

## Reviews

### Species concepts, process analysis, and the hierarchy of nature

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**Abstract.** Species figure prominently in all biological studies, but what a species actually is and how we recognize it in practice is still a much-debated issue. Present discussion revolves around five major species concepts: the biological, the evolutionary, the cladistic, the recognition and the phylogenetic concepts. Each of these species notions has its theoretical and practical problems. One important point that has emerged from recent discussions on the ontological status of species is that there is a tension between species concepts based on interbreeding and those based on genealogy, and that practical application of these two kinds of concept may give rise to incompatible results. Species recognized by one species concept appear to be essentially different entities compared with species demarcated by another. However, these different species may all represent real and objective entities in nature. What we perceive as a species depends on the evolutionary processes that we have made objects of our research. Some of these processes are between entities of the genealogical hierarchy of nature, while other processes relate to nature's ecological hierarchy. It is essential that our species concept should be adjusted to the focal level of our research program, thereby taking into full account the two process hierarchies of nature.

**Key words.** Species concepts; theoretical and practical problems; ontological status; interbreeding; monophyly; genealogical hierarchy; ecological hierarchy; evolutionary processes; focal research level.

#### Introduction

It is now generally accepted that Darwin did not solve the problem formulated by the title of *The Origin of Species*. He made a convincing argument for the existence and importance of variation within species, especially in the time dimension, but failed to provide an analysis of the multiplication of species. In retrospect this is hardly surprising because Darwin was not at all sure about the nature of species<sup>31</sup>. But it is more surprising that after a further 130 years of study the same problem, the origin and diversity of species, is still with us today and that the ontological status of species is more hotly debated than ever before.

The continuing uncertainty about the precise nature of species becomes even more of an embarrassment for evolutionary biologists when it is realized that the notion or concept of species is essential to the current, neo-Darwinian, evolutionary theory. Species, defined in one way or the other, are usually seen as basic units of evolution. The proliferation of species concepts that we have witnessed in the last decades resulted from the desire to formulate one concept that would be applicable to all levels of evolutionary biology. However, it turns out that the various concepts proposed stress different, and frequently incompatible properties of species, depending on the different angles from which students have approached nature's diversity. Thus we have reached a point where more of the same is not expected to give us finally the ultimate, all-applicable characterization of

species. It has already become apparent that adopting a different way of looking at the species problem is much more constructive in furthering our understanding of the nature of species and may be able to assess the usefulness of the various existing characterizations of species.

Firstly this paper reviews the characteristics and problems of the major alternative definitions of species; more exhaustive discussions on the pros and cons of the various species concepts can be found in other publications<sup>20, 35, 49</sup>. Secondly, the paper examines the implications of a hierarchical way of looking at species for the theory and practice of systematic biology and for our perception of species.

#### *Systematic practice and alternative species concepts*

The systematic literature abounds with descriptions of new species and it is well known to every practising taxonomist that the most pervasive species concept used in these accounts is that of the morphospecies. This means that in daily systematic practice the majority of taxonomists follow the practical approach taken also by Darwin in that they still "... look at the term species as one arbitrarily given, for the sake of convenience, for a set of individuals closely resembling each other..."<sup>12</sup>. In that respect current taxonomic practice is only one step removed from the essentialistic or typological species concept used by Linnaeus and his followers. These workers did not recognize in variation an important characteristic of nature, because they believed that God had creat-

ed immutable entities according to a limited number of structural types. These idealized entities could be characterized through the description of typical specimens, one good specimen in principle being sufficient for a complete description. Current practice only differs from the essentialists' method in that we now carefully document the full range of variation within what we perceive as a morphospecies; this change is due in no small part to the appreciation of variation within species that originated with Darwin's detailed analysis in *The Origin of Species*. The "new systematics" and "modern synthesis" of the 1940s focused on the population level and incorporated notions such as interbreeding, genetic unit, and reproductive community, emanating from the rapidly developing field of population genetics. One result of the renewed activities embodied by the "new systematics" was the formulation by Mayr<sup>30</sup> of the first modern species notion, the biological species concept: "Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". In later formulations Mayr<sup>32, 33</sup> omitted the phrase "actually or potentially".

