

Species

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Abstract: This article discusses the many usages and meanings of the term *species* in biology, as currently applied (1) to named taxa such as *Homo sapiens* and *Panthera tigris*, (2) to a rank (usually but not necessarily the lowest and/or the most fundamental one) of the biological classification, and (3) as a variegated set of notions, the most important among them being the morphospecies, the biospecies, the ecospecies, the evolutionary species, the agamospecies and the taxonomic species. The debatable relationship between the Aristotelian “definition by species and genus” and the historical roots of the usage of genus and species as basic ranks in biological classification are outlined, as are the historical roots of the scientific nomenclature applied to biological species.

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1.0 Introduction

Species is both (a) a specific kind of something and (b) a taxonomic group in biology, but also (c) a general concept in knowledge organization (KO) about units being classified, often used synonymously with, for example, *element*, *entity*, *individual* and *item*.

As stated by Hull (1998), “The fundamental elements of any classification are its theoretical commitments, basic units and the criteria for ordering these basic units into a classification”. It is, therefore, of great interest to explore issues related to such units. The identification of the units is one of the most important issues in any classification and the present article will illuminate this in relation to biology. Surprisingly perhaps, the units in biological taxonomy (the species, the focus of this article) are subject of controversy, as are also the units in other scientific taxonomies, e.g., in chemistry (the chemical elements arranged in the Periodic Table; see, for example, Ruthenberg and Jaap 2008; Scerri and Ghibaudo 2020) and mineralogy^[1], which are not treated here.

The focus of this article about species is biological, but there are important problems involving biological species that must be approached from the perspective of philosophy and other disciplines, e.g., questions about natural kinds (not treated here) and the contrast between monistic and pluralistic approaches, briefly treated in Section 7 below.

The species in biology is a complex topic and a controversial issue. This is due in part to the polysemic nature of the term *species*, which is used to denote (1) a taxon (a named aspect of biological diversity, such as Indian Elephant, or Baobab), (2) a category or rank (often regarded as the fundamental one in the biological classification) and (3) a unity of biological diversity recognized in a particular biological discipline or as defined according to a particular delimitation criterion. These different notions are currently mixed together in dictionary definitions, for example:

species (biology) taxonomic group [taxon] whose members can interbreed [biological species defined according to a criterion of reproductive compatibility, cf. section 6.2.2] (WordNet 3.1)

Zoology and Botany. A group or class of animals or plants [taxon] (usually constituting a subdivision of a genus [thus, referred to a precise taxonomic rank]) having certain common and permanent characteristics which clearly distinguish it from other groups [biological species defined according to criteria of objective diagnosability, cf. section 6.2.6] (Oxford English Dictionary)

The next section of this article is intended to characterize the three usages of the term *species* in biology (species as taxon, species as category, and species concepts), discussed in detail in Sections 4 to 6, while Section 3 offers some historical background.

2.0 Species as taxon, species as category, and species concepts

Like any other set of objects, animals and plants could be classified according to a number of different criteria, nevertheless it is often taken for granted that there should be only one classification of living species. A frequently advocated reason for preferring a general-purpose classification is the expected possibility of getting a stable and universal nomenclature to be used as common currency in the different biological disciplines and also in nonscientific contexts, e.g., agriculture, trade, and legislation^[2].

In its traditional formulation, the biological classification is hierarchically structured by ranks (called the *taxonomic categories*). Some of these ranks are still those of *Systema Naturae* (Linnæus 1758 and other editions), i.e., classes, orders, genera, and species, in descending order; other ranks have been added later, some of them (family, between order and genus; phylum, above the class) used regularly, others (e.g., subclass, superfamily; or domain, at the top of the hierarchy) less frequently and to some extent optionally.

All named items in the classification are called *taxa* (sing., *taxon*). Species taxa are thus the taxa to which a taxonomist assigns species rank, i.e., the taxonomist's choice between the rank of species and other ranks in classification, e.g., genus, and thus presupposes a classification system in which "species" is a defined rank^[3]. For example, our species (*Homo sapiens*) is a species level taxon classified in the genus *Homo* within family Hominidae, order Primates, class Mammalia, phylum Chordata, kingdom Animalia.

Most biologists, and probably a number of philosophers of biology too^[4], will accept that "species taxa, as all other taxa in biological classification [e.g., genera and families], serve as the foundation for all other biological analyses and hence should be as similar to one another as possible" (Bock 2004, 183). However, general agreement on this issue has emerged as highly controversial and possibly beyond hope of a definitive solution.

Problems arise because of the conflict between the diversity of meanings the term *species* takes in disciplines other than taxonomy, such as evolutionary biology, ecology, etc., contrasting with the uniform nomenclature applied to the taxa of Linnaean tradition. Indeed, the units of biodiversity recognized in biology are mostly named by using the binomials of Linnaean taxonomy, although in some circumstances researchers use instead a diversity of non-Linnaean formulas (Minelli 2019). However, the use of the same Linnaean binomials in taxonomy, evolutionary biology, ecology, etc., is a consequence of the fact that we call *species* all the different biodiversity units worth recognition in all these disciplines, but does not attest that these units are, or can be, coextensive.

This is the origin of what is widely known as the *species problem*: "there are multiple, inconsistent ways to divide biodiversity into species (on the basis of multiple, conflicting species concepts), without any obvious way of resolving the conflict. No single species concept seems adequate" (Richards 2010, 5). This issue was first brought to the attention of naturalists by Bernard (1902), Bessey (1908) and Cowles (1908) but became matter of debate following the publication of Robson (1928), the first book on the species problem. Among the monographs on this subject are Hey (2001a), Stamos (2003), Richards (2010), Pavlinov (2013), Zachos (2016), Wilkins (2018), and Wilkins et al. (2022).

"The species problem is caused by two conflicting motivations; the drive to devise and deploy categories, and the more modern wish to recognize and understand evolutionary groups" (Hey 2001b, 329); further motivations might be added. The focus of the dispute is the biological nature of the biodiversity units that are represented as species taxa in the classification. These have been tentatively defined in ecological, evolutionary, genetic, phylogenetic terms, etc., giving rise to a plurality of alternative notions. These will be discussed in detail in Section 6.2, but three principal issues need be addressed here.

First, about the use of the term concept^[5]. It can be argued that the notions traditionally known as the biological species concept, the evolutionary species concepts, etc., are not really different concepts, but merely alternative definitions. Wilkins (2011; 2018), after discussing in detail the nature and the mutual relationships of the many "species concepts" proposed to date, ends up with the reasonable conclusion that there is in fact only one species concept, upon which (even if often implicitly) rests the classification of the living species, i.e.: "Species are those groups of organisms that resemble their parents" (Wilkins 2018, 307). All the different "concepts" would thus be alternative (and often more or less extensively overlapping) conceptions, for which more or less precise definitions have been formulated, or simple operational criteria for species delimitation. However, the usage of "concepts" for the individual notions of species is

so deeply entrenched in the literature, that in practice Wilkins himself uses concept and conception as synonyms, often in the same sentence, for example: “I distinguish between two *phylospecies* concepts that go by various names, [...] to remedy this terminological inflation, I have christened them the *autapomorphic species conception* and the *phylogenetic taxon species concept*” (Wilkins 2018, 370, italics as in the original). Therefore, this critical issue (the legitimacy of the use of concept for the different species notions proposed thus far) needs be flagged, but, in practice, the access to the current literature (biological and of philosophy of biology alike) continues to go through the application of the term *concept* to the different notions of species, as presented in the subsection 6.2.

Second, it can be argued that species concepts are not subject matter of systematic biology, but a question of general biology, although not necessarily an integral part of the theory of evolution, as suggested by Szalay and Bock (1991)^[6]. However, adopting one or the other of the many species notions proposed thus far (see subsection 6.2) can have dramatic consequences on classificatory practice, especially in so far as it may involve a choice between monism and pluralism (see subsection 6.3).

Third, species concepts do not necessarily translate into operational guides allowing the assignment of specimens to species. For example, despite the popularity of the so-called biological species concept, the instances in which biologists actually check if living specimens *x* and *y* actually interbreed, to decide whether they belong to the same species, are an extremely minor exception. Most identifications are made on preserved museum specimens; additionally, the name-bearing type specimens are nearly always preserved specimens and the exceptions to this rule are the living types of bacteria to which the biological species criterion would hardly apply. A great many researchers would probably accept the biological species concept in the abstract but, in their daily practice, to establish conspecificity of specimens they will use proxies, such as morphological or genetic similarity.

3. Historical background: philosophy vs. natural history

3.1. Aristotle

Modern commentators have expressed contrasting and often unjustified interpretations regarding the meaning of the term *species* in zoological or botanical works published since classical antiquity up to Linnaeus (1707-1778), the author in whose works the modern classification and nomenclature of animals and plants has taken shape

The first point to be fixed is how far the term species, as used by biologists today, agrees with its meaning in the con-

text of the so-called Aristotelian “definition by species and genus.” It is a widespread opinion that “formalization of individual kinds (species) and of collective groups (genera) [by Aristotle] was the point of departure for the more perceptive and elaborate classifications of the later period” (Mayr 1982, 153), but this assumption is arguably ill-founded.

Let’s move from Aristotle’s *Metaphysics*, where this logical scheme is introduced, to subsequently see if and how, as often stated, this notion becomes the foundation of biological taxonomy, irrespective of the fact that Aristotle’s texts do not contain any explicit classification of animals or plants. Aristotle’s terms *γένος* and *εἶδος* will be translated here as “genus” and “species” respectively, but without any commitment to take these words as meaning the same as in modern classification.

