.
Ecureuil volant.
Chauve-souris.
Autruche.
OISEAUX.
Oiseaux aquatiques.
Oiseaux amphibies.
Poissons volans.
POISSONS.
Poissons rampans.
Anguilles.
Serpens d'eau.
SERPENS.
Limaces.
Limaçons.
COQUILLAGES.
Vers à tuyau.
Teignes.
INSECTES.
Gallinées.
Termites, ou Solitaires.
Polypes.
Orties de Mer.
Sensitives.
PLANTES.
Lichens.
Mouffures.
Champignons, Agarics.
Truffes.
Coraux & Coralloïdes.
Lithophytes.
Amianthe.
Talcs, Gyps, Sépénites.
Ardoises.
PIERRES.

Fig 1. The *Scala Naturae* (Great Chain of Being) represented nature as a hierarchy of continuous relationships from the most simple to the most complex. This idea influenced classification thinking until the late 19th century (from Bonnet, 1745).

example *Homo sapiens*, which cannot be said to be the group of currently existing people, or that it always existed in its present form, nor that anyone has ever seen or will ever see *Homo sapiens*; you shall, during your short contribution to the existence of our species, encounter a few organisms that, just like you, are not *Homo sapiens* itself but ephemeral parts of it.

Historical organismal lineages such as ours have been identified through all life forms. In prokaryotes they show differences compared with eukaryote species in terms of cohesion, trait evolution, and mechanisms of gene exchange (Woese, 2000; Gogarten, Doolittle & Lawrence, 2002; DeSalle & Riley, 2020). Even though we have traditionally applied binomials to both eukaryote and prokaryote organismal lineages, they may refer to different kind of historical lineages. The terms ‘prokaryospecies’ and ‘eukaryospecies’ could perhaps be used to refer to the different kinds of cohesive lineages that originate as a result of the way organisms reproduce. To be sure, there are other kinds of lineages within eukaryotes that are not, but evolve from, phylogenetic lineages of sexually reproducing organisms and that are still called species for practical rather than ontological reasons [e.g. uniparentals (see Frost & Wright, 1988; Frost & Hillis, 1990)].

This paradigm shift is still underway and undergoing revision, but the view of species as the branches of the tree of life pervades our world view. Evolutionary trajectories of lineages such as ours, their origin, diversification and extinction, is what gives form to the abstract hierarchy that underlies the necessarily imperfect metaphor of the Tree of Life. This notion has brought humans from the top of the divine ladder down to a rather small branch from where we witness in distress the unfolding ecological disaster caused by our species. The very idea of an Anthropocene, and for that matter of any other geological period, also entails a genealogy of species not as human abstractions but as real complex wholes (hyperobjects in the emerging terminology around the Anthropocene; Morton, 2013), systems woven by phenomena, endowed with unique properties and with beginnings and ends and enough agency to modify the climate or drive other species to extinction. Likewise, the growth and pruning of this Tree of Life – species diversification and extinction – emerge as factual processes that shape the history of life into successive episodes of which the Anthropocene is but the latest. Processes and history have supplanted ideas of a fixed order and ideal abstractions of ranks, of unbroken continuity and progress, and with it our claim for a position of honour within the order of things.

III. A BRIEF GENEALOGY OF PROGRESS

The metaphor of the budding tree replaced the metaphor of a ladder that inspired the Linnaean system, yet contemporary classifications retain the hierarchical structure of the system because it captures, in a more or less rudimentary form, a “truly wonderful fact” (Darwin, 1859, p. 128), a genealogy of evolving lineages. Darwin realised, for example, that Linnaeus’ grouping of *Homo sapiens* with apes and within primates made sense not because it revealed an order instituted in the Creation, but because it reflected relatedness of lines of descent that had departed from an ancestral species through the action of organic evolution (Winsor, 2009; De Queiroz, 2011). What Linnaeus’s System had comprehended was not the successive layers of the *Scala*

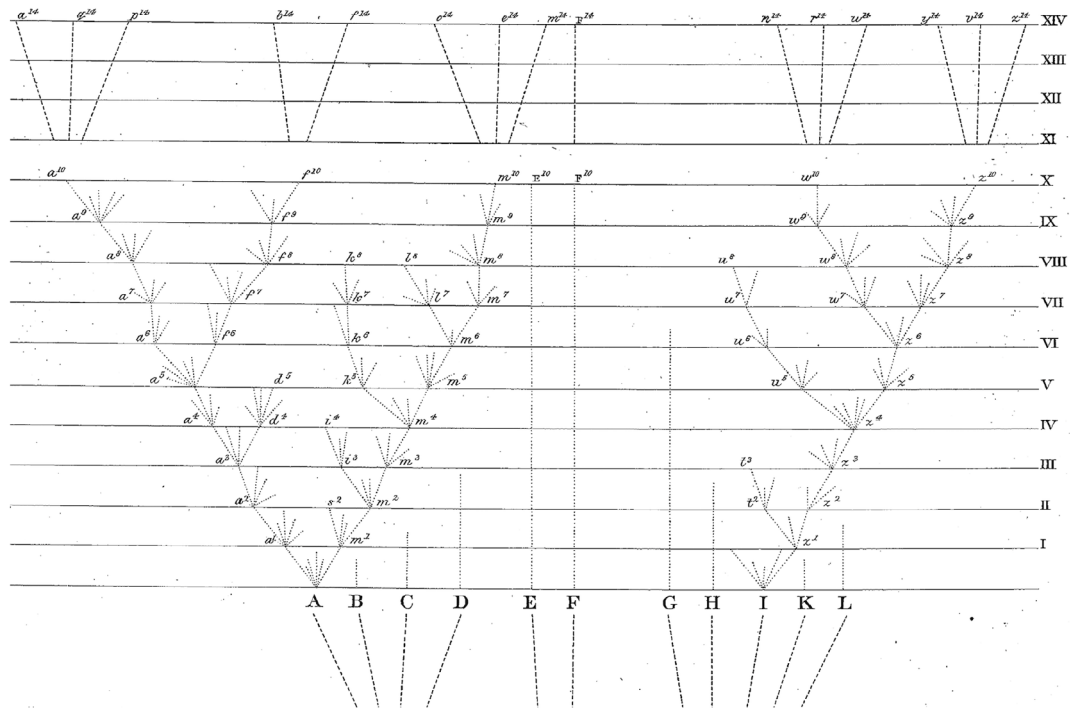


Fig 2. Darwin’s (1859) sole diagram in the *Origin of species* representing the lines of descent of ancestral genera (A–L) departing through the effects of natural selection acting on existing variation.

Naturae but a natural genealogy of departing lines of descent within the unity of life. As Darwin (1859, p. 420) put it, “community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike”. Darwin was so convinced of his own insight that he did not hesitate to announce that “classifications will come to be, as far as they can be so made, genealogies” and that these would one day be reconstructed by “characters of any kind which have long been inherited” (Darwin, 1859, p. 486).

As reservations about organic evolution subsided, the shifting branches of the budding evolutionary tree replaced the stacked layers of the Great Chain of Being (for an historical analysis of tree representation, see Stevens, 1994; Tassy, 2011) (Fig. 3). Yet for a 100 years, biologists would fail to develop a rigorous method to transform observations of trait variation into rigorous hypotheses of genealogical descent (Fig. 4). The metaphor of the Tree of Life finally took empirical form with Hennig’s (1950) *Foundations of a theory of phylogenetic systematics* – the bedrock of tree-thinking –, in which Hennig succeeded both in establishing the basic tenets of phylogenetic systematics and in developing a method to infer lines of descent by heritable characters of any kind (Hennig, 1950, 1966). Hennig’s phylogenetic theory also solved one of Darwin’s most pervasive problems: the problem of species. For although Darwin conceived species as departing lines of descent, he hesitated about the equivalence between these lines of descent and the taxonomist’s ranking of them as species, subspecies and races (see Hull, 1965;

Stamos, 2007; De Queiroz, 2011). For Darwin, any geographic variant produced by natural selection was indicative of the existence of a line of descent or an incipient line of descent and, as a result, classifying them as either species, varieties and races made no difference. Hennig, following the geneticists of the Modern Synthesis, clarified this issue by distinguishing between two different processes affecting geographic variation, tokogeny and phylogeny, describing the different patterns of trait variation they produced, and identifying the entities involved in such processes (Fig. 5). He distinguished, on the one hand, interbreeding among organisms (tokogeny) and, on the other hand, the formation of phylogenetic lineages through the prolonged isolation of generations of populations (phylogeny). At a practical (empirical) level the key difference between these two processes resided in the different patterns in trait variation that they produce as a result of reproduction/isolation. Thus, the anastomosis of population lineages, merging and departing recurrently, results in inferences of polymorphous or scattered patterns of trait variation (reticulated). On the other hand, prolonged isolation and limited or no interbreeding among organisms of different population lineages produces hierarchical patterns in trait variation that can be traced back to the time when they were still connected. Hennig’s method of phylogenetic reconstruction assumed therefore a correspondence between the hierarchical structure in trait variation (lineages of traits, i.e. homology) and the history of species as phylogenetic lineages, from which he deduced that the reconstruction of the homologous transformations of traits provided empirical approximations to the origin and