That the biological species concept has its problems has been pointed out by many workers and also by Mayr himself. The practising taxonomist is immediately confronted with the problem that the biological species notion is generally non-operational. But this is not such a major drawback as it seems because it applies to any theoretical definition for which we need further criteria enabling us to establish whether in particular instances the conditions of the definition are met. Such operational tests can be found in morphological gaps<sup>32, 33</sup> and in characteristics that signal reproductive isolation by pre-mating isolating mechanisms such as ethological differences (e.g. song structure), which are also applicable to allopatric populations. The fact that generally these rules provide reliable inferences about reproductive isolation between sexual species (excepting those cases where reproductive isolation has been acquired without corresponding morphological or ethological change, or cases where differentiation has not been accompanied by reproductive isolation) does not exhaust the practical and theoretical problems which beset the biological species concept.

One of the major shortcomings of the biological species concept is its restriction to bisexual species and its inapplicability to uniparental organisms. This problem has already been amply discussed by Mayr<sup>32, 33</sup>. It is not so much a practical problem, because we can use morphological differences for delimiting asexual species in the same manner that these operational criteria are used for recognizing sexual species. The problem is of a theoretical nature, in that relative morphological similarity cannot determine the probability of interbreeding among individuals that do not interbreed; in other words: the operational criteria do not relate to the biological species definition<sup>45</sup>.

Rosenberg<sup>45</sup> concluded, rightly, that the qualification that a species occupy a specific niche, as proposed by Mayr<sup>34</sup>, does not adequately answer the theoretical shortcomings of the biological species notion and suffers from being non-operational<sup>9, 21</sup>. Other workers, however, do not see the existence of asexual organisms as a problem for the biological species concept because (a) it is considered unlikely that asexuality can give rise to independent lineages, while it is seen also as "a possibly insignificant phenomenon"<sup>20</sup>, or (b) the attainment of reproductive isolation is considered to be synonymous with speciation and to be the essential aspect of the biological species notion (instead of interbreeding); it is argued that both sexual and asexual organisms can form reproductively isolated groups of natural populations, i.e. species<sup>57-59</sup>. Templeton<sup>50</sup>, however, recently argued that nonsexuality cannot be considered as an insignificant problem for the biological species concept (and the recognition concept as well) because (a) asexual organisms appear to be subdivided into well-delimited taxa, in the same manner as sexual species, and (b) a continuum exists between panmictic populations and genetically closed demes; there is no clear-cut distinction between sexual and genetically closed reproductive systems.

Another major and persistent problem of the biological species concept is that it is difficult to apply in the time dimension. In a temporal sequence of interbreeding individuals there is continuous gene flow and there are therefore no natural break-points dividing this lineage into several biological species. Therefore, it has been suggested<sup>2</sup> that the biological species notion is a non-dimensional concept, applicable only to "horizontal" cross-sections of a phyletic lineage. Willmann<sup>58, 59</sup>, however, has argued, in contrast to most workers, that in the time dimension biological species are delimited by cladogenetic speciation events.

The second modern major species notion, the evolutionary species concept propounded by Simpson<sup>47</sup>, should accommodate much better the notion that species extend in time and space – according to its proponents. This species concept has become best known in the modified version proposed by Wiley<sup>53, 54</sup>: "A species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate". According to Wiley<sup>54</sup> this species concept is in agreement with the viewpoint that interbreeding is an important component in species cohesion in bisexual organisms, while at the same time the definition deals with the time dimension by introducing the notion of lineage.

In the time dimension, species would be delimited by punctuations resulting from mostly allopatric speciation events<sup>53</sup>. Wiley<sup>53</sup> argues that at these speciation events the ancestral species will generally become extinct and give rise to two or more daughter species. Thus, according to Wiley, we are in the happy circumstance that the methodological necessity of delimiting species in the time

dimension, and thus of postulating extinction of the ancestral species, generally corresponds with a biological phenomenon. However, Wiley also admits that there are cases where part of the ancestral species survives the punctuation event or split by maintaining its own identity and tendencies. Although the evolutionary species definition can deal with both of these situations, Wiley<sup>53</sup> does not provide us with operational rules enabling us to discriminate between them. Thus, judged from a practical point of view, the evolutionary species concept does not form an adequate answer to the problem that the biological species concept faces with respect to the temporal dimension.

Ax<sup>1</sup> and Willmann<sup>57</sup> argued that the punctuation or bifurcation event giving rise to two daughter species coincides with the establishment of reproductive barriers between the new species. Wiley<sup>54</sup> appears to express a similar idea when he states that species can only maintain their identities, tendencies, and historical fate through reproductive isolation from each other. But this brings us right back to all the problems related to the notion of reproductive isolation and its necessary operational tests, problems which also apply to the biological species concept.