In Aristotle, everything that differs from something else differs either in genus or in species: in genus, when both things have neither matter nor the way in which they are generated in common, whereas matter and way of generation are instead shared by the species of the same genus^[7] (for example, a human is a species of the genus animal that differs from the other animals by being rational). Therefore, what a genus differs from every other genus (otherness, *ἕτερότης*) is other than what a species differs from other species of its genus (difference, *διαφορά*): to recognize a genus, it is not necessary to compare it with other genera, but a species is defined only based on its differences from the other species of the same genus^[8]. A popular visualization of Aristotle’s logics based on the genus and species is Porphyry’s tree. This embodies the method of binary (dichotomous) division upon which most modern keys to the identification of plant and animal species are built, but Aristotle did not commit himself strictly to dichotomy (Franklin 1986). Aristotle used *eidos* and *genos* at multiple levels (Lennox 1980; Pellegrin 1982; Balme 1987; Sloan 1987; Richards 2010); as a consequence, these were not taxonomic concepts. Specifically, “it is implausible that Aristotle was generally using the term *eidos* to refer to those groups of organisms that we identify as species taxa. *Sparrow*, for instance, does *not* refer to a species taxon in our usage. In modern classificatory terms, *sparrow* is the family *Passeridae*, which includes multiple genera, and many species” (Richards 2010, 33). Therefore, we cannot accept that “Linnaeus’s system of static and discrete species was simply the result of filling in the abstract [Porphyry’s] Tree with the names of actual species” (Franklin 1986, 252).

As used in his works on animals, Aristotle’s genus was not a formal taxonomic category but just a group of fairly similar organisms on which attention was focused and stable diagnostic characters (*differentiae specificae*) identified subgroups within each genus, whenever required (Reydon 2020).

3.2 Alphabetical order vs. classification

Philosophers (from Neoplatonists to Scholastics) who took up the categories of genus and species from Aristotle used them as two terms in a logical relationship, without linking them to the natural world as levels of a taxonomy (Pavlinov 2022). Reciprocally, Renaissance zoologists and botanists who used these terms do not seem to have been directly inspired by the Aristotelian-Scholastic tradition.

In many 16th and 17th century books on plants or animals, entries were ordered alphabetically; examples are Leonhard Fuchs' herbal *De historia stirpium* (1542) and John Ray's early botanical works, *Catalogus plantarum circa Cantabrigiam nascentium* (1660) and *Catalogus plantarum Angliae* (1677).

Deciding on the place of these works in the history of biological systematics depends on what we mean by classification and, as a consequence, on whether we accept alphabetical ordering as a peculiar kind of classification. These issues are clearly discussed in Hjørland (2017), on which the following paragraph is based.

A dictionary, e.g., of animal or plant names could be described as a classification, where the ordering principle is the alphabetical sequence of the entries: this arrangement satisfies indeed Bliss' (1929, 143) definition: "A classification is a series or system of classes arranged in some order according to some principles or conception, purpose or interest, or some combination of such". Specifically, the alphabetical ordering of entries fits into Suppe's broad definition of *conceptual classification*, as "intrinsic to the use of language, hence to most if not all communication. Whenever we use nominative phrases, we are classifying the designated subject as being importantly similar to other entities bearing the same designation; that is, we classify them together" (Suppe 1989, 292). However, to regard the simple alphabetical ordering of plant or animal names would not add any scientific content to the mere identification of phenomenological entities worth a name (*phenomenological species sensu*) (Sterelny 1999). A taxonomy, or *systematic classification* requires instead the arrangement of these units within a scheme in which at least two levels are recognized (Suppe 1989, 292).

A transition from a roughly alphabetical ordering to a distribution of items ("species") into named groups ("orders") is found in Conrad Gesner's works (Enenkel 2014). While in his first zoological treatise, on quadrupeds (Gesner 1551), mammals are arranged alphabetically, in the second edition of the *Icones Avium* (Gesner 1560) birds are distributed in eight orders some of which, e.g., the nocturnal birds of prey, broadly correspond to those of modern ornithology.

Ordering by alphabet is not the only way to arrange items in a list, as shown for example by the Great Chain of Being,

once popular since classical antiquity into modern times, linking God, angels, humans, animals, plants, and minerals in the order (Lovejoy 1936).

In any case, ordering and classifying are two different operations and, to some extent, either of them can be present in the absence of the other. When Lamarck (1815-22) in the *Histoire naturelle des animaux sans vertèbres* arranged the main groups of invertebrates from the simplest to the most complex, thus reversing the traditional order, he demonstrated that the link between classification and ordering is not indissoluble.

3.3 Linnaeus

Before finding a point of arrival in Linnaeus' encyclopedic work covering both animals and plants, zoological and botanical taxonomy evolved separately. Even Ray, the most prominent of taxonomists before Linnaeus and one of the few major scientists who published important works in both fields, never dealt with plants and animals in the same work and adopted very different treatments for plant and animal species. Plant taxonomy matured faster than animal taxonomy and this is well reflected in Linnaeus' scientific production.

Linnaeus (1751, aphorism 155) suggested an equivalence between the sequence of categories adopted in his botanical classification (*classis, ordo, genus, species, varietas*, in descending order from the most inclusive) and the philosophical categories *genus summum, intermedium* and *proximum, species* and *individuum*. However, this correspondence was offered by Linnaeus only by way of example, as evidenced by two further equivalents, a geographical sequence (*Regnum, Provincia, Territorium, Parœcia, Pagus*) and a military one (*Legio, Cohors, Manipulus, Contubernium, Miles*). In fact, Linnaeus derived from the scholastic tradition (through his predecessors in natural history) the names, rather than the meanings, of these categories (Minelli 2022).

4. Species as taxon

4.1 Species delimitation

A number of criteria and algorithms that would reduce subjectivity in species delimitation have been proposed (e.g., Wiens and Servedio 2000; Pons et al. 2006; Wiens 2007; Leliaert et al. 2009; Monaghan et al. 2009; Hausdorf and Hennig 2010; O'Meara 2010; Yang and Rannala 2010; 2014; Ence and Carstens 2011; Dupuis et al. 2012; Fujita et al. 2012; Puillandre et al. 2012a; 2012b; Carstens et al. 2013; Flot 2015; Rannala 2015; Luktanov 2019; Sukumaran et al. 2020).

Deciding whether the morphological or genetic differences between two sets, A and B, of individuals justify clas-

sifying these as distinct species is often uncontroversial when A and B are sympatric, i.e., occur in the same area: the absence of specimens with intermediate traits strongly suggests reproductive isolation.

Species delimitation based on apparently fixed differences was codified as a methodology called population aggregation analysis (Davis and Nixon 1992). Although satisfactory in principle, this criterion may fail when applied to limited population or character samples. On the one hand, if A and B have been compared for a few characters only, characters with alternative states fixed in A vs. B may not be observed; on the other hand, if sampling is limited to few specimens, an overlap between the ranges of variation of the putative species A and B may go unnoticed. As a consequence, the number of species will be easily underestimated in the first case and overestimated in the second.

The real problem, however, is delimiting species in conditions of allopatry, i.e., when comparing similar but distinguishable populations living in geographically isolated area, e.g., on different islands or mountains. In this case, some degree of morphological divergence is often accepted as a proxy for a real proof of reproductive isolation. However, what “some degree” may actually mean, remains undecidable. Thus, to avoid or at least to reduce this subjectivity, alternative approaches have been proposed, often advocating an “integrative taxonomy” (Dayrat 2005) resting on different sources of data, such as molecular, morphological, behavioral, and ecological, to delimit species.

Other approaches are based on dedicated bioinformatics tools newly developed at the interface between two traditional biological disciplines: phylogenetic analysis and population genetics. The General Mixed Yule Coalescent (GMYC) method (Pons et al. 2006; Monaghan et al. 2009; Leliaert et al. 2009) is used to analyze trees depicting the relationships of a sample of individuals representing an unknown number of related species, to discover the splits of related species from their common ancestor. The Automatic Barcode Gap Discovery (ABGD) method (Puillandre et al. 2012a) detects discontinuities (“barcode gaps”; Hebert et al. 2003) in the distribution of pairwise distances between DNA sequences. This is not easily distinguished from genetic differences internal to the populations. New mathematical models are currently being developed to address this difficulty (e.g., Sukumaran et al. 2020).

4.2 Cryptic species

Experimental tests of the reproductive compatibility between individuals of different populations have frequently revealed the existence of reproductive barriers between groups of individuals not distinguishable from each other by diagnostic morphological characters. These *cryptic species* (Darlington 1940) have been regarded as a precious study

object by evolutionary biologists, but as a source of difficult problems by systematists. In recent times, the increasingly widespread use of molecular characters in taxonomy has shown that the number of cryptic species and their occurrence in the most diverse groups have been strongly underestimated.

Many, only partly overlapping definitions of cryptic species have been given (for a list, see Struck et al. 2018), but most authors would agree with Bickford et al. (2007), that two or more species deserve to be defined “cryptic” if they are currently classified, or have been classified in the past, as a single species due to the apparent lack of diagnostic morphological characters. Thus, the status of cryptic species does not describe a natural phenomenon, but only a temporarily problematic formalization of the delineation of species (Korshunova et al. 2017).

Despite the fact that the term was introduced by a botanist (Darlington 1940), the literature would suggest that cryptic species are much more frequent in animals than in plants (Bickford et al. 2007). To some extent, this might be a consequence of the fact that quick, cheap and reliable diagnostic tools by which indications of the existence of cryptic species can be rapidly obtained are available for animals, but not yet for plants (Shneyer and Kotseruba 2015). In most animal groups, individual specimens can be assigned quite reliably to a species by extracting and sequencing a diagnostic DNA segment that evolves fast enough as to differentiate between closely related species, but also shows very modest or no variation within each species. A nearly universally accepted “molecular barcode” for animals is a segment of the mitochondrial DNA, a part of a subunit of the cytochrome oxidase gene CO1 (Hebert et al. 2003). But in most plant lineages, mitochondrial DNA evolves too slowly; alternatives have been suggested (e.g., Chase and Fay 2009), including the sequence of the whole plastidial genome, i.e., the DNA associated with the chloroplast (Erickson et al. 2008; Parks et al. 2009; Nock et al. 2011), but no satisfactory solution has been obtained thus far (Li et al. 2015; Saddhe and Kumar 2018).