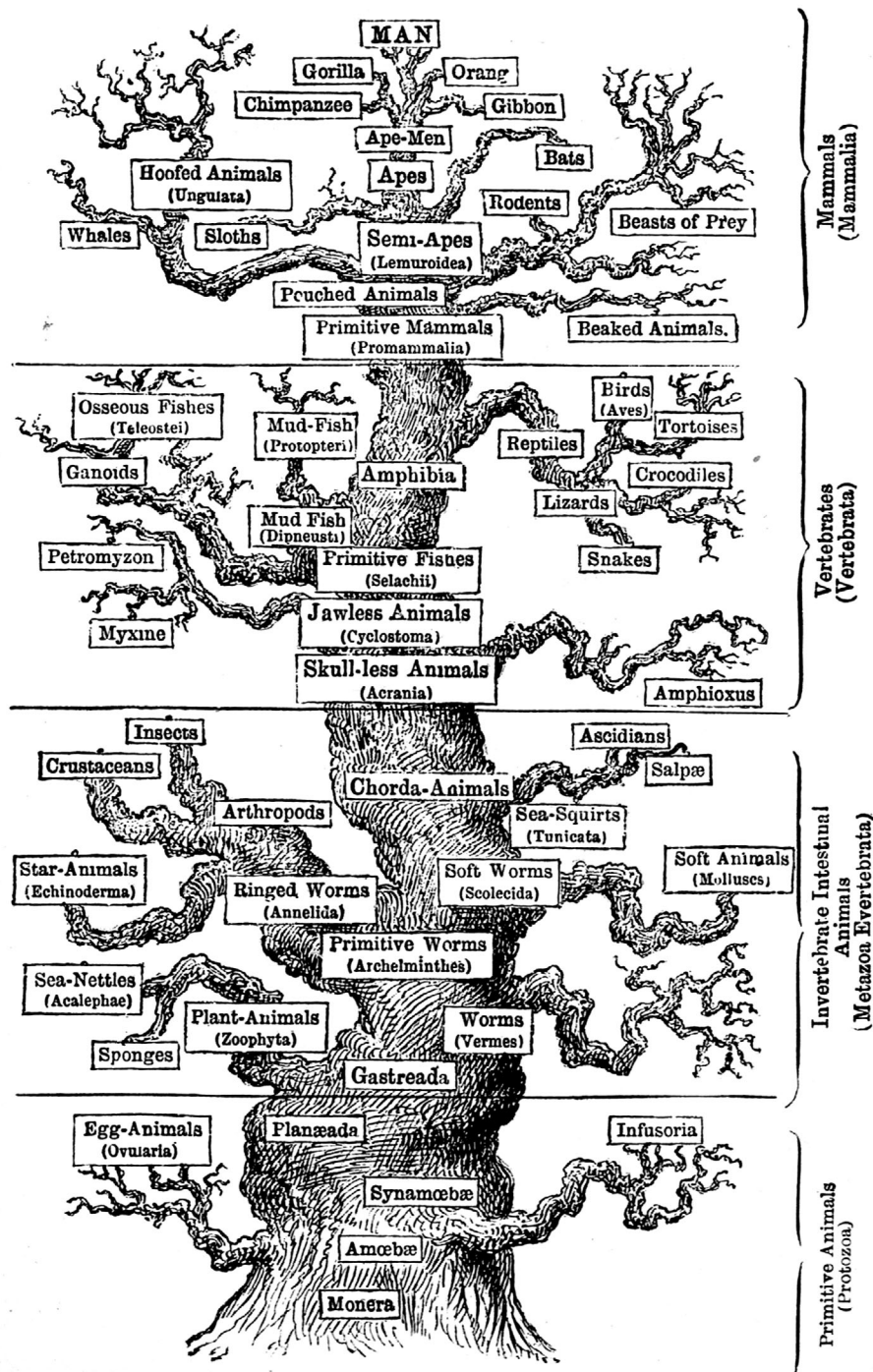


Fig 3. Darwin's metaphor of a genealogical Tree of Life represented by Haeckel (1897) in the first edition of *The Evolution of Man*. Note that Haeckel's diagram retains the teleological and hierarchical assumptions of the Great Chain of Being. For example, Primitive Animals, Invertebrate Intestinal Animals, Vertebrata, and Mammalia, exist both in the present and as levels of the ladder, and form a progression that culminates with 'Man'.

relationships of species (the species tree), testable by addition of more species and traits.

Although Hennig's and the Modern Synthesis' view of species have often been portrayed as conflicting (e.g. phylogenetic *versus* biological species concepts), they are more different in form than

in content (see De Queiroz, 2005). Hennig's ideas drew on findings in population genetics (e.g. Dobzhansky, 1935), that refuted the old idea that variation was continuous and that species were more or less arbitrary partitions of variation (e.g. de Vries, 1904); he understood a certain kind of discontinuous variation as

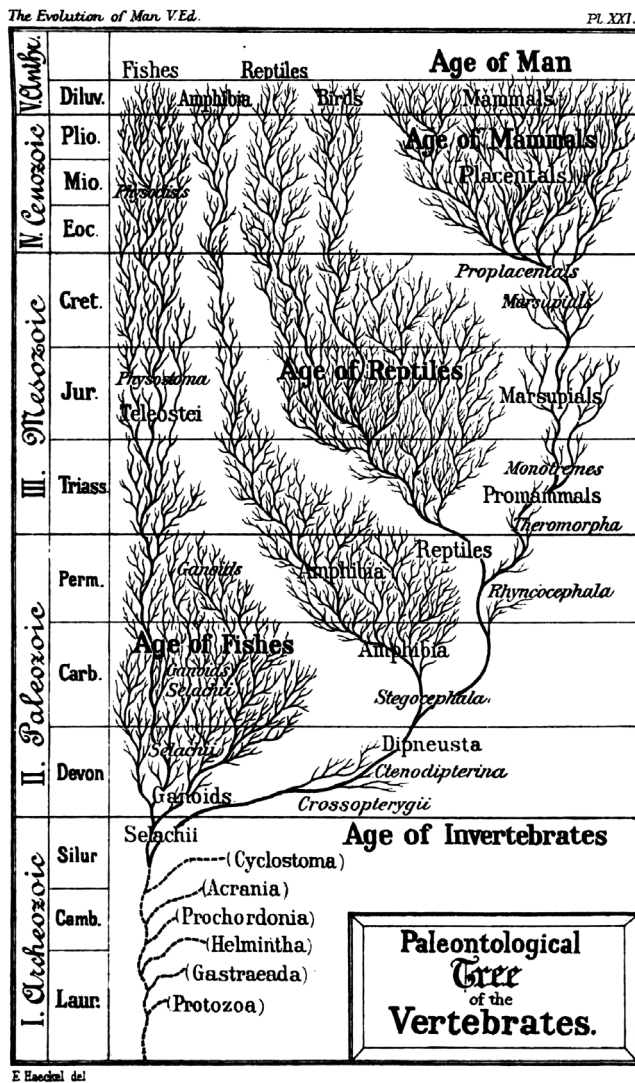


Fig 4. By 1910, in a new edition of *The Evolution of Man* (Haeckel, 1910), evolutionary thinking had eroded the logic of the Great Chain of Being and the Tree of Life had become an abstract representation of genealogical lineages changing in a non-directional way. The vertical axis now represents time and not levels of a hierarchy. Lineages that exist in the present are represented at the same level of the tree as the terminal branches, while their ancestors lie in the past. The hierarchy is no longer established *a priori* but shaped by the origin, diversification and extinction of lineages.

evidence for the existence of phylogeny as a factual process and of species as real entities (Fig. 5). He also viewed reproductive isolation as a key factor in the formation of species (e.g. Hennig, 1975). But, foremost, Hennig gave species the deeper historical dimension necessary to study them as parts of a genealogy of life. In other words, to understand mechanisms shaping trait variation, the biologists of the Modern Synthesis focused on the genetics of populations – the only observable part of a species, or their upper, flat surface (Fig. 6) – while Hennig attempted to apprehend the whole historical dimension of

species all the way back to their ancestors in order to explain how variation observed in the present came to be. This difference in spatiotemporal focus may have prevented an earlier synthesis between the findings of population genetics and Darwin’s idea of a genealogy of life.

