Classes or Individuals? The Paradox of Systematics Revisited

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Abstract

The circumscription of taxa and classification of organisms are fundamental tasks in the systematization of biological diversity. Their success depends on a unified idea concerning the species concept, evolution, and taxonomy; paradoxically, however, it requires a complete distinction between taxa and evolutionary units. To justify this view, I discuss these three topics of systematics. Species concepts are examined, and I propose a redefinition for the Taxonomic Species Concept based on nomenclatural properties, in which species are classes conventionally represented by a binomial. Speciation is subsequently discussed, to demonstrate that concepts on the evolutionary process are damaged when species are considered as evolutionary units. Speciation should be considered a transition among patterns of a population (anagenesis) and, consequently, always a sympatric process. This view contrasts with the majority of speciation models, which analyze cladogeneses and classify speciation geographically, usually considering allopatry the essential condition for the differentiation process. Finally, taxonomy is considered, to show that the equivalence between evolutionary and taxonomic units may also damage the practice of biological systematization. Principles and rules of nomenclature and classification should offer freedom to accommodate divergent opinions about systematics and to incorporate the evolution of knowledge; therefore, they should remain independent of biological theories.

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Biosystematy seeks (1) to delimit the natural biotic units and (2) to apply to these units a system of nomenclature adequate to the task of conveying precise information regarding their defined limits, relationships, variability, and dynamic structure. (Camp & Gilly, 1943, p. 327)

Classical taxonomy and biosystematy will have to learn to live together. (Camp, 1951, p. 120)

1. Introduction

Systematists organize biological diversity in taxa defined for convenience, creating a hierarchical taxonomic system that suggests relationships among the classified organisms. Circumscription of taxa and classification of organisms are objectives of any study in systematics, and these tasks are elaborated according to the concepts and evolutionary mechanisms in which the systematist believes. Nowadays, many systematists are confusing taxon with evolutionary unity and, consequently, attributing characteristics of a historical entity (an individual in a philosophical sense) to a class of organisms. This mistaken equivalence between taxonomic classes (e.g., species and genera) and biological systems (e.g., populations and lineages) has generated misinterpretations and threatened the evolutionary independence of the taxonomic system (that is, rules and principles of classification and nomenclature). The aim of this article is to discuss the distinction between the natural system and its representation in an analogical system of taxa.

In the first section, the discussion on species is used to contrast the thesis of taxa-as-individuals and the thesis of taxa-as-classes. Species concepts are classified, a method often used to treat this subject (e.g., Baum & Donoghue, 1995; Luckow, 1995; Hull, 1997; Mayden, 1997; De Queiroz, 1998; De Pinna, 1999). I try to demonstrate that they usually do not define what the species really is. In my view, an *a posteriori* definition should be evaluated by its universality (generality) and exclusivity (precision), differing from criteria used by Hull (1997) and Mayden (1997), who argued for universality, theoretical significance, and applicability to evaluated species concepts. If the species concept has no theoretical significance or no applicability, it is possible to use other concepts, such as lineage (see e.g., Dupré, 2001) or population for theoretical significance, or criteria and methods for applicability. I conclude this section defending the Taxonomic Species Concept and arguing for a pure nominalistic view of species, in which any taxon, even at the species level, must have a class concept.

After separating species from individual concepts, speciation models are compared. The objective is to point out that evolution, including speciation, depends basically on time, and then, to demonstrate the mistaken concept of speciation models associated with concepts of species as individuals, which advocate for a space-depending speciation. The last section discusses some limitations of the traditional taxonomic system and the necessity to substitute it for a new one, as advocated by phylogenetic taxonomists (e.g., De Queiroz & Gauthier, 1990, 1992, 1994; Welzen, 1997, 1998; Cantino, 2000; Bryant & Cantino, 2002). In my opinion,
instead of being discarded, the traditional taxonomy should be, as has been done in the last decades, adjusted in order to offer freedom for any biological theory.

In summary, I discuss the three main topics of systematics—species concepts, speciation, and taxonomy—to reconsider a recurrent problem of this discipline: the equivalence between taxa and units of evolution (classes and individuals, respectively; for more discussions about class/individual contraposition in systematics, see also Frost & Kluge, 1994, and references therein). The central objective of this issue is to present arguments that taxonomic units are not the natural entities that evolve, but cognitive tools used to order them. Hence, I attempt to demonstrate that the equivalence (or confusion) of taxonomic units with units of evolution has disadvantageous effects in evolutionary concepts, as well as in taxonomic procedures, damaging the comprehension of biological diversity as a whole.