The evolutionary species notion is closely related to the cladistic species concept. Because the latter has received a different name and sometimes is discussed without reference to the evolutionary species concept it is treated separately here. The term "cladistic" refers to the branching hierarchy of a phylogenetic tree, which consists of clades or branches based on recency of common ancestry.

Several authors<sup>1,43</sup> have argued in favor of the cladistic species concept, based on Hennig's<sup>22</sup> deviation rule which postulates that the beginning and end of a species are demarcated by speciation events and particularly that the ancestral species ceases to exist after the split. According to the deviation rule a speciation event gives rise to two new sister species, of which one may be similar to the ancestral species. Remane<sup>42</sup> analyzed the texts of Hennig<sup>22</sup> and Ax<sup>1</sup> and noticed difficulties and inconsistencies in the application of this cladistic species concept, especially with respect to the temporal extension of ancestral species and the isolation of marginal populations. For example, Ax<sup>1</sup> discussed two theoretical examples in which an ancestral species survives the split. But this is theoretically inconsistent with the cladistic species concept, while we also lack operational criteria enabling us to determine whether a species survives one or more splits<sup>42</sup>.

Ridley admits that there may be a problem with practical recognition criteria, but argues that nevertheless the cladistic species notion is theoretically sound. But defining species as branches<sup>43,57</sup> is not sound cladistic reasoning at all but is resorting to tree-of-life thinking, in the terminology of Sluys<sup>48</sup>. The branches of a phylogenetic tree represent genealogical *relationships* between taxa but

do not correspond with any physical reality in nature, and therefore cannot be used to deal with the ontology of species.

Although the cladistic species concept has its roots in the writings of Hennig<sup>22</sup> it is also fair to note that this author was aware of the fact that in determining the temporal extension of species, application of the deviation rule may produce statements contradicting observations made from another point of view<sup>23</sup>. In particular, Hennig already noticed the tension and incompatibility between the notions of interbreeding and genealogy, thus preceding more recent discussions on the pluriformity in species concepts (see below): "If both systems (the biological and genealogical) are mixed up, then inextricable confusion is the result. In the study of affinities one deals exclusively with genealogical relationships, from which it follows that the question into the biological identity between different species in different time horizons is here totally irrelevant" (cited in Sluys<sup>48</sup>).

The biological, cladistic, and evolutionary species concepts see the establishment of reproductive isolation as an important component of speciation in bisexual organisms. Reproductive isolation is seen as resulting from gradual adaptive or even drift-induced divergence between allopatric populations, in the manner described by Mayr<sup>33</sup>. Paterson<sup>40</sup>, however, took quite a different view, suggesting that genetic isolation is not so much an incidental product of geographic isolation but comes about through direct selection, on the basis of the Specific Mate Recognition System (SMRS). According to the recognition concept a species is "that most inclusive population of individual biparental organisms which share a common fertilization system"<sup>41</sup>.

It has been argued that one advantage of the recognition concept is that it is non-relational because it enables recognition of a species without reference to other species, in contrast to the biological species concept<sup>26,29</sup>. Under the recognition concept a group of organisms that share a common fertilization system, or, more specifically, reproductive adaptations constituting the SMRS, form a species. Others, however, have argued that the recognition concept also necessarily becomes relational when one tries to assign individuals to one of *two* species<sup>6</sup>.

One other postulated advantage of the recognition concept is that it focuses on real biological properties related to mate recognition which are meaningful to the organisms themselves. In contrast, the biological species notion concentrates on isolation, which is just an incidental effect and, as such, not experienced by individual organisms<sup>26</sup>. The self-defining<sup>26</sup> properties of a recognition species, i.e. aspects of the mating system, concern properties of individual organisms that have a biological function in the male-female communication system. Each species defines itself by a unique system of recognition signals between conspecific mates; species are delimited by a unique combination of individual elements of the

mate recognition system. The elements themselves need not be unique<sup>26</sup>.

In the temporal as well as the present dimension, species are delimited by reproductive divergence as a result of SMRS discontinuity. As long as reproductive bonds are unbroken and the SMRS is maintained by strong stabilizing selection there is only a question of a single species, and there is no reason for chopping up a lineage into several arbitrarily defined species, irrespective of the degree of economic or morphological differentiation accrued over time.