A newer and more complete synthesis is already taking form around the tokogeny/phylogeny divide that traditionally separated population genetics and phylogenetics. History has become increasingly relevant in understanding genetic variation in extant populations, and as geneticists attempt to track variation back in time, they deem it necessary to differentiate between the phylogenetic and tokogenetic processes. For example, like Hennig’s phylogenetic theory, coalescent theory – now the dominant model in population genetics – is retrospective and expects variation in gene lineages produced by tokogeny to converge with the history of phylogenetic lineages that forms the tree of species (e.g. Rosenberg & Nordborg, 2002; Edwards, 2009; Fujita *et al.*, 2012; Sukumaran & Knowles, 2017; Smith *et al.*, 2020; Fig. 7). In other words, without the constraints imposed by phylogenetic lineages to free reproduction, variation would be endlessly reticulated and there would be no phylogeny nor would hierarchical classification be possible. Thus, and although model assumptions and processes such as gene duplication, deep coalescence, different rates of trait change, hybridisation and horizontal gene transfer are known to create mismatches between the history of phylogenetic lineages and the lineages of genes, the analysis of such phenomena presumes the existence of phylogenetic lineages (Brower, 2019). This new framework accommodates the ideas that phylogenetic lineages can originate and persist in spite of genes occasionally flowing from lineage to lineage (e.g. Petit & Excoffier, 2009), and that the origin of reproductive incompatibilities is often the result of lineages evolving in isolation and not necessarily a cause, shifting the emphasis from intrinsic reproductive isolation as the only cause of the origin of species to a more comprehensive genetic view of speciation (e.g. Wiens, 2007; Presgraves, 2010; Seehausen *et al.*, 2014).

There is surely a great deal to learn about how species form and how traits change, but overall our understanding of species has become more explanatory through the confluence of inductions across disciplines approaching evolution from different angles – a major step in the growth of scientific knowledge according to William Whewell, one of Darwin’s friends and favourite philosophers of science.

IV. SIMPLY LINEAGES

The most important implication to our notion of species resulting from carrying the genealogical theory of lineages to its logical conclusions is that species are simply lineages of organisms (Figs 8 and 9). Yet, not all lineages of organisms are species or, as Hillis (2019, 2020) succinctly put it, although all species are lineages not all lineages are species. Populations, colonies and laboratory mice form lineages of

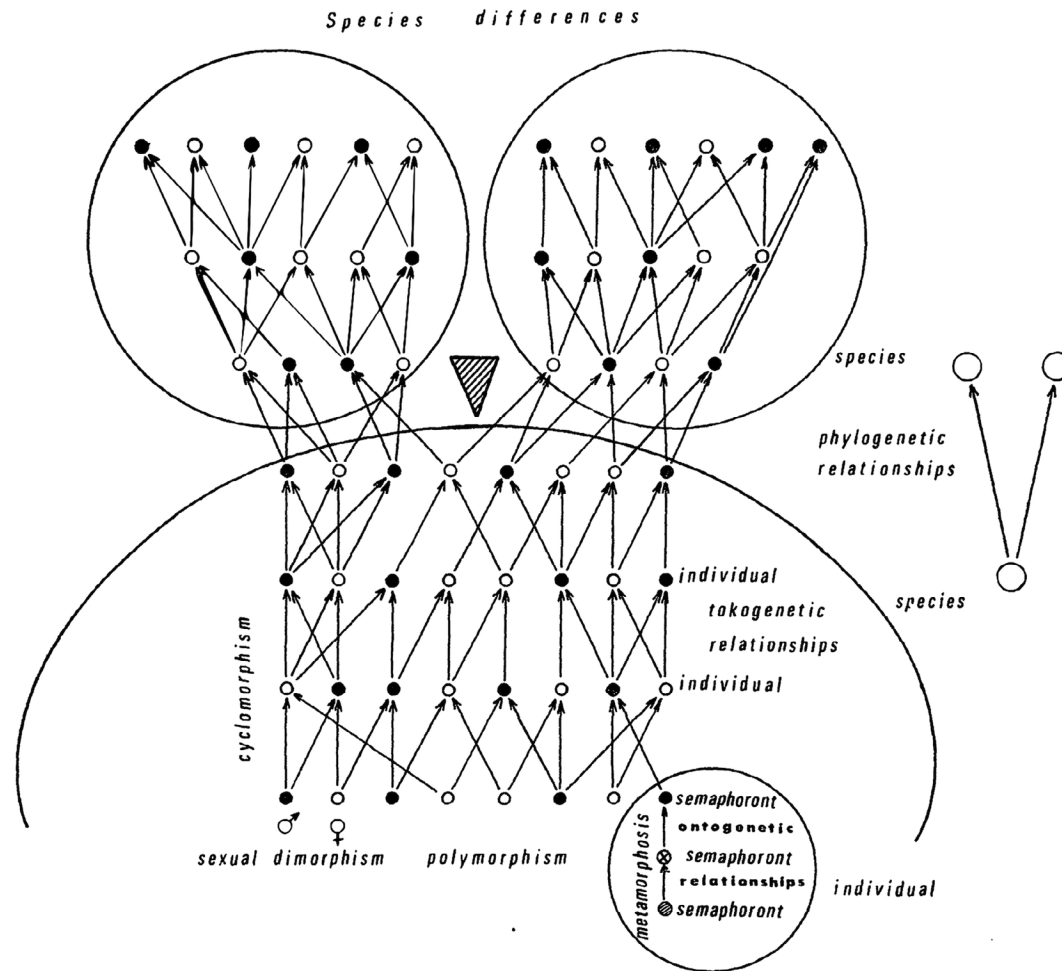


Fig 5. Hennig's (1966) diagram showing the hierarchical structure of phylogenetic relationships among species (resulting from the process of phylogeny), and the non-hierarchical (reticulated) relationships among organisms composing a phylogenetic lineage (tokogeny). Species differences are represented as circumferences surrounding species lineages.

organisms that are not species; nor are lineages of genes species, as acknowledged by the distinction between gene trees and species trees in molecular phylogenetic reconstruction.

By arguing that all species are phylogenetic lineages we do not claim that all species are similar or that there are not different kinds of historical lineages (e.g. unisexuals). We claim the opposite: no species is alike because each is the result of a unique evolutionary history. What this view of species entails is that there is a level of organization (perhaps restricted to eukaryotes yet not shared by all of them) that we identify with the category of species, in the same way that the metazoan organism reflects a level of biological organization that includes things (metazoan organisms) that are all inherently different. Thus, even if the category 'species' refers to a mixed bag of things (a mixed bag of lineages each unique in their own way), it remains useful for it captures a certain kind of emergent property of life resulting from a certain kind of process (phylogeny) recurrently happening through the biological realm.

Species as phylogenetic lineages can be conceived as unique systems or networks of anastomosing lineages of

populations integrated through reproduction and collective genomic and phenotypic evolution over successive generations (Hennig, 1950, 1966; Simpson, 1951; Wiley, 1978; Frost & Hillis, 1990; Frost & Kluge, 1994; Mayden, 1997; De Queiroz, 1998, 2007). This view is far from new or radical, for all traditional species concepts take into consideration the processes through which lineages of populations remain collectively integrated within species, and look for evidence to discriminate between the reticulated patterns produced by anastomosing population lineages and the discontinuous hierarchical structure that results from the prolonged reproductive isolation of population lineages (i.e. the tokogeny/phylogeny divide; Figs 8 and 9). For example, the Biological Species Concept (Dobzhansky, 1937; Mayr, 1942) looks at how intrinsic barriers to reproduction integrate population lineages within a species and isolate different species lineages, while the Phylogenetic Species Concept looks for congruent patterns of divergence across traits that should result from the integration that follows prolonged isolation after phylogenetic lineage splitting (see Frost & Kluge, 1994). Speciation

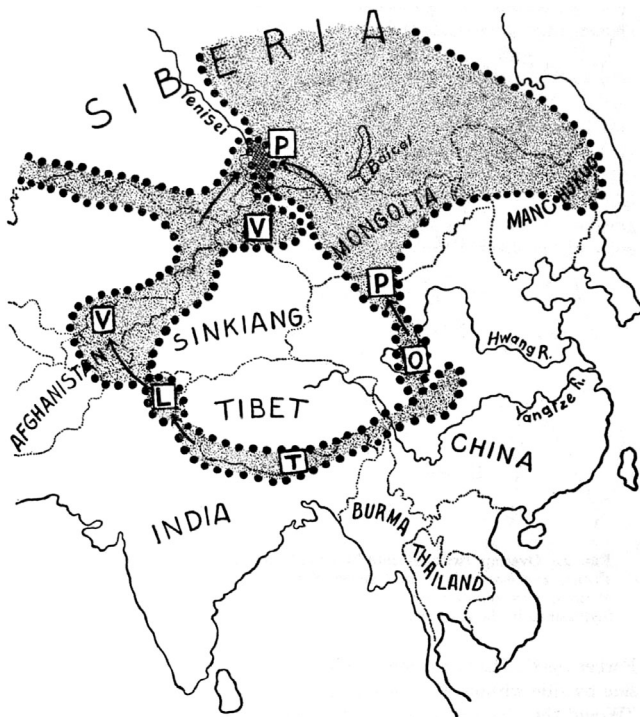


Fig 6. Standard representation of species and subspecies during the Modern Synthesis, where species were represented as non-dimensional, flat distributions of variation in space. In this figure Mayr (1942) depicts Ticehurst's (1938) delimitation of subspecies of the warbler *Phylloscopus trochiloides* forming a ring (V = *P. trochiloides viridamus*; L = *P. trochiloides ludlori*; T = *P. trochiloides trochiloides*; O = *P. trochiloides obscuratus*; and P = *P. trochiloides plumbeitarsus*; the dashed area represents the zone of contact of *P. trochiloides viridamus* and *P. trochiloides plumbeitarsus*, which do not interbreed.