2. Species concepts

Among various hierarchical ranks of classification, the species rank has received particular attention and is considered the basic biological unity. The nature and definition of the species have been among the most discussed subjects in systematics (Wiley, 1978); however, despite many species concepts, few have been explicitly and consistently considered in practice (Luckow, 1995; McDade, 1995). Slobodchikoff (1976), Ereshefsky (1992), Claridge, Dawah and Wilson (1997), Wilson (1999), and Wheeler and Meir (2000) included articles about this theme in many different views. Whereas one may interpret them as parts of a primary evolutionary concept (Mayden, 1997) or variations of a unique evolutionary concept (the General Lineage Concept of Species, De Queiroz, 1998, 1999), others (Ereshefsky, 1992; Hull, 1997, 1999; Mishler, 1999; Hey, 2001) have concluded that there is no agreement on the subject.

Several species concepts have used interpretative models of speciation in the definition, treating species as populations. Others have proposed criteria or methods to circumscribe taxa. The majority of these concepts, instead of offering an ad hoc definition, used the relationship among species to define them. In my view, the species definition should be dissociated from evolutionary concepts and the methods used to circumscribe taxa. Thus, I propose a redefinition of the Taxonomic Species Concept.

2.1. Species as populations and processes

The central problem of many controversies concerning the species concept is not related to the definition of the species, but with the models of the process that results in discontinuous patterns that may be recognized as species. The inclusion of processes and models of speciation in species definitions began with the development of genetic studies: ‘species is a stage in a process, not a static unit’ (Dobzhansky, 1937, p. 312)—and its influence on species concepts was initially based on interbreeding capability. Mayr (1942) suggested the geographic model of speciation, emphasizing the importance of reproductive isolation in species definitions and establishing the Biological Species Concept (BSC), also called Isolation
Concept (Paterson, 1985). In parallel, the Ecological Species Concept (EcSC, Van Valen, 1976) considers the environment as the main factor in the speciation process. Unlike the BSC, the EcSC also includes asexual organisms, but it focuses on vague terms, such as adaptive zone or ecological niche. The Cohesion Concept (Templeton, 1989), on the other hand, stresses the importance of natural selection in the integrity of the cohesive relationship among organisms of a same species, incorporating gene flow as a mechanism of cohesion.

These mechanistic concepts of species (Luckow, 1995) include models of evolution or explanations of the speciation process. They confuse patterns and processes and give temporality to a taxon (Lidén & Oxelman, 1989; Lidén, 1992, 1997). In the BSC, cohesion is related to gene flow, whereas in the EcSC, cohesion is maintained by environmental selective restrictions. In these concepts, species used by taxonomists are confused with populations studied by geneticists or even with taxonomic ranks created by Linnaeus, as in Dobzhansky’s (1951, pp. 256–263) commentary:

There is obviously no conflict between these aims and endeavors of systematists and of geneticists. In fact, they are complementary. It should, nevertheless, be made explicit that what a systematist is operating with are categories of classification. A category of classification is a group concept. Its adequacy is judged by the accuracy with which it describes the characteristics of the things classified. A population geneticist is, on the other hand, concerned with mating and parentage bonds and reproductive relationships which unite certain organisms into breeding communities. The most important and most highly integrated form of breeding communities, are Mendelian populations. Categories of classification are constructs devised by the student for his convenience; in this sense, they are sometimes called ‘arbitrary’ or ‘subjective’. Mendelian populations are spatio-temporal objects, and hence can be designated as ‘real’ or ‘objective’ …

The system of Linnaeus recognized only five systematic categories: species, genus, order, class, and kingdom … It must be reiterated that Mendelian populations are not synonymous with any groupings or categories of systematics …

In short, a species is the most inclusive Mendelian population.

Several authors have mixed taxonomic categories, taxa, and populations, even when they are trying to distinguish them. Systematists operate with taxa, which are constructs idealized by the student. A species (taxon) is neither a taxonomic category, nor a Mendelian population. It includes populations and, in another perspective, is included in a taxonomic category (Fig. 1).

### 2.2. Species as criteria and methods

Some species concepts emphasize criteria and methods to establish patterns or kinds of relationships that could be used to recognize taxa. In this context, morphology has been the main criterion adopted. Empirical circumscriptions based on morphological data are usually associated with the Morphological Species Concept (MSC). According to the followers of the MSC, species are groups of similar
organisms that are morphologically distinct from each other. That is, species are morphologically discontinuous sets of organisms (cf. Mayr, 1942, 1958; Coyne, 1992) or ‘the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means’ (Cronquist, 1978, p. 15). However, the occurrence of polymorphic species or hybrids between ‘good species’ that are not morphologically distinct from their ancestors makes a universal application of this concept difficult. Thus, Mallet (1995) readjusted the MSC to include genetic information and to evaluate polymorphic or geographically isolated populations more objectively, an approach that was called Genotypic Cluster Definition.

The BSC s.l. (e.g., Dobzhansky, 1937, 1951; Mayr, 1942, 1970) is the most influential concept of the last decades (Ereshefsky, 1992). However, it has been criticized (e.g., Jonsell, 1984; Baum, 1992; Mayden, 1997; De Queiroz, 1999) because it is not operationally viable (e.g., Sokal & Crovello, 1970) or it is restricted to sexual
organisms (e.g., Templeton, 1989). This concept is based on interbreeding capacity, a characteristic unnecessary and insufficient for the establishment and maintenance of a species (Ehrlich and Raven, 1969; Sokal & Crovello, 1970; Van Valen, 1976), and it considers gene flow as the major determinant in the formation of patterns. Instead of morphology, as in the MSC, the BSC uses fertility, sterility, or recognition as criteria, at least theoretically, to define species.

