

Problèmes de philosophie de la biologie contemporaine

Semestre 1 : Patrons

Dossier 1 : Espèce

Le concept biologique de l'espèce (Nouvelle systématique)

Des ornithologues comme Stresemann et Rensch appliquèrent avec conséquence le concept biologique de l'espèce dans les années 1920 et 1930. En 1919, Stresemann souligna que ce n'est pas le degré de différence qui caractérise les espèces, mais que ce sont des formes « qui se sont élevées durant un isolement géographique au rang de l'espèce, en devenant physiologiquement si différentes les unes des autres [...] qu'elles peuvent de nouveau revenir ensemble sur le même territoire sans se croiser » (p. 64). La définition de l'espèce selon Dobzhansky, pour lequel il s'agit de formes « physiologiquement incapables de se croiser » (1937 : 312), est virtuellement identique. L'histoire des nombreuses tentatives de définition de l'espèce biologique a été souvent racontées (voir par exemple Mayr, 1957 ; 1963). La définition donnée par Mayr en 1942 – « Les espèces sont des groupes de populations dont les membres peuvent se croiser entre eux, réellement ou potentiellement, et qui sont reproductivement isolés d'autres groupes » (p. 120) – contenait encore quelques faiblesses. La distinction entre « réel » et « potentiel » n'est pas nécessaire puisque l'expression « reproductivement isolés » renvoie à la possession de mécanismes d'isolements, et il n'est pas important pour le statut de l'espèce que ces mécanismes soient mis en jeu ou non à un moment ou à un autre. Voici une définition meilleure : *Une espèce est une communauté reproductrice de populations (reproductivement isolées d'autres communautés) qui occupe une niche particulière dans la nature.*

Cette règle ne nous dit pas comment on reconnaît les taxa de niveau spécifique. Elle permet seulement de déterminer la catégorie à laquelle se situe un taxon. En revanche, le degré de distinction morphologique n'est pas un caractère convenable, comme le prouvent les espèces jumelles et les morphes bien tranchés. Le concept biologique de l'espèce, exprimant des relations au sein des populations, n'a de valeur, et n'est vraiment applicable, que dans un cadre non-dimensionnel [= dépourvu de toute dimension temporelle et/ou spatiale]. Il ne peut être étendu à des situations multi-dimensionnelles que par inférence.

L'expression « reproductivement isolée » est l'expression-clé de la définition biologique de l'espèce. Elle soulève immédiatement le problème de la cause de cet isolement, résolu par l'élaboration du concept de *mécanismes d'isolement*. Les prémices de ce concept remontent au critère de stérilité, avancé par Buffon et resté en vogue chez les botanistes jusqu'au cœur du XX^e siècle. Les zoologistes, en particulier les ornithologues et les spécialistes des papillons, ont observé toutefois que dans la nature, la barrière de stérilité est rarement testée chez les animaux, et que la conspécificité est déterminée d'après la compatibilité comportementale. On a découvert de plus en plus de dispositifs empêchant le croisement entre espèces, comme par exemple les différences dans les habitats, dans les saisons de floraison, ou d'accouplement. Le botaniste suédois du Rietz (1930) a été le premier à fournir une liste détaillée et une classification de ces barrières empêchant le croisement entre espèces. Leur étude fut handicapée par l'absence de termes techniques convenables. Dobzhansky suggéra l'expression « mécanisme d'isolement » pour désigner « tout agent qui entrave le croisement de groupes d'individus [...] ». Les mécanismes d'isolement peuvent être divisés en deux grandes catégories, géographiques et physiologiques » (1937 : 230). Même si Dobzhansky réalisa que l'isolement géographique était « sur un plan différent de n'importe quel mécanisme physiologique », il ne comprit pas que seul ce dernier type de mécanisme fait vraiment partie des propriétés de l'espèce. Pour cette raison, Mayr restreignit le terme de « mécanisme d'isolement » aux propriétés biologiques de l'espèce, excluant expressément les barrières géographiques (1942 : 247). Il restait cependant encore une difficulté : un individu pouvait exceptionnellement s'hybrider, bien qu'appartenant à une « bonne espèce ». En d'autres termes, les mécanismes d'isolement pouvaient bien préserver l'intégrité des populations, mais pas jusqu'au dernier individu. Cette remarque conduisit Mayr à proposer une définition améliorée : « Les mécanismes d'isolement sont des propriétés biologiques d'individus grâce auxquelles le croisement entre populations réellement ou potentiellement sympatriques est prévenu » (1963 : 91). Ces