Eventually, cryptic species may turn out not to be so rare among plants as recent reviews (e.g., Shneyer and Kotseruba 2015) suggest, thus fulfilling Grant’s (1957; 1981) prediction that they may be frequent among plants too. Cryptic species may also represent a significant part of the still undescribed species of algae (Guiry 2012) and perhaps also of fungi, judging from some reports of cryptic diversity among plant pathogenic fungi (Pavlic et al. 2009; Bennett et al. 2011).

An important amount of cryptic diversity would be better described in terms of MOTUs (molecular operational taxonomic units) (Floyd et al. 2002). These clusters of individuals or populations recognizable through molecular markers do not necessarily correspond to conventional taxonomic species, as pointed out for the first time by Blaxter et al. (2005) and confirmed by a large number of studies us-

ing a diversity of markers and different species delimitation criteria. More disturbing, there is no universal rule for translating MOTUs into named species with a place in the Linnaean classification. Not an easy job, considering the very large number of cryptic species that some studies have suggested need recognition within what was hitherto described as a single species. For example, a morphologically very uniform set of populations of subterranean crustaceans living in the desert springs of the Southern Great Basin of California and Nevada, USA, previously referred to one species (*Hyalella azteca*), was reported to correspond to 33 cryptic species (Witt et al. 2006). A still higher number (62 or 78, depending on the method used to delimit species) has been identified using ribosomal DNA sequences from 401 samples across the global distribution of the tiny flatworm *Gyraatrix hermaphroditus* (Tessens et al. 2021).

In most instances, for a newly discovered cryptic species no formal description and naming is provided, for a while at least (Horton et al. 2017). Struck et al. (2018) analyzed 606 publications citing cryptic species, issued before June 2016; of these, less than one in five contains formal descriptions of the hypothesized species. However, despite the difficulties and size of the task, detailed study and formal description of this species diversity is seen by many researchers as a necessary effort (e.g., Trontelj and Fišer 2009; Pérez-Ponce de León and Nadler 2010; Minelli 2017).

4.3 Linnaean nomenclature

The international scientific nomenclature of animal and plant species has its origin in the works of Carolus Linnaeus: more precisely, in the first edition of *Species Plantarum* (Linnaeus 1753) for plant and the tenth edition of *Systema Naturae* (Linnaeus 1758) for animal names. We, therefore, speak of Linnaean nomenclature, where each species is indicated with an expression (the Linnaean binomial) consisting of two words: the generic name and the specific epithet. The generic name is identical for all the species that zoologists or botanists group in the same genus. For example, *Solanum tuberosum* (potato) and *Solanum melongena* (aubergine) are two species classified in the genus *Solanum*.

The specific epithet was introduced by Linnaeus (under the name of “*nomen triviale*”), as an advantageous mnemotechnical alternative to the polynomial formulas then in use, which summarized the main diagnostic traits on the basis of which a species was considered to differ from other species of the same genus. Some of these polynomial formulas were actually binomial, especially in the case of more common species, or of species attributed to genera with few species, where a single differential character, expressible with a single word, was sufficient to characterize a species (e.g., *Asphodelus autumnalis* and *Asphodelus bulbosus*, two plants listed under these names in Bauhin 1596). But in the

most species-rich genera, the formulas tended to lengthen considerably, therefore the convenience that resulted from the introduction of the Linnaean binomials is evident. For example, the Old World swallowtail, a butterfly that Linnaeus himself had indicated (Linnaeus 1746) as *Papilio hexapus; aliis flavo nigroque variegatis: secundariis angulo subulato maculaque fulva*, becomes *Papilio Machaon* (Linnaeus 1758), the name by which it is still called, apart from the loss of the capitalization of the specific epithet. Linnaeus was the first author to adopt binomial nomenclature systematically, but the idea had been floated before him (Choate 1912) by some botanists, most explicitly by Rivinus (1690), who remarked that it would be easy to suggest the specific difference diagnostic for a plant species by simply attaching a second term to the genus name^[9]. Before the deliberate systematic adoption of binomial nomenclature in *Species Plantarum*, an extensive although still unsystematic use of binomials is also found in the dissertation *Pan suecicus* defended in Uppsala on December 9, 1749, by Linnaeus' pupil Nicolaus L. Hesselgren (Linnaeus 1749). Of the 866 plant names listed there, 754 are binomials. A number of them, but not all, were retained by Linnaeus in *Species Plantarum*.

The rapidly growing popularity of Linnaeus' works, including his encyclopedic *Systema naturae* that provided a classification both for animal and plant species (and also minerals, classified at the time as the third kingdom of nature) contributed strongly to aligning zoological and botanical practices and to convince the scientific community of the enormous benefits that would derive from a general agreement, both in the delimitation of the phenomenological units recognized as species, and in the adoption of a unique name for each of them. On the latter issue, binomial nomenclature was an obviously advantageous choice; this caused a dramatic loss of interest in the pre-Linnaean literature, encumbered by its unmanageable nomenclature.

However, this revolution was neither easy nor complete. The main remaining issue was that just adopting the Linnaean system did not guarantee the uniqueness and universality of nomenclature. Two main problems showed up: synonymy and homonymy. If different names have been used for one and the same species, which of them should be accepted and used? If one and the same name has been used for two or more different species, for which of them should it be retained as valid? Common sense and legal practice may suggest to resolve these conflicts by applying a principle of temporal precedence (priority given to the oldest synonym or homonym), but this was just the tip of an iceberg that deserved a serious debate before a possible agreement on a precise set of rules.

Taxonomic traditions in botany and zoology began to diverge again soon after Linnaeus' death. This was annoying, especially in so far as this affected nomenclature.

In zoology, the British Association for the Advancement of Science made a first attempt to regulate these matters by setting up a Committee “to consider the rules by which the Nomenclature of Zoology may be established on a uniform and permanent basis”. This Committee eventually produced a *Report* (Strickland et al. 1842) that is regarded as the first official set of rules for zoological nomenclature. However, this initiative was still at a national level. Only towards the end of the 19th century did an international effort eventually produce a nomenclature code on which the entire zoological community could converge. A Commission appointed by the third International Congress of Zoology, held in Leiden in 1895, produced the document known as *Règles internationales de la nomenclature zoologique* (International Commission on Zoological Nomenclature 1905). This Commission has continued to work, both to resolve problematic cases that emerged from the application of the rules and to integrate or modify the latter. In the long run, the need for an overall rewriting of the rules was recognized; a new document was issued in 1961 as the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1961). In the following years, this text was subjected to further revision, until the fourth edition (International Commission on Zoological Nomenclature 1999), in force since January 1, 2000. For a history of zoological nomenclature, 1895-1995, see Melville (1995).

In botany, a series of principles were more or less widely accepted as normative for the nomenclature of plant taxa, starting from a document prepared by Alphonse de Candolle for the International Congress of Botany held in Paris in 1867 (Candolle 1867), but the first official Code was voted on only at the Seventh International Congress of Botany, held in Stockholm in 1950 (Lanjouw et al. 1952). The current edition of the botanical code (Turland et al. 2018) was adopted by the Nineteenth International Botanical Congress, Shenzhen, China, in July 2017. For a history of botanical nomenclature, 1737-1989, see Nicolson (1991).

At the time the committee of the British Association for the Advancement of Science was about to publish a first set of rules aimed at ensuring stability and universality in the creation and use of names for animal species and higher taxa (Strickland et al. 1842), the Italian zoologist Luciano Bonaparte (Napoleon's nephew) initiated a cooperative effort towards the definition of common rules for the nomenclature of animals and plants, but this project was abandoned quite soon (Minelli 2008).

Coordination of animal and plant nomenclature would not be simply a formal exercise but would address two sets of problems that have been growing through time. First, the independence of zoological vs. botanical nomenclature has allowed the creation of names for animal genera identical to the names of plant or fungal genera. Second, the nomenclature of a certain number of genera of unicellular organisms, which

over time have been classified sometimes as animals (“protozoans”) and sometimes as plants (“algae”), is currently intractable. Some of them have two names, according to the zoological and the botanical nomenclature, respectively. There are also organisms recognized today as closely related to each other, one of which carries a zoological name, the other a botanical name. An additional problem is the lack of rules for fixing the name of an organism that has been originally described as an animal, but is now treated as a plant, or vice versa.

A new attempt at unifying the different traditions into a single set of rules intended to govern the nomenclature of all organisms (Hawksworth 1997) lead to the formulation of a BioCode (Greuter et al. 1996; 1998), but the Bionomenclature Committee which met in Naples in 2000 on the occasion of the General Assembly of the International Union of Biological Sciences (IUBS) decided to abandon the initiative (International Commission on Zoological Nomenclature 2001). A further attempt to relaunch the BioCode project (Greuter et al. 2011) was ephemeral. Therefore, the BioCode has remained at the level of a hypothesis to work on and has never been adopted by the scientific community.

Special codes of nomenclature have been created for prokaryotes (Eubacteria and Archaea), for viruses and for cultivated plants. The current editions of these three documents are Parker et al. (2019), International Committee on Taxonomy of Viruses (ICTV) (2021), and Brickell et al. (2009), in the order. Binomial nomenclature is applied to prokaryotic species taxa, but not to viruses or to cultivated plants as such. However, ongoing discussion (e.g., Hull and Rima 2020; Siddell et al. 2020) suggests that virologists may also adopt binomial nomenclature before long. As for cultivated plants, nomenclature is centered on naming cultivars. A *cultivar* is defined (Brickell et al. 2009, Art. 2.3) as “an assemblage of plants that (a) has been selected for a particular character or combination of characters, (b) is distinct, uniform, and stable in these characters, and (c) when propagated by appropriate means, retains those characters”. Rules for naming cultivars are very flexible and do not presuppose a clear hierarchy from genus to species to cultivar, but names that include a Linnaean binomial, such as *Chamaecyparis lawsoniana* “Silver Queen” (Brickell et al. 2009, Example 5 to Recommendation 8A) are accepted.