Concepts based on cladistic principles emerged with the development of phylogenetic systematics (Baum, 1992). Originally, the Phylogenetic Species Concept (PSC, Nelson & Platnick, 1981; Cracraft, 1983, 1989) considered species to be any diagnosed and irreducible group of organisms, that is, ‘the smallest detected samples of self-perpetuating organisms that have a unique set of characters’ (Nelson & Platnick, 1981, p. 12). Nevertheless, scientific progress, mainly based on macro-molecular data, will soon make possible the recognition of diagnostic characters (or apomorphies) for almost every organism (Mallet, 1995). Any organism or clone could be recognized by a set of genetic characters and would represent a different species according to this concept. Other distinct concepts based on cladistics are also known as PSC (Nixon & Wheeler, 1990). Baum and Donoghue (1995) and De Pinna (1999) recognized two different approaches: one based on characters (pattern-based concepts) and another based on history and ancestry (lineage-based concepts). Wheeler & Nixon (1990, p. 80), for example, considered that ‘[a] necessary and sufficient species concept for phylogenetics involves products of the evolutionary history’, which are recognized through fixed changes; that is, it should be ‘based on character state patterns and not on a particular model of evolutionary process’. On the other hand, De Queiroz and Donoghue (1988), and Graybeal (1995) looked for systems or historical entities resulting from interbreeding (toko-genetic or reticulated) or common descent (monophyly or exclusivity). They value history and evolutionary relationships, using characters as evidence, and interbreeding or ancestry as criteria to circumscribe taxa, independently of the methods of analyses.

The MSC, BSC, and PSC are stipulative definitions, intending to establish a method for group circumscription. They proposed criteria to recognize relationships among organisms, but they do not define the species.

2.3. Circularity of species concepts

Many species concepts are supported by relational definitions. According to Mayr’s BSC, ‘species are groups of interbreeding natural populations that are reproductively isolated from other such groups. Thus it is quite clear that the word “species” in biology is a relational term’ (1970, pp. 12–13; my italics). In this manner, species are defined in relation to other species, which does not represent an ad hoc definition (Paterson, 1985). The same happens in the Evolutionary Species Concept (EvSC) and in the EcSC. In the first, a species ‘is a lineage evolving separately from the others and with its own unitary evolutionary role and tendencies’ (Simpson, 1961, p. 153; my italics), a definition subtly modified by Wiley: ‘[it is] a single lineage of ancestral-descendent populations of organisms which maintains its
identity from other such lineages and which has its own evolutionary tendencies and historical fate’ (Wiley, 1978, p. 18; my italics). According to the EcSC, ‘a species is a lineage (or closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range’ (Van Valen, 1976, p. 233; my italics).

The MSC (above) emphasizes morphological discontinuity in the definition, and consequently, it also uses the relationship among species to define a species. This situation is evident in the practice of plant taxonomy; the diagnosis of a species does not usually define the taxon using intrinsic characters but rather indicates characters to differentiate it from one or more related species. Nevertheless, a diagnosis, contrasting with the description, does not intend to define a species; it represents a hypothesis of pattern based on discontinuities.

2.4. Are species special?

The previous species concepts, as well as presenting operational problems as generally criticized, also present problems in their theoretical scope. Many biologists still accept species as objective evolutionary units, justifying themselves with confused arguments: ‘Furthermore, most biologists appear to agree that there are real discontinuities in nature that can be designated as species’ (Rieseberg & Brouillet, 1994, p. 22). Discontinuities do exist; the problem is to choose which discontinuities are significant (Mishler & Donoghue, 1982). In fact, discontinuities are useful only as a relational artifact to order variations found in nature according to their uniformity, be it at the level of species, genus, family, etc.

Dobzhansky (1970, pp. 353–358) stated that ‘a species is a supra-individual biological system ... more than a group concept ... [It] is composed of individuals as an individual is composed of cells ... The species mankind is not an invention of a taxonomist but a biological (as well as sociological and existential) reality’. This viewpoint was shared with Mayr, 1942, 1970) and also followed by several authors: ‘we have adopted and defend ... that species are real entities existing in nature, whose origin, persistence, and extinction require explanation’ (Eldredge & Cracraft, 1980, p. 15); or ‘we assume that species are biologically real entities and feel they should be treated as such unless proven otherwise’ (Rieseberg & Brouillet, 1994, p. 22).