quarante dernières années, l'étude des mécanismes d'isolement est devenue l'un des champs les plus actifs de la biologie.

L'isolement reproductif n'est cependant que l'une des deux caractéristiques majeures de l'espèce. Les premiers naturalistes avaient déjà observé que les espèces sont restreintes à certains habitats, et que chaque espèce est adaptée à une niche particulière. Ces idées étaient proposées par Buffon et tous les auteurs des XVIII^e et XIX^e siècles qui parlaient de l'économie de la nature. Darwin était convaincu que l'aire de distribution géographique d'une espèce est déterminée par les frontières des espèces concurrentes. Pourtant, dans l'élaboration du concept moderne d'espèce, l'accent fut d'abord porté sur l'isolement reproductif. Celui qui a le plus fait pour susciter un retour d'intérêt à la dimension écologique de l'espèce est David Lack (1944 ; 1949). Il est intéressant, sur le plan historique, de se pencher sur l'interprétation évolutionniste qu'il a donnée de la taille du bec chez différentes espèces de pinsons des Galapagos. Dans un premier article (1945 ; en réalité écrit avant 1940), il avait interprété la taille du bec comme un signal de reconnaissance spécifique, donc comme un mécanisme d'isolement, tandis que dans son livre ultérieur (1947), il le comprit comme une adaptation à un mode d'alimentation lié à une niche particulière, interprétation depuis largement confirmée.

Le processus de spéciation n'est pas achevé par l'acquisition de mécanismes d'isolement, il requiert aussi l'acquisition d'adaptations permettant la coexistence avec des concurrents potentiels. Il est difficile pour une espèce d'envahir l'aire d'un concurrent potentiel : ceci est bien mis en évidence par les modes de distribution parapatrique d'espèces étroitement apparentés (des populations ou des espèces sont *parapatriques* lorsqu'elles sont en contact géographiquement, mais ne se recouvrent pas, ne se croisent que rarement, voire jamais). Dans ces circonstances, une espèce se trouve mieux adaptée d'un côté de la ligne de séparation, et l'autre espèce de l'autre côté. La situation parapatrique peut aussi être provoquée par une stérilité croisée en l'absence de mécanismes d'isolement pré-copulatoires.

Van Valen a tenté de baser la définition de l'espèce sur l'occupation des niches : « Une espèce est [...] une lignée [...] qui occupe une zone adaptative différant, même peu, de celle de n'importe quelle autre espèce rencontrée dans son aire de distribution » (1976 : 233). Cette définition reflète le principe d'exclusion par concurrence, mais elle n'est pas très pratique comme définition de l'espèce, parce qu'il est souvent difficile de découvrir la petite différence entre les niches des deux espèces, comme les recherches écologiques l'ont montré. En outre, beaucoup d'espèces (par exemple celles comprenant un papillon et une chenille) occupent des niches très différentes aux divers stades de leur cycle vital et dans différentes portions de leur aire géographique. Chacun de ces stades constitue-t-il une lignée, et donc une espèce différente ? Ces cas montrent à l'évidence que la communauté reproductive est le noyau dur du concept d'espèce. De fait, le genre de niche occupée et l'isolement reproductif sont deux aspects de l'espèce non exclusifs mutuellement (sauf chez les espèces parapatriques), Lack (1947), Dobzhansky (1951), Mayr (1963 : 66-68) et d'autres l'ont montré. En fait, la grande signification biologique de l'isolement reproductif est qu'il fournit une protection pour le génotype adapté à l'utilisation d'une niche spécifique. L'isolement reproductif et la spécialisation dans une niche (exclusion par concurrence) sont donc simplement les deux faces d'une même pièce. Dans le cas où le critère d'isolement reproductif ne tient plus, comme pour les clones asexués, on doit employer le critère du genre de niche occupée (Mayr, 1969 : 31) ¹.

