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La notion d'espèce en paléontologie : ontogenèse, variabilité, évolution

The species concept in palaeontology: ontogeny, variability, evolution

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General palaeontology

Species and “strange species” in zoology: Do we need a “unified concept of species”?

Espèces et « drôles d'espèces » en zoologie : avons-nous besoin d'un « concept unifié d'espèce » ?

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ABSTRACT

Eidonomy is the field of taxonomy, which addresses the “species problem”. The latter has several dimensions. The first is the confusions frequently made between species as an evolutionary unit, a taxon, a taxonomic category and a nomenclatural rank. The second is the reductionist temptation to recognize in nature only one kind of “basic entities” of biodiversity. From a practical viewpoint and for all non-systematist users of specific *nomina*, any animal organism should be referred to a taxon of nomenclatural rank *species*, designated by a Latin *binomen*. These *nomina* are indispensable for administrative and legal documents, for management and conservation of biodiversity, as well as for all biological research. But this does not imply that all these taxa should be referred to a single taxonomic category, a “unified concept of species”. In nature, several kinds of entities correspond to different “species concepts” or *specions* that are irreducible one to another. These categories can be defined according to the modalities of their reproduction, i.e., of their *gametopoesis* (mode of formation of gametes), of their *kinetogenesis* (mode of initiation of the development of the ovum) and of the *gene flow* between individuals. The best known of these categories is that of *mayron* or “mixiological species concept”, which points to an independent bisexual panmictic entity, constituting a protected gene pool, but others do exist. In order to better understand their differences, it is useful to consider the various *patterns of speciation*. These can be referred to three main categories: *monogeny* (change within a single lineage), *diplogeny* (birth of two specions from a single one) and *mixogeny* (hybridization between two specions). The splitting in two of a single initial gene pool is a rather long process, which often shows different stages. The latter can be expressed taxonomically through the use of particular eidonomic categories. Speciation can be considered completed only when it has become irreversible in case of new contact between the two stocks after a period of separation. In allopatry, it is difficult or impossible to know if this stage has been reached. This is not a reason for abandoning the mixiological criterion for identifying sympatric or parapatric specions. In allopatry, the method of inference can be used and, in the absence of sufficient information, it is fully possible to use “by default” the “phylogenetic concept of species” or *simpson*. The situation is further complicated by the fact that some of the basic

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entities of biodiversity of hybrid origin, the *kyons*, are not mayrons, as they have particular reproductive modes. Contrary to isolated and “normal” hybrids, such entities may persist in the long term in nature. Their gametopoiesis implies either an *ameiosis* (mitoses) or a *metameiosis* (modified meiosis), and their kinetogenesis implies *zygogenesis* (fertilization), *gynogenesis* or *parthenogenesis*. *Kyons* are of two main categories. The *klonons* are unisexual female entities in which genetic transmission is clonal, reproduction being often through parthenogenesis, or following other mechanisms with similar results in genetic terms. The *kleptons* are unisexual or bisexual entities, which depend for their reproduction, at each generation, on a mayron or another klepton. Their metameiosis produces particular gametes, which start their development either by *zygogenesis* (*zygokleptons*), by *gynogenesis* (*gynokleptons*) or by a combination of both systems (*tychokleptons*). All these particular cases do not constitute, as it has long been believed, “evolutionary dead ends”. On the contrary, some of these forms are advantaged in some conditions, and may also, in some cases, be at the origin of allopolyploid specions. The latter include both “normal mayrons” or *eumayrons* (allotetraploid bisexual entities) and *heteromayrons* (allotriploid bisexual entities with metameiosis). Mayron, klepton, klonon and simpson, and their subcategories, are different taxonomic categories which correspond to a single nomenclatural rank, that of species. The existence of interspecific hybridization in nature is a very common phenomenon in animals, the importance of which has long been underestimated. Reticulous relationships between specions have played a major role in the scenario of evolution. This should be acknowledged by the rejection of the “universal tree of life” model for organic evolution and its replacement by a “network of life” model.

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R É S U M É

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Klonon
Klepton
Simpson
Arbre du vivant
Réseau du vivant

L'*éidonomie* est le domaine de la taxinomie qui traite du « problème de l'espèce ». Ce dernier présente plusieurs dimensions. La première réside dans les fréquentes confusions entre espèce en tant qu'unité évolutive, taxon, catégorie taxinomique et rang nomenclatural. La seconde est la tentation réductionniste de ne reconnaître dans la nature qu'une seule sorte d'« entités de base » de la biodiversité. D'un point de vue pratique et pour tous les utilisateurs non systématiciens des *nomina* spécifiques, tout organisme animal doit être rapporté à un taxon de rang nomenclatural *espèce*, désigné par un *binomen* latin. Ces *nomina* sont indispensables pour les documents administratifs et légaux, pour la gestion et la conservation de la biodiversité, et pour toute la recherche en biologie. Mais cela n'implique nullement que tous ces taxons doivent être rapportés à une seule catégorie taxinomique d'espèce, un « concept unifié d'espèce ». Dans la nature, plusieurs sortes d'entités correspondent à différents « concepts d'espèce » ou *spécions* qui sont irréductibles les uns aux autres. Ces catégories peuvent être définies selon les modalités de leur reproduction, c'est-à-dire de leur *gamétopoïèse* (mode de formation des gamètes), de leur *kinétogénèse* (mode d'initiation du développement de l'ovule) et du *flux génique* entre les individus. La catégorie la mieux connue est celle de *mayron* ou « concept mixiologique d'espèce », qui désigne une entité bisexuelle panmictique indépendante, constituant un pool génique protégé, mais d'autres existent. De manière à mieux comprendre leurs différences, il est utile de considérer leurs divers *patrons de spéciation*. Ceux-ci peuvent être classés en trois catégories principales : la *monogénie* (transformation au sein d'une même lignée), la *diplogénie* (un spécion donnant naissance à deux spécions distincts) et la *mixogénie* (résultant de l'hybridation entre deux spécions). La division en deux d'un pool génique initial unique est un processus assez long, qui passe souvent par plusieurs stades. Ceux-ci peuvent être traduits taxinomiquement grâce à l'emploi de catégories éidonomiques particulières. On peut considérer la spéciation achevée seulement quand elle est devenue irréversible en cas de remise en contact des deux stocks après une période de séparation. En allopatrie, il est difficile ou impossible de savoir si ce stade a été atteint. Ce n'est pas une raison pour abandonner le critère mixiologique pour identifier les mayrons sympatriques ou parapatriques. En allopatrie, une méthode reposant sur l'inférence peut être employée et, en l'absence d'information suffisante, il est toujours possible d'employer « par défaut » le « concept phylogénétique d'espèce » ou *simpson*. La situation est encore compliquée par le fait que certaines des entités de base de la biodiversité, d'origine hybride, les *kyons*, ne sont pas des mayrons, car elles ont des modalités reproductives particulières. Contrairement aux hybrides isolés et « normaux », de telles entités peuvent persister longtemps dans la nature. Leur gamétopoïèse implique, soit une *améiose* (suite de mitoses), soit une *métaméiose* (méiose modifiée), et leur kinétogénèse implique une *zygogénèse* (fécondation), une *gynogénèse* ou une *parthénogénèse*. Il existe deux catégories principales de *kyons*. Les *klonons* sont des entités unisexuées femelles, au sein desquelles la transmission génétique est clonale, la reproduction s'effectuant souvent par parthénogénèse, ou au moyen d'autres mécanismes ayant des résultats similaires en termes génétiques. Les *kleptons* sont des entités unisexuées ou bisexuées qui

dépendent, pour leur reproduction, à chaque génération, d'un mayron ou d'un autre klepton. Leur métaméiose produit des gamètes particuliers dont le développement est initié par zygogenèse (*zygokleptons*), par gynogenèse (*gynokleptons*) ou par une combinaison des deux phénomènes (*tychokleptons*). Tous ces cas particuliers ne constituent nullement, comme on l'a longtemps cru, des « culs-de-sacs évolutifs ». Au contraire, certaines de ces formes sont avantageées dans la nature dans certaines conditions, et peuvent également, dans certains cas, être à l'origine de spéciations allopolyploïdes. Ces derniers incluent à la fois des « mayrons normaux » ou *eumayrons* (entités bisexuées allotétraploïdes) et des *hétéromayrons* (entités bisexuées allotriploïdes à métaméiose). Mayron, klepton, klonon et simpson, et leurs sous-catégories, sont des catégories taxinomiques différentes qui correspondent à un seul et même rang nomenclatural, celui d'espèce. L'existence d'hybridation interspécifique dans la nature est un phénomène très commun chez les animaux, dont l'importance a longtemps été sous-estimée. Les relations réticulées entre les spéciations ont joué un rôle majeur dans le scénario de l'évolution. Cette découverte devrait se traduire par le rejet du modèle de l'« arbre universel du vivant » pour décrire l'évolution organique, et son remplacement par un modèle du « réseau du vivant ».