The importance attributed to the species category is related to the apparent reality, integrity, and independence present in the BSC, EcSC, and EvSC (Levin, 1979). Those concepts have considered taxa based on population and/or lineage inferences and give evolutionary traits to species. Following Ghiselin’s (1974; see also Ghiselin, 1987) ‘radical solution to the species problem’ and proponents of the species-as-individual concepts (e.g., Hull, 1981; Minelli, 1993; Mayden, 1997), ‘[t]axonomy categories, in the sense of all taxa of a given rank, are like “national state”: everybody agrees that these entities are classes’ (Ghiselin, 1974, p. 537); ‘[o]rganisms remain individuals, but they are no longer members of their species. Instead an organism is part of a more inclusive individual, its species’ (Hull, 1976, pp. 174–175).
Species (identification unity) and population (evolutionary unity) are distinct concepts (Ehrlich & Raven, 1969; Mishler & Donoghue, 1982). Organisms are parts of a population as well as parts of a lineage; they are tied to a space and time, operating together as a historical entity (or individual). The same organisms, however, may be also included in taxa (classes) defined by common properties of their members, independent of space and time (Dupré, 1999). Although the correlation between taxa and evolutionary units is useful, their relationship is based on derivation (Knox, 1998). They are different things, and complete equivalence is therefore inappropriate and responsible for many semantic problems and discussions (Woodger, 1952; Blackwelder, 1962). By saying *Tyrannosaurus rex*, for example, the image of an aggressive, carnivorous dinosaur comes to mind for most of us. This species is alive as a concept even though it includes only members of an extinct lineage and therefore no current population belongs to it. This is possible because taxa are cognitive concepts, that is, intentions that survive regardless of their extensions.

### 2.5. Taxonomic Species Concept (TSC)

The classification system used in taxonomy, characterized as hierarchical and nominalistic, is a conceptual method elaborated to order knowledge about biological diversity, and species are operational tools for this systematization procedure. The Taxonomic Species Concept (TSC), also known as nominalistic, differs from the others because it is not based on any biological theory but on a system of hierarchical classes, in which species as taxa are classes of organisms (Fig. 1a) included in the species as category class (Fig. 1c). Unfortunately, the view that species are classes may lead one, erroneously, to associate this concept with a typological-essentialist concept, which would remit us to a creationist explanation of biological diversity (Sober, 1980). The TSC is often confused with or equated to the MSC (e.g., Rieseberg & Brouillet, 1994), and the lack of an explicit definition of the species in the TSC may be the main reason why it is misinterpreted in discussions of systematics.

According to the TSC, nature produces individuals; species are mental concepts invented so that one may refer to a great number of individuals collectively (Bessey, 1908). A clear definition of species, however, must be universal and accurate, providing exclusive properties presented in any taxon recognized at the species level. Thus, to make the definition of the TSC more explicit, the species is here proposed as *the taxonomic category* (a class of taxa) *in which each taxon is a class of organisms represented by a valid binomial following the current code of nomenclature*. Whereas taxonomic categories are classes of classes (Caplan, 1981), taxa are classes of organisms that received a name (Gregg, 1950)—a Latin binomial, at the species level. Therefore, species (and taxa at other taxonomic categories) have a logical or analogical existence, but not a real one (Burma, 1954). They should not be confused with names that represent them nor with the group of organisms that are included in their intention. They are concepts, belonging to Popper’s worlds of knowledge, differing from the individuals or group of individuals that are their
extension and that belong to the world of objects. Therefore, taxa are created and modified, but do not exist in the real world and cannot evolve (Loevtrup, 1987; see also Bernier, 1984).

Evolution is the only unanimous principle in biology, and the TSC is criticized (e.g., Mayr, 1942, 1958) because it does not consider evolution of taxa. In fact, taxa do not evolve, but populations do; based on patterns of these populations, systematists inductively define taxa and then classify the organisms. Arbitrariness is another criticism of the TSC; however, it does not proclaim the absence of criteria but admits its convenience. The criteria to establish a taxon at the species level—or at any other taxonomic category—is defined by the author. There is no universal criterion to circumscribe a taxon (Kitcher, 1984), nor an evolutionary unity; each group of organisms is the result of different evolutionary factors and situations (Mishler & Donoghue, 1982). Like Dupré (1999), I am arguing for a monistic definition of species that allows a pluralistic theoretical concept, but I do not agree that it is a semantic monism. Even after establishing criteria, the other concepts also fail to avoid convenience. After all, how morphologically or genotypically different does a group need to be so that a taxonomist recognizes it as a species? How many apomorphies? What kinds of diagnostic characters? What level of gene flow and/or niche differentiation is necessary to break the cohesion of a population and, consequently, enable a taxonomic recognition of a species?

Concepts based on processes or criteria and methods fail to demonstrate necessary and sufficient properties to every taxon classified in the species category, and thus they do not propose an accurate and universal definition for this taxonomic category. Some authors (Beckner, 1959; Hull, 1965; Nixon & Wheeler, 1990) tried to solve this problem with a disjunctive (polythetic) definition, that is, there should be two or more conditions to recognize a species, and it should be necessary and sufficient to satisfy one or some of them. Other authors (Crowson, 1970; Mishler & Donoghue, 1982; Kitcher, 1984) adopted a pluralistic concept in which each group has particular properties and deserves specific treatment. All taxa classified at the species level invariably receive a binomial, which must be validly published. Though simple, these conditions are necessary and sufficient for any ‘kind of species’. As pointed out by Davis & Heywood (1963, p. 92) in their classical statement, ‘species are only equivalent by designation, and not by virtue of the nature or extent of their evolutionary differentiation’.