Le concept évolutif de l'espèce (Nouvelle systématique)

It is the fact of evolution that has made genetical species [= biological species *sensu* Mayr] separate and that keeps them from always being sharply, clearly separate. It is also evident that the genetical definition of species has evolutionary significance. Still it is striking that the definition does not actually involve any evolutionary criterion or say anything about evolution. It would apply equally well, or in fact a great deal better, to species that did not evolve. Mayr (1957) has pointed out that pre-evolutionary taxonomists advanced almost identical definitions, for example, Voigt in 1817 : "Whatever interbreeds fertile and reproduces is called a species."

Given the fact that the genetical definition of species [= the biological definition of species *sensu* Mayr] is consistent with evolution, its lack of any direct and overt evolutionary element certainly does not invalidate it. Nevertheless it is desirable also to have a broader theoretical definition that relates the genetical species directly to the evolutionary process that produce it. I have elsewhere (Simpson, 1951) proposed such a definition, which may be slightly modified as follow :

1. Ernst Mayr. 1989. *Histoire de la biologie. Diversité, évolution et hérédité*. Paris : Fayard, p. 266-268.

An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.

That definition not only is consistent with the genetical definition but also helps to clarify it and to remove some of its limitations. At any point in time, or taken in temporal cross section, an evolutionary species of biparental organisms will almost invariably coincide with a genetical species. That is precisely why the genetical species has evolutionary significance, and in a broader sense it is why genetical species do exist. It also tends to remove some of the conceptual difficulties remaining in the purely genetical concept. It is (to me, at least) clearer to see why disjunct populations should be placed in one species if they retain the same evolutionary role than if they have the rather vague potentiality to interbreed. It is also clear that two species may interbreed to some extent without losing their distinction in evolutionary roles and that this is the really important point for evolutionary taxonomy. The amount of interbreeding allowable by definition is then precisely as much as does not cause their role to merge. The taxonomic value of the genetic criteria of interbreeding and isolation lies not in those characteristics in themselves but in their evidence as to whether populations are or are not capable of sustaining separate and unitary roles over considerable periods of time. Interbreeding helps to keep a role unified; isolation makes possible separation of roles.

The evolutionary definition given above omits the criterion of interbreeding. Interbreeding promotes the unity of role involved and is also evidence that the criterion of unity is met. It is not, however, the only way in which unity is maintained or the only evidence that it exists. The evolutionary definition is thus broader than the genetical, while including it as the most important special case. Uniparental populations also have separate and unitary roles, and the evolutionary definitions can also be applied to them, as discussed later in this chapter.

The evolutionary species implicitly bring in the element of time. Species do in fact have a long time dimension, and a concept that omits this consideration is incomplete if not quite inappropriate. The evolutionary concept is thus more readily related to paleontological sequences, a point also discussed farther along in this chapter.

The one important difficulty in the evolutionary concept of the species is the definition and recognition of roles. That is rarely a serious problem to a field naturalist or an ecologist, who can almost always see clearly that the various species he encounters do have recognizably different roles. Roles are definable by their equivalence to niches, using "niche" for the whole way of life or relationship to the environment of a population of animals and not for its micro geographic situation.