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1. Introduction

The term *species* is of very general use in all domains of human activity and thought, where it may take very diverse meanings. Its use in biology and zoology is very old. Since the beginnings of these disciplines, it designates, as in common language and since thousands of years in all societies, a “kind” of animal (Pierre, 2002).

For *taxonomy*, the discipline of biology in charge of establishing a classification of living beings, the species is the basic unit, the “brick” of classification. The study of species is a particular domain of taxonomy, called *alpha-taxonomy*, *microtaxonomy* (Mayr and Ashlock, 1991) or *eidonomy* (Dubois, 2008a) (the term used here), which deserves to be distinguished (by its questions, concepts and methods) from supraspecific taxonomy.

Besides, since the emergence of the theory of evolution, the species is also considered as the basic unit of evolution, the latter resulting mostly from the phenomenon of *speciation* (appearance of new species).

In fact, even within the wide domain of research of systematics, the term species is used in several distinct senses. It may designate:

- an *evolutionary concept*, the basic unit of evolution;
- a classificatory unit or *taxon*;
- a *taxonomic category*, applying to several taxa sharing some properties or peculiarities (e.g., “biological species” or “phylogenetic species”);
- a *nomenclatural rank*, shared by all taxa named in a similar way, through Latin *binomina* (*binomen* = generic *substantive* + specific *epithet*; Dubois, 2000), and occupying a given rank in the nomenclatural hierarchy.

The rather frequent confusion between taxonomy (classification) and nomenclature (nomination) (Dubois, 2005, 2007, 2008b) is here particularly harmful. The fact that different taxa share the same nomenclatural rank of species does not mean that they belong necessarily to the same taxonomic category.

Although ancient in biology, and particularly in zoology, the “species problem” has been renewed in the

recent decades, in part because of the development of cladistic thinking, and in part through the discovery in animals of many unexpected evolutionary situations and “strange species”, often of hybrid origin, that reproduce in an unusual way (parthenogenesis, gynogenesis, etc.). The latter situations are diverse and deserve an appropriate taxonomic treatment. The aim of the present work is not to present again these unusual situations in detail, which has already been done in many publications, but to focus on the following aspects of this question, that have attracted much less attention so far:

- the appropriate terminology for the description of these biological phenomena, in particular the reproductive modes of such zoological entities;
- the patterns of speciation involved in these situations;
- the appropriate eidonomic treatment for these taxa.

The rather complex and sometimes entangled situation regarding the “species problem” has an important linguistic dimension. It would be difficult to explore seriously the various facets of this question without dealing first with some terminological problems. As often in science, these problems cause ambiguities in communication and errors of interpretation (Mayr, 1997). Two major terminological problems exist regarding the questions related with species, speciation and “reproductive modes”. The first one concerns the difficulties posed by the ambiguous use of the term *species*, and the second the terms ending in *-genesis*.

A most harmful confusion for communication is that between “species” as a nomenclatural rank and as a taxonomic category. One way to remove this ambiguity is to use two distinct terms for the two concepts (Dubois, 2007). Currently, the most frequently used meaning for the term species is that of a particular nomenclatural rank. This meaning is found in all “official lists” of taxa and other administrative or legislative texts, as well as in most publications of conservation biology, general and experimental biology, biomedical, veterinary and agronomic disciplines, etc. It seems therefore justified to retain the term *species* for this nomenclatural concept, and the root species for other related nomenclatural ranks (subspecies,

supraspecies) (Dubois, 2008a, 2009a). When it comes to designate a taxonomic category, the use of the term *specion* (Dubois, 2007, 2008b, 2009a) allows avoiding confusion. In other words, in zoological nomenclature, a single rank species exists but, in zoological eidonomy, several *specion* concepts are currently in use. To avoid confusion with nomenclatural terms, these eidonomic concepts are designated below by terms ending in *-on* like the term *taxon* (Dubois, 2008a, 2009a).

Problems also derive from the existence of many scientific or technical terms (such as cladogenesis, parthenogenesis or hybridogenesis) based on the same root *genesis*. Their similar aspects may wrongly suggest that they are somehow “homologous” and that they designate comparable or parallel phenomena (Dubois, 1991). In Greek and Latin, the term *genesis* designates the origin, the source of life, hence the derived meanings generation, creation, birth, etc. The use of this root to create technical terms is ambiguous, as it has been employed in various branches of science to designate different kinds of “origin”, thus giving birth to similar or even identical terms (homonyms) pointing to widely different phenomena: e.g., *pedogenesis*, used both for the process of formation of soils and for the process of reproduction by “larval” animals. In the field here explored (species, speciation and related phenomena), the use of this root has covered a particularly high variety of concepts. In some cases (e.g., cladogenesis) it has referred to a pattern of speciation. In others, it has referred to a “reproductive mode”, but the latter formula itself has been used in an ambiguous sense. The reproductive process in metazoa includes several phases: formation of gametes, fertilization and starting of embryonic development. Although similar and often considered alternative terms describing parallel situations, terms like parthenogenesis or hybridogenesis do not refer to homologous stages in the reproductive process. Stating that an organism reproduced by parthenogenesis means that the development of its ova did not require the intervention of sperm. This term, as such, does not provide any information about the cytological process that produced these ova. The information whether such an organism also had, or did not have, a peculiar mode of formation of gametes, is not carried by the term “parthenogenetic”. Terms like parthenogenesis or gynogenesis refer to the mode of initiation of development, whereas the term hybridogenesis, in the sense given to it by Schultz (1969), designates a particular mode of formation of gametes in organisms of hybrid origin (see below). The resemblance between these terms is therefore misleading and results in confusions.

In order to contribute to terminological clarification, it was suggested (Dubois, 1991, 2008a, 2009a, 2009b) to restrict the use of the root *-genesis* to some of the phenomena mentioned above only, and to use other endings for the others. In the field of biology of speciation and species here covered, three main domains have received designations in *-genesis*:

- patterns of speciation (e.g., cladogenesis);
- processes involved in the formation of gametes (e.g., gametogenesis, hybridogenesis);

- processes involved in the initiation of embryonic development (e.g., parthenogenesis, gynogenesis).

The suggestion made was to restrict the use of the root *-genesis* (adjectives in *-genetic*) to the latter category of phenomena and to use the following roots, also meaning “origin” or “production” for the other two: *-geny* (adjectives in *-genic*) for the patterns of speciation and *-poiesis* (adjectives in *-poietic*) for the modes of formation of gametes.

2. Species as a nomenclatural rank

In the traditional taxonomic system, as used since Linnaeus (1758) by the overwhelming majority of zoologists, the taxonomic information is indexed thanks to a system of Latin scientific names or *nomina* (Dubois, 2000). This system is organized in a hierarchical way by means of *nomenclatural ranks* successively fit into each other, from kingdom and phylum to variety and form. The *International Code of Zoological Nomenclature* (Anonymous [ICZN], 1999) (“the Code” below) provides Rules for the unambiguous and automatic allocation of a unique and universal valid nomen for each taxon, at least for most *nomina* (excepting the higher and lower ranks). From a nomenclatural point of view, a species is simply a taxon of rank lower than genus (or subgenus or species-group if relevant) and higher than subspecies (or subspecies-group if relevant). Species as a nomenclatural rank is essential outside systematics. For this purpose, which is intended mostly to non-systematists and even to non-biologists, it is indispensable to have a universality of use over the whole zoology. All taxa of rank species must be designated in the same way in the whole world, by a Latin *binomen* such as *Drosophila melanogaster*.

3. Species (*specion*) as a taxonomic category

3.1. The main traditional concepts

The situation is different if the term species is considered as designating a taxonomic category, based on biological criteria. Many distinct “species concepts” have been proposed and several are still in force in zootaxonomy. It is possible to compile lists of 22 “species concepts” (Mayden, 1997) and probably more, but many of these definitions are largely equivalent, and the useful number can be reduced to a few main categories. Three concepts have by far been most frequently used in the zoological literature: the phenetic, mixiological and phylogenetic concepts.

According to the *Phenetic Species Concept* (Sokal and Crovello, 1970), *specions* are groups of individuals that resemble each other “closely”. The units so defined, or *phenons* (Mayr, 1969), are not genetic units, as individuals with similar phenotypes may have different genotypes, whereas individuals with different phenotypes may have the same genotype (e.g., the same organism all along its development). Such units are not reproductive or mixiological units either, as individuals with different phenotypes may breed together whereas similar individuals may be intersterile.