The four modern species concepts discussed above (the biological, evolutionary, cladistic, and recognition concepts) are to a greater or lesser extent genetic concepts, in that they define species in terms of gene exchange. Such is not the case with the fifth modern species concept to be mentioned, the phylogenetic species concept sensu Cracraft<sup>7</sup>. Cracraft shifts away from the emphasis on process that is inherent in many species concepts, and focuses attention on the result of the evolutionary process. A species is then defined in terms of the resulting pattern: "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent"<sup>7</sup>, or "A species can be defined as an irreducible cluster of organisms, within which there is a parental pattern of ancestry and descent, and which is diagnosably distinct from other such clusters"<sup>9</sup>. This means that in practice species are diagnosed either by apomorphic characters or by unique combinations of plesiomorphic features (Cracraft<sup>7</sup> mentions unique combinations of primitive *and derived* features, but surely these characters must all be plesiomorphic on the level of the species, otherwise we would have at least one synapomorphy, and reference to primitive features would be superfluous).

It has been argued that species thus delimited represent fundamental evolutionary units<sup>7,9</sup> and are eminently suited for phylogenetic studies and the analysis of biogeographic differentiation. This may be perfectly true for clearly monophyletic species, i.e. for organisms sharing a uniquely derived character, because of these it can be said that they have an objective reality in nature, as is true for any monophyletic group. But is a phylogenetic species diagnosed by a combination of plesiomorphic features a real "evolutionary unit"<sup>7,9</sup> or an entity? It may be a monophyletic group (in cases where diagnostic apomorphies remain undetected), or it may not. There is a distinct possibility that a phylogenetic species diagnosed by plesiomorphic characters is in fact a paraphyletic species and thus a genealogical non-entity. It is clear that the phylogenetic species concept is not always in accordance with cladistic principles, but then Eldredge & Cracraft<sup>17</sup> have argued a way out of this dilemma by suggesting that the concept of monophyly does not apply very well to species; in a similar vein Nixon and Wheeler<sup>38</sup> stated recently that species are neither monophyletic nor paraphyletic.

The viewpoint that monophyly is a concept that loses its usefulness on the level of species runs counter to the phylogenetic species concept sensu Mishler and Donoghue<sup>37</sup> (see also ref. 36). According to Mishler and Brandon<sup>36</sup> organisms should be grouped into species through application of the cladistic concept of monophyly. This implies, in practice, that organisms will usually be assigned to a species on the basis of the possession of synapomorphies. But derived features can be used to arrive at monophyletic groups at any level. Therefore, Mishler and Brandon<sup>36</sup> suggest that the basal systematic taxon (i.e. the least inclusive monophyletic group, or species) be delimited, or ranked, in more or less the usual manner, i.e. by morphological discontinuities related to the number of synapomorphies between internodes of a cladogram. They suggest that this ranking criterion delimits individualistic groups of organisms that are held together by interbreeding, selective constraints, developmental canalization, or other agents. Thus, they de-emphasize interbreeding as an evolutionary agent in the origin and maintenance of species.

#### *Monophyly and interbreeding*

With regard to species the value and applicability of the concept of monophyly have been variously perceived by systematists. Ax<sup>1</sup>, for example, stated that the concepts of monophyly and non-monophyly have nothing to do with species as real entities in nature. Also Willmann<sup>56</sup> and Wheeler and Nixon<sup>52</sup> express the opinion that the term monophyly only applies to groups of species and not to a single species, because they perceive a fundamental difference between phylogenetic and tokogenetic relationships (tokogenetic relationships result from reproductive interactions between individuals). In contrast, McKittrick and Zink<sup>35</sup> "believe that species not only can but must be monophyletic". Wiley<sup>54</sup> formulated still another option: the term monophyletic does not apply to natural species because these are a priori monophyletic.

One major problem with the requirement that species be monophyletic is that it fails to assess the specific status of an ancestral species because the latter lacks derived features and is non-monophyletic by definition. This is precisely why some cladists have settled for mere diagnosability of species (see above) and others have denied the usefulness of the concept of monophyly for species and have instead stressed reproductive criteria in species delimitation<sup>56,59</sup>. De Queiroz and Donoghue<sup>13</sup> amply discussed the tension and non-overlap that exists between species concepts based on interbreeding and on common descent, and they correctly concluded that a combination of these two aspects into one species definition would probably enlarge the number of practical and theoretical problems.