can then be seen as a rare successful breach in the collective of population lineages bonded by a genomic architecture, that drives some population lineages away from their maternal phylogenetic lineage (Fig. 9). If they are pushed away strongly enough or manage to stay away for long enough (as in long-term isolated allopatric populations), new genome-level changes will accumulate and spread across the network of organisms over successive generations, eventually driving linked, coordinated evolution across populations, that culminate in a new binding genetic architecture (e.g. Presgraves, 2010; Seehausen *et al.*, 2014; Lewis *et al.*, 2020). These lineages eventually take hold of the population lineages that are parts of them as, for example, through the integration of functional traits involved in courtship (e.g. Ligon *et al.*, 2018), metabolic pathways (Hill, 2019), or exclusive gamete compatibility (Springate & Frasier, 2017). Such lineages can become bullet-proof to the import of genes or be tolerant and resistant to some degree of introgression with other lineages (Petit & Excoffier, 2009; Feder, Egan & Nosil, 2012; Ottenburghs, 2018; Hill, 2019). Sometimes a unique cocktail of genes results from the reproduction of organisms from different species, and the hybrid organisms are retained in their own lineage by their novel genetic architecture (Rieseberg, 1997; Mallet, 2007; Lamichhane *et al.*, 2018). On the other hand, if lineages reunite before any combination of changes precludes full reintegration, organisms will freely reproduce again and unique traits acquired during their period of isolation will diffuse (reticulate). Observed variation across extant human populations supports this last scenario for the recent history of our species (Tattersall & DeSalle, 2011).

Although many evolutionary biologists have adopted this view of species as phylogenetic lineages and its epistemological implications (and limitations), the delimitation of species is still seen as arbitrary and based on methodological inclinations rather than empirical and increasingly grounded on one unifying view of species as phylogenetic lineages. For

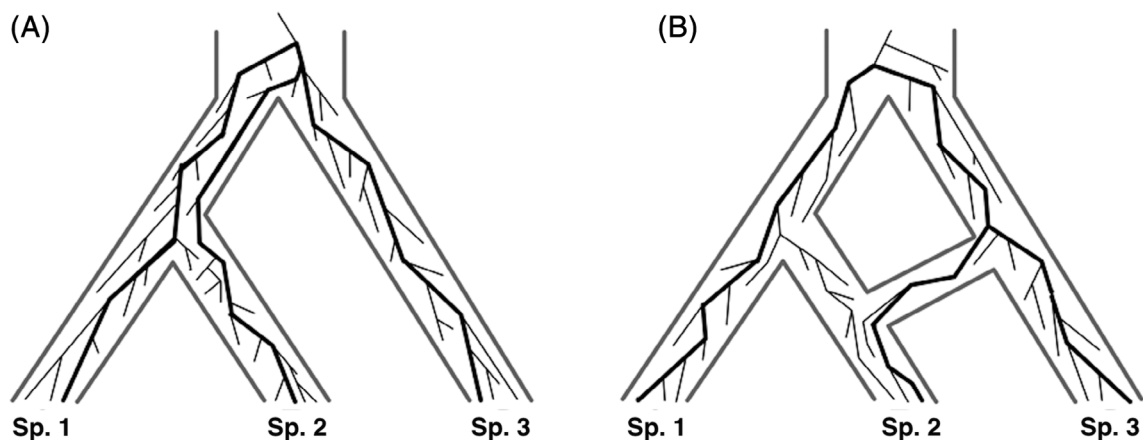


Fig 7. Representation of phylogenetic and gene lineages under the multispecies coalescent (MSC) theory (from Wen, Yu & Nakhleh, 2016). (A) A hypothetical MSC scenario where variation over time in populations is represented by gene lineages changing within the branches of a species tree. Note that the history of genes is partially incongruent with the species tree due to incomplete lineage sorting. (B) An alternative hypothetical scenario modelled under the multispecies network coalescent (MSNC) theory, where observed variation in populations has to account for an ancient hybridisation event.

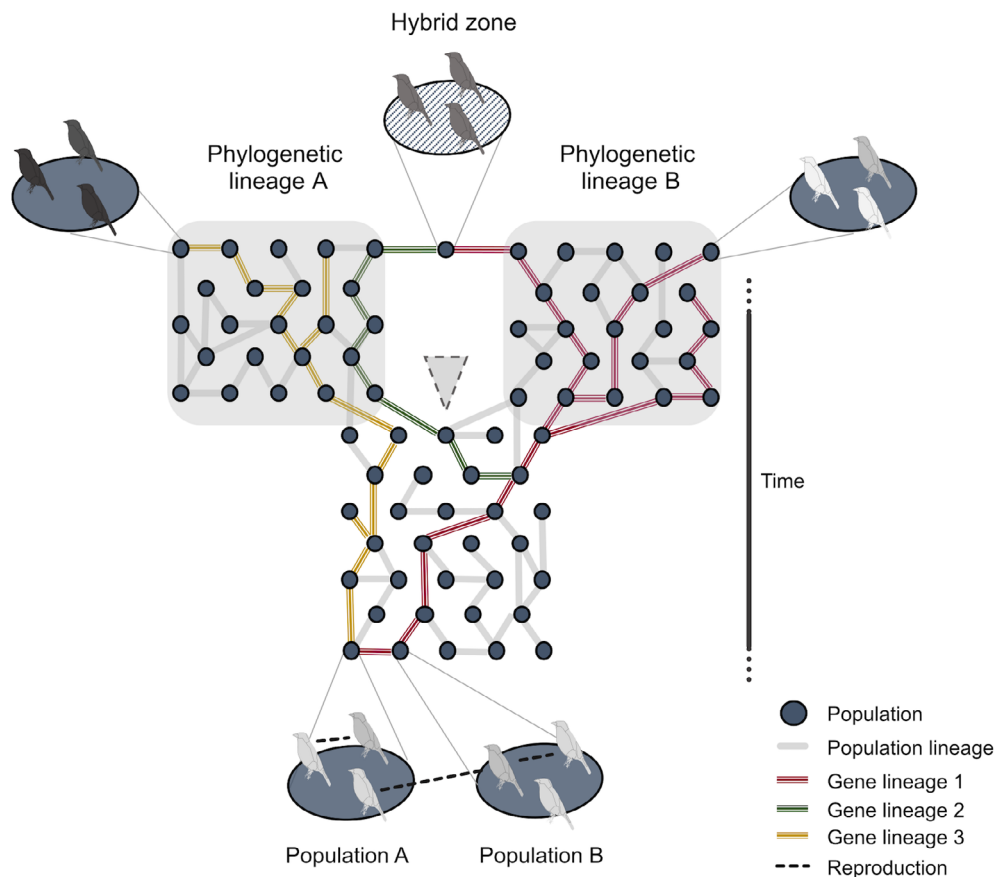


Fig 8. Branches of the eukaryotic Tree of Life as an encaptic system of lineages within lineages that result from different processes. Genes form lineages through organismal reproduction (tokogeny) and diversify through, for example, mutation and crossing over. Reproducing organisms also form population lineages that anastomose by diverging and merging and that diversify through drift, selection or epigenetic phenomena. Phylogenetic lineages are the result of prolonged isolation of population lineages from other such lineages; they diversify through changes in the genetic and phenotypic architecture spreading through all population lineages of which they are composed (see Fig. 9). Hybridisation occurs between organisms that are part of population lineages of different phylogenetic lineages. Hybrid organisms can be part of one, both or none (hybrid sterility) of the phylogenetic lineages depending on which other organisms they mate with (see Fig. 9). Note that even though the internal structure of phylogenetic lineages is reticulated (non-hierarchical), gene genealogies can be hierarchical, and incomplete sampling of gene or population lineages can lead to methodological results mimicking the hierarchical structure of phylogeny, leading to an overestimation of phylogenetic lineages.

example, Garnett & Christidis (2017, p. 25) contend that in spite of “reasonable agreement among taxonomists that a species should represent a distinct evolutionary lineage... there is none about how a lineage should be defined. ‘Species’ are often created or dismissed arbitrarily, according to the individual taxonomist’s adherence to one of at least 30 definitions”. As Zachos *et al.* (2019, p. 2) put it: “The Tree of Life, however, is an encaptic system displaying a nested hierarchy with a fractal pattern (lineages within lineages). Lineages can legitimately be delimited by grouping individuals together using diverse criteria, but, if criteria for grouping differ, the resulting taxa are necessarily different kinds of entity [sic]”. Because phylogenetic lineages are composed of other sublineages of populations, deciding which of these many lineages of the same type are species is arbitrary, and “given the same raw data, taxonomists often arrive at different species classifications because there is no single correct

taxonomic solution above the level of the population itself” (Zachos *et al.*, 2019, p. 3).