3. Speciation

3.1. Models of speciation

The most accepted evolutionary model is that of geographic speciation (Mayr, 1942; but see Jeanmonod, 1984, for a review of alternative modes of speciation), and allopatry (or at least isolation) is probably the only ‘speciation rule’ widely accepted (Coyne & Orr, 1989). According to this model, two or more populations should be geographically isolated from each other with no gene flow between them.
Such isolated populations with different genetic backgrounds and under the influence of distinct environmental pressures tend to evolve gradually, and independently, into different species. When they come together again, the organisms of each population will be incapable of interbreeding with organisms of the other population. In this case, speciation, reflected in reproductive isolation, is not adaptive but a pleiotropic subproduct of evolution.

Ayala (1982), for instance, as in the model of reinforcement (Dobzhansky, 1937), divided the speciation process into two phases: initially, gradual genetic divergence occurs because of geographic isolation and the consequent interruption of gene flow, producing a post-zygotic incompatibility. Hybridization between individuals of different populations generates less viable descendants and mechanisms of reproductive isolation are selected, producing rapid changes in those populations. From this point of view, speciation is related to the formation of pre-zygotic barriers but is a consequence of post-zygotic barriers.

Paterson (1985) assumed an alternative hypothesis proposed by Dobzhansky (1970). He explained speciation as a result of disruptive selection and proposed an inversion to the interpretation of the process: populations do not become two distinct species because they are reproductively isolated, but they are reproductively isolated because they are two distinct species. The occupation of different environments or distinct niches results in distinct characteristics; intermediates are less fitted and, consequently, negatively selected. In this case, the development of isolation mechanisms is adaptive and results from speciation.

The discussion, therefore, is about what is important during the speciation process: the reproductive isolation, according to the BSC, or the restrictions imposed by environment, as in the EcSC. Recent studies (e.g., Schneider, Smith, Larison & Moritz, 1999; Rundle, Nagel, Boughman & Schluter, 2000; Huey, Gilchrist, Carlson, Berrigan & Serra, 2000) have concluded that speciation may be primarily a product of environmental selection, rather than resulted from geographic isolation. Grant (1992) argues that the adaptation process is in the biological model approach and that the EcSC is included in the BSC. The Cohesion Concept (Templeton, 1989) unites the BSC and the EcSC, considering environmental restrictions and gene flow as parts of the intrinsic mechanisms of cohesion responsible for speciation. Finally, Andersson (1992) related the differences found in the BSC and EcSC according to the emphasis given to species formation in the first concept and its maintenance in the second one.

Maynard Smith (1966; see also Thoday & Boam, 1959) was one of the first to demonstrate the viability of sympatric speciation: stable polymorphisms would have the chance to develop in heterogeneous environments as a crucial step in sympatric speciation. Sympatric speciation has been considered an important component in diversification of some groups, and restrictions to this model have been less severe (e.g., Kondrashov & Mina, 1986; Tauber & Tauber, 1989; Tregenza & Butlin, 1999). However, it has been considered only an occasional process by many biologists (Lynch, 1989), mostly resulting from hybridization.
3.2. Speciation as anagenesis

Given the TSC above, the process, or event, called ‘speciation’ may be interpreted as that part of the evolution of a lineage in which the population becomes distinct from its ancestors. Therefore, it is always a sympatric process. In this context, geographic (or allopatric) speciation discussed above is the combination of the evolution of isolated populations; that is, it is the result of one to several sympatric speciations. For example, with the emergence of a geographic barrier in a continuous population ‘A’, recognized as *Fulana beltranii* (a putative species), two populations ‘B’ and ‘C’ appear but, initially, the members of each population do not form an exclusive lineage and do not have any difference from the members of the other population; all organisms in this stage, therefore, remain taxonomically classified as *F. beltranii*. Subsequently, one or both populations could differentiate and would be included in a species that is distinct from the original *F. beltranii*. For instance, members of ‘B’ are now included in *F. siclanii* because of sympatric speciation in that population, whereas ‘C’ does not differentiate, remaining in *F. beltranii*.

The models of speciation are mainly tied to the BSC and, as well as in that concept, they are relativistic and confuse species with populations. Those models analyze only cladogenesis or, in a broad sense, a lineage transformation according to another lineage that evolves independently: ‘species are formed when a once actually or potentially interbreeding array of Mendelian populations becomes segregated in two or more reproductively isolated arrays’ (Dobzhansky, 1951, p. 262). If ‘C’ of the example above becomes extinct, would speciation not occur in ‘B’? Members of ‘B’ diverge from their ancestors that, initially, were similar to members of ‘C’. The difference between modern populations (or metapopulations), such as ‘B’ and ‘C’, that can be recognized in distinct species, such as *F. siclanii* and *F. beltranii* respectively, is a consequence of divergence from their respective ancestors and not one from the other.