Here again the question of definition and evidence comes up. The role cannot be directly observed in a series of dead specimens, recent or fossil, in a museum. Valid and sufficient evidence of separation and unity in role can, however, be obtained from observation on such specimens. Morphological resemblances and differences (as reflected in *populations*, not individuals) are related to roles if they are adaptive in nature. The assumption that over-all resemblance and difference is, on balance or as an average, adaptive is adequately justified by general evolutionary theory. It is helpful but it is not necessary for purely taxonomic purposes that specification of the nature of the adaptation, or of the role, be possible. The definition requires only that the roles be separate but each unified, and that is, as a safe enough rule, shown by somatic differences and resemblances between populations. That may at first sight look like a circular procedure, but it is not. The normal correlation between role and morphology has been amply established for populations in which the roles were independently determined on quite different grounds, notably those of environment and behavior. Another check and further aid in applying criteria as to roles is, moreover, provided by adequate field data, which even for fossils yield at least some information on environment.

Intraspecific groups may differ somewhat in roles. As a rule, however, these differences, like morphological differences, grade through adjacent populations, and the criterion of distinct separateness of roles would not make such groups different species. Again there are and in the nature of things must be doubtful cases, for nascent species do not suddenly acquire separate roles at a determinable instant.

The definition neither states nor implies that the unitary role of any one species is necessarily unchanging. Evolution (apart from quite exceptional saltations) could not occur if roles did not change *within* species. The concept involves a species having a unified role at any one time (not necessarily the same role at all times) and that its role always be separate in some way (not always in the same way) throughout its duration².

2. George G. Simpson. 1961. *Principles of Animal Taxonomy*. New York, NY : Columbia University Press, p. 152-155.

L'espèce comme unité taxinomique opérationnelle (UTO) (phénétique)

What taxonomic units can be classified by numerical taxonomy? The logical fundamental unit in a large majority of instances is the individual organism. While this is usually an unambiguous entity, it is generally not feasible to use numerous conspecific individuals of each of several apparent taxonomic groups to compute a classificatory hierarchy. Matrices of excessive size would have to be processed—a formidable enterprise even by the standards of the most modern computers. Furthermore, such studies would throw light largely on resemblances among infraspecific variants and would not be likely to offer much scope for comparisons at the subgeneric, generic, and higher levels. Thus, except for special studies aiming at intraspecific classification, the most customary unit in zoology and botany will be the species (strictly speaking, the taxonomic unit with a binomial name, the *bin* of Camp, 1951, which is believed to correspond to one or other of the biological units which are given the name of species). Since the hierarchic level of the taxonomic unit employed in numerical studies will differ, we cannot speak of fundamental taxonomic units but shall refer to them as *operational taxonomic units (OTU's)*.

Should numerical taxonomy rely on the validity of species erected by conventional methods? We believe (probably in agreement with most present-day biologists) that of the categories established in the present system of nature the different entities which have been called species have more reliability than any others, with the possible exception of the very highest taxa. So far as numerical taxonomy is concerned, it does not matter that there are many species concepts and species definitions, so long as these are clearly understood and used fairly consistently within a study. Some kinds of species, furthermore, can be defined by biological (analytical and experimental) criteria (see Mayr, Linsley, and Usinger, 1953, for some definitions) and differ in this respect from the higher and lower taxa, which are defined on more ambiguous bases. However, it should be pointed out that the criteria of specific difference actually applied by most systematists to most taxa are phenetic and do not satisfy the genetic definition of specific status (see also, Blackwelder, 1962, and Sokal, 1962b, 1964). Although taxonomists make objective tests of the criteria for specific distinction in only a small minority of cases, their judgment in this matter generally inspires confidence (certain difficult taxa and indifferent taxonomists excepted).

Zoologists in recent years have turned to a genetic definition of species (*sensu* Mayr, 1942). However, there are many groups—including, for example, the bacteria—where such a species definition seems at present inapplicable. Since a single bacterium can seldom be studied sufficiently, taxonomy is based on pure culture of strains. In plants there are many genera in which the individuals are apomictic—vegetatively propagated, parthenogenetic, or self-fertilized—and here it is generally the clone which is taken as the unit of classification. Yet clones may throw off mutant forms, which may or may not be considered as distinct units. The important point is to avoid prejudice in choosing the OTU's and if need be to explore by preliminary analyses the phenetic relations of the specimens which are to form them. In both plants and animals there may be a choice between stages in the life cycle, or between different castes in social insects. The special problems raised by these possibilities have been discussed in Section 5.4.3.