The tension perceived by De Queiroz and Donoghue<sup>13</sup> between species concepts based on interbreeding and on

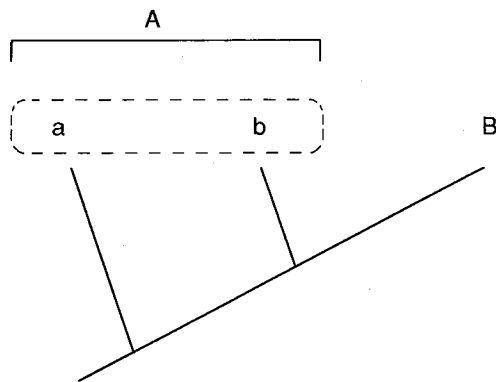


Figure 1. Phylogenetic relationships between taxonomically differentiated populations *a* and *b* of biological species A and biological species B. *a* and *b* are reproductively isolated from B but not from each other (modified from Willmann<sup>56</sup>).

genealogy is related to the fact that there is no a priori reason why reproductive isolation would coincide with taxonomic diversification<sup>7,10</sup>. Thus, we may encounter in nature cases where application of the criteria of common descent and reproductive isolation produce incompatible results. Willmann<sup>56</sup>, for example, illustrated the situation that a well-differentiated population (subspecies) of biological species A is genealogically more closely related to a second species B than to the other subspecies of A, with which it interbreeds (fig. 1). Cracraft<sup>11</sup> provided a similar example from the Australian bird genus *Cinclosoma*, in which two pairs of hybridizing taxa (species) were separated in the phylogenetic tree by three and four speciation events, respectively. Templeton<sup>50</sup>, too, discussed the situation that in both plants and animals natural hybridization frequently occurs between genetically, morphologically, and ecologically very distinct taxa. Templeton concluded that syngameons exist not only in the plant kingdom but also in the animal kingdom and that natural hybridization and gene exchange within these units does not exclude the existence of objective and stable morphological, ecological, or genetic units within a syngameon.

Such seemingly contradictory results become much more understandable when it is realized that (1) reproductive isolation is an incidental by-product of geographical isolation (see above), (2) reproductive isolation is not an attribute of populations but indicates a *relationship* between populations<sup>10,11</sup>, and (3) interbreeding between individuals of taxonomically differentiated populations may simply result from retention of the primitive character state, viz. genetic compatibility<sup>4</sup>. That species concepts based on interbreeding and on genealogy may frequently be fully incompatible, and that consequently application of genetic and taxonomic operational tests or criteria produce contradictory conclusions, is due to the fact that these concepts relate to different biological entities, which again result from different biological processes.

Some of these entities or species are produced by genetic cohesion, while others result from descent from a common ancestor.

#### *Different entities*

Cracraft<sup>10</sup> made a very similar point when he noted that systematists have generally used species definitions for two different purposes: (1) classification of organismal diversity, and (2) identification of entities thought to be participants in biological processes. Similarly, Rieppel<sup>44</sup> distinguished between a taxic and a transformational approach followed by systematists in their studies on species diversity. The taxic approach deals with the pattern of species diversity as brought about by genealogical branching events which give rise to hierarchically arranged organismal discontinuities. In the transformational approach, in contrast, systematists examine the gradual transformation of morphologies within an evolutionary lineage and concentrate on temporally and genealogically continuous populations.

So, it appears that over the years systematists have conceptualized two different entities, both called species and both considered to have a real existence in nature. The reality of these entities, species, has now been acknowledged due to the realization that they are individuals and not classes (for a recent listing of relevant literature on the species-as-individuals debate, see Rosenberg<sup>45</sup>). But seeing particular species as individuals solves only part of the species problem, because there may well be different kinds of individuals that function as discrete and real entities in different domains. De Queiroz and Donoghue<sup>13</sup> noted that, "Simply asserting that something is an individual... does little to clarify the nature of its existence". Therefore, we have to examine in which domains or contexts these different individuals function or belong. And it is especially here that the notion of the hierarchical organization of nature has provided valuable insights.

#### *The hierarchy of nature*

Three books<sup>15,16,46</sup> have advocated a restructuring of evolutionary theory by taking into account two hierarchies that they recognize in nature, the genealogical and the ecological hierarchies. This distinction between two different process hierarchies in nature reflects Hull's<sup>24</sup> earlier distinction between replicators and interactors as entities that function in biological processes. The entities that make up each of the two hierarchies (fig. 2) are thought to be spatiotemporally restricted, i.e. to be individuals. Entities of the genealogical hierarchy are held together by the capacity to produce more individuals of themselves. The upper limit of the genealogical hierarchy is reached with monophyletic taxa (all life being a very special monophyletic taxon), to which the rule of more-making does not apply: monophyletic groups do