Finally, such units are not always cladistic units, as resemblance is not equivalent to kinship and similar phenotypes may result from evolutionary convergence or parallelism. However, this specion concept is sometimes the only one that can be operational, in the case of organisms about which little biological information is available, for example, in paleontology.

According to Coutagne's *mixiological criterion* (Audibert and Vivien, 2007; Coutagne, 1895), *specions* are groups of individuals that, *in natural conditions*, breed together and recombine their genes to produce viable and fertile offspring. At each generation, new genomes are created as a result of random sampling and recombination during the formation of the gametes of the parents followed by fertilization. This *Mixiological Species Concept* was termed by Mayr (1942, 1963) the *Biological Species Concept* (BSC), a well-known but ill-chosen denomination as it does not point to the particularities of this concept. Even more ambiguous, the shorter terms *biological species* or *biospecies* (Cain, 1953, 1954) should be banished from scientific literature, as all the species recognized by biologists, whatever species concept they use, are “biological”! The simple and brief term *mayron* (Dubois, 2007) is used below for this *specion* concept.

Despite its simple formulation, this concept is complex, as it implies several distinct phenomena. In order to breed together, animals must be able to meet; therefore they must occur in *sympatry* and *synchrony*. In such conditions, the ability to produce together a fertile offspring (interfertility) testimonies to genetic compatibility between them. In any discussion of this concept, instead of stressing this compatibility, attention can be called on the opposite characteristic: sympatric animals that do not breed together show breeding *isolation*, a fact used by Paterson (1985) to coin the formula *Isolation Species Concept*. The same idea can be expressed by stating that a *mayron* is a “closed gene pool”, or, more generally, a “protected gene pool”. This means that in some relatively rare cases, the gene pool may be slightly “leaking” (e.g., in exceptional hybridizations).

Breeding isolation between distinct *specions* may be due to different kinds of barriers between them (Dubois, 1988). Individuals potentially interfertile may never pair in natural conditions for various reasons, e.g., behavioural. Instead of stressing the criteria of interfertility or of genetic isolation, it is therefore possible to stress such ethological criteria, as done in the *Recognition Species Concept* (Paterson, 1985). The *unity of the genotype* (Mayr, 1975), i.e., the fact a *mayron* forms an integrated entity with a high level of cohesion, may also be stressed in the formula *Cohesion Species Concept* (Templeton, 1989). All other “criteria” allowing one to establish that various individuals belong in the same *mayron* also result, directly or indirectly, from this genetic and behavioural cohesion. These different characteristics are just different facets of the same reality. The *Mixiological Species Concept* or *mayron* implies them all and is sufficient to account for them.

Beside this family of concepts, another school of thought developed, initiated mainly by paleontologists. For these researchers working usually in allochry and with very limited biological information on the organisms studied,

the implementation of the *mayron* concept is difficult, and another approach was proposed. It was so first under the form of the *Evolutionary Species Concept* (Simpson, 1961; Wiley, 1981), which defines a species as an independent lineage. After the works of Hennig (Hennig, 1950, 1966) and the spread of cladism, this concept was reformulated as *Phylogenetic Species Concept* (PSC) (Cracraft, 1983), a species being understood as a group of individuals liable to be defined by a particular diagnosis, more precisely an *apognosis* (Dubois, 1997, 2007, 2008b), i.e., a set of *autapomorphies* shared by its members (Donoghue, 1985; Mishler, 1985). This species concept was recently given the shorter designation of *simpson* (Dubois, 2007, 2008a, 2008b, 2009a), used below.

An attempt of synthesis of several *specion* concepts was recently proposed (de Queiroz, 1998) under the designation of *General Lineage Species Concept* (GLSC). This concept is meant as being global but it does not take into account various real evolutionary situations, discussed below.

3.2. A critical approach to tradition

The “species problem” is one of those which mobilized the highest numbers of practitioners and theoreticians of systematics and it would be impossible, and largely useless, to simply list, let alone summarize and discuss, all the theories and opinions that have been devoted to it. All along this history, two very different attitudes have co-existed regarding the definition of the taxonomic category of species. The first one, often preferred by the theoreticians and historians of sciences, and by laboratory biologists with little experience of organisms in nature, consists in defining a priori one or several models, then trying to match reality with them, sometimes at the expense of strange contortions and deliberately ignoring some embarrassing exceptions that do not fit with the models. The second one consists in starting from the organisms as observed in the field, from the particular concrete characteristics of their situations and relations, then trying to extract from this information some general concepts, but without ignoring the existence of exceptions and difficulties. This second approach, often privileged by field naturalists, is adopted here. Whatever interest one may have for theories, concepts and generalisations, they are meaningful only when they are appropriate for accounting for *all* phenomena observed in nature, without distorting them and without ignoring all the particular cases which do not fit with the general theories or concepts.

Currently, two main groups of concepts of species as a taxonomic category have numerous supporters among taxonomists: the *mixiological species concept*, BSC or *mayron*, as a protected gene pool; and the *phylogenetic species concept*, PSC or *simpson*, as an isolated, independent evolutionary lineage, characterized by autapomorphies. In nature, undeniably many entities correspond to both concepts, and some to only one of them. Why should we imagine, however, that these concepts have a general value, and that all the “basic units of evolution” should be entities as defined under one of these concepts, or a third one like the GLSC? For which theoretical reason should there exist

“a single kind of species” in the world? The search, pursued by many taxonomists and for a long time, for *the* species concept, which would account for all concrete situations, appears to be due to the influence of reductionist thinking. Such an approach is appropriate in sciences, like physics, chemistry or physiology, the main objective of which is to find invariants and general laws, but it is not appropriate for the study of the diversity of living organisms (Mayr, 1997). The careful study of concrete situations in nature testifies to its “inventiveness” and unpredictability. The quest for a “unified species concept” will prove to be a sterile Quest for the Holy Grail if the study of facts leads us to recognize the existence of several kinds of “basic units of evolution”, irreducible one to another.

Understood as a lineage, the *specion* is a basic unit of evolution. The multiplication of lineages has allowed the diversification of living organisms and their progressive adaptation to changes in environment. The concept of *simpson* places the *specion* in a temporal context. Within such a framework, it is possible to consider ontologically each *specion* as an “individual” (Ghiselin, 1974), the existence of which is limited in time, from its “birth” (speciation) until its “death” (extinction). This image is interesting, but it is only an *image*. Biological species do not share all the peculiarities of individuals, particularly integrity, cohesion and centralisation. The individuals that make up a species can have a rather high level of autonomy and a distinct fate, particularly in terms of descent. If it were not so, no *specion* could give birth to two distinct *specions*. A dangerous connotation of this image is that it brings apparent support to the misleading idea that *specions* follow an internal ageing process that leads them to “natural extinction”, although there exists no such “law of extinction” (Raup, 1991).

In order to be able to apply the concept of “independent evolutionary lineage”, it is necessary to have criteria allowing to state that a lineage is fully separated from all other ones. A problem of interpretation appears at low level in the case of entities the geographic distributions of which have become disjunct, but which may come again in contact later on. A second problem concerns the entities composed of individuals between which the only existing gene flow is from mothers to daughters, without genetic recombination between individuals. In such situations, which meaning should be given to the term “independent”? On the other hand, the distinction between “independent evolutionary lineages” at low level (“species”) and at higher level (“clades”) appears largely artificial and subjective. Finally, a still more difficult problem is posed by the existence in nature of stable and well-characterised entities that are not “independent”. How should eidonomy account for their existence?

Before examining these points in more detail, we have to consider first the main categories of *specions* that can be recognized to account for the diversity of observed situations, then the different kinds of reproductive modes (Dubois, 1991, 2008a) and of gene flow between individuals in these natural entities (Dubois, 2008a, 2009a), and finally the different patterns of speciation in nature. This will allow us to propose a general framework for dealing with zoological eidonomy.

4. Categories of specions

4.1. Mayron

The most “classical” case of *specion* is that of *mayron*, i.e., a “panmictic bisexual species”. At each generation, the chromosomes and alleles are distributed and recombined randomly, so that no two individuals are genetically identical, apart from identical twins (except for recent mutations). Such entities, which also qualify as independent evolutionary lineages, are numerous in nature. Such *specions* have been the matter of countless studies dealing with the most diverse groups of animals. As tackled below, “borderline situations” can be observed in cases of speciations still “under way”, where hybrid zones exist between two entities.