Problems may arise if a taxon used as an OTU proves to be variable for one or more characters. This brings up the question of whether we can use as OTU's higher taxa (such as genera, families, and orders) in which the majority of characters within a taxon will of course vary. Such taxa can be used, in principle, for the reasons discussed in Section 6.4.

A second equally serious problem is the low degree of relevance of most lists of characters (see Section 6.5.5). Since these considerations have not yet been discussed, we shall postpone an evaluation of the analysis of higher taxa until Chapter 6³.

Le concept hennigien de l'espèce (cladistique hennigienne)

Figure 1, reprinted from Hennig's (1966) figure 14 should make the cladistic species concept immediately clear. Hennig, at least in paleontology, defined species as the set of organisms between two speciation events. It needs to be generalized slightly in the letter, if not the spirit, for the cases of extinction and of living species. A species is then *that set of organisms between two speciation events, or between one speciation event and one extinction event, or that are descended from a speciation event*. A speciation event produces at least (but usually only) two new species; the ancestral species automatically goes ex-

3. Robert R. Sokal & Peter H. A. Sneath. 1973. *Principles of Numerical Taxonomy*. San Francisco, CA : Freeman, p. 120-122.

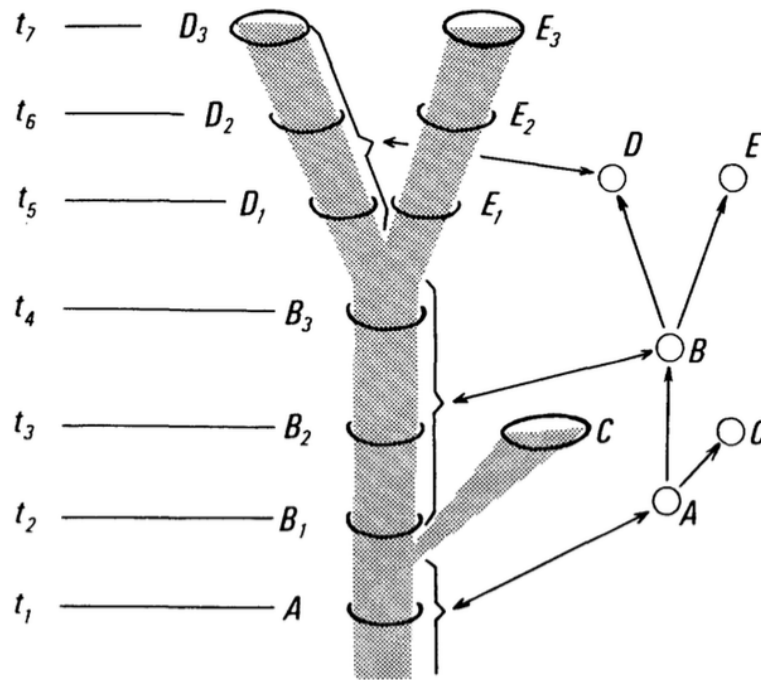


FIGURE 1 – Cladistic species, illustrated by Hennig (1966). The segments of the tree marked with different alphabetic letters are different cladistic species.

tinct when it splits. Cladistic species are monophyletic in the sense of including all the descendants from a speciation event, up to the next speciation event, when the cladistic species comes to an end. (The full definition, with all those disjunctive conditions, is long winded, and I shall informally abbreviate it in this paper : a cladistic species is the set of organisms between two speciation events ; the other conditions are implied.)

Non-cladists most often raise two difficulties of the cladistic definition of species : it denies phyletic (or anagenetic) speciation (species C in Figure 1 remains the same species no matter how much it changes) and it, apparently artificially, generates a new species even when the species has not changed (e.g. A and B in Figure 1), just because a species happens to have branched off. It sounds like saying a mother changes into a new person when she gives birth to a child. Rosenberg (1985, 1987) objects to cladism for this reason. Hennig (1966, see also Ridley 1986) dealt with both these difficulties. The objections are phenetic in inspiration and share the general defects of phenetic classificatory systems (Johnson 1970, Ridley 1986). The virtue of the cladistic definition is its perfect objectivity. Species are defined unambiguously as branches, or, in Ghiselin's expression, chunks of the phylogenetic nexus.