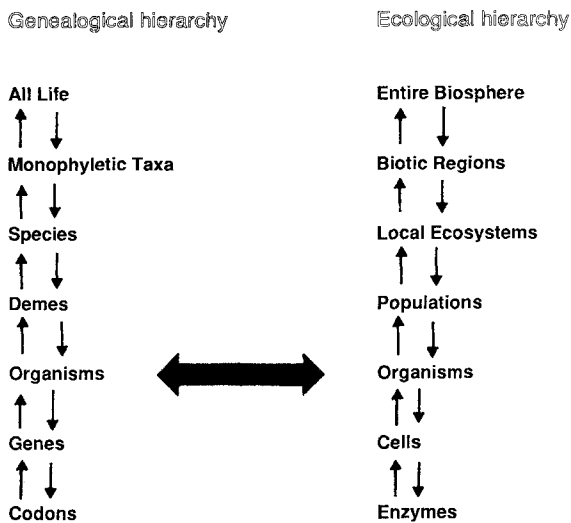


Figure 2. The genealogical and ecological hierarchies; interaction between entities indicated by arrows<sup>15, 18</sup>.

not produce monophyletic groups of like kind. Nevertheless, monophyletic taxa belong to the genealogical hierarchy because "they are historical units formed by the ongoing production of new species from old"<sup>15</sup>. Genealogical entities are replicators, albeit imperfect ones, and are involved in the transmission and transformation of information<sup>15</sup>.

Entities from the ecological hierarchy derive their cohesion from matter-energy transfer between individuals of a particular level in the hierarchy: ecological entities are interactors. Energy exchange between individuals on one level of the ecological hierarchy lends cohesion to individuals on the next-higher level<sup>15</sup>.

In the present context, the most important insight provided by the notion of two twin hierarchies of nature is that species belong to the genealogical hierarchy. Species are seen as spatiotemporally localized individuals with a beginning and an end, they are historical entities or individuals, but they are not interactors. It is here important to note that proponents of a hierarchical view of nature support a genetic species concept; species are seen as reproductive communities that arise through disruption of the SMRS<sup>15, 16</sup>.

#### Process analysis

Apart from advocating, the process of more-making, Eldredge and Salthe<sup>18</sup> identify another kind of process operating within the genealogical hierarchy, viz. "shuffling of lower-level individuals within upper-level individuals". Natural selection is the best known example of such shuffling process; it brings about an altered distribution of gene frequencies, due to differential reproductive success among organisms within demes. Although shuffling is seen as a process within the genealogical hierarchy it is evident that natural selection is also a reaction

to events within the ecological hierarchy<sup>15</sup>: individual organisms are selected because of particular interactions with other organisms, and interaction is a process characteristic of the ecological hierarchy.

Eldredge and Salthe<sup>18</sup> argued that similar shuffling occurs at other levels of the genealogical hierarchy, and as an example they mention species selection. We can speak of species selection if differential rates of origin or extinction directly result from selection on species level properties. This is an example of the rule that there is only a case of true selection when selective processes act on properties emergent on the focal level of analysis<sup>3, 10, 51</sup>, in this case the species level. In other words: differential sorting at the focal level should not be reducible to sorting among lower-level individuals, i.e. there should not be upward causation from phenomena at lower levels than the focal level. Thus, the question is whether species have emergent properties that can be selected. This question has been answered in the affirmative by some (e.g. ref. 51, which mentions characteristic population size, spatial and genetic separation between populations, and the nature of a periphery as possible candidates for species characters) and in the negative by others<sup>10</sup>. It appears that earlier proponents of species selection now recognize the absence of true emergent species characters and ascribe differential rates of origin and extinction among species to effects of lower-level processes<sup>16</sup>. But if sorting among species and higher-level individuals merely results from causes emanating from lower hierarchical levels, that is, from upward causation, not much remains of Eldredge and Salthe's<sup>18</sup> claim that within the genealogical hierarchy "in general individuals are shuffled within the next higher individuals".

The ecological hierarchy lends itself much better to an analysis of characteristic processes acting on each level. This is, of course, due to the fact that individuals on each level are interactors involved in the exchange of energy. Eldredge and Salthe<sup>18</sup> have amply discussed the various processes taking place at each of the ecological levels. A matter of no small importance is the interaction between the two hierarchies of nature, for it is only through interaction that "results" from the ecological level can become incorporated in entities of the genealogical hierarchy; only then is there evolution.

One obvious possibility for interaction is the level of the organism, because organisms belong to both hierarchies. Organisms are the carriers both of reproductive and economic adaptations and therefore take part in processes going on in each of the hierarchies. Viewed in a somewhat different way one could say with Eldredge<sup>15, 16</sup> that the genealogical hierarchy provides the organisms that function as interactors in the ecological arena.