Besides the principle of temporal precedence, accompanied by less general rules for determining which name must be used in specific cases of homonymy or synonymy, the codes are also based on additional principles that should help achieve the desirable aim of stability and universality of nomenclature. Among these principles, the most important is the permanent association between taxa and types, as explained in the following paragraph.

The association between species and types is double. On the one hand, through the specimen(s) selected as the species’

type(s); on the other, through the species, among those classified in the same genus, chosen as that genus' type. Both *type specimens* and *type species* have a double significance: taxonomic and nomenclatural, respectively. This is better visible in the case of a type specimen. As taxonomic type, it is a voucher documenting the characters based on which a species taxon was first recognized, as well as a material store of additional information available for possible subsequent mining. As nomenclatural type, it fulfills the role spelled out in the following rule of the zoological code: "No matter how the boundaries of a taxonomic taxon may vary in the opinion of zoologists, the valid name of such a taxon is determined [...] from the name-bearing type considered to belong within those boundaries" (International Commission on Zoological Nomenclature 1999, Art. 61.1.1). In other terms, the type specimen is an onomatophore, or name-bearer (Simpson 1940; Dubois 2011; Witteveen 2016). Similarly, taxonomists may disagree on the validity or delimitation of a genus, but so long as this is considered valid, the genus' type species will remain associated forever with it.

4.4 Open nomenclature and non-Linnaean nomenclatures

Nomenclature codes do not contain a definition of the species category, but rules for the adoption and use of the names by which species taxa must be designated.

The formal description and naming of species is not the same action as the identification of specimens (Collins and Cruickshank 2013), which often remains uncertain even in the hands of a specialist. To hide this uncertainty under an unflagged Linnaean name would carry a wrong message. To avoid this, some formats have been used, as in the following examples: "*Harpalus* sp." (the specimen can be confidently identified as belonging to one of the species of the beetle genus *Harpalus*, but a more precise identification has not been possible); "*Lannea* cf. *schimperi*" (the specimen belongs to the wasp genus *Lannea*, possibly to *L. schimperi*, but it might instead belong to a different species, including a still undescribed one). The set of these formulae and related ones that depart from pure Linnaean binomials is sometimes called open nomenclature (nomenclature *aperta*: Richter 1943; see also Matthews 1973). This includes cases where the identification at the species level is uncertain because of contingent difficulties, e.g., incomplete specimens, or the suggested identification is potentially but not certainly correct, or the identification at the species level is uncertain because no sound taxonomy is currently available for the group to which it belongs. Last but not least, a still undescribed species may be involved, but an exhaustive study and, if this is the case, the description and naming of the new species are reserved for a later time. Sigovini et al. (2016) have provided a detailed discussion of open nomen-

clature, with a detailed glossary of the terms in use and preliminary suggestions for their standardization (see also Minelli 2019).

Besides the necessary, frequent use of open nomenclature, current practice frequently deviates from Linnaean nomenclature because of the deliberate rejection of a specific rule of the Code, or even of its basic philosophy.

A biological nomenclature in which taxa and names are not fixed by reference to types has been proposed by a group of researchers who regard this departure from the traditional codes as a necessary implication of the adoption of the so-called phylogenetic systematics. This approach to biological systematics, which moves from the conceptual and methodological reform initiated by Hennig (1950; 1965; 1966), questions the maintenance of the ranks (e.g., genus, order, class) of the Linnaean classification (Griffiths 1976). More recently, some followers of phylogenetic systematics have launched a new "phylogenetic nomenclature" eventually formalized in a new Code (Cantino and de Queiroz 2020). This proposal, strongly defended by some authors (e.g., de Queiroz 1997; de Queiroz and Cantino 2001; Bryant and Cantino 2002; Pleijel and Rouse 2003; Cantino 2004; Pleijel and Härlin 2004; Laurin et al. 2006), has been strongly rejected by others (e.g., Lidén and Oxelman 1996; Dominguez and Wheeler 1997; Benton 2000; Forey 2002; Carpenter 2003; Keller et al. 2003; Nixon et al. 2003). According to some authors, in a consequent taxonomic system based on phylogenetic principles, there would not even be room for species; the lowest unit recognized in the system should instead be an operationally defined LITU (least inclusive taxonomic unit; Pleijel and Rouse 1999) (see 6.2.6).

Another deviation from the official nomenclature is the proposed addition of a numerical code to the names formed according to the rules. This was suggested in the early 1990s to address a perceived shortage of scientific names as keywords for retrieving information from databases (Heppel 1991). Alphanumeric formulas have also been recommended as a useful complement to the unconventional names suggested by de Smet (1991) as a new biological nomenclature largely accepting the Linnaean hierarchy but represented by terms based on Esperanto rather than Latin.

5. Species as category

5.1. The species rank in biological classifications

It is generally assumed that the species category is the fundamental level in the taxonomic hierarchy of biological classifications. However, it would be more correct to reverse the sentence: today, the basic taxonomic category in biological classifications is generally called species.

The fundamental unit in a classification is not necessarily the lowest one, especially if lower ranks are optional

and not acknowledged to deserve a standardized nomenclature. This is the case of subspecies, varieties, etc. in a classification in which the species is explicitly chosen as the basic unit.

Moreover, caution is necessary in examining early taxonomies up to Linnaeus, where the author's choice between genus and species as the unit of the classification is not always easy to determine (Minelli 2022).

Like the "species" of folk taxonomies (Berlin 1973), e.g., willow and oak among plants, sparrow and eagle among animals, those described by Renaissance herbalists are only groups of organisms that are easily recognizable and quite consistently identifiable, those that Sterelny (1999, 119) characterizes as *phenomenological species*: even where nomenclature might suggest otherwise, the "species" of 16th and early 17th century botanists and zoologists are not always the same as the species of Linnaeus and often correspond to taxa recognized today as genera (Arber [1912] 1986). For example, Bauhin (1596) described 29 species of *Narcissus* (daffodil), however, he added that of one of them, *Narcissus albus, medio croceus vnico flore*, "there are three species, mainly differing in flowering time" (79).

5.2 Infraspecific taxonomic categories and their names

That animals and plants of the same species can exhibit regional peculiarities, is something that could easily fit into the framework of pre-Linnaean zoology and botany. However, geographic variation was not considered an issue really worth of study: "*varietates levissimas non curat botanicus*" (Linnaeus 1751, aphorism 310). Eventually, geographic variation began to attract the attention of naturalists, at least since Pallas (1778) compared putatively conspecific populations of rodents from many localities and documented with great accuracy variation both within and between populations, highlighting the frequent difficulty in tracing with certainty the boundaries between one species and another.

In geographical terms, intraspecific variation is also quite diverse, sometimes continuous (clinal), sometimes discontinuous. The latter case makes it easier to identify distinct units, usually called *subspecies*.

The scientific nomenclature of infraspecific taxa is much more articulated and flexible for plants than for animals. The zoological code (International Commission on Zoological Nomenclature 1999) recognizes only taxa at one subordinate rank (subspecies; a term first defined in ornithological circles (Allen 1877), while the International Code of Botanical Nomenclature (Turland et al. 2018) allows the use of names for subspecies, varieties, sub-varieties, forms and subforms.

6.0 Species concepts

6.1 The debatable plurality of species concepts

Nor shall I here discuss the various definitions which have been given of the term species. No one definition has yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species (Darwin 1859, 44)

As mentioned in section 2, the controversial issue of species concepts belongs in principle to general biology rather than to taxonomy because it involves concepts and theories that range over most of the biological disciplines, e.g., ecology, genetics, biology of reproduction, and evolutionary biology. Nevertheless, it deserves to be treated here because its many ramifications extend well into aspects of language and communication, in particular, when the contrasting positions are monism vs. pluralism (cf. subsection 6.3), with obvious implications for nomenclature. Philosophical debates that started in the late '60s have even questioned the nature of the species as a kind of class (the "species-as-sets" conception), suggesting that biological species are instead historical individuals (the "species-as-individuals" thesis).^[10]

As noted by Hey (2006, 448)

the current long list of [species] concepts spans a wide variety of inspirations, histories and purposes [Mayden 1997; Endler 1989; Hull 1997]. Indeed, it is now generally necessary when addressing general questions on species concepts to first attempt a classification of them on the basis of various properties [Mayden 1997; Endler 1989; Baum and Donoghue 1995; de Queiroz 1998; Pigliucci 2003].

Mayden's (1997) classic overview listed 22 definitions of species; subsequent revisitations by Wilkins (2009a; 2011; 2018) have added five more items. These definitions, or at least a core selection from them, are traditionally discussed and contrasted as alternative (but also in part overlapping) *species concepts*; a list of works mentioning "species concept(s)" in the title is found in the note.^[11]

But there are several reasons for disagreement on the number of definitions of biological species thus far proposed, e.g., (i) when introducing a new term, some authors did not provide an explicit definition, thus leaving a degree of uncertainty as to the precise intended meaning; (ii) because of minor differences in the definition, it is questionable if some of the proposed terms should be better regarded as synonyms of others, or not; (iii) more intriguingly, several species definitions overlap to some extent with others, but this translates only in part into a hierarchy of more inclusive vs. less inclusive terms.