Anagenesis, or phyletic speciation, has been largely criticized and lost consideration, mainly after the incorporation of Hennig’s (1996) rule of dichotomous speciation. This convention is, however, only a methodological principle of cladistics (Hull, 1979; Platnick, 1979); theoretically, anagenesis is the basic type of evolution responsible for intrinsic modifications in a population (‘speciation’), and cladogenesis (‘diversification’) is a non-obligatory co-product of this process. Geographic isolation may influence the number of speciations and, then, the diversification of life, but it will not be the cause of speciation in each population per se. The use of species (taxa) as evolutionary units (populations) causes conceptual problems in biology, such as the geographic classification of modes of speciation, which have maintained the allopatric speciation as a paradigm in evolutionary theory.
4. Taxonomy

I understand biological systematics as a discipline that orders organisms and taxonomy as the method to express this discipline, a way of communication. Changes in procedures of systematics (principles of group arrangement, concepts of classification, or rules of nomenclature) are frequent, but taxonomy remained almost unquestioned until the diffusion of cladistics (phylogenetic systematics; Hennig, 1966) and its influence on taxonomic classifications. Some (e.g., De Queiroz & Gauthier, 1992; Brummitt, 1997; Sosef, 1997) have argued that the exclusive utilization of monophyletic groups cannot be adapted to the current system of taxonomy, and the use of paraphyletic groups is still debated (e.g., Brummitt & Sosef, 1998; Brummitt, 2002). In the last few years, some authors have argued for a complete substitution of the current taxonomy with a new one that equates phylogeny and classification, such as Phylogenetic Taxonomy or ‘Phylocode’ (e.g., De Queiroz & Gauthier, 1992; Cantino, 2000).

Promoters of the Phylogenetic Taxonomy advocate a complete equivalency between units of evolution and units of taxonomy. However, most of their criticisms to the current taxonomy, such as automatic propagation of paraphyletic taxa, are not inherent in the system and can be easily fixed with some changes in the concepts of arrangement. Other criticisms are not related to the taxonomic system itself, such as ideas that taxa are derived from other taxa, but to the concepts used by particular taxonomists. Finally, other arguments criticize the versatility of the taxonomy reflected as nomenclatural instability, which may be considered healthy for progressions in systematics (e.g., Lidén & Oxelman, 1996; Moore, 1998; Jorgensen, 2000).

4.1. Phylogenetic Taxonomy

Phylogenetic systematics searches for biological systems or entities composed of organisms related to each other through common ancestry (Hennig, 1966; De Queiroz & Donoghue, 1988). The expression of these systems has shown incompatibility with the traditional taxonomy, which encouraged the elaboration of Phylogenetic Taxonomy (De Queiroz & Gauthier, 1990, 1992, 1994; De Queiroz, 1996, 1997). This new system of nomenclature and classification is based on the principle of monophyly, proposing changes in classification, nomenclature and typification procedure of the traditional taxonomy (Cantino, Olmstead & Wagstaff, 1997; Moore, 1998).

The best method for reconstructing the phylogeny of a group of organisms is still questioned. Cladistic analyses are a source of information, offering to the systematist the most congruent or likely distribution of characters based on a particular set of data. Although widely used to evaluate hypotheses of relationship, they have uncertainties and limitations, such as the failure to detect and accurately represent reticulation and multiple speciations and the subjectivity of the division of morphological characters and their states, as well as the way to combine data from different sources (e.g., Bremer & Wanntorp, 1979; Hull, 1979; Platnick, 1979;
Cronquist, 1987; Chappill, 1989; Stevens, 1991; Kluge & Wolf, 1993; Davis & Nixon, 1992; Hedberg, 1995). For most taxa there are no phylogenetic hypotheses, and in other groups they are controversial. Thus, the primordial monophyletism principle, or clado nomination, initially proposed by Phylogenetic Taxonomy (De Queiroz & Gauthier, 1990, De Queiroz & Gauthier, 1992) was later (De Queiroz & Gauthier, 1994) modified to preserve taxonomic freedom of thought and action, accepting classifications of groups empirically circumscribed or unresolved.