4.2. Klonon

The term *parthenogenesis* (Owen, 1849) designates the development of a virgin ovum, without genetic input from a male gamete, into a viable organism. The term *clone* (Webber, 1903) designates a lineage of females transmitting their genome unchanged (except for recent mutations) to their daughters, but this term had no taxonomic connotation. The discovery in nature of animal entities that reproduce exclusively by parthenogenesis has long been problematic for evolutionary biologists and zootaxonomists, inasmuch as these entities appear as exceptions to the “rule” of the “panmictic bisexual species”. They have long been treated as “curiosities” of little importance, but this becomes more and more difficult as more cases are discovered and as it becomes clear that such entities do exist in many distinct zoological phyla and may even, in some groups like the bdelloid rotifers (Welch and Meselson, 2003), become the rule. Such entities received several designations (Dubois, 2008a). In order to avoid the use of the stem *species*, here reserved to a nomenclatural rank, the term *klonon* (Dubois, 1991) is used here. Being short, it may be combined with other roots to build longer terms. As will be discussed below, recent researches have shown that many *klonons* are of hybrid origin.

Beside experimental parthenogenesis, a variety of cytological phenomena can be responsible in nature for a female being able to give birth to other females without any intervention of male gametes (Dawley and Bogart, 1989; Loxdale and Lushai, 2003; Mogie, 1986; Oliver, 1971; Simon et al., 2003). Two main categories of such entities may be distinguished, according to their mode of formation of gametes.

In the first one, meiosis is replaced by an *ameiosis* (Rieger et al., 1968) consisting simply in a series of mitoses, which result in a diploid ovum that will develop until adulthood. This phenomenon, which has received various designations (Dubois, 2008a), such as *apomixis* (Winkler, 1906), is really *asexual* (Rieger et al., 1968), and results in a clonal transmission of the genome from mother to daughters. All children are genetically identical, except for recent mutations. From the viewpoint of its results, *apomixis* is equivalent to simple *vegetative multiplication* (by stolon, rhizome, tubercle, etc.). Natural entities which reproduce exclusively through

one of these two phenomena can be designated as *mitoklonons* (Dubois, 2008a, 2009a).

The reproductive mode of the second category, *meioklonon* (Dubois, 2008a, 2009a), has also received various designations, including *automixis* (Rieger et al., 1968). In this case, meiosis is present, but “abnormal”. It may be preceded by a *premeiotic endomitosis* (Dawley and Bogart, 1989) or include an *endomeiosis* without separation of the two cells and followed by a gathering of the two chromosomal sets (Simon et al., 2003). This gathering may also concern two cells resulting from distinct meioses. These various *parasexual* (Pontecorvo, 1954) processes rely on several kinds of *metameioses* (Dubois, 2008a) followed by caryogamy. Depending upon the stage at which chromosomal duplication and caryogamy occur, the organisms resulting from automictic gametopoiesis may bear identical genomes (except for recent mutations) or not, but in the long run, in all cases, this reproductive mode tends to produce homozygous organisms (except for recent mutations) (Simon et al., 2003).

In both cases, *klonons* are entities composed exclusively of females. Genetic transmission within such *specions* is fully clonal (in all *mitoklonons* and some *meioklonons*), each daughter having the same genome as her mother (except for recent mutations), or *meroclinal* (Dubois, 2008a, 2009a), i.e., partially clonal, at least for some generations (in some *meioklonons*).

The entities composed exclusively of females reproducing only by parthenogenesis are not *mayrons*. Individuals do not pair to recombine their chromosomes and genes, and the only connection between them is from parents to offspring. These entities are however well characterised and delimited, being composed of organisms with a well-defined morphology, and sharing the same phylogenetic “macro-origin” (usually the hybridization between organisms belonging in two precise *mayrons*; see below), even if their “micro-origin” may be distinct (independent hybridization events between different individuals). All individuals of such entities have very similar genomes, modes of life and behaviour, they share the same habitat and have similar interactions with other organisms (predation, competition for resources and space, etc.). It is therefore justified to recognize these entities as taxa of nomenclatural rank species, and to name them.

All individual organisms reproducing by parthenogenesis do not deserve to be referred to *klonons*. In many animal species, exceptional cases of parthenogenesis occur. These cases of occasional or optional parthenogenesis, or *tychoparthenogenesis* (Suomalainen, 1950), may be at the origin of some parthenogenetic taxa (Kramer and Templeton, 2001), but by themselves they do not justify a special taxonomic status. More complex is the case of species whose “normal” life history involves temporary or cyclical phases of parthenogenetic reproduction, or in which some individuals (e.g., the members of one sex) are always produced by parthenogenesis. These phenomena do not challenge the existence of a gene flow between most of the individuals of the taxon. This gene flow is maintained because some or most individuals of these taxa have a normal meiosis followed by normal fertilization. This prevents the taxon from being a clone composed of almost

identical individuals, or even a hemiclone or meroclone (see below). In the long run, such taxa behave genetically as panmictic groups of individuals with genetic mixing and free recombination of alleles over generations, and they therefore remain *mayrons*. However, to point to the fact that not all specimens involved in the normal life cycle of such taxa have a normal reproductive pattern, these taxa can be referred to a category of *heteromayron* (from the Greek *heteros*, “other, different”), opposed to that of *eumayron* (from the greek *eu*, “well, properly, rightly”).

4.3. *Klepton*

This evolutionary situation was discovered much more recently than the two former ones, which may explain that few theoreticians of systematics really discussed its taxonomic treatment. However, here also the discovery in the last decades of many new cases requires one to take them into account. The entities concerned, called *kleptons* (Dubois and Günther, 1982), which all result from phenomena of hybridization between two *mayrons* (see below), are unable to maintain themselves alone in nature, as they need at each reproduction the intervention of individuals belonging in a distinct entity, usually a *mayron* (but sometimes another *klepton*). Such entities are known to exist in various groups of vertebrates and in a few groups of insects, bivalves and turbellarians (Dubois, 2008a, 2009b), but it is very likely that various other “strange” cases of transmission of characters or of composition of populations, which until now have defied the interpretations of geneticists and evolutionary biologists, are in fact examples of such phenomena. Three main categories of *kleptons* can be distinguished (Dubois, 1991, 2008a, 2009a).

Gynokleptons only include females. At each generation, the gametes they produce are not fertilized, but the start of their development is induced by sperm provided by a related *mayron* or *klepton* (gynogenesis). Genetic transmission within such *specions* is clonal, just like in *klonons*.

As for *zygokleptons*, which are composed either of females alone or of individuals of the two sexes, their peculiar meiosis produces gametes with a chromosomal complement inherited from only one of the two parental *mayrons* of the *klepton*. These gametes undergo normal fertilization with “normal” gametes produced by an individual of opposite sex belonging to a related *mayron* or *klepton*. In such cases, although fertilization and amphimixy occur, there is no panmixy in the population, as the possible genetic combinations are half-constrained. The hemigenome of one of the two parental *mayrons* is transmitted in a clonal way, without recombination, within the *klepton* (*hemiclinal* heredity), whereas the other hemigenome usually comes from a *mayron* and has therefore gone through the multiple standard recombinations that characterise panmictic entities. Such a reproductive mode has received the designation of *hybridogenesis* (Schultz, 1969), which poses problems that will be discussed below. More detailed descriptions of these phenomena are available (Dawley and Bogart, 1989; Dubois, 1977, 2008a).

A third category of kleptons was revealed quite recently, in North American salamanders (Bogart et al., 2007). In this group, various kinds of populations composed only of females display various levels of ploidy (from diploidy to pentaploidy) and various genome combinations originating from five ancestral *specions*. Genetic transmission in these populations is very complex (Dawley and Bogart, 1989). At each generation, the females transmit to their offspring a part only of their genome, sometimes half (hemigenome) and sometimes more (merogenome). Contrary to the situation in *zygokleptons*, no particular genome is transmitted in a constant and clonal or hemiclinal way by the females of a population. The fate of the ova of these females is variable. In some cases, genuine crosses occur with sympatric males belonging to other *mayrons* or *kleptons*, so that paternal hemigenomes are added to the maternal genome. In other cases, the sperm of the male is not incorporated into the ovum, so that gynogenesis occurs and the ovum develops only with the maternal genome. The occurrence, or not, of true fertilization with caryogamy in such crosses seems to be related to environmental factors, such as temperature (Bi et al., 2009). Such *tychokleptons* (Dubois, 2009a) combine features of both *gynokleptons* and *zygokleptons*. Their mode of heredity is *mero-clonal* (partially clonal).