The best characterized and/or most popular among the many definitions of species thus far proposed are analyzed in the following subsection, largely following Wilkins (2011). This author identifies seven main notions of species, respectively defined (1) as classes of morphologically similar individuals (*morphospecies*), (2) as reproductively isolated sexual species (*biospecies*), (3) by their common gene pool (*genetic species*), (4) as occupants of distinct ecological niches (*ecospecies*) or (5) as evolving lineages (*evolutionary species*), plus (6) a notion introduced for organisms without sexual reproduction (*agamospecies*) and (7) a term to describe whatever a taxonomist calls a species (*taxonomic species*; incl. those recognized by palaeontologists, i.e. *chronospecies*).

However, as also noted by Wilkins (2011), some of these notions are more or less equivalent (e.g., *biospecies* and *genetic species*, treated together in 6.2.2 below; *evolutionary species* and *ecospecies*, cf. 6.2.3 below). Two additional groups of concepts are presented here in separate subsections. First, *cladistic* and *phylogenetic species concepts* (cf. 6.2.4), which are indeed a mix either of *morphospecies*, *biospecies* or *ecospecies* or all of them (Wilkins 2009a) but are characterized by their specific background in phylogenetic systematics, either in its original formulation (Hennig 1950; 1965; 1966) or in its subsequent development commonly known as *cladistics*. Similarly, *phenetic* and *diagnosable species*, *LITU* and *OTU* (treated in 6.2.5) are a variegated set of definitions that differ from the taxonomic species because of the specific theoretical contexts (*phenetic* or *numerical taxonomy* and *phylogenetic systematics*) in which they have been formulated.

Before moving to detail about the different definitions, let's remark that Wilkins (2011) eventually recognizes only one species concept, in strict agreement with Ray's (1686) approach to plant species^[12]. As noted by Richards (2010, 69), "From Ray through Linnaeus and Buffon, there was a turn to a historical and genealogical conception of species. [...] An organism was a member of a species taxon not because it was similar to other members of that species – not because they shared essential traits — but because its parents were members of that species taxon". In Wilkins' (2011, 59) explicit reformulation of this *generative concept*, "species are those groups of organisms that resemble their parents".

6.2 Species definitions

6.2.1 Taxonomic species and morphospecies

Before the development of methods to investigate the diversity of life at the molecular level (proteins, but especially DNA and RNA sequences), the diagnostic characters used by taxonomists were provided by morphology, with few exceptions such as the mating calls of crickets and grasshop-

pers. It has become customary to say that delimiting species based on morphology amounts to adopting a morphological species concept (*morphospecies*), but this is mostly accepted without a formal definition like those provided for other species notions.

Eventually, in the absence of further specifications, the selection of morphological traits deemed to be diagnostic at the species level rests on the subjective choice of the taxonomist. Therefore, out of this tradition of morphology-based classificatory efforts, this vaguely circumscribed approach has been sometimes described as a *taxonomic species concept*, usually defined, by Regan (1926, 75), as "a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name".

6.2.2 Species concepts based on reproduction and genetic exchange

In everyday practice, all species taxa are commonly perceived as equivalent, since they are all named by a Linnaean binomial. However, according to Bock (2004) they should be offered uniform taxonomic status and identical nomenclatural treatment only on condition that they are, as far as possible, "biologically equivalent".

Efforts to define species in biological terms have been traced back to the work of John Ray (1627-1705) and Georges Louis Leclerc de Buffon (1707-1788).

According to Cain (1997), Ray published the first attempt to define living species based on their constancy throughout the generations. However, it is hard to construe Ray's actual words^[13] as a definition of biological species, rather than as an empirical (experimental) criterion to check the conspecificity of similar but not identical kinds of plants, i.e., to verify how much variation can be accepted within the limits of genealogical continuity. Moreover, there is no evidence that Ray extended this view to animals too. On the contrary, some passages in his zoological books seem to exclude, on Ray's part, the adoption of a "true breeding" criterion to recognize animal species (Minelli 2022).

There are also problems with Buffon, who is credited of introducing a concept of species as a reproductive community. In the pages of the *Histoire naturelle, générale et particulière* dealing with hybrids, Buffon (1749; 1766) made clear that the nearly complete reproductive isolation between horse and donkey cannot be generalized as providing a biological criterion revealing that two animals belong to different species. Like Ray, he was not interested in reproductive isolation *per se*, as a criterion to separate species, but in ascertaining the continuity of a lineage through the generations.

In the last century, the *biospecies* has been most frequently defined as a reproductive community of sexual individuals that do not cross with individuals of the other species, or as the most inclusive set of individuals sharing a common gene pool. In this latter form, the notion is also called *genetic species* (Simpson 1943; Dobzhansky 1950).

According to Dobzhansky (1970, 354), “a biological species is an inclusive Mendelian population; it is integrated by the bonds of sexual reproduction and parentage”. In Mayr’s (1963, 21) more detailed characterization,

species are reproductive communities. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction [...]. The species, finally, is a genetic unit consisting of a large, intercommunicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short time.

In practice, however, it is not always easy, or possible, to recognize a clear boundary between interfertile and reproductively isolated populations. In extreme situations, e.g., among the hundreds of taxa of the cichlid fish family present in Lake Victoria, Africa, the reproductive communities seem to literally come and go in real time (Spinney 2010). New species are taking shape from hybridization between pairs of survivors from the severe crisis caused in the recent past by the introduction of an alien big predator, the Nile perch *Lates niloticus*: an example is the hybrid currently forming in the lake’s Mwanza Gulf between the blue *Pundamilia pundamilia* and the red-back *P. nyererei* (Meier et al. 2018).

The biological species concept has been primarily applied to animals. Some botanists (e.g., Raven 1980) have been skeptical as to the possibility of applying it to plants; others, however, have openly sided in favor of its validity, e.g., Grant (1971; 1981; 1992), more recently Rieseberg et al. (2006).

According to an alternative view of the biological species concept, a species does not exist based on its relations with other species, but by virtue of a property that unites the individuals referable to it, thus forming a system that “defines itself” (Paterson 1985; Lambert et al. 1987; White et al. 1990). This was recognized long ago by Plate (1914)^[14]. According to the recognition species concept developed by Paterson (1979; 1985, and also by Lambert and Paterson 1984), species are reproductive communities the members of which share a “specific mate recognition system”, i.e. an interpretative code for a series of information elements — for example, acoustic signals or pheromones — that are exchanged between potential partners.

A problem with species notions based on sexual reproduction, both in Mayr’s and in Paterson’s sense, is that these may work only for populations that are far from both of two opposite, extreme conditions: the absence of sex, in which case no species would exist, and the absence of barriers to sexual exchanges, as repeatedly observed in bacteria, where strongly different kinds of organisms would be classified as one species because transfer of genetic material between them is possible in natural conditions. To avoid these disturbing consequences, Templeton (1989, 12) proposed a *cohesion species concept*, according to which a species is “the most inclusive population of organisms having the potential for phenotypic cohesion through intrinsic cohesion mechanisms”. Mechanisms favoring cohesion are not necessarily the same in all instances; in particular, both interfertility and the presence of shared mating recognition systems are included.

Hybrids, both natural and artificial, also continue to challenge modern definitions of species (Wagner 1983). In many plant groups, hybrids are very common in nature and a large number of hybrid forms are described in the floras. Examples are abundant e.g., among the European orchids and willows. The well-defined, stable morphology of these hybrids suggests that they represent F1 (first generation) hybrids between the two parental species; a backcross with one of the parents would blur the distinction. But many hybrid individuals found in nature, especially among animals, are just elements of a chain, each of which shares to a different degree similarities with either parental species. Hewitt (1988) described this situation as a “hybrid zone”.

Over time, the need for a concept and a term to indicate the whole set of populations linked by hybridization has repeatedly emerged among systematists. The term *syngameon* was introduced by Lotsy (1925) and used mainly by botanists (e.g., for oaks, *Quercus* species; see Cannon and Petit 2020). In zoology, Dubois (1982) proposed an operational definition of genus that practically coincides with Lotsy’s syngameon. In recent times, the term has been borrowed by zoologists to describe cases where the boundaries between species are difficult to establish, due to reticulate evolution, e.g., among Darwin’s finches of the Galápagos islands (Grant and Grant 1996), the cichlid fishes of the large African lakes (Seehausen et al. 1997), the South American *Heliconius* butterflies (Beltrán et al. 2002) and the reef corals of the genus *Acropora* (Oppen et al. 2001; Mao et al. 2018; Mao 2020). Seehausen (2004, 198) has provided a new definition of syngameon as “a complex of selection-maintained, genetically weakly but ecologically highly distinctive species capable of exchanging genetic material”.

Within the biological species concept, additional taxonomic categories have been proposed to accommodate groups of closely related groups of populations in an evolutionary condition intermediate between still interbreeding subspecies, or races, and reproductively isolated species

(Mayr 1931; Amadon 1966; Mallet 2013). The term species in *statu nascendi*, used for a while to describe them, has lost favour. A complex of imperfectly isolated, closely related taxa was called *Artenkreis* by Rensch (1928; 1929), a term largely replaced in later use by Mayr's (1931) *superspecies*. Mayr's (1963, 672) eventually revised definition of a superspecies is: "a monophyletic group of entirely or essentially allopatric species that are too distinct to be included in a single species", where "allopatric" means "with non-overlapping geographical distribution".

The term *semispecies* was originally introduced to denote the component species of a superspecies, whatever the degree of reproductive isolation between them, as in the following definition: "Semispecies – In systematic zoology the species of which a superspecies is composed" (Mayr et al. 1953, 313). However, the term has been increasingly used in the sense of species in *statu nascendi*, to denote borderline cases between subspecies and full species: "populations that have acquired some, but not yet all, attributes of species' rank; borderline cases between species and subspecies" (Mayr 1963, 671).

A number of botanists realized that the different degrees of reproductive isolation between populations or groups of populations observed in nature could not be adequately expressed in terms of the categories of the Linnaean classification but required a special purpose classification (Stace 1989) for which Camp and Gilly (1943) coined the term *biosystematics*.