According to this view, the tokogeny/phylogeny divide is inconsequential for it provides no theoretical or empirical solution. Lineages of populations do not form phylogenetic lineages that are in any way distinct from other population lineages, and no level of organisation or genetic architecture exists beyond that of the lineage of organisms forming populations. The branched shape of the Tree of Life metamorphoses into a gorgonia with endlessly anastomosing population lineages, the variation and origin of which theory of population genetics would alone explain. We could still choose to maintain the category of species, but as an arbitrary one, for selected groups of populations, but we would have to give away all theoretical claims of unique species limits and of species trees as a result of phylogeny.

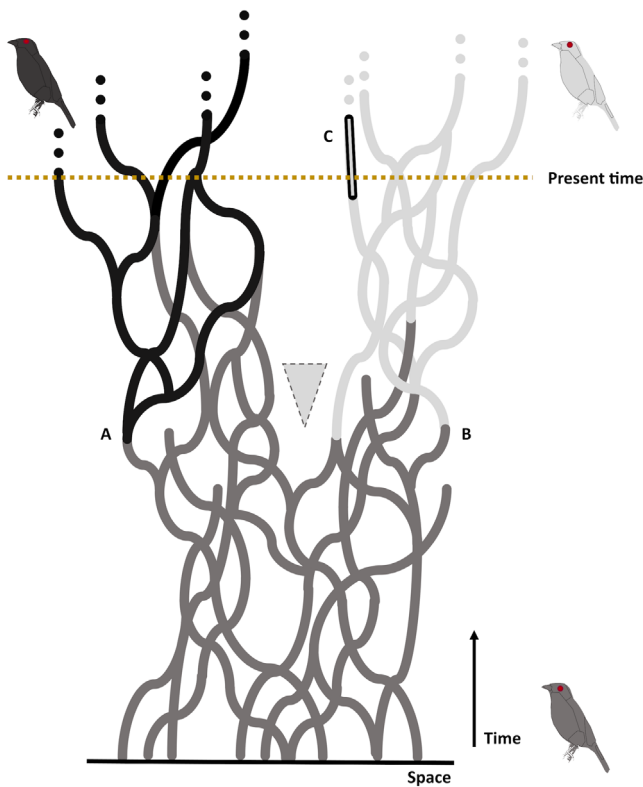


Fig 9. The origin of two phylogenetic lineages from population lineages of an ancestral phylogenetic lineage as a result of isolation (inverted triangle). (A) One population-level lineage undergoes changes in its genetic architecture that propagates towards the present time (and plausibly beyond) through all other anastomosing population lineages. (B) Two population-level lineages undergo changes in their genetic architecture that propagate toward the present time (and plausibly beyond) through all other anastomosing population lineages. (C) One population lineage shows part of the genetic architecture of another phylogenetic lineage as a result of hybridisation where hybrids reproduced exclusively with organisms of population lineage C. The fate of lineages is unknown and prospective guesses about whether present-time population lineages will fully merge in the future or would lead to other phylogenetic lineages falls outside the task of species delimitation.

We can agree with Zachos (2016) that our classifications will never truly capture with precision the genealogy of life; our taxon names will remain approximations to an slippery reality with which we lack face to face contact, for such is the nature of every empirical business. We also accept that evolution produces situations that are not consonant with the expectations of common sense ‘yes or no’ species classification, such as hybrid zones or uniparental species of hybrid origin; further, species might not have existed through all the history of life. But we do not endorse the claim that these limitations render species delimitation necessarily arbitrary. It is not the fuzziness of natural phenomena that make scientific attempts to apprehend them arbitrary, but our resistance to change our viewpoints in the face of new evidence. No hypothesis offers more than a provisional representation of

reality, plagued with inconsistencies and imperfections, but so long as our hypotheses remain open to falsification, our representations of reality will be empirical (based on evidence) and not arbitrary (based on personal inclinations).

We can also think about the Tree of Life as an encyclopaedic system of lineages within lineages – lineages of genes, proteins, cells, organisms, populations, or species – existing on each other from the lower to the higher level of organisation. But this fractal structure does not entail sameness, equivalence or transitivity across levels (Fig. 8). Each level shows unique emergent properties that result from processes operating or generated at each level of complexity [for emergent properties of systems/parts and ontological considerations see, e.g. Ghiselin, 1974, 1997, Griffiths, 1974, Hull, 1976, Frost & Kluge, 1994 and Mayden, 1997]. As a result, and while species are made of population lineages, not all population lineages are species. It is this lack of transitivity across the levels of population and species that renders theory and methods of population genetics insufficient to explain all organismal variation (Frost & Kluge, 1994; Smith *et al.*, 2020) and what impelled evolutionary biologists to develop a theory of phylogeny to explain some of the patterns we observe. We can use population genetics to study, for example, the prevalence of colour blindness in an isolated population lineage through founder events and population-level processes, but not to infer the traits we share with our extant primate ancestors nor to explain how all humans acquired cognitive and anatomical traits that made speech possible. Population genetics and phylogenetics remain nonetheless necessarily interdependent because of the nested nature of gene lineages within population lineages and within phylogenetic lineages, but each discipline focuses on different levels of organisation and different processes.

In spite of the vertical continuity of all sorts of biological lineages, evidence from both population genetics and phylogenetics supports the existence of phylogenetic lineages as branches of the Tree of Life: their tips can be observed at the present time as horizontal discontinuities in the wonderful variety of organisms with their traits and modes of existence. This view is supported by the fact that it is hard to refute the existence of *Homo sapiens* and other such lineages as cohesive phylogenetic lineages while the reticulated pattern of variation within *Homo sapiens* precludes any unbiased internal subdivisions other than the identification of reticulating population lineages (Tattersall & DeSalle, 2011). It is the existence of species lineages such as ours as well as species of hybrid origin and introgression along the edges of overlapping lineages that indicates that at least in some parts of the Tree of Life species do exist as phylogenetic lineages and that populations and species are not equivalent levels of biological organisation.

V. THE EMPIRICAL FRAMEWORK

Under the view of species just explained, species delimitation consists in determining which population lineages belong to which individual phylogenetic lineage, or lineages, as in the

case of hybrid zones (Figs 8 and 9). The condition that species delimitation has to meet to be objective and empirical is straightforward: we need testable (i.e. refutable) evidence supporting the hypothesis that patterns of variation observed across sampled populations are best explained by an instance of phylogeny (e.g. Wiley, 1978; Frost & Kluge, 1994; Dayrat, 2005; DeSalle *et al.*, 2005; De Queiroz, 2007; Padial *et al.*, 2010; Padial & De la Riva, 2010). However, we need some evidence to put forward the hypothesis that the observed variation is the result of the phylogenetic process. In this sense, De Queiroz (2007, p. 884) explains: “To the extent that the possession (by a set of populations) of even a single relevant property provides such evidence, it may be considered evidence for the existence of a species. This is not to say that the properties are infallible; on the contrary, any line of evidence can be misleading if interpreted inappropriately.... Thus, the point is not that the presence of a single property guarantees that a set of populations possessing that property represents a separate lineage (i.e., a species) but only that the presence of a single property constitutes evidence (which is always fallible) supporting that hypothesis... On the other hand, it would seem to go without saying that recognizing a species is inappropriate in the absence of any positive evidence for its existence... Although presence of a single property provides evidence for lineage separation, a highly corroborated hypothesis of lineage separation (i.e., of the existence of separate species) requires multiple lines of evidence.” In short, it is the lack of evidence about the process of phylogeny that forms the basis for grouping populations into single species. As Wiley (1978) stated, we do not consider North American and Eurasian wolverines different species because they are not different lineages, but because we lack evidence that they are, even if they are. Thus, and although the expression ‘evolutionary tendencies and historical fate’ (Wiley, 1978) has been interpreted as a prospective guess of whether phylogenetic lineages are or will remain independent (e.g. Conix, 2018), Wiley (1978) himself emphasised that species delimitation is necessarily retrospective. What matters is thus not whether we can claim complete evolutionary independence but whether we can attribute observed variation to the process of phylogeny and refute tokogeny as the best explanation of observed variation, even if some organisms are currently mating with organisms of another lineage along the edges where they encounter each other, or whether they completely merge in the future (Fig. 9).