4.4. Kyon

The taxonomic categories of *specion* discussed above (*mayron*, *klonon* and *klepton*) are *alternative eidonomic* categories that can be used for taxa all referred to the nomenclatural rank *species*. They are therefore not in a relation of hierarchisation or subordination. In some cases however, it may be useful to highlight the main opposition between two main kinds of *specions*, i.e., between *mayron*, the “classical mixiological species concept”, on the one hand, and *klonon* and *klepton* (with their subcategories) on the other hand. The latter situations show a great diversity. The term “unisexual” is sometimes used (Dawley and Bogart, 1989) as a general term to designate organisms with unusual reproductive modes. This term does not designate a taxonomic category and, furthermore, is sometimes employed in an improper way, in situations where both sexes are represented (Dawley and Bogart, 1989). It should not be used for the *formal designation of taxa*.

Dobzhansky (1970) proposed the general term *pseudospecies* for all *specions* having a parasexual or asexual reproductive mode, i.e., which do not behave as *mayrons* from the reproductive, genetic and evolutionary points of view. In order to avoid the root “species” and to have a shorter term, the term *kyon* was substituted for it (Dubois, 2008a). The main advantage of the taxonomic category *kyon*, which includes both categories *klonon* and *klepton*, is that it can be used provisionally, in case of uncertainty regarding the exact modes of gamete formation and of initiation of development in some organisms or populations that do not behave as *mayrons*, a rather frequent situation indeed. The two main categories of *kyons* include several subcategories that can be characterised by various particularities related to two basic features:

- the existence, or not, of two sexes, of panmixy, of reproductive independence and of sexual parasitism;
- the mode of heredity.

Until information is available on these features, it is impossible to know whether a recently discovered *kyon* is a *klepton* or a *klonon*.

It seems likely that still other categories of *kyons* remain to discover. This is suggested by the many cases of “strange species”, with “aberrant” genetic transmission of characters, that have long been known, but have not yet been studied in an appropriate way, and some of which only start being better understood (Loxdale and Lushai, 2003). Be that as it may, the existence of *kleptons* raises a major problem regarding the “generality” of the concept of *specion*, as these entities are by no way “independent lineages”.

5. Modes of formation of gametes (gametopoiesis)

Several modes of formation of gametes have been described in animals, some involving a normal or modified meiosis (with a reductional cell division), and some an ameiosis (consisting only of normal mitoses). For reasons given above, the term *gametopoiesis* is here used instead of the traditional term “gametogenesis”. The term *metameiosis* (Dubois, 2008a) designates any modified meiosis, i.e., any meiosis different from *eumeiosis* (Battaglia, 1945, 1955) as described in all treatises of biology. The term *metameiosis* is in no way descriptive but simply points to the presence of an “abnormal meiosis”, irrespective of its peculiarities.

The study of all the “strange species” mentioned above suggests that most, if not all, cases of natural *gametopoiesis* in animals may be referred, from the viewpoint of their results in terms of genetic complement of the gametes, to five main categories, very briefly characterised below but presented in more details elsewhere (Dubois, 2008a, 2009a). What is relevant and important here, in the frame of a reflection on the *taxonomy* of these entities, is not the cytological processes involved in the formation of gametes, but the genetic composition of the latter.

Mixopoiesis is the kind of *gametopoiesis* at work in most *mayrons*, but also in some *kyons*. It involves an *eumeiosis*.

In *phylactopoiesis*, the gametes produced are all diploid and contain a genome identical to that of the mother. This may be the result of two distinct *gametopoietic* pathways: ameiosis (in apomictic and some gynogenetic entities) or *metameiosis* (in some gynogenetic entities) (Dawley and Bogart, 1989; Simon et al., 2003).

Airetopoiesis concerns the taxa with automictic reproduction, the *metameiosis* of which involves an intracellular doubling of the parental chromosomal stocks, followed by a meiotic reduction and then by a fusion that produces diploid gametes. This results in both heterozygous and homozygous gametes, but in the long run the entity tends towards becoming homozygous (Simon et al., 2003).

Elasopoiesis occurs in some taxa of hybrid origins, the *kleptons*. Their *metameiosis* produces only “pure” gametes containing only chromosomes from one of the two parental *mayrons*.

Finally, in the recently discovered *tychopoiesis* (Bogart et al., 2007), the gametes produced contain one or several

hemigenomes of variable origins, either maternal or paternal. These gametes depend on sperm for the initiation of their development, but may, or may not, be fertilized, so that a great variability is observed in the offspring of any given female.

6. Modes of initiation of development (kinetogenesis)

Several modes of initiation of embryonic development in an ovum or *kinetogenesis* (Dubois, 2009b) exist, some only being known to occur spontaneously in nature.

Zygogenesis (Dubois, 1991; Pilger, 1989, 1997; Tomlinson, 1968) is the fertilization of an ovum by a sperm, producing a zygote. In this system, except for identical twins, each individual possesses its own assortment of chromosomes and genes.

Parthenogenesis is the development (either spontaneous or experimentally induced) of a virgin ovum without any contact with sperm. Apomixis concerns ova of phylactopoietic origin, whereas automixis occurs in ova of airtopoietic origin. The offspring of a parthenogenetic female may thus bear the same genetic complement as the mother, or not.

In *gynogenesis* (Wilson, 1925), the development of the ovum is initiated (either spontaneously or experimentally induced) by its contact with a sperm, but without incorporation of the genetic material of the latter into its nucleus. All the children of a female thus have the same genome.

In *androgenesis* (Verworn, 1891; Wilson, 1925), the development takes place only with the paternal chromosomes, after expulsion or destruction of the maternal chromosomes. Although rare, this phenomenon exists in nature in some animal groups (McKone and Halpern, 2003).

Two modes of kinetogenesis recently described can be designated as cases of *pseudozygogenesis* (Dubois, 2008a). In these cases, a *pseudozygote* is obtained by fusion of two gametes from one or several individuals of the same sex. In *corydogensis*, the fusion concerns two sperms introduced in an enucleated ovum, whereas in *lesbogenesis* the fusion is between two ova.

7. Patterns of speciation

The *specion* concepts that we considered above (*mayron*, *klonon* and *klepton*) underline the patterns of genetic flow within the entities examined or between them. This approach is not sufficient. It describes *specions* as static, fixed entities, and ignores the conditions of their appearance and evolution. In an evolutionary perspective, it must be completed by a dynamic approach of *specions* as historical entities. Here we will consider the *patterns of speciation*, i.e., the characteristics of the “birth” of a *specion* and its relationships with its ancestral *specion(s)*. In the discussion that follows, speciation is considered, by definition, as a phenomenon *unique* and *irreversible*, separating in a definitive way (but sometimes incompletely, in the cases of *kleptons*) two or more evolutionary entities.

Because its purpose is taxonomic, the following discussion is strictly targeted. It is not focused on the *modes* but on the *patterns* of speciation. The *speciation modes*, i.e., the *mechanisms* operating in the separation of entities,

can be classified according to the *geographic relationships* between the latter (allopatry, sympatry, etc.) or to the *biological mechanisms* (genetic, behavioural, etc.) involved. As concerns *speciation patterns*, they simply refer here to the *structure* of the phylogenetic relationships and of genetic transmission between the individuals and the lineages.

The patterns of speciation in the animal kingdom can be referred to three main categories (Dubois, 2009a). In *monogeny*, a *specion* is replaced in nature by another one; in *diplogeny*, a *specion* gives birth to two distinct *specions*; and in *mixogeny*, a new *specion* is produced through hybridization between two, or more, *specions*. These three patterns of speciation were reviewed in detail elsewhere (Dubois, 2009a) and are only briefly presented below.

7.1. Speciation by monogeny

In monogenic speciation, the two entities are not contemporaneous but successive. A *specion* replaces another one, so that speciation is concomitant with the extinction of the ancestral *specion*. Two main distinct kinds of speciation by monogeny may be recognized.

Speciation by *anageny* corresponds to the classical speciation pattern by “gradual change” through genetic drift within a single lineage. Although this speciation pattern is mentioned in many books on evolution, mostly by paleontologists, our current knowledge in population biology suggests that it cannot be very widespread. In demes of large size, homeostatic mechanisms make genetic drift much more difficult than in small populations.

In contrast, speciation by *stenogeny* requires survival to a demographic “bottleneck”, i.e., a population reduced to a few individuals. These only bear a randomly impoverished sample of the genetic pool of the *mayron* from which they originated. These conditions are favourable to “genetic revolution” and “founder effect” (Dubois, 1988; Mayr, 1954). In such small-sized founder populations, genetic drift may be a powerful factor responsible for rapid speciation.