Three partly overlapping schemes of biosystematics categories were developed by Turesson (1922a; 1922b), Danser (1929), and Gilmour and Heslop-Harrison (1954), respectively. These categories are uniquely based on the extent of possible interbreeding between individuals or populations. In Turesson's nomenclature (the first to be introduced and eventually the most popular), individuals capable of hybridizing with one another form a *coenospecies* (= *comparium* of Danser = *syngamodeme* of Gilmour and Heslop-Harrison). The terms *commiscuum* of Danser or *coenogamodeme* of Gilmour and Heslop-Harrison have been used if hybrids show some degree of fertility, whereas complete interfertility characterizes the *ecospecies* of Turesson (same as Danser's *convivium* and Gilmour and Heslop-Harrison's *hologamodeme*).

6.2.3 Agamospecies

A strict, exclusive application of the biological species concept would imply that no species exist among those kinds of organisms that reproduce from a single parent. Mechanisms include asexual multiplication in the strict sense (i.e., through the detachment of body parts), self-fertilization (both male and female gamete being produced by the same individual, as in several tapeworms and other hermaphro-

dites) and thelitoky (development of a new individual from an unfertilized egg; see Fusco and Minelli (2019) for these and other, less common and often complex mechanisms).

Taxa recognized (and named) among uniparental organisms have been called *agamospecies* by Turesson (1929). The terms have been accepted by several authors, including Cain (1954), who regarded the agamospecies as a subset of the morphological species. A synonym is *paraspecies* (Mayr 1987), but this term had been used before by Ackery and Vane-Wright (1984) with a different meaning, for species lacking uniquely derived traits. With a beautiful metaphor, Ghiselin (1984) compared agamospecies to dead leaves forming a heap at the foot of the phylogenetic tree from which they originated but to which they no longer belong. Camp (1951) and Grant (1957) called them *binoms*, to stress the fact that those taxonomic entities deserve anyway a place in a classification using Linnaean names.

6.2.4 Evolutionary and ecological species concepts

Simpson's (1961, 153) *evolutionary species concept* identifies the species as "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies", a definition slightly revised by Wiley (1978, 17) in the following terms: "An evolutionary species is a single lineage of ancestral-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate".

This notion applies equally to organisms with sexual or asexual reproduction, because the evolutionary processes give rise in either case to lineages subject to changes over time.

A related *ecological species concept* was introduced by Van Valen (1976, 333) as "a lineage or set of closely related lineages, occupying an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all other lineages outside its range".

Conservation biologists have long disputed about the nature and circumscription of *evolutionarily significant units* (a term introduced by Ryder 1986) as the units of biodiversity individually worth of monitoring and eventually action to ensure their survival (Moritz 1994; Nielsen 1995; Waples 1995; 1998; Cracraft 1997; Pennock and Dimmick 1997; Dimmick et al. 1999; Crandall et al. 2000; Casacci et al. 2013; Reydon 2019). It is still an open question how far evolutionarily significant units may correspond to taxa of the Linnaean tradition.

6.2.5 Cladistic and phylogenetic species concepts

Evolution is not just matter of adaptation^[15], but also one of genealogical relationships (phylogeny), and biological

systematics has been revolutionized since the relationships expressed in phylogenetic trees have been targeted as the first (or only) criterion on which to base the classification (Hennig 1950; 1965; 1966). In this context, there have been repeated efforts to define the species in relation to phylogeny. Wilkins (2009b) classifies the resulting definitions under six terms: *Hennigian species*, *cladospecies*, *internodal species*, *phylogenetic taxon species*, *autapomorphic species* and *composite species*. Here, we recognize two main notions: a cladistic species concept and a phylogenetic species concept.

With reference to an explicit (albeit hypothetical) reconstruction of the phylogenetic relationships among a given set of extant and/or extinct organisms, Ridley (1989, 3) defines a *cladistic species* as the “set of organisms between two speciation events, or between one speciation event and one extinction event, or that are descended from a speciation event”.

Again, with reference to hypothesized phylogenetic relationships, a *phylogenetic species* identifies, according to Rosen (1978) and de Queiroz and Donoghue (1988), the smallest recognizable biological entity that is monophyletic, i.e., includes all descendants from a given ancestor, to the exclusion of any other organism. The proof of monophyly is the presence of one or more autapomorphies (derived characters present only within the group considered).

In a different version (McKittrick and Zink 1988), the phylogenetic concept of species requires both monophyly and unambiguous diagnosability.

In addition to these two formulations, Mayden (1997) grouped also a third one (as the diagnosable version) under the umbrella term of phylogenetic species concept, but it seems more reasonable to classify it in the group of phenetic species concepts, as described in the next subsection.

6.2.6 Phenetic and diagnosable species, LITU and OTU

Definitions of Mayden's (1997) diagnosable version of the phylogenetic species concept, mentioned in the previous subsection, were proposed by Eldredge and Cracraft (1980), Nelson and Platnick (1981), Cracraft (1983; 1987) and Nixon and Wheeler (1990). According to Cracraft (1983, 170), “A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent”. Adopting this notion of species may easily cause a phenomenon described as species inflation (Zachos et al. 2013). An example was provided by Cracraft (1992) himself with his taxonomic revision of the birds of Paradise. Within this group, the taxonomy of previous authors, based on the biological species concept, recognized 40-42 species, whereas Cracraft, under his “minimalist” species concept, raises this number to about 90. More recently, species inflation has repeatedly occurred in mammal taxon-

omy, two examples being the three species recognized by Cracraft et al. (1998) among tigers instead of the only species (*Panthera tigris*) accepted by traditional taxonomy, and the three species recognized by Groves and Grubb (2011) among the European red deer hitherto classified as one species (*Cervus elaphus*).

According to Nelson (1989) and Lidén (1992), in nature there are no objects such as species or processes such as speciation (formation of two or more species by splitting of a previously existing one), therefore no aspect of biological diversity can be unambiguously referred to a hypothetical species rank. Due to the common ancestry of all living beings, it is possible to recognize relations of relative inclusion of a lower taxon within a higher taxon, without one or the other being assigned an absolute (and named) rank, e.g., species. In the same vein, a *least inclusive taxonomic unit* (LITU) was proposed by Pleijel and Rouse (1999; see also Pleijel 2000). The word *species* does not appear in this denomination, therefore this operational unit should perhaps not be included in a list of species concepts. In a nutshell, LITUs are the smallest taxonomic groups that can be diagnosed based on derived traits (apomorphies). They do not refer to any hierarchical level, nor are they necessarily labeled with Linnaean binomials. The prospect of abandoning the species category was discussed by LaPorte (2007), who concluded that no alternative to the use of *species* among those proposed for a rankless taxonomy has provided an adequate substitute for it. The current edition of the PhyloCode (Cantino and de Queiroz. 2020) does not include rules for “species” (or LITUs) names, contrary to previous plans (cf. Dayrat et al. 2008).

Strictly operational, thus free from this kind of ontological implications, is the *phenetic species concept* developed by Sokal and Sneath (1963) and Sneath and Sokal (1973) in the context of their numerical approach to taxonomy. Setting an objective and reproducible classification as the only target of their effort, and deliberately ignoring phylogenetic relationships, these authors classified organisms on the basis of overall similarity (a phenetic approach). Rather than species defined by biological properties such as descendancy or interfertility, the units of their classification are thus *operational taxonomic units* (OTUs). Eventually, OTUs may overlap with Eldredge and Cracraft's (1980) diagnosable species mentioned in the first lines of this subsection.

6.2.7 Successional species

Extinct animals and plants did not find a place in the Linnaean classification of living organisms. In the 12th edition of *Systema Naturae*, Linnaeus (1768) listed eight genera of fossils, but classified them with minerals. Eventually, however, extinct species found their places in the classification in close proximity of the living forms to which they are most similar. As in collection drawers the shells of both living and

fossil molluscs were often arranged together, i.e. sorted out according to their similarities rather than to their age, so Lamarck (1815-22) arranged living and extinct species according to their presumed affinities.

The species recognized by paleontologists are morphospecies (e.g., Hallam 1988) that are difficult to reconcile with current concepts of biological species. Different terms have been suggested to stress their distinctness from the latter, such as *chronospecies* (George 1956) or *successional species*, a more suggestive alternative proposed by Imbrie (1957, 151) to designate a not better delineated segment of evolutionary lineage and accepted by Simpson (1961, 166), who regarded this entity as “a segment of an evolutionary species delimited in a certain span of time”, as opposed to a species recognizable among contemporary organisms as “a cross section of an evolutionary species at any one time”. This clearly indicates an effort to reconcile within one definition (evolutionary species concept) the taxonomic units recognized both in extant and extinct organisms, but also denounces the unavoidable arbitrariness, explicitly acknowledged by George (1956), in the temporal delimitation of successional species.

7.0 Species monism or pluralism?

7.1. Ontological and epistemological aspects

As mentioned in subsection 6.1, Wilkins (2011) reduces the dozens of species notions thus far proposed to seven distinct definitions — all referable to one species concept — with 27 variants and mixtures. Most of these different definitions (or variations) refer to the different aspects of biological diversity relevant in the context of different biological disciplines; however, the corresponding taxa are almost always called “species” and receive Linnaean names, similar to the phenomenological species of the Linnaean taxonomy (Sterelny 1999). Nevertheless, if Linnaean binomials are to be useful in evolutionary biology, ecology, etc., they should refer to units overlapping as much as possible with the different units in which this or that discipline is interested. Ideally, for all of them, hence the so-called species problem mentioned in section 2. This problem has been mostly addressed in one of two ways (Brigandt 2020).

A first way is to decide that the units of taxonomy must be, for example, those of evolutionary biology, or segments of the phylogenetic tree, to the exclusion of any other criterion.