#### Species concepts: pluralism, monism, or pragmatism?

Awareness of the twin hierarchies of nature – the ecological and the genealogical – ensures that we attempt to

determine precisely in which hierarchy and at what level particular evolutionary processes operate. For example, population genetics deals with processes restricted to local populations, i.e. the research program concerns a particular focal level within the ecological hierarchy. This implies that an understanding of population genetic processes does not automatically lead to insights into the origin of species diversity. The entity "species" belongs to the genealogical hierarchy, and does not only result from processes in the ecological hierarchy – specifically, natural selection mediated through the organism level – but is also subjected to upward and downward causation within the genealogical hierarchy. Natural selection is not the only cause of pattern<sup>51</sup>; species diversity is also controlled by downward causes such as epigenetic constraints. Because of previously acquired and subsequently stored (epi)genetic information the emergence of morphological novelties is constrained by the dynamics of existing developmental programs<sup>39</sup>. It appears once more (see also above) that a species is not an interactor, and does not participate in evolutionary processes but is the result of such processes<sup>10, 28</sup>. Being a resultant of evolutionary processes, a species is a component of a historical pattern instead of a functioning unit in processes.

A particular pattern is identified through diagnostic, or defining features. Consequently, this line of reasoning leads to the conclusion that a species is a historical entity or product in the genealogical hierarchy of nature that can be recognized with the help of diagnostic and/or defining characters. The best indication of membership of a species is that of synapomorphic characters, evolutionary novelties shared by a number of organisms. With the help of the principles and methods of phylogenetic analysis apomorphic characters can be unequivocally evaluated. In such cases species demarcation is easy: members of a species form an irreducible cluster of organisms characterized by a shared uniquely derived character. But systematic practice reveals that frequently apomorphic characters cannot be found on the species level, contrary to what has been suggested by Cracraft<sup>11</sup>, but again in correspondence with some earlier studies of this worker<sup>8</sup>. This is a frequently encountered practical problem, but it does not make a species less real; species, or monophyletic taxa in general, are not defined by apomorphic characters but are only recognized with the help of these features<sup>14</sup>. Therefore, we may well look for other criteria in cases where apomorphic characters cannot be found for species identification.

Alternative criteria can be found in unique combinations of diagnostic features characterizing clusters of organisms. It must be realized that the use of such unique combinations of characters goes together with the assumption that they indicate species similar to, and as real as, the ones suggested by the distribution of apomorphies. There are two grounds on which this assumption can be based. Firstly, one may consider species recogni-

tion on the basis of diagnostic character combinations to be a working hypothesis that eventually should be supported by apomorphies. One sees in practice that in these cases the search for derived characters shifts away from traditional features to other data sets, e.g. ultrastructural characters.

The second reason for accepting species recognized by diagnostic characters as objective realities in nature may be based on the notion that their "wholeness" derives from historical information. This historically-acquired information is stored in the organism's genetic make-up and developmental program. This notion of historical information incorporates aspects of Templeton's<sup>50</sup> cohesive species concept, because the latter ascribes the unity of species to the organisms' intrinsic cohesion mechanisms resulting from developmental, genetic, and phylogenetic constraints. Organisms with the same genealogical history share the same information and therefore constitute a historical entity, and thus an individual, which is different from other such entities. In itself this is a sufficient causal explanation for a species' reality and unity<sup>14, 55</sup>. It is, however, the expression of this historically acquired information that may cause practical problems in the recognition of species, notably in the absence of distinct apomorphies. A synapomorphy is a sure sign of shared historical information, but there is no biological principle dictating that every re-organization of stored information must lead to a discernable apomorphic modification. Modifications may very well express themselves as relatively minor variations (often of a quantitative nature) in plesiomorphic traits, or as different combinations of primitive characters. It is these kinds of diagnostic modifications that we take to be signals of a species' reality and individuality.

In this respect, species are treated differently from other taxa. Taxa higher than species are not used in all sorts of analyses (e.g. historical biogeographic studies) unless their monophyletic status, i.e. their reality in nature, is supported by derived characters. But if we apply this policy to species then there is the grave danger that much of our taxonomic, phylogenetic, and biogeographic work grinds to a halt because species are the basal units for all further studies. Systematic practice teaches that the workings of nature are such that apomorphies are scarce in species taxa. This appears to hold true for invertebrates and vertebrates alike and is probably based on a common principle, which needs further exploration.