It has to be clarified that the empirical aspect of species delimitation is not grouping populations according to methodological criteria such as similarities or differences, or degree of divergence (for such criteria are endless), or about diagnosing populations (for any population or group can be diagnosed to some extent), but to determine which populations belong to which phylogenetic lineage. Since phylogenetic lineages cannot be observed, species delimitation involves inferences of phylogenetic lineages and hence explanations about the evolutionary processes producing observed patterns of variation (Wiley, 1978; Frost & Kluge, 1994; Sites & Marshall, 2004; De Queiroz, 2007; Wiens, 2007;

Fujita *et al.*, 2012; Sukumaran & Knowles, 2017). We do not need to decide whether large or small differences grant our groups the rank of species or subspecies: we need to discriminate what variation observed in populations is the result of the phylogenetic process and what variation is the result of other processes (e.g. tokogeny or epigenetic processes). Large differences may indicate a long history of isolation or a short one driven by strong forces affecting traits (Rundell & Price, 2009), but small ones may reveal young and cryptic or sibling species that are of great interest for the study of speciation and the evolution of traits (Bickford *et al.*, 2007), or may otherwise indicate lineages that have changed little in spite of their age (Eldredge *et al.*, 2005). Likewise, that phylogenetic lineages are different from each other does not imply that diagnosability of populations is the rule of thumb on which we base our decisions. Populations may differ for various reasons, such as the effect of local ecological conditions on ontogeny (e.g. Barton & Boege, 2017), local adaptation (e.g. Hämälä, Mattila & Savolainen, 2018; Sork, 2018), genetic surfing (Excoffier & Ray, 2008) or drift (e.g. Funk *et al.*, 2016). Consequently, to explain the causes of variation in our data we need to study the history of as many traits as possible, ideally simultaneously, and with good geographic sampling (e.g. DeSalle *et al.*, 2005; Padial *et al.*, 2010; Pante *et al.*, 2015a). The combined use of hundreds of genes and phenotypic data across the range of two species would be as powerful to assess species limits as the strongest evidence on reproductive isolation. This is not because of any *a priori* expectations about the merits of selected evidence but because if species are real things built on external forces and an internal genetic architecture, the burden of proof should reveal their existence. Alternatively, when names are given to groups that do not reflect species (either because of sampling biases or partial evidence), we are unable to explain how the genomes and phenotypes of these ‘species’ evolved, and end up instead explaining how groups were created.

It could be argued that hybridisation, introgression, horizontal gene transfer, or different rates of trait change pose a problem for the empirical framework, either because species might not be real or because these processes make it hard to determine which organisms belong to which phylogenetic lineage (e.g. Willis, 2017). On the other hand, we can argue that the discovery of these processes suggests that species do exist as entities and that their populations can exchange genes and eventually merge totally or partially, and, more importantly, that we are able to identify their existence, although not always. Through this change of perspective we have been able to discover that hybrid species are phylogenetic lineages that result from the reproduction of organisms of maternal species crossing with each other, or that uniparental lineages can originate from the reproduction of organisms of two sexual species. We have also learned that sometimes not every organism is part of just one phylogenetic lineage, such as when hybrids are able to mate with organisms of either one of their maternal species. Thus, while horizontal gene transfer, endosymbiosis, or incomplete lineage sorting can mislead species delimitation, if detected and

recognised such processes provide insights into the complexities of species evolution and the causes of patterns of variation (e.g. McGuire *et al.*, 2007; Cardoso, Serrano & Vogler, 2009; Andújar *et al.*, 2014; Pante *et al.*, 2015a; DeJaco *et al.*, 2016; Papakostas *et al.*, 2016; Kindler *et al.*, 2017). No doubt mistakes are made, for conflict of evidence is not only unavoidable but constitutes the very bread of scientific progress. It is the clash of evidence that determines the degree of corroboration of any hypothesis, and the interplay between theoretical assumptions and inconsistent evidence that helps us reconsider our assumptions so that mistakes are identified and corrected, and new hypotheses brought forward. As exemplified by recent studies showing that methods of species delimitation based on the multiple coalescent model can overestimate phylogenetic lineages, it is through conflict of evidence and disparate results that we can discover what we are doing wrong and learn how to do it better (e.g. Carstens *et al.*, 2013; Naciri & Linder, 2015; Sukumaran & Knowles, 2017; Hillis, 2019, 2020; Leaché *et al.*, 2019).

VI. RESOLVING POWER

In optics, the greater the resolving power of a lens, the smaller the distance between two lines or points that can still be perceived. Similarly, under the theoretical framework of species as phylogenetic lineages, the higher resolving power is provided by the discovery of sister species, as these inform speciation and species limits. Although the relevance of sister species for understanding speciation was recognised long ago, and they played an important role in the ideas of the Modern Synthesis and in early phylogenetic approaches to species delimitation (e.g. Cracraft, 1983; Frost & Kluge, 1994), the presumption that only sister species are relevant for species delimitation and the study of speciation is now fundamental for all phylogenetic and population genetics methods of species delimitation (e.g. Sites & Marshall, 2004; De Queiroz, 2007; Wiens, 2007; Fujita *et al.*, 2012).

With the development of methods designed to discover sister relationships and with increasing access to dense geographic and character sampling, our resolving power has improved considerably. As a result, the limits of many species have been redrawn, often with the consequence that familiar species are split into two or more species. This splitting trend is criticised for recognising species that are not as conspicuous as those usually recognised in the past (e.g. Isaac *et al.*, 2004; Garnett & Christidis, 2007; Meiri & Mace, 2007). Arguably, lineages recognised as species in the past were more sharply distinct, often intrinsically isolated by reproductive incompatibility, while those recognised nowadays are less distinct and often hybridise [but see Mayr, 1942 for an early discussion on the many species accepted in birds under the biological species concept in spite of widespread interbreeding, even between distant relatives; see recent reviews by Ottenburghs *et al.*, 2016 and Ottenburghs, 2018]. However, while

sister species that split and diverged recently will likely hybridise along contact zones and be more similar than distantly related ones, the fact is that we knew very little about whether those species recognised in the past were indeed sister species, which challenges any general perception of how distinct and reproductively isolated species are supposed to be. Indeed, recognizing species that include multiple phylogenetic lineages or phylogenetic lineages that are distantly related is less relevant, if at all, for understanding species limits and speciation. This is not to say that methods used in the past (and that remain in use today) have no bearing on the inference of species; indeed they do. Traditional phenotypic species delimitation consists of detecting breaks in trait variation across space that seem to be explained better by phylogeny than tokogeny, evidence that can be tested by further sampling and different methods to refine species limits (e.g. DeSalle *et al.*, 2005; Padial & De la Riva, 2010; Pante *et al.*, 2015a). All approaches are therefore fundamentally the same in the sense that they can provide evidence of the existence of species, but those approaches that reconstruct genealogical descent are more rigorous at identifying sister species (have higher resolving power) and hence at rejecting alternative hypotheses about the nature of trait variation.

Rigorous species delimitation and classification stability is to a large extent limited by our understanding of sister relationships. For various if not all groups or organisms, evidence indicates a vast underestimation of species diversity, sparse sampling and, hence, limited resolving power (e.g. Köhler *et al.*, 2005; Padial & De la Riva, 2006; Ceballos & Ehrlich, 2009; Vieites *et al.*, 2009; Mora *et al.*, 2011; Guiry, 2012; Pimm & Joppa, 2015; Barrowclough *et al.*, 2016; Christenhusz & Byng, 2016; Stork, 2018). While many species are now being discovered, not all are formally described and named, and this backlog of unnamed species are not included in evolutionary, ecological, or conservation studies (Sangster & Luksenburg, 2015; Pante, Schoelinc & Puillandre, 2015b). Often enough familiar species names seem to capture very distinct and reproductively isolated species only because the closest relatives are unknown or have not been named. This situation is not endemic only to poorly known taxa and areas (e.g. Gehara *et al.*, 2014), but affects charismatic taxa and well-sampled areas as well (e.g. Ceballos & Ehrlich, 2009; Milá *et al.*, 2012; Sangster & Luksenburg, 2015). The recent discovery of a species of frog from New York City (Feinberg *et al.*, 2014), a snake in Central Europe (Kindler *et al.*, 2017), and a wolf in northern Africa (Koepfli *et al.*, 2015) should make us wary of old names, no matter how familiar and stable they seem.

We are often looking at species diversity through a lens with low resolving power. Due to this poor species resolution, a young and diverse radiation may look old and homogeneous if multiple species are hidden under a single name, and a ring of species may not look like a ring if several species are missing. Furthermore, increasing understanding of species diversity and increasing species resolution do not necessarily go hand in hand, as many non-sister species can still be discovered even if sampling is sparse. Poor species

resolution may also explain other patterns, such as why for many taxa and areas sibling parapatric or geographically close allopatric species are rare and hence why large (and perhaps rapid) radiations remain uncovered for decades (e.g. De la Riva *et al.*, 2017). Low species resolution could also explain highly discordant patterns of genetic differentiation, divergence times, and degree of gene flow, often attributed to ancient ecological and orogenic processes (e.g. Weir & Schluter, 2007; Smith *et al.*, 2014), especially when we take into account biases in species resolution across areas (e.g. Feeley & Silman, 2011). The elephant in the room of species resolution is, nonetheless, extinction. *Homo sapiens* stood out against a background empty of close relatives until more hominins and genomic material of Denisovans and Neanderthals were discovered and turned the simple story of modern humans into a more challenging one (e.g. Hajdinjak *et al.*, 2018; Chen *et al.*, 2020). Still, extinction is a process, affecting both populations and species, amongst the myriad evolutionary processes that shape the limits and diversity of species and should be as present in our explanations as our evidence allows.