Modifications proposed by Phylogenetic Taxonomy look for a stable and objective classification but, since a hierarchical system of classification is compatible with a phylogenetic system or its correspondence (De Queiroz & Gauthier, 1992; de Queiroz, 1997; Dominguez & Wheeler, 1997; Knox, 1998), these changes became restricted to a nomenclature system (De Queiroz, 1996, 1997; Cantino, 2000). Instability of the traditional system of nomenclature reflects divergent interpretations or the evolution of systematic knowledge of the groups studied, and it would also be present in a phylogenetic system, at least above the species level. In a phylogenetic nomenclature, content instability would be even greater than in the traditional system (Schander & Thollesson, 1995; Dominguez & Wheeler, 1997; Moore, 1998; Nixon & Carpenter, 2000); a name once created may represent a non-relevant clade in a new topology (Härlin, 1998), and a well supported clade may need to be renamed because of changes in ideas of the relationships in its internal subgroups (Lidén & Oxelman, 1996). In fact, Phylogenetic Taxonomy does not bring any improvement, not even to nomenclatural practice, as we may conclude from words of De Queiroz (1997, pp. 137–139) himself:

one might ask why—from the viewpoint of the practicing taxonomist – we would want to make such a fundamental change. The reason is simple and concerns the basic goals and purposes of nomenclatural systems in general and the current codes in particular; that is, to provide nomenclatural clarity, universality, and stability . . . Linnaean definitions also promote the unambiguous application of names to taxa and the development of a universal and stable nomenclature . . . neither phylogenetic nor Linnaean systems guarantee clarity, universality and stability in terms of hypotheses about relationship and composition of taxa.

4.2. Traditional taxonomy

Brummitt (1997, p. 725) correctly affirmed that ‘biological systematics should aim to produce two things side by side, a classification and a phylogeny, and not confuse the two’ (see also, Camp & Gilly, 1943; Camp, 1951; Lidén & Oxelman, 1989; Knox, 1998; Dupré, 2001). He (see also, Brummitt, 2002) considered it to be a logical impossibility to combine both activities—to establish phylogeny and classify organisms—and include only monophyletic taxa in a traditional classification (that is, paraphyletic taxa would be inevitable in the current taxonomy). This interpretation is supported by taxonomic views and principles of classification that could be adjusted to accept the combination of these practices more properly.
a) The current system of classification has mandatory categories in which any taxon must be classified. Similarly, according to the exhaustive subsidiary taxa principle, when a particular group has a subgroup recognized at a subjacent taxonomic level below, any remaining taxa of the group must be automatically included in a taxonomic level similar to that one. These fundamentals may imply recognition of paraphyletic taxa or result in proliferation of uninformative taxa, but their abandonment (except at the genus level), as advocated by some authors (e.g., De Queiroz & Gauthier, 1992; Schander & Thollesson, 1995; Cantino, Olmstead & Wagstaff, 1997), would not produce significant changes in the current taxonomy.

b) Ideas applying evolutionary concepts to taxa, as exemplified by Hull (‘if species are classes, it’s difficult to see how they can evolve—but they do!’, Hull, 1976, p. 75), and Brummitt (‘if one believes in evolution, every taxon must have evolved from a precursor which must, by definition, in Linnaean classification, be placed in a different taxon at the same rank’, Brummitt, 1997, p. 726), should be discarded. As presented in the first and second sections of this paper, taxa are class concepts; thus, although their members (populations) do evolve, they (taxa) do not. Questions like: ‘if one denies paraphyletic taxa, where do genera and families come from?’ (Brummitt, 1996), make no sense.

Brummitt (1997, p. 728; see also Brummitt, 2002) considered it ‘nonsensical to argue that a derived taxon … cannot be recognized just because it leaves the parental group paraphyletic’. This does not occur. The ‘derived taxon’ and the ‘derived taxon’ with the ‘paraphyletic parental group’ are both recognized as monophyletic. The paraphyletic group is not recognized separately since it actually does not constitute a relevant group and, generally, is defined by the absence of evolutionary novelties. Asclepiadaceae (‘derived taxon’), for instance, are included in Apocynaceae as a subfamily rather than rejected; however, Apocynaceae s. str. (‘parental paraphyletic group’), traditionally recognized by absence of translators, are not considered a separate taxon (e.g., Judd, Sanders, & Donoghue, 1994; Struwe, Albert, & Bremer, 1994; Sennblad & Bremer, 1996).

Another common criticism of the traditional taxonomy is the use of categories, either because of their essentialist connotation (Griffths, 1974, 1976) or because they give a false impression that nature is ordered in hierarchical ranks and that each taxon at a taxonomic level is comparable to others at the equivalent level (e.g., Ereshefsky, 1997, 2001). Comparisons among taxa classified at the same taxonomic category seem inevitable by biologists and are widespread in phytosociological studies. In fact, there is no ranking criterion to define taxa and the level at which one recognizes a taxon is only a convention (Stevens, 1998); therefore, comparisons among taxa of the same taxonomic category are inappropriate (e.g., Welzen, 1998). Since the evolutionary process is asymmetric and we currently know only a minute draft of the diversity of organisms, this inconvenience will be the most difficult one to solve, independently of the taxonomic system employed. The use of taxonomic categories provides information, such as exclusivity, that is, two taxa at the same rank do not have any member in common (Schander & Thollesson, 1995). The names in Phylogenetic Taxonomic, on the other hand, do
not provide information on circumscription in the absence of a cladogram; furthermore, it has not abandoned the ranks since PhyloCode recognizes species and clades (Stuessy, 2001).