7.2. Speciation by diplogeny

Speciation by *diplogeny* occurs whenever two *specions* succeed to a single *specion*. This happens in two widely distinct situations, *schizogeny* and *blastogeny* (Dubois, 2009a).

Speciation by *schizogeny* corresponds to the splitting of an original *specion* into two new *specions*, e.g., after instauration of a geographic discontinuity between two groups of populations. This is the classical Hennigian concept of speciation by “cladogenesis”.

Speciation by *blastogeny* or “budding” (Donoghue, 1985) corresponds to the case where a small group of members of a *mayron* is isolated from all other populations of the latter, and cannot interact genetically with their individuals any more. This isolated “founder population” is then in conditions similar to those mentioned above for speciation *stenogeny*. It may then give birth to a new *mayron*, whereas the initial *mayron* continues to exist. Speciation by *blastogeny* does not really consist in the “subdivision” of a *specion* in two. Just like in the case of the reproduction of an organism, which usually does not die when its offspring appears, the original *specion* persists, and gives birth “lat-

erally” to a new *specion*, with which it does not interfere any more, except in case of secondary disappearance of the barriers that separate them.

In both cases of speciation by diplogeny, the two entities are contemporaneous (at least for a while). They are initially separated geographically, but may later on come again in contact. It is then possible to study the dynamics of their interactions, in some cases with appearance of a hybrid zone, a situation that we will tackle below. Speciation by diplogeny corresponds to the majority of speciations studied by biologists. If in paleontology speciation by monogeny seems more frequent, this is most likely due to the very incomplete nature of fossil documentation: what appears to us today to be a unique lineage in which *specions* succeed to each other consisted in fact most probably in many cases in an arborescence, a few branches of which only have left fossils that we found.

7.3. Speciation by mixogeny

In speciation by *mixogeny*, new entities are created by hybridization between two distinct *specions*. This phenomenon was sometimes called *hybridogenesis* in botany (Mattfeld, 1930) or zoology (Darevsky et al., 1989), but this term is confusing because of the existence of its homonym *hybridogenesis* in the sense of Schultz (1969) (see above and below).

In mixogeny, two previously geographically separated *mayrons* hybridize when they come again in contact. The hybrids give birth to a new entity of its own, whereas the two parental *specions* continue their independent existence. Here also, several different situations can be distinguished. In order to understand them better, it is necessary to come back to general questions related to interspecific hybridization in animals, their evolutionary meaning and taxonomic interpretation.

A crucial distinction must first be made between *hybrid individuals* as such and *taxa of hybrid origin*. As we have seen, the concept of *mayron* is a *naturalist* concept. *Mayrons* are sets of animals between which gene flow in nature is non-existent or very reduced or insignificant, whatever the causes responsible for this absence or restriction of gene flow may be (Dubois, 1988). The data on interspecific hybridization in nature are precious for the establishment of the specific taxonomy of a group. These facts are of a great diversity and can be considered in three major situations:

- isolated cases of hybridization;
- hybrid zones;
- taxa of hybrid origin.

7.3.1. Isolated hybrids and hybrid zones

Two animal species that normally do not hybridize may do so in exceptional conditions. Often their hybrids will not live long, or will not succeed in finding partners and producing offspring. Such individual hybrids do not deserve special taxonomic recognition.

Hybrid zones, which are rather common in zoology, correspond to a different situation. In such cases, two biological entities of common origin have been separated geographically for a while. During the separation period,

they may have diverged only slightly, in various characters. When they come in contact again, if they have remained genetically compatible they may hybridize in the zone of sympatry. Several kinds of hybrid zones may be distinguished (e.g., Bocquet et al., 1976, 1977, 1980; Short, 1969; White, 1978). A thorough bibliographic survey and a synthesis of the data and ideas on these peculiar situations are available (Bernardi, 1956, 1957, 1980; Haffer, 1986). The wide variety of situations observed in hybrid zones can be accounted for by the recognition of several distinct taxonomic categories of nomenclatural rank species (such as *quasimayron*, *vicemayron* and *promayron*) or subspecies (*submayron*) (Dubois, 2009a). These situations correspond to successive *evolutionary stages* in the process of speciation by diplogeny, which lead either to the separation of two distinct *mayrons*, or to reunification of the two entities as a single *mayron*.

Besides reunification as a single gene pool and ultimately complete separation as two distinct *mayrons*, a third possibility exists when two entities of common origin meet again in nature. In such cases, genetic divergence between them during their separation has touched the complex mechanisms of genetic regulation of meiosis, mitosis or caryogamy. When hybrids are produced between such entities, they may be confronted to perturbations in their mechanisms of gametopoiesis and/or karyogenesis. Even if for most of them we do not yet know their intimate mode of functioning, we now know that these phenomena do occur, and are not that rare, as we observe their consequences in some mixogenic speciations that we will now consider.

7.3.2. Allopolyploidisation

Natural polyploidy has been known for a very long time in plants, but long considered virtually impossible in nature in animals because of the so-called “Müller’s rule” (Müller, 1925), until a few researchers started surveying natural populations for ploidy. Numerous cases of allopolyploid (mostly allotetraploid) entities were then discovered and studied, particularly in the vertebrates and insects (Bogart et al., 2007; Dawley and Bogart, 1989; Loxdale and Lushai, 2003; Stöck et al., 2010). In some cases, when they meet again, two formerly separated entities give birth to hybrids whose perturbed meiosis produces unreduced diploid gametes with a haploid chromosome set from each parent. Allotetraploid individuals may then be produced by fusion of two such gametes. When pairing, allotetraploids of both sexes may then give birth, in a single generation, to a new *mayron* the members of which will not produce a viable and fertile descent with any individual of their parental diploid *mayrons*. In other cases, the appearance of polyploidy does not seem to be immediate, but follows an intermediate stage through a *klonon* or *klepton* (Bogart and Wasserman, 1972; Dubois, 1977). Allotetraploid *mayrons* include individuals of both sexes and behave genetically as normal *mayrons*, with a random distribution of chromosomes in gametes and random fertilization of gametes in panmictic populations. They therefore are “just” *eumayrons*, and do not deserve any particular taxonomic treatment.

Although most natural polyploids known so far in animals are tetraploids, a few of them have other ploidies. Pure

triploid animal populations composed of specimens of both sexes and using zygogenesis at each generation were long believed to be impossible, until their discovery in some populations of toads (Stöck et al., 2002, 2005, 2010). The maintenance of pure triploids populations is made possible in these cases by the existence of unusual meiotic pathways, sometimes different in the two sexes. In such all-triploid entities, random recombinations and distribution of chromosomes and genes occur in some individuals only. Clonal transmission of chromosomes without recombination occurs in some individuals but, sooner or later, genetic mixing occurs for all chromosomes and genes. In the long run, these entities behave as *mayrons*, just like for the *specions* having an alternation of parthenogenetic and zygogenetic generations mentioned above. In this case also, it is relevant to point to the fact that the individuals of such entities show unusual meiotic pathways, by referring them to the taxonomic category of *heteromayron*.

7.3.3. *Klonophore mixogeny*

The perturbations of gametopoiesis and kinetogenesis in entities of hybrid origin can be stronger than in allopolyploid *mayrons*. In some cases, the gametopoiesis of hybrid females goes through an ameiosis and produces unreduced gametes, that may develop spontaneously, without fertilization. These females reproduce parthenogenetically over generations and transmit their genome in a clonal way. Taxonomically, this situation is that of *klonon*, and this category of mixogeny qualifies as *klonophore* (Dubois, 2009a). As we have seen, two different categories of *specions* can result from klonophore mixogeny (Dubois, 1991, 2008a), corresponding to two categories of perturbation of gametopoiesis (airetopoietic metameiosis and phylactopoietic ameiosis).

7.3.4. *Kleptophore mixogeny*

Hybridization between two *mayrons* put again in contact after a period of separation can result in other kinds of perturbations of meiosis. *Kleptophore mixogeny* (Dubois, 2009a) gives birth to *kleptons* (Dubois and Günther, 1982). As we have seen, three taxonomic subcategories of *kleptons* may be distinguished (Dubois, 1991, 2008a, 2009a).

The category of *gynoklepton* corresponds to a situation, which reminds that of *mitoklonon* by its modes of gametopoiesis (ameiosis or phylactopoietic metameiosis) and by the clonal transmission of the genome from the mother to her daughter. It differs from it however by a crucial element: such entities are not “independent lineages”, as they require, for their reproduction and therefore for their perennality, at each generation and for the initiation of the development of each ovum, the intervention of a sperm provided by a male of a sympatric *mayron*. This sperm is not incorporated into the ovum, but stimulates the beginning of the process of divisions by which the ontogenesis starts (gynogenetic kinetogenesis).