In addition to the challenges posed by limited evidence, the discovery of young and slightly distinct lineages is in itself a very difficult task that requires more evidence, complex methods, and risky assumptions that are also prone to errors (e.g. Roux *et al.*, 2016; Sukumaran & Knowles, 2017; Hillis, 2019; Leaché *et al.*, 2019). Taxonomy is relatively easy when describing distantly related species in comparison to the complexity of inferences and the amount of evidence necessary to identify true sister species (i.e. with higher resolving power) and especially if these diverged recently. The discovery of sister species requires discriminating between patterns that mimic phylogeny, such as the temporal split of anastomosing populations or the divergence of gene lineages (Figs 8 and 9). Such inferences require large and diverse sampling of traits and fine-grained geographic sampling to test for the existence of contact zones, signs of past hybridisation, incomplete lineage sorting, or other phenomena that may hamper a satisfactory resolution of lineage relationships or could lead to overestimation of species. These challenges have made species delimitation, historically the territory of taxonomists, a field of broader interest that now attracts population geneticists, ecologists, computer scientists, and others interested in the complex scenarios that our new understanding of species provides.

VII. SUBSPECIES

The category of subspecies entered biological classification in the 20th century to formalise, within the Linnaean system, what previous naturalists had been considering as varieties or races. Subspecies names quickly proliferated along with studies of geographic variation. By midcentury, polytypic species abounded (Dobzhansky, 1937; Huxley, 1942; Mayr, 1946), and Ernst Mayr, who alone named over

400 subspecies, cautioned about the proliferation of subspecies for “minutely differing” populations (Mayr, 1935, p. 23); he later wrote, “I estimate that the number of valid subspecies of birds described by the end of 1945 amounted to about 28500. This figure is increasing annually by about 200” (Mayr, 1946, p. 68). Less constrained by the expectations of rigour associated with species, the category of subspecies quickly degenerated into a ‘trashcan’ fit for a diversity of predilections: populations showing signs of phenotypic differentiation, segments of clines, and lineages of various levels of divergence (Huxley, 1942; Wilson & Brown, 1953; Burt, 1954; Gillham, 1956). Trinomina did not, however, become equally popular across all taxa and areas. Subspecies became more prevalent in highly variable species, charismatic groups and well-sampled areas. Birds were perhaps the most affected by subspecies classification (Paynter, 1987; Zink, 2004), but trinomina also became common in mammals (Burt, 1954; Wilson & Mittermeier, 2009; Gippoliti *et al.*, 2018), especially primates (Rylands & Mittermeier, 2009), and plants, where subspecies proliferated rapidly together with other lower ranks because of complex variation and reproductive relationships (Huxley, 1942). The classification of amphibians and reptiles acquired few if any subspecies in tropical regions but more in North America and Europe (Frost & Hillis, 1990; Frost, 2020). Invertebrate taxonomists were less fond of subspecies except in Lepidoptera, and again mainly in North America and Europe (Gillham, 1956).

The uneven use of subspecies raises the question of whether subspecies refer to biological processes common in some groups and areas and rare in others, or whether their recognition is more a matter of taste and tradition than of their nature. The fact is that although biologists now tend to agree that species are the result of the phylogenetic process, there is no consensus as to what kind of process the category subspecies represents. Should subspecies also represent phylogenetic lineages? And if so, just young sister lineages, or lineages that show little difference independently of their age? Should they be restricted to phylogenetic lineages partially isolated from other such lineages? Or should trinomina be applied only to any conspicuous local variation as often is the case for the names of varieties and races?

We could retain the category subspecies for young phylogenetic lineages (i.e. young species) or phylogenetic lineages that show little divergence independently of their age (e.g. Braby, Eastwood & Murray, 2012), but this would be confusing. We would be using two taxonomic categories (species and subspecies) for entities that are the same kind of thing (phylogenetic lineages), just older or younger or more or less distinct, falling again into the pitfalls of arbitrariness and biased expectations about the entities assigned to the two categories. For example, since subspecies are deemed less relevant than species in conservation we would implicitly assume that young or inconspicuous lineages deserve less protection. We would also treat young or less conspicuous species as if they were less relevant for the study of evolution or as if they emerged from different processes.

An alternative is to restrict the category subspecies to geographical variants within a species and hence, to treat trinomina not representing phylogenetic variation as synonymous with geographical races and varieties. Subspecies names could be retained at that level to communicate peculiarities of populations within species (Hillis, 2020). But we would have to bear in mind that the partition of that variation involves arbitrary thresholds for one or a few correlated traits, which is what fostered the subjective classification of human variation into races (Tattersall & DeSalle, 2011) and led to concerns about consistency in the criteria of subspecies classification in the first place (Huxley, 1942; Mayr, 1946; Wilson & Brown, 1953; Burt, 1954; Gillham, 1956; Zink, 2004; Braby *et al.*, 2012). Another alternative is to recognise as subspecies “incompletely separated lineages within a more inclusive lineage” (De Queiroz, 2020, p. 460), such as phylogenetic lineages with hybrid zones at areas of contact (e.g. sections of ring species), and use trinomials not to represent a rank, but as representational devices to indicate the process of gene exchange between phylogenetic lineages. In this way a phylogenetic lineage could be considered a subspecies and a species simultaneously, in the same way a subclade is a clade and a subpopulation is a population.

One more option is to eliminate trinomina altogether and use vernacular names for the diversity observed within lineages, as suggested early on by Wilson & Brown (1953). The advantage of eliminating subspecies altogether is that we could get rid of unjustified expectations associated with trinomina while maintaining a way of communicating about variation that is less loaded with assumptions about how relevant, objective or conspicuous that variation is. As taxonomy becomes increasingly phylogenetic, this last option is gaining adepts and subspecies are raised to species when evidence shows that variation is the result of the phylogenetic process while variation caused by other processes is left formally unnamed (Padial & De la Riva, 2006; Sangster, 2009). The problem that remains is that trinomina are currently applied to different types of variation shown by different entities. Thus, among the thousands of subspecies names still in use, some refer to distinct phylogeographic breaks such as mitochondrial gene lineages (Moritz, 1994; Culver *et al.*, 2000), while others capture things as different as incompletely isolated phylogenetic lineages (De Queiroz, 2020), segments of clines, or groups of organisms affected by similar epigenetic phenomena (e.g. xeric conditions). As currently used, trinomina do not necessarily refer, nor even attempt to refer, to the same kind of variation.

Consider the case of the California gnatcatcher (*Poliophtila californica californica* Brewster, 1881), singled out by Garnett & Christidis (2017), as an example of how different notions of subspecies may create conflicts with implications for conservation. This subspecies corresponds to phenotypically distinct populations of *Poliophtila californica* in Baja California that are considered endangered and listed under the U.S. A’s Endangered Species Act. Zink *et al.* (2000), based on mitochondrial genes, found reticulated and continuous genetic variation among the subspecies and recommended

their rejection. But deprived of the subspecies status, these populations would also lose their protection and 77,000 ha of their range would be cleared for development. The U.S. Fish and Wildlife Service asked for additional evidence before making a decision. Zink *et al.* (2013) analysed additional molecular evidence (nuclear and mitochondrial genes) and tested whether patterns of variation could be explained as the result of phylogenetic lineage splitting in relation to ecogeographic breaks. In other words, they tested whether variation could be explained as a result of a process of speciation in allopatry or parapatry and their analyses rejected both hypotheses. McCormack & Maley (2015) reanalyzed Zink *et al.*’s (2013) DNA data and found diagnostic differences in nuclear loci and contested their taxonomic decision. But since the subspecies was indeed proposed on the basis of diagnostic phenotypic traits along a cline, diagnosability was out of the question; what was at stake was whether variation was clinal or not, and whether a break in variation is explained by phylogeny or some other process. Regardless, disagreements may not be solved by evidence because for Zink *et al.* (2013) subspecies should represent phylogenetic lineages or be rejected (see Zink, 2004), while for McCormack & Maley (2015) subspecies can represent diagnosable populations along a cline. Until we reach an agreement about what to do with the subspecies category, instability will remain and its effects will affect both research and conservation.

VIII. WHAT CAN TAXONOMY DO FOR CONSERVATION?

Species and subspecies are considered useful taxa for conservation. Their latinised scientific names are unambiguously associated with particular populations (type localities) through vouchers and rules of nomenclature, and they can be easily inventoried, tracked, and incorporated into regulations. The IUCN *Red List of Endangered Species* works closely with taxonomists to curate updates and maintain an effective connection between taxon names and their conservation status (e.g. Taylor *et al.*, 2019), but changes to names can still create a disconnect between a name listed in a bill and the populations that we want to protect. For example, the long time required to update CITES listings and national legislations create legal loopholes from which illegal traders, developers and other interested parties can profit (Zhou *et al.*, 2016).