Radical changes in the traditional taxonomic system will bring confusion and chaos (Lidén et al., 1997), but, it has been argued that a system of classification and nomenclature elaborated before the advent of the evolutionary theory has restricted the practice of modern systematics (De Queiroz & Gauthier, 1992, De Queiroz & Gauthier, 1994; Ereshefsky, 2001). No one disagrees about the importance of a system of classification that allows an evolutionary perspective, and the problems with paraphyletic groups fall within this context. In the traditional taxonomic system, however, a taxon intention may be reduced to apomorphies like the apomorphy-based phylogenetic definition, allowing a statement interpretation without any modification into a nomenclatural system. The replacement of traditional taxonomy would necessitate needless transformations in the organization of the biological knowledge accumulated over the centuries. Practical damage to access of information could be drastic and the advantages of this substitution are still difficult to visualize (e.g., Forey, 2001, 2002).

Limitations imposed by Phylogenetic Taxonomy are not only a perception because the taxa content cannot be controlled by taxonomists, as suggested by Bryant and Cantino (2002). Phylogenetic Taxonomy constrains taxa to a phylogenetic hypothesis based on the assumption that taxa are historical entities. Nevertheless, as I have defended throughout this issue, taxa are classes regardless of their taxonomic rank. I do not expect to convince everybody of this, but it is relevant to be aware that the thesis of taxa-as-individuals is not the only one in systematics. Therefore, the current system of taxonomy should not be replaced by another system that is constrained by phylogenetic thought, and which name only supposed historical individuals (particulars); on the contrary, it only needs to be adjusted to properly accept epistemological changes taking place in biology.

5. Conclusion

a) The species is a taxonomic category; a species is neither a lineage nor a population. Its definition should not be linked to explanatory models of the evolutionary process or to criteria and methods commonly used to circumscribe taxa. The Taxonomic Species Concept, as previously defined, does not deny evolution but recognizes the use of classes in taxonomic work. In contrast to other species concepts, it is the only one that establishes a universal and intrinsic definition, using the nomenclatural system (of binomials validly published) to discern common properties to every taxon classified at the species level. This concept defines the species category explicitly by the simple, necessary, and sufficient conditions of their members (species as taxa).

b) The equivalence between species (classes) and units of evolution (individuals) and consequently the inappropriate use of ‘speciation’ to designate the differentiation of contemporary populations, have damaged theoretical concepts of
evolution. Taxonomic categories and taxa are classes and classes do not evolve. Thus, a taxon cannot originate from another one, whether a species (‘speciation’), genus, or family. The models of speciation are supported by circular and relativistic ideas of species-as-individual theses and by patterns of dichotomy usually produced by cladistic analyses. Speciation, understood as the process that leads a population (or set of organisms) to form a pattern distinguishable from the ancestral one and capable of being recognized as a new species, is part of the evolution of a lineage, or anagenesis, and this is always sympatric. Therefore, speciation basically depends on time and not on space, as has been advocated by the majority of speciation models.

Proposals to equate classification and phylogenetic hypotheses, which have been advocated by phylogenetic taxonomists, are undesirable. Systematics seeks to reflect phylogenetic inferences through taxonomy, which, in some instances, has been limited by the traditional system. Poly- or paraphyletic taxa should be avoided, but this is a phylogenetic and not a taxonomic requirement, as congruence may be used as a cladistic but not necessarily an evolutionary. Traditional taxonomy should be adjusted to increase taxonomic freedom to organize biological diversity, but it should remain based on principles and rules independent of biological theories. Thus, current taxonomy should not be substituted by another system, restricted to phylogenetic (or cladistic) thought based on ancestry, which, although a widely held consensus today, may be questioned in the future.

Systematists search for biological entities or systems of organisms. We may use many approaches to find the best hypotheses of biological units, and these approaches are based on the principles in which we believe. Based on those hypothetical entities, we define taxa and classify the organisms according to taxonomy, that is, following the rules of nomenclature and hierarchical principles of classification. Each taxon stores much information in a few words, working like a tool in the process of ordering biodiversity. Taxa help us evaluate phylogenetic hypotheses, as phylogenies help us evaluate knowledge about evolution. In a feedback process, changes in ideas of evolution may alter phylogenetic ideas, and modifications in phylogenetic ideas produce changes in the classification of organisms. Those parts of the process of ordering biodiversity—to propose hypotheses of biological entities and to classify organisms—are completely different but perfectly integrated disciplines, which constitute the epistemological system of biology known as systematics.

Unity of classification (taxon) and unity of evolution (population) are both necessary concepts in systematics. Whereas the first is a kind of class, the second is a kind of individual. They are completely distinct philosophical concepts, and their implied equivalence damages theoretical concepts about the evolutionary process and in the practice of taxonomy. Therefore, a unified concept of systematics, paradoxically, requires a clear distinction between taxa and evolutionary entities.
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