I believe the cladistic concept is, in a sense, the "solution" to the species problem. It accurately defines the nature of species in evolutionary theory ; in a theoretical sense, there is no species problem. If we accept that phylogenetic relations exist, species must exist in this unambiguously defined sense. The only problems will be practical questions of whether we can recognize them. But even then the cladistic concept is useful. It provides the external reference system against which to judge proposed practical rules.

[...] ⁴

L'espèce comme genre ou le concept synapomorphique de l'espèce (cladistique procédurale) [texte facultatif]

An Alternative Concept of Species

An alternative perspective on species as genealogical, theoretically significant taxa has been developed by Mishler and Donoghue (1982), Donoghue (1985), and Mishler (1985) and called the "phylogenetic

4. Mark Ridley. 1989. The Cladistic Solution to the Species Problem. *Biology and Philosophy* 4 : 3-5.

species concept" (not to be confused with the concept proposed by Cracraft, 1983, with the same name). This concept explicitly recognizes a grouping and a ranking component, is monistic with respect to grouping yet pluralistic (in the sense advocated above) with respect to ranking, and produces species taxa with at least some aspects of individuality.

The grouping criterion advocated by Mishler and Donoghue is monophyly in the cladistic sense. Further discussion of the meaning of "monophyly" is needed (see below), because the term is not normally applied to species in a substantive way by cladists. For now it suffices to say that "monophyly" here is taken to refer to a grouping that had a single origin and contains (as far as can be empirically determined) all descendants of that origin.

Monophyletic groupings as roughly defined above exist at all levels of inclusiveness, thus a ranking criterion for species is needed as the basal systematic taxon (i.e., the least inclusive monophyletic group recognized in a particular classification). It is here that Mishler and Donoghue have advocated a pluralistic adjustment in the number of ranking criteria allowable for consideration in particular cases. They argued that the currently favored monistic ranking concept of absolute reproductive isolation is not the most appropriate for all groups of organisms. The ranking concept to be used in each case should be based on the causal agent judged to be most important in producing and maintaining distinct lineages in the group in question. The presence of breeding barriers might be used, but so might selective constraints or the action of strong developmental canalization (Mishler, 1985). In the great majority of cases, little to nothing is actually known about any of these biological aspects. In such cases grouping (estimation of monophyletic groups) will proceed solely by study of patterns of synapomorphy (i.e., shared, derived characters), and a practical ranking concept must be used until something becomes known about biology. This preliminary and pragmatic ranking concept will usually be the size of morphological gaps (i.e., number of synapomorphies along any particular internode of a cladogram) in most cases, a concept in accord with current taxonomic practice.

The phylogenetic species concept (PSC) of Mishler and Donoghue can be summarized as follows :

A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly (usually, but not restricted to, the presence of synapomorphies), that is ranked as a species because it is the smallest "important" lineage deemed worthy of formal recognition, where "important" refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case.

Relating the PSC back to the earlier discussion of individuality, it is clear that species so defined (as with monophyletic taxa at all levels) will at least meet the restricted spatiotemporal criterion of individuality. They may or may not be integrated or cohesive. However, these criteria may often prove useful in ranking decisions. Since the strength of integrative or cohesive bonds tends to gradually weaken as more and more inclusive groups of organisms are taken (see for example discussion by Mayr, 1987), it may be possible in many cases to objectively fix the species level as the most inclusive monophyletic group that is integrated or cohesive with respect to "important" processes. Again, "important" has a context-dependent meaning, and will often not refer to reproductive criteria. It may often be difficult to apply this standard, especially if macroevolutionary processes occur (even rarely) involving groups at high taxonomic levels (Gould, 1980; Jablonski, 1986). If so, integrated and/or cohesive groups may occur at much more inclusive levels than anyone would wish to name as basal taxonomic units.