The category of *zygoklepton* differs from the preceding one both by its gametopoiesis (elasopoietic metameiosis) and by its kinetogenesis (zygogenesis). Several cytological mechanisms may be responsible for the production of “pure” monoparental gametes, including premeiotic exclusion of one of the parental hemigenomes, followed by an

endoduplication of the remaining hemigenome (Graf and Polls Pelaz, 1989). These entities are not “independent lineages”, as they also require sperm for their kinetogenesis. This sperm may be provided either by a male of a sympatric *mayron*, or sometimes, in more complex situations, of another *klepton* (Polls Pelaz, 1991, 1994).

Finally, the category of *tychoklepton*, still only partially understood, provides a still more complex pattern, as it combines features of both *gynoklepton* and *zygoklepton*, thus stressing that these are just different modalities of a general situation (Dubois, 1991, 2008a, 2009a; Dubois and Günther, 1982). In this system, up to five different initial *mayrons* may be involved in the origin of some populations, and a high variety of genomic compositions exist, with ploidies ranging from diploidy to pentaploidy (Bogart et al., 2007). This complexity is due to the fact that in such a system several different mechanisms may be at stake both during gametopoiesis and kinetogenesis. According to the individuals and the conditions, gametopoiesis may combine characters of phylactopoesis and elasopoiesis. Similarly, kinetogenesis may occur either by gynogenesis or by zygogenesis.

8. Discussion and conclusion

Tables 1 and 2 give the main evolutionary, genetic and reproductive characteristics of the eidonomic categories (categories of *specions*) presented above.

The main category, to which is most generally applied the “species concept”, is the “mixiological species”, or BSC, here termed *mayron*. *Mayrons* are usually panmictic bisexual entities, with complete eumeiosis and ovum fertilization, and therefore a complete reproductive independence from all other *specions* and a non-clonal heredity with recombination between parental genomes at each generation. Except for identical twins, each individual of such an entity possesses its own genetic identity, no two individuals having the same genome. It is not necessary that all the individuals of a *mayron* have the reproductive mode summarised above for the taxon to be referred to this taxonomic category. This reproductive mode may be “dormant” for one or a few generations or absent in some individuals without challenging the fact that the entity in which they belong is bisexual and (on the whole, and sometimes virtually) panmictic. For example, the taxa with facultative or cyclical parthenogenesis include individuals that may reproduce without ovum fertilization, but these events are not at the origin of real clones, as their descendents, sooner or later, take part again in bisexual reproduction and therefore in a redistribution of chromosomes and genes. Even in very particular cases like some all-triploid taxa mentioned above, the existence of metameiosis in some individuals is associated with eumeiosis in other individuals, so that, in the long run, genetic mixing occurs. These entities, in which panmixy exists only over several generations, should be referred to the taxonomic category of *mayron*, although in the subcategory of *heteromayron*.

Although several other eidonomic categories were recognized above (*klonon*, with two subcategories, and *klepton*, with three subcategories), the main opposition is

Table 1

Main genetic and reproductive characteristics of seven eidonomic categories (*specions*) of nomenclatural rank *species* recognized here in zoology (see text for details). More detailed lists of higher taxa of metazoa in which taxa referred to these categories are currently known to be present are available elsewhere (Bogart et al., 2007; Normark et al., 2003; Scali et al., 2003; Simon et al., 2003; Vrijenhoek et al., 1989). The abbreviations given in the headings of columns are those, which when placed between the generic substantive and the specific epithet, designate the eidonomic category in the nomen of any taxon referred to this category (Dubois, 1991, 2008a, 2008b; Dubois and Günther, 1982).

Tableau 1

Principales caractéristiques génétiques et reproductives de sept catégories éidoniques (*spécions*) de rang nomenclatural *espèce*, reconnues ici en zoologie (voir le texte pour plus de détails). On trouvera ailleurs (Bogart et al., 2007; Normark et al., 2003; Scali et al., 2003; Simon et al., 2003; Vrijenhoek et al., 1989) des listes plus détaillées de taxons supérieurs de métazoaires, au sein desquels des taxons rapportés à ces catégories sont actuellement connus. Les abréviations qui figurent en tête des colonnes sont celles qui, placées entre le substantif générique et l'épithète spécifique, désignent la catégorie éidonique au sein du nomen de tout taxon rapporté à cette catégorie (Dubois, 1991, 2008a, 2008b; Dubois and Günther, 1982).

Eidonomic category	Mayron (m.)		Kyon (k.)				
	Eumayron (em.)	Heteromayron (hm.)	Klepton (kl.)			Klonon (kn.)	
			Zygoklepton (zykl.)	Tychoklepton (tykl.)	Gynoklepton (gykl.)	Meioklonon (mekn.)	Mitoklonon (mikn.)
Higher taxa of metazoa in which taxa of this category are known	Animalia	Crustacea, Insecta, Mollusca, Platyhelmintha, Vertebrata	Anura, Phasmatoptera, Teleostei	Urodela	Bivalvia, Lepidoptera, Teleostei, Turbellaria	Anostraca, Lepidoptera, Squamata	Anostraca, Bdelloidea, Cladocera, Coleoptera, Gastropoda, Homoptera, Hymenoptera, Isopoda, Oligochaeta, Orthoptera, Ostracoda, Phasmatoptera
Main speciation patterns	Monogeny, diplogeny or mixogeny	Monogeny, diplogeny or mixogeny	Mixogeny	Mixogeny	Mixogeny	Mixogeny	Mixogeny
Gametopoiesis: mechanism > result	Eumeiosis > mixopoiesis	Eumeiosis, metameiosis or ameiosis > mixopoiesis or phylactopoiesis	Metameiosis > elasopoiesis	Metameiosis > tychoipoiesis	Ameiosis or metameiosis > phylactopoiesis	Metameiosis > airetopoiesis	Ameiosis > phylactopoiesis, or absence of gametopoiesis (vegetative multiplication)
Kinetogenesis	Zygogenesis	Zygogenesis, gynogenesis or parthenogenesis	Zygogenesis	Zygogenesis or gynogenesis	Gynogenesis	Parthenogenesis	Parthenogenesis or absence of gametopoiesis (vegetative multiplication)
Sexes present	♂ + ♀	♂ + ♀	♀ or ♂ + ♀	♀	♀	♀	♀
Free crosses between the members of the taxon	Yes	Yes or no	No	No	No	No	No
Reproductive mode	Sexual	Sexual	Sexual	Sexual or parasexual	Parasexual	Parasexual	Asexual
Intervention of sperm required for reproduction	Yes	Yes or no	Yes	Yes	Yes	No	No
Sexual parasitism of another <i>specion</i> required for reproduction	No	No	Yes	Yes	Yes	No	No
Reproductive independence	Yes	Yes	No	No	No	Yes	Yes
Mode of heredity	Non-clonal (recombinations between parental genomes at each generation)	Non-clonal (recombinations between parental genomes over several generations)	Hemiclonal (clonal heredity of one of the two parental hemigenomes)	Meroclonal (clonal heredity of part of the maternal genome)	Clonal	Clonal or meroclonal (clonal heredity of part of the maternal genome)	Clonal

Table 2

Main genetic characteristics of five eidonomic categories (*specions*) here recognized in zoology (see text for details). The table gives the genomes of the parents (adults of generation G1), of their gametes (of generation G1) and of their descendants (ova or adults of generation G2). The letters and numbers (A1, A2, B1, etc.) represent the genomes (chromosomal and genic complements) of the individuals or gametes. Different letters point to different initial parental species for the taxa issued from interspecific hybridizations (*kleptons* and *klonons*). The numbers that follow them show different chromosomal and genic composition of the gametes, with presence (different numbers: A1 > A5) or absence (same number: A1 > A1) of a modification of this composition in G1 adults relatively to the genomes received from their own parents of generation G0. In the latter case, clonal transmission of this part of the genome is involved. The presence of a genome between square brackets, [C3], indicates that it is not incorporated in the genome of the descendant. A dash – indicates the absence of intervention of males in reproduction. Two categories of *specions* mentioned in the text (heteromayron and tychoklepton) are not shown in this table, as they are heterogeneous categories that cover varieties of situations. Despite their diversity, all heteromayrons have in common that they: (1) include specimens with different gametopoieses and kinetogeneses; and (2) show recombinations between parental genomes over several generations, so that, in the long run, their heredity is not clonal. Tychokleptons also show a variety of gametopoieses and kinetogeneses, but their heredity is meroclonal (see text for details).