Concerns about taxonomic instability are therefore not ill-founded, but they have engendered misguided ideas about how classification should assist conservation better. For example, Garnett & Christidis (2017, p. 26) proposed “creating boundaries for species (and other taxonomic units) that can be applied consistently across multiple life forms”, so that species attain “legally defensible boundaries” and stakeholders procure “objective criteria against which to argue the case for a different outcome”. Their solution assumes

that species delimitation rests on conventions and that the species category contains abstract classes (populations or groups of populations we agree to name as species) defined by a set of properties on which we have to agree (rules that can be applied consistently across life forms). Such a perspective is at odds with the view of species as phylogenetic lineages and with empirical species delimitation. Furthermore, the growing community of scientists involved in species delimitation constitutes a global avenue for appeal, for evidence provides stakeholders and everyone else with objective criteria to refute species. Conflict of evidence or conflict of decisions based on the same evidence call for further evidence and do not require legally defensible boundaries established *a priori*. Cases where non-taxonomists participate in taxonomic decisions are now far from rare. The fact is that nowadays not only taxonomists but increasingly ecologists, conservationists, and molecular biologists stumbling upon results conflicting with accepted species limits are responsible for changes, often with critical repercussions for conservation (e.g. Culver *et al.*, 2000; Feinberg *et al.*, 2014; Hrbek *et al.*, 2014; Koepfli *et al.*, 2015; Fennessy *et al.*, 2016; Bercovitch *et al.*, 2017; Nater *et al.*, 2017). For example, the work of non-taxonomists was key to the recognition of Southern European endemics such as the Iberian imperial eagle and the Iberian lynx, and their protection arrived just in time to avoid further declines as a result of hunting, habitat loss, and disease (see Ferrer & Negro, 2004). Not only were key endemics saved, but they have become icons of Spain's biodiversity richness, attracting funds for conservation, research and sustainable development.

Disputes about classification trends and conservation remain, not because taxonomy stands on a shaky ground at odds with our understanding of evolution, but precisely because of the resistance to accept the implications (and limitations) of applying our understanding of evolution to biological classification. Taxonomy is criticised when populations recognised as subspecies are raised to species if they are found to be part of a unique phylogenetic lineage, or when populations recognised as a single species are split into multiple ones if they are found to be different lineages, while familiar classifications often remain stable for decades even when evidence shows that they are deceptive (Gippoliti *et al.*, 2018). As explained above, we have no theoretical arguments to reject the existence of young phylogenetic sister lineages or slightly diverging sister lineages as species if evidence supports their existence. We could decide not to name all those species, treat as species only the very conspicuous and perfectly isolated lineages, and apply other categories for the rest. But if species are to start somewhere and evolve at different rates, what is the rationale for discriminating young or slightly divergent lineages supported by evidence? Should we dismiss evidence indicating the existence of phenomena such as rapid radiations, cryptic and sibling species, hybrid zones, and hybrid species? Furthermore, placing less-divergent species or younger ones into the category of subspecies would not change the nature of the entities we are studying nor solve the problem of the proliferation of names

and units to protect: it would just place names at a level where some feel more comfortable. What is more problematic is placing the same sort of entities into different categories and assuming that they represent different entities and processes. Likewise, fixing species limits and making arbitrary decisions about what to place in different categories would not only bring taxonomy back to the authoritarianism of pre-evolutionary times, it would yield a shaky theoretical foundation for biology and conservation.

Although the disuse of subspecies taxonomy is often judged detrimental for conservation as shown by the current controversy about the California Gnatcatcher described above, the Florida panther (*Felis concolor coryi*; another example singled out by Garnett & Christidis, 2017), provides a good example of successful conservation in spite of, or perhaps because, its status as subspecies has been contested. At the beginning of this century, Culver *et al.* (2000) provided a thorough analysis of mitochondrial and microsatellite DNA variation of puma populations across the Americas. They found six mitochondrial lineages that could be associated to only six of the 32 subspecies names then in circulation. All North American populations were found to be almost identical genetically and almost indistinct to the southern subspecies; they recognised only one North American subspecies, *P. concolor concolor*. Although their decision was initially controversial, The IUCN's Cat Classification Task Force has recently accepted their results and does not list *P. c. coryi* among the six subspecies of pumas still recognised (Kitchener *et al.*, 2017). Yet the Florida populations have remained the focus of conservation programs because scientists and managers were well aware that, subspecies or not, these pumas constitute the only surviving population east of the Mississippi and play a key role as top predators in the unique and endangered ecosystem of cypress swamps in southern Florida. They have been working hard to preserve this last population (Culver, 2009) and one of the fundamental measures involved the introduction of pumas from Texas (formerly considered another subspecies, *P. c. stanleyana*) to mitigate inbreeding depression manifested through different conditions (Johnson *et al.*, 2010; Ochoa *et al.*, 2019).

Our recommendation is that, since biological classification must reflect rigorous evidence about the existence of particular biological processes – evidence that can be either corroborated and contested but that remains open to empirical testing – taxon-based conservation should emphasise species. In other words, the use of Linnaean classification for conservation should be restricted to species because using taxa that reflect variation partitioned in arbitrary ways and assuming that those taxa are natural, discrete, and incontestable units is misleading. We are not arguing that only species should be the target of conservation. On the contrary, we agree with the paradigm shift in conservation biology that focuses on the preservation of all sorts of variation that make ecosystems functional and resilient (Primack, 1995; Crandall *et al.*, 2000; Des Roches *et al.*, 2018). The preservation of Evolutionarily Significant Units (Moritz, 1994) is a good step in this direction because it constitutes a precise non-Linnaean

category that targets intraspecific genetic variation explained by historical processes such as postglacial migration routes or forest refugia (Newton *et al.*, 1999). But preserving the results of historical processes is not enough. Other processes such as gene flow, ecological interactions, and functional traits are more relevant for ecosystem resilience and require the preservation of all organisms participating in the economy of ecosystems, diagnosable or not (Crandall *et al.*, 2000).

Whether the label subspecies is ultimately retained, conservationists and legislators should be aware of the kind of variation and processes subspecies represent and how it has been partitioned, so that solid arguments can be used to solve conflicts. Taxonomists, on our part, should assist conservation by providing well-corroborated evidence about the existence of species as single phylogenetic lineages and their distribution. Even though our inferences can fail because of sampling biases, methodological shortcomings, and confounding processes, disagreements can be solved by leaving hypotheses open to further empirical testing by any interested party. Ultimately, increasing stability will be the result of species limits being well corroborated by multiple lines of evidence.

IX. A NEW ORDER OF THINGS

Order, the order that Linnaeus sought to represent, has finally imposed itself into our world view. The patterns he observed turned out to be the results of the process of phylogeny, the understanding of which has decisively shaken our world view. It was not any kind of order that Linnaeus was seeking, but the particular one that makes us see lions and cats and apes and humans as parts of an extended family; an order that was telling us something about the material world and which we now understand as the phylogenetic process. The discovery of phylogeny not only challenges our traditions of classification but also the way we look at the world. It has produced a rift in culture that splits us apart from an order of things that held us at the top of the progressive Great Chain of Being. The discovery of phylogeny also challenged simplistic notions of species: notions thought simply to emanate from careful observation of their traits. As with any major scientific revolution, there is resistance to abandoning old beliefs and traditions. We are equally resistant to change or remove familiar taxa; we hold our taxonomies dearly and dislike changes in the common and scientific names through which we learned to look at the natural world. But biological classification is no longer an apparently simple process of naming a visible order; it is about inferring parts of the genealogy of lineages that form the Tree of Life, a genealogy that is hypothetical and amenable to refutation. Our classifications are not permanent because the lineages and their genealogy cannot be established with certainty, let alone be decided. We confront real, complex historical phenomena to which we have only partial access through indirect and scattered evidence analysed through assumptions that are

themselves subjected to refutation. We may not have unambiguous answers all the time; we will make mistakes. How many tests our hypotheses can withstand is therefore the issue we should pay attention to. Many species have yet to be discovered, others were named but never tested, and only the smallest minority has been subjected to tests by multiple sources of evidence; our understanding of the natural history, range, population size and many other pieces of information fundamental for species delimitation remains insufficient in the vast majority of cases. We cannot assume or expect classifications to be stable under such a dearth of evidence. Even in supposedly well-known groups there will be surprises because we have taken for granted age-old classifications. We should be wary of these facts, both when contemplating changes to classifications and when relying on accepted ones.

X. CONCLUSIONS

- (1) Current trends in species classification are the result of a paradigm shift in our view of species towards which both population genetics and phylogenetics have converged and that regards species as phylogenetic lineages.
- (2) Species delimitation consists in identifying which populations belong to which unique phylogenetic lineage, and this operation is not based on perceptions of difference but on inferences of the history of traits and of sister relationships. The rigour of species delimitation resides in determining how much of the genomic and phenotypic variation observed in populations is explained by phylogeny better than by any other process shaping variation in populations.
- (3) The increase in geographical and character data sampling and the proliferation of methods to infer sister relationships has increased resolving power in species delimitation. Species resolution – our understanding of sister relationships – remains nonetheless poor for many taxa and areas, including charismatic and relatively well-known groups, which biases our understanding of species diversity and divergence, and we can expect changes to classifications as we address these problems.
- (4) The demise of trinominal nomenclature is a consequence of the conceptual shift, as subspecies are raised to species if they are found to correspond to phylogenetic lineages, while they are rejected as fabricated taxa if they reflect arbitrary partitions of continuous or non-hereditary variation.
- (5) Species classification is not subjective but empirical, and rests on evidence about the existence of species as individual phylogenetic lineages, evidence that can be either corroborated or contested but that remains open to scrutiny by any interested party.
- (6) Conservation based on taxa should emphasise species and reduce the use of subspecies to avoid preserving arbitrary partitions of continuous variation.

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