[...]

It is our argument that the PSC is superior to the biological species concept (or to the evolutionary species concept of Simpson, 1961, and Wiley, 1978, which is similar in these ways to the biological species concept) in two fundamental ways. First, monophyly as a grouping criterion is superior to ability to interbreed because it will lead to a consistently genealogical classification. Second, the pluralistic ranking concept of the PSC is superior to the monistic insistence on breeding barriers of the biological species concept because it can more adequately reflect evolutionary causes of importance in different groups.

[...]

Monophyly

One final area in need of clarification is the concept of monophyly. Traditionally, the cladistic definition of monophyly (which we favor) has not been applied to the species level. Hennig (1966) did not do so because he was committed to a biological species concept and thought that there was a clean break at the species level, with reticulating genealogical relationships predominating below and diverging genealogical

relationships predominating above. Later cladists (e.g., Wiley, 1981) have followed Hennig and defined a monophyletic taxon as one that originated in a single species and that contains all descendants of that species. Species are taken to be monophyletic a priori, therefore it is argued that they need not possess synapomorphies or really be monophyletic in the sense of higher taxa (e.g., Wiley, 1981). One major reason for this is the supposed problem of "ancestral" species.

It is our view that properly clarified, there are no insurmountable problems with applying the concept of monophyly explicitly to species (as the basal systematic taxon). Furthermore, this application must be carried out in order to have a consistently genealogical classification.

Monophyly should be redefined in such a way as to apply to species :

A monophyletic taxon is a group that contains all and only descendants of a common ancestor, originating in a single event.

"Ancestor" here refers, not to an ancestral species, but to a single individual. By "individual" here, we do not necessarily mean a single organism, but rather an entity (less inclusive than the species level) with spatiotemporal localization and with either cohesion or integration or both (as defined above). In particular cases this ancestral individual could be a single organism, a kin group, or a local population. We would argue that it would never be a whole species because we share the widespread view that new species come about only via splitting, not by any amount of anagenetic change.

The originating "event" of a monophyletic group referred to in the definition above could be due to the spatiotemporally restricted action of a number of different causes. These could include, in different cases, the origin of an evolutionary novelty which causes a new monophyletic group to be subject to a different selective regime than the rest of the "parent" species or which causes a disruption of the normal developmental canalization of the "parent" species. These could also include acquisition of an isolating mechanism or even the origin of a new species by hybridization between parts of two "parent" species. This diversity of causes for evolutionary divergence reinforces the need for a pluralistic ranking concept.

[...]

This concept of monophyly is, of course, only a grouping criterion. It does not imply that any particular peripheral isolate or hybrid population must be recognized as a species. It only specifies the genealogical conditions under which such groups can be recognized if the ranking criterion applied in a particular case supports recognition at the species level. The grouping and ranking criteria can thus be seen to interact in producing a species classification. Note that a corollary of the PSC is that not all organisms will belong to a formal Linnaean species since some monophyletic groups (e.g., hybrid populations that arise, but then quickly go extinct) will not be judged to be "important" monophyletic groups. The hybrid organisms in such a case would not formally belong to either original species.

The definition of monophyly given above solves the problem perceived by Hennig (1966), Wiley (1981), and Cracraft (1983) with "ancestral species." No such things exist. Only parts of an original species give rise to new ones, as in the above examples. If a currently recognized species is found to be paraphyletic because parts of it can be demonstrated to be more closely related to another species (Fig. 1; see also discussions and diagrams of such a situation in Bremer and Wanntorp, 1979; Avise, 1986), then the paraphyletic species should be broken up into smaller monophyletic species⁵.

Le concept diagnostique ou autapomorphique de l'espèce (cladistique structurale)

Biological classification is a very old enterprise, arising from humankind's ability to generalize about the natural world. The type of generalizations of concern may be termed kinds. For example, one may observe a particular organism and give it a name : "cat." Early in life, humans learn that names such as "cat" ally not to one particular organism, but rather to a kind of organism. There is not only one cat, there are many. And there are even different varieties of them.