This strategy has been adopted by Mayden (1997), based on Mayr’s (1957) distinction between “primary” and “secondary” species concepts. A primary species concept would embody the most important properties shared by all entities assigned to the species category, whereas secondary species concepts are intended as operational tools to be used to dis-

cover species in practice. Mayden’s primary species concept is the evolutionary species concept.

Subjectively restricting the choice to one primary species concept may bring to the rejection of the species category as a privileged rank in the Linnean hierarchy or even to denying that it constitutes a rank at all (species eliminativism; e.g., Mishler 1999; Cellinese, Baum, and Mishler 2012).

A second way to solve the species problem is to look for a general concept of species within which the greatest number of independent and sometimes conflicting criteria can be accommodated. According to de Queiroz (1998; 1999; 2005), recognizing the common features of a *general lineage* (or *metapopulation*) species concept would represent a simple solution to the species problem. Indeed, “all modern species definitions either explicitly or implicitly equate species with segments of population level evolutionary lineages” (de Queiroz 1998, 60). Similarly, Van Valen (1988) advanced a *polythetic species concept*, according to which we accept as species all populations or sets of populations that fulfill a majority of a set of stated criteria, but none of them is expected to fulfill all of them^[16].

However, there is also a third way out of the “species problem”, that is to accept a certain degree of taxonomic and nomenclatural pluralism, to account for the different units of representation of biological diversity required in the different disciplinary or operational contexts, most of which were not foreseeable in the times of Linnaeus or Ray (Pavlinov 2020).

Some authors (Mishler and Donoghue 1982; Kitcher 1984b; Stanford 1995; Dupré 2001; Ereshefsky 1998; 2001; Slater 2013^[17]; Conix 2019) support taxonomic pluralism, others (Ghiselin 1987; Hull 1987; Hey 2006) reject it. At any rate, despite the intentions and efforts of many taxonomists, current taxonomic practice is already, to some extent, pluralistic (Minelli 2019).

Nathan (2019) distinguishes two independent versions of pluralism. According to the first, various kinds of species are present in nature. A plurality of species concepts may thus be adopted. This corresponds to Davis and Heywood’s (1963) remark that among living forms, there are many kinds of discontinuities, all of which may be of interest. As a consequence, “a variety of species concepts are necessary to adequately capture the complexity of variation patterns in nature. To subsume this variation under the rubric of any one concept leads to confusion and tends to obscure important evolutionary questions” (Mishler and Donoghue 1982, 500). The species category is thus heterogeneous in the sense that it encompasses multiple types of species taxa, likely produced by a number of phenomena (Nathan and Cracraft, 2020).

The other version of species pluralism claims that the assignment of species-level taxa is always relative to a theory, explanatory aim, or classificatory purpose (Dupré 1981;

1999; Kitcher 1984a; 1984b). Accepting this form of pluralism seems to require that the different species concepts adopted in circumscribing different sets of taxa are always evident and possibly stated in explicit terms (Conix 2019). This form of pluralism has been often regarded (e.g., by Ereshefsky 1992; 1998; Hull 1999) as a reason for rejecting species realism, i.e., species realism would necessarily accompany species monism. But it should be noted that other authors have merged pluralism with realism (Kitcher 1984b; Dupré 1993; 1999; Boyd 1999; Wilkins 2003; Slater 2013).

7.2 Soft (taxonomic) species pluralism

As noted quite long ago by Kitcher (1984b), description and naming of the different kinds of units relevant to the different biological disciplines require pluralism of species notions. This is not without consequences, however, because the resulting classifications are not the same: number and circumscription of the units recognized following the adoption of different criteria may differ in an unpredictable way and to an unpredictable extent (Conix 2018; Brigandt 2020). Moreover, pluralistic taxonomy necessarily requires some degree of *nomenclatural pluralism* (Minelli 2019; 2020).

A somehow cryptic form of nomenclatural pluralism is due to the instability of taxonomy. The following is an example of ambiguity in the meaning of species names caused by differences in taxonomic treatment (Minelli 2019). According to Zachos et al. (2013) the red deer *Cervus elaphus* Linnaeus (1758) includes the Mediterranean subspecies *C. e. corsicanus* (Erxleben, 1777), which is instead treated by Groves and Grubb (2011) as a distinct species (*Cervus corsicanus* Erxleben, 1777). As a consequence, in the absence of further qualifications, Linnaean names may become semantically unstable. The problem can be solved by specifying *taxonomic concepts* (Berendsohn 1995), i.e. the precise meanings of names in the different sources and the semantic relationships among them. In the above example, “*Cervus elaphus* Linnaeus (1758) sensu Groves and Gubb (2011)” is part of “*Cervus elaphus* Linnaeus (1758) sensu Zachos et al. (2013)”. Taxonomic groups for which two or more, conflicting taxonomies coexist are all but rare. For example, ca. 10,000 species and 22,000 subspecies of birds are currently recognized (Lepage 2019), but over 1.5 million distinct taxonomic concepts are available for them in the literature (Lepage et al. 2014).

To contrast the standing instability of taxonomy and, as a consequence, of species names, an international effort towards establishing a global list of accepted species has been launched. Conceptual, political, and technical aspects of this initiative have been discussed in a set of articles in the December 2021 issue of the journal *Organisms Diversity and Evolution* (Conix et al. 2021; Hobern et al. 2021; Lien

et al. 2021; Pyle et al. 2021; Thiele et al. 2021; Thomson et al. 2021).

8.0 Conclusion

“The diversity of life is not seamless but comes in relatively discrete packages, species” (Sterelny 1998, 78). However, much of the difficulty in classifying living organisms and defining a unit for such a classification is that the more closely the biological world has been studied, the more exceptions have been found for what formerly was considered a relatively well-defined system of species. Taxonomy’s unceasing developments remind us of Thomas Kuhn’s view: “the history of developed science shows that nature will not indefinitely be confined in any set which scientists have constructed so far” (Kuhn 1970, 263).

This article has also demonstrated that “the species problem” has been growing in recent years. If somebody has expected that the unit of classification is given and that just the criteria for classifying them has to be decided, we have now learned another lesson: conceptions of species, and thereby the way to specify them, is closely related to the general approach to classification such that, for example, cladistics tends to develop a cladistic species concept, while phenetics and numerical taxonomy provide alternatives.

The question is whether science can ever reach a consensus about one classification of animals and plants reflecting evolutionary history (the “tree of life”)^[18]. Richards (2016) thinks not. He speaks about an innate tension between our psychological biases and the theory that governs biological classification, which has played out in the history of classification from Aristotle to the present, for example in the disputes between evolutionary taxonomists and phenetists and (284-285):

until human psychology changes, and there is little reason to believe it will soon, and as long as we learn and apply general terms, this tension will remain. We can learn the theoretical framework of modern evolutionary biological classification, but we cannot avoid our psychological tendencies in learning the general terms that we apply to biological taxa. We cannot avoid thinking about all the kinds of organisms we see in the world as timeless sets of things, where set inclusion is determined by a set of properties, even though we also believe these kinds to be historical and branches on an evolutionary tree. If so, then the practice of biological classification will continue to be fraught with the problems that arise from this fundamental tension.

Other kinds of tensions may also be relevant, perhaps even more so. Different social interests may be associated with

classification, including different demands by different biological subdisciplines and goals for producing classifications, such as demands to simply communicate versus demands to reflect the evolutionary history. When all comes to all, the lesson we have learned is that further empirical discoveries themselves cannot solve this problem, which involves deep conceptual, theoretical and philosophical issues.

Endnotes

1. Interestingly, the term *species* is also used in mineralogy. The mineralogical species was first critically discussed by Dolomieu (1801); its current notion is comparable to the diagnosable biological species discussed in subsection 6.2.6 of this article, as shown by the following quote: “*The concept of a mineral species*. A mineral species is defined mainly on the basis of its chemical composition and crystallographic properties, and these must therefore be the key factors in determining whether the creation of a new mineral species and a new mineral name is justified. If a mineral is found whose composition and/or crystallographic properties are substantially different from those of any existing mineral species, there is a possibility that it may be a new species. A general guideline for compositional criteria is that at least one structural site in the potential new mineral should be predominantly occupied by a different chemical component than that which occurs in the equivalent site in an existing mineral species” (Nickel and Grice 1998, 238-239).
2. However, “One might think that there is a single best way of grouping entities: the grouping that exactly represents the various kinds of organisms that exist “out there”. This is not the case: “To see this, consider a fundamental dichotomy that is made in philosophical discussions of scientific classification between *natural* systems of classification and *artificial* systems of classification. One could say that a natural system of classification represents “the natural order of things” [...] while an artificial system of classification groups things together in a way that suits whatever purposes we might have but does not represent the natural order. [...] While artificial systems of classification may be useful for some purposes, in science the focus is usually on natural systems of classification [note 2 here omitted]. [...] An important aim of science is to produce knowledge that, once obtained by studying a sample of a kind, can be extrapolated to all other members of the same kind” (Reydon 2020, 219-220, italics in original).
3. This definition is thus not about what Wilkins (2018, 376) wrote: “27 Taxonomic Species [...] Also: Whatever a competent taxonomist chooses to call a species [...] Synonyms: Cynical species concept (Kitcher 1984b)”. Wilkins and Kitcher are concerned with the notion of taxonomic species, as discussed in subsection 6.2.1.
4. Dupré (2001) describes his own view as “contrary to the prevailing orthodoxy” and it is an exception to the view that species taxa should be as similar to one another as possible. He wrote (204): “The fact that classification cannot, at least, be closely tied to the central theory of biology leaves room for the thoroughly pragmatic and pluralistic approach to biological taxonomy that I shall advocate”.
5. Hjørland (2009, 1522-3) defined: “Concepts are dynamically constructed and collectively negotiated meanings that classify the world according to interests and theories. Concepts and their development cannot be understood in isolation from the interests and theories that motivated their construction, and, in general, we should expect competing conceptions and concepts to be at play in all domains at all times”. Brigandt (2020) discussed the nature, use and transformation of “concept” in biology. On p. 80, he wrote “Philosophers construe a concept as the mental content associated with a term, and because of its content, the concept plays a distinctive role in reasoning, from theorizing to practical action”.
6. Dupré (2001) argues the other way round: *species* has always been a well-established term in biological taxonomy and should remain so, but should not be considered a unit of evolution, although often confused with this.
7. “πάν γάρ τὸ διαφέρον διαφέρει ή γένει ή εἶδει, γένει μὲν ὁν μὴ ἔστι κοινὴ ή ὅλη μηδὲ γένεσις εἰς ἀλληλα, οἷον δυων ἄλλο σχῆμα τῆς κατηγορίας, εἶδει δὲ ὁν τὸ αὐτὸ γένος” (Aristotle, *Metaphysics* I, 3, 1054b27) (For everything which is different differs either in genus or in species—in genus, such things as have not common matter and cannot be generated into or out of each other, e.g., things which belong to different categories; and in species, such things as are of the same genus; transl. after Aristotle, *Metaphysics* (English), Perseus Digital Library; <http://data.perseus.org/citations/...>, accessed January 14, 2022).
8. “διαφορὰ δὲ καὶ ἑτέροτις ἄλλο. τὸ μὲν γάρ ἑτερον καὶ οὗ ἑτερον οὐκ ἀνάγκη εἶναι τινὶ ἑτερον: πάν γάρ η ἑτερον η ταῦτα διαφέρονται τινός τινὶ διάφορον, ὥστε ἀνάγκη ταῦτα τι εἶναι φ διαφέροντιν” (Aristotle, *Metaphysics* I, 3, 1054b23) (but “difference” is distinct from “otherness”. For that which is “other” than something need not be other in a particular respect, since everything which is existent is either “other” or “the same”. But that which is different from something is different in some particular respect, so that in which they differ must be the same sort of thing; transl. after Aristotle, *Metaphysics* (English), Perseus Digital Library; <http://data.perseus.org/citations/...>, accessed January 14, 2022).