Diagnostic and apomorphic characters may be restricted to one ontogenetic stage or to a single sex. Therefore, the species notion developed above requires one additional criterion, viz. reproductive cohesion among members of the irreducible cluster of organisms, or species. But then, Cracraft<sup>9, 10</sup> has pointed out that such a very general statement about cohesion is a necessary component of all species concepts.

The species notion, and its criteria, as developed in this paper, combine elements of the phylogenetic species con-

cepts of Cracraft<sup>7,9</sup>, Mishler and Donoghue<sup>37</sup>, and Mishler and Brandon<sup>36</sup> (see above). The present notion utilizes synapomorphies in the recognition of basal systematic taxa in the genealogical hierarchy, as suggested by Mishler and Donoghue<sup>37</sup>, Mishler and Brandon<sup>36</sup>, and also Cracraft<sup>11</sup>, but resorts to diagnostic features (as suggested by Cracraft<sup>7,9</sup>) in cases where apomorphies cannot be found. Furthermore, the species concept and operational criteria developed above incorporate explicitly the notion that a species' members, i.e. organisms, share the same, historically acquired genetic and epigenetic information (an aspect also discussed by Mishler and Brandon<sup>36</sup>).

The species notion and criteria for it developed in the present paper may be compared with a phylogenetic species concept formulated recently by Nixon and Wheeler<sup>38</sup>: a species is "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)". The term "phylogenetic", used by Nixon and Wheeler in the propagation of their species concept, seems ill-chosen because they do not require their species to be monophyletic; in their view the concept of monophyly is not applicable to species. Therefore, Nixon and Wheeler maintain that species might be diagnosed solely by plesiomorphic characters because "no criterion of monophyly" would be necessary while delimiting species. In the present paper it is argued that there are frequently situations in which the *criterion* of monophyly (viz. presence of apomorphies) cannot be used (as recognized also by Nixon and Wheeler), but that in such cases application of diagnostic features goes together with an *assumption* about the monophyletic status of the presumed species.

The operational criteria for species recognition proposed in this paper derive from the notion that a species represents a particular evolutionary pattern and therefore fall under the rubric of the taxic approach in comparative biology, in the terminology of Rieppel<sup>44</sup>. This particular approach to species recognition has elements in common with the traditional, typological way of working and it will rather often lead to "morphospecies" which are recognized already in traditional studies. Because this taxic approach to species predates genetic species concepts one could argue that the former should have priority over the latter, i.e. that the term species ought to be applied only to clusters of organisms recognized by taxic operational criteria.

However, the current practice of systematists, ecologists, and geneticists does not suggest that usage of the term species will be governed by historical priority. Scientists will continue to use the term species for biological entities that function in, or derive their existence from, the various evolutionary processes which are subjects of investigation<sup>13, 19, 25, 42</sup>. It is to be expected that the term species will continue to be applied, for example, to groups of genetically cohesive organisms that are isolated from

other such groups, or to populations of individuals which share a potential for genetic and phenotypic cohesion<sup>50</sup>, or share a common specific mate recognition system (see above). All these different "species" may represent real biological entities with respect to particular evolutionary processes at a specified focal level of analysis. Therefore, it is essential in discussions about species and speciation to make absolutely clear which evolutionary processes and results one has made the object of study, and to be aware of the focal level of analysis in the appropriate hierarchy of nature.

Realistically, it is to be expected that what scientists call a species, i.e. which species concept they use, depends on their field of investigation. Returning to the title of this section, it is a case of pluralism and pragmatism. From the various species notions available, that one is chosen which fits the evolutionary mechanisms under study and therefore can be used as a tool for understanding these processes. For example, if we are interested in the amount of gene-flow between organisms of various populations, we shall use a genetic species notion, e.g. the biological species concept. But if we are interested in the diversity of biological taxa, and their history in time and space, we shall deploy a taxic species concept. This view – that species notions are related to the evolutionary processes under investigation – runs counter to the suggestion of Chandler and Gromko<sup>5</sup> that there should not be a link between species concepts and processes of speciation. But how can we study any phenomenon in the natural sciences if our concepts are not adjusted to the particular processes giving rise to this phenomenon? Quantum mechanics represents a powerful tool in the description of the microstates in gases, but if we are interested in the relationships between macroscopic variables such as temperature, volume, and pressure we gain more insight by using thermodynamic concepts. The present diversity in species notions is not a sign of conceptual weakness, but signals real biological diversity, different research interests and necessarily different scientific approaches.

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