Biological classification is an attempt to specify all of the different kinds of organisms. In its modern form, it is basic to understanding the natural world. But the enterprise of classification is problematical. Nature is rich in different kinds of organisms, and persons disagree on exactly what kinds there are. When disagreement occurs, a person is apt to reflect on the nature of that disagreement and may ask : what is a "kind" ? Most biologists have been too busy to give much thought to this general question. For most

5. Brent D. Mishler & Robert N. Brandon. 1987. Individuality, Pluralism, and the Phylogenetic Species Concept. *Biology and Philosophy* 2 : 405-410.

practical problems of humanity and science, it does not matter. With reference to a particular kind, an appropriate answer is usually available. Asked “what is a mammal?”, a biologist is apt to respond with a definition : “a tetrapodous vertebrate with homeothermy, hair, internal fertilization, milk glands, and a dentary-squamosal articulation.” Or the response may consist of examples : “a monotreme, marsupial, or placental.” Further inquiry is apt to proceed away from the general question “what is a kind?” to more particular questions, such as “what is hair?” or “what is a monotreme?” To such particular questions, answers can usually be given that satisfy most day-to-day curiosity. But if there is to be a general theory of classification, the general question must be answered. Most biologists might answer it in a preliminary way by stating that there are two kinds of “kinds” : species and groups of species. As a result, the initial question (what is a kind?) may be restated in two forms : (1) “what is a species?” and (2) “what is a group?”

The second question will be explored at length in this book, but the first question will be considered only here, and only briefly. Unlike the general question (what is a kind?), the question “what is a species?” has been extensively debated by biologists. Numerous different species concepts have been proposed : there are biological species, evolutionary species, morphological species, polytypic species, phenetic species, ecological species, paleontological species, essentialistic species, nominalistic species, and doubtless many others. Most considerations of this topic have been attempts to define the word “species”, but as Popper has pointed out, controversies about the possible definitions of terms are not themselves productive, because all definitions utilize other words that are themselves in need of definition, resulting in a never-ending process (an infinite regress). For example, almost all definitions of the word “species” that have been proposed utilize the word “population”—species are populations, or groups of populations, that meet one or more criteria. But the word “population” is itself in need of definition, and is fully as difficult to define as is the word “species.”

All of these varied species concepts do share some elements in common. All of them admit that we can never study species a wholes, but only samples of them, and all of them provide criteria by which, in some cases, we may be able to say that a given sample of organisms represents not one but two (or more) species. Non of them, however, can ever guarantee the integrity of a sample ; none can ever guarantee that a sample contains only one species. The most we can say is that we have not yet been able to differentiate species within the sample. So no matter what species concept a biologist claims to use, there is an upper limit to the number of species, set by the number of samples that can be differentiated in some way. To a very large extent, this is the species concept actually used in practice : those samples that a biologist can distinguish, and tell others how to distinguish (diagnose), are called species.

This, however, is not in itself a sufficient concept, because there are samples that can be distinguished but which do not appear to exist independently in nature. In many groups of organisms, for example, we can distinguish samples representing males and females : or eggs, larvae, pupae, and adults. We find, however, that males by themselves do not produce other males, or larvae other larvae, so that these samples, by themselves, have no independent existence in nature. Thus the concept of species must include a criterion of self-perpetuation : males and females together ; eggs, larvae, pupae and adults together ; form self-perpetuating species.

If we call any attribute of an organism by which we can distinguish samples a character, we can say that to be diagnosable, a sample of specimens must have a unique set of characters. It need not have even a single character that is unique to it, but the total set of its known characters must be different from that of all other known samples, or we will not be able to distinguish it. In this book, then, species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters. As such, they include as species the “subspecies” of those biologists who use that term⁶.

6. Gareth J. Nelson & Norman I. Platnick. 1981. *Systematics and Biogeography : Cladistics and Vicariance*. New York, NY : Columbia University Press, p. 10-12.