9. “*levissimo artificio superaddi potest nota specificae differentiae per modum cognominis*” (Rivinus 1690, 11) (by a very simple trick, through the added name [Linnaeus' nomen triviale, i.e. the specific epithet in modern parlance] it is possible to add a remark pointing to the specific difference).

10. Following a first publication (Ghiselin 1966), where he first rejected the traditional view of species as classes of individuals, in an article titled “A radical solution to the species problem” Ghiselin (1974, 538) defined species as “the most extensive units in the natural economy such that reproductive competition occurs among their parts”. Thus, treating species as separate reproductive communities, Ghiselin regarded them as individuals endowed with unity, space-time continuity, cohesion and integration, their parts being linked together by historical-genealogical links. This means that species have a birth (speciation) and a death (extinction); between these events the species may undergo significant phenotypic changes. On this contentious issue, see also Hull (1976; 1978); Ghiselin (1987; 1988; 1997); Stamos (2003); Wilkins (2009a; 2009b; 2018); Richard (2010) and Zachos (2016). Richard's (2010, 176, italics in original) found: “The bottom line is that this metaphysical framework based on *individuality* promises to be a fertile way to think about species within the evolutionary context that coheres with what evolutionary theory tells us about species and that is confirmed by empirical investigations”. Richards (ibid.) also wrote: “[G]iven that species taxa have various characteristics and function within evolutionary theory in specific ways, what is the best general, fundamental way to think about them – as sets or individuals? The species-as-individuals answer seems most promising in terms of coherence with evolutionary theory, fertility in thinking about species taxa, and in the development of evolutionary theory. If the species-as-individuals conception is so superior for its value to biological thinking, why is the *species-as-sets* conception so attractive to philosophers? There is, I believe, a clash of two disciplines here – philosophy and biology – with different goals, methods, tools and traditions. Natural kind and set thinking has been an important part of philosophy for a very long time – at least since Plato. Because philosophers have been trained in this tradition, it is natural for them to turn to it to make sense of the world”.

While agreeing that biological species are not classes, Mayr (1987) was inclined to call them populations, rather than individuals, because the term population conveys the impression of the multiplicity and composite nature of species, but his view has never gained much favor.

11. See also: Dobzhansky 1935; Ramsbottom 1938; Burma and Mayr 1949; George 1956; Sylvester-Bradley 1956; Mayr 1957; 1992; 2000a; 2000b; Sokal and Crovello 1970; Ghiselin 1977; 1987; Kottler 1978; Wiley 1978; Mishler and Donoghue 1982; Cracraft 1983; 1987; 1992; 1997; 2000; Lambert and Paterson 1984; Paterson 1985; 1993; Atran et al. 1987; Mishler and Brandon 1987; Mckitrick and Zink 1988; Avise and Ball 1990; Nixon and Wheeler 1990; Mayr and Ashlock 1991; Grant 1992; Eldredge 1993; Kornet 1993; Baum and Donoghue 1995; Lambert and Spencer 1995; Mayden 1997; Davis 1997; Hull 1997; de Queiroz 1998; 1999; 2007; Pleijel and Rouse 1999; Wheeler 1999; Meier and Willmann 2000a; 2000b; Mishler and Theriot 2000; Wheeler and Meier 2000; Wheeler and Platnick 2000; Wiley and Mayden 2000; Hey 2001a; 2006; Wilkins 2003; 2011; Bock 2004; Vos 2011; Hausdorf 2011; Zachos 2015; 2016.

12. “*Quæ specie differunt speciem suam perpetuo servant, neque hæc ab illius semine oritur, aut vice versa*” (Ray 1686, 40) (those [plants] which differ in species keep their own species forever, and one does not arise from the seed of the other and *vice versa*; transl. after Lazenby 1995, 1157).

13. “*Quæcumque ergo Differentiæ ex eiusdem seu in individuo, seu specie plantæ semine oriuntur, accidentales sunt, non specificæ. Hæ enim speciem suam satione iterum non propagant [...] aut si inter duas aliquas comparatio instituatur, quæ plantæ ex alterutrius semine non proveniunt, nec unquam semine satae transmutantur in se invicem, eæ demum specie distinctæ sunt*” (Ray 1686, 40). (Therefore, whatever differences arise from a seed of a particular kind of plant, either in an individual or in a species, they are accidental and not specific. For they do not propagate their species again from seed; [...] if a comparison is made between two kinds of plant, those plants which do not arise from the seed of one or the other, nor when sown from seed are ever changed one into the other, these finally are distinct in species; transl. after Lazenby 1995, 1157).

14. “*Ein [reales] Band [...] welches ganz unabhängig ist von der menschlichen Betrachtung [...] ist vorhanden zwischen den Gliedern einer Art, insofern sie sich als Zusammengehörige erkennen und miteinander fortpflanzen*” (Plate 1914, 117) (Totally independent from human perspective, among the members of a species there is a real bond, in so far as they perceive themselves as relatives and reproduce among themselves).

15. If evolution was just a matter of adaptation, similarity due to similar adaptation would not be distinguished from similarity due to common ancestry, therefore we would probably continue classifying whales with fishes, bats with birds etc. — For a while, especially between

1965 and 1974, Ernst Mayr and others defended their approach to biological systematics as the one that took into account both aspects of evolution, i.e. adaptation and phylogenetic relationships; this contrasted Hennig's approach, strictly focused on phylogeny. Only the phenetic school, championed by Sokal and Sneath, deliberately took distance from phylogeny — eventually, however, the numerical methods developed in order to implement this approach were extensively “translated” to the service of phylogenetic reconstruction.

16. “a population is a species to the extent that it has most of the members of some such list of criteria as [...]”

- (1) A single origin and final extinction, with reproductive (informational) continuity between these events.
- (2) Origin taking many, rather than several or one, generations.
- (3) Limited but real extension in both time and space.
- (4) Origin by transformation of a population of individuals, not from one or two parents.
- (5) Capacity to evolve.
- (6) Capacity to act as a unit in evolution.
- (7) Occurrence in spatially disjunct populations.
- (8) Potential reproductive continuity among all included populations; compatibility for development and fitness of offspring as well as for mating and fertilization.
- (9) A mechanism for recognizing other individuals or gametes of the same species.
- (10) Reproductive isolation from other species.
- (11) Being composed of individuals.
- (12) Capacity to speciate, either with or without phyletic branching.
- (13) Capacity to remain the same species while, and after, part becomes another species after phyletic branching.
- (14) Possession of phenotypic, genic, and genotypic characters jointly distinct from those of any other species.
- (15) Occupancy of a perhaps broad and flexible niche (in the sense of a perhaps arbitrarily bounded part, or even disjoint parts, of the [biotic and abiotic] environmental hyperspace) different from that of any sympatric species.
- (16) Ultimate regulation of population or metapopulation density being causally different from that of any sympatric species” (Van Valen 1988, 51; 53).

17. In his review of Slater (2013) Richards (2015) wrote: “Slater [...] distinguishes between taxic pluralism, a plurality of partitions of organisms into species taxa, and category pluralism, a plurality of ways to conceive the species category. According to Slater, the former, but not the latter, challenges the idea that species are real.

That different species are different kinds of things does not by itself imply that species are unreal. But taxic pluralism, the partitioning of organisms in multiple inconsistent ways, is a challenge to realism in that if there is no single way to divide biodiversity into species taxa, it is not clear that there really are species things. Rather there would just be different ways to divide biodiversity, based on our interests”. Richards also found that Slater underplays the role that the species concept plays in biological theory.

18. The metaphor “tree of life” is itself subject to criticism. See Makarenkov et al. (2004), Rivera (2004), Gontier (2017), Quammen (2018).

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