Tableau 2

Principales caractéristiques génétiques de cinq catégories éidoniques (*spécions*), reconnues ici en zoologie (voir le texte pour plus de détails). Le tableau donne les génomes des parents (adultes de génération G1), de leurs gamètes (de génération G1) et de leurs descendants (œufs de génération G2). Les lettres et nombres (A1, A2, B1, etc.) représentent les génomes (compléments chromosomiques et géniques) des individus ou gamètes. Des lettres différentes indiquent l'existence d'espèces parentales différentes pour les taxons issus d'hybridation interspécifique (*kleptons* et *klonons*). Les nombres qui les suivent indiquent des compositions chromosomiques et géniques différentes des gamètes, avec intervention (nombres différents : A1 > A5) ou non (même nombre : A1 > A1) d'une modification de cette composition chez les adultes G1, par rapport aux génomes reçus de leurs propres parents de génération G0. Dans ce dernier cas, cette partie du génome est transmise clonalement. La présence d'un génome entre crochets, [C3], indique que celui-ci n'est pas incorporé dans le génome du descendant. Un tiret – indique l'absence d'intervention de mâles dans la reproduction. Deux catégories de *spécions* mentionnées dans le texte (hétéromayron et tychoklepton) ne figurent pas dans ce tableau, car il s'agit de catégories hétérogènes regroupant chacune plusieurs situations. Malgré leur diversité, tous les hétéromayrons ont en commun (1) de comporter des spécimens ayant différentes gamétopoièses et kinétogénèses, et (2) de manifester des recombinaisons entre génomes parentaux sur plusieurs générations, de telle manière que, à long terme, leur hérédité n'est pas clonale. Les tychokleptons ont également diverses modalités de gamétopoièse et de kinétogénèse, mais leur hérédité est méroclonale (voir le texte pour plus de détails).

Taxonomic category	Parents (G1)		Gametes (G1)		Descendant (G2)
	Parent ♀	Parent ♂	Gamete ♀	Gamete ♂	
Eumayron	A1/A2	A3/A4	A5	A6	A5/A6
Zygoklepton	A1/B1	B2/B3	A1	B4	A1/B4
Gynoklepton	A1/B1	C1/C2	A1/B1	[C3]	A1/B1
Meioklonon	A1/B1	–	A1/A1 or A1/B1 or B1/B1	–	A1/A1 or A1/B1 or B1/B1
Mitoklonon	A1/B1	–	A1/B1	–	A1/B1

between *mayron* and all the other categories, which may be united under the common designation of *kyon*. *Specions* of this second group are probably much less numerous in nature than those of the first one. They show very diverse characteristics which challenge generalisation. They will most likely have to be complemented by a few other very rare or still not understood situations which will probably deserve the creation of other eidonomic categories – in particular, entities with androgenetic and corydogenetic kinetogeneses (see above). According to the information currently available (Loxdale and Lushai, 2003), these entities are all of hybrid origin, but they all persist over long periods in nature, contrary to “normal hybrids”.

As a matter of fact, and contrary to what was long believed by evolutionary biologists, all these “particular cases” are not “evolutionary dead ends” bound to rapid extinction. Despite the fact that some of them depend on sympatric *mayrons* for their reproduction, they may perpetuate themselves over millions of generations (Bi et al., 2009; Bogart et al., 2007). In some particular conditions (e.g., small isolated populations of *klonons* of lizards and snakes on very small islands), *kyons* are advantaged compared to bisexual *mayrons*. Some *kleptons* clearly show heterosis compared to their parental *specions*. However, they may not replace them completely in nature because they need them for their reproduction and perpetuation, so that an equilibrium must be found that allows the maintenance of both taxa in sympatry, except in some cases involving polyploidy where some members of the synkleptic complex can provide sperm and allow elimination of

the parental species from some populations (Bogart et al., 2007; Polls Pelaz, 1991, 1994). Moreover, in some cases, it is likely that *kyons* can be at the origin of allopolyploid *mayrons*, thus so to speak “restoring” a “normal” situation after an intermediate “abnormal” stage (Dubois, 1977). All these questions, and many others (concerning behaviour, ecology, competition, selection, etc.) are of great interest for evolutionary biologists, so that, although unusual, these “strange species” deserve close attention.

As for *mayrons*, although they are the “normal” situation for many animals, this should not obscure the fact that intermediate and temporary situation are not uncommon. Categories like *submayron*, *quasimayron*, *vicemayron* and *promayron* testify to the fact that *specions* are not eternal “essences”, corresponding to a “type” and to characters given once and for all, but living, evolutionary entities, the fate of which is not written in advance but will depend on the conditions of environment, of competition and other interspecific relationships. In other words they are changing entities in the permanent dynamics of evolution.

These taxonomic categories are no doubt simplifications of the real evolutionary situations, which all have their own particularities, but they provide a rather rich and diversified frame of reference for such situations, which allows to account rather finely for their main features.

The approach presented here is quite different from that adopted by many contemporaneous authors who showed interest in the “species problem”. Most of them were clearly obsessed by the search at all costs of a “unified species concept”, allowing one to account altogether for all situa-

tions observed in nature. This search seems to take its roots in philosophical convictions tied to a reductionist conception of science, according to which, as stated by Aristotle, science only deals with universal concepts. This formula applies to non-historical sciences like physics or mathematics but not to the study of organic evolution. There exists no theoretical reason why all animal organisms in the world should be referred to a single kind of evolutionary unit or “brick of evolution”. The analysis presented above shows that nature is richer than our a priori expectations. To account for the observed facts, it is necessary to recognize several eidonomic categories of “bricks of evolution” or *specions*. These major categories are alternative, that is, they are not reducible or infeodated to each other. These different evolutionary situations (and most probably others) exist “in parallel” in nature, and the role of evolutionary biology and taxonomy is to identify them, through a fine analysis of their concrete particularities, rather than starting from general and reductionist “models”.

The requirement for a “unified species concept” results in a considerable impoverishment, in an abusive simplification of the situations observed. Given the diversity and richness of real evolutionary situations, and the incompleteness of the data we have on many organisms (in particular fossils), for which we lack information on gene flow and the dynamics of hybrid zones, the only “unified species concept” that could be implemented would be the “smallest common denominator” to all situations, and the only possible species concept would be that of *simpson*. This concept is misleading, as it would lead us in certain cases to treat as two “species” two groups of individuals geographically isolated, even if this isolation is of short duration and has entailed no evolutionary divergence between these two groups, which remain able to hybridize freely, with unrestricted bidirectional gene flow between them, if they come in contact again. Besides, the use of this unique species concept in all situations results in important information losses, for two distinct reasons.

The first reason is that this concept does not account for some evolutionary situations (the *kleptons*), where a well-individualised but partial lineage depends for its perpetuation of the intervention at each generation of a sympatric bisexual entity. This *mayron* would not be threatened with extinction if the *klepton* was to disappear. There exists therefore no *mutual* dependence between a *mayron* and its associated *klepton*. The *mayron* is indeed an “independent lineage”, but the *klepton* is a “half-lineage” that is dependent from the *mayron*. There is a *formal* way to solve this problem in order to try and “save” the “unified species concept”: it is simply to negate the existence of these peculiar entities, and to include formally each *klepton* into the *mayron* that permits its reproduction and perpetuation, despite the fact that the two forms are fully distinct genetically, cytogenetically, morphologically, ethologically, bioacoustically and ecologically, may have existed as such for millions years, and may have distributions covering a whole continent, where they play fully different roles in the ecosystems (Dubois, 1977, 2008a; Dubois and Günther, 1982; Graf and Polls Pelaz, 1989). For example, some authors (Frost and Hillis, 1990) considered that from a taxonomic point of view the entities

that transmit a hemigenome from generation to generation in a hemiclonal way (*zygokleptons*) do not deserve to be treated as taxa of their own, just like the males of organisms bearing a heterochromosome Y do not belong in a *specion* different from that of the females having an XX genome! However, comparisons may be misleading, and this one is fully inadequate: males and females of all *mayrons* having a chromosomal sex determinism cannot breed and therefore subsist without each other, they are in a situation of mutual dependence! If our aim is to found eidonomy, the “science of species”, not on a priori general models and theories, but on observations of the real characteristics of natural entities, we need a peculiar category for those which depend, at each generation, on gametes provided by another, more “normal”, entity.

Ignoring generally the case of *kleptons*, the supporters of the *simpson* concept claim that it accounts for the evolutionary situation of *klonons* as well as of *mayrons*, both kinds of entities being qualified by them as “independent lineages”. There is however a difficulty here, as the meaning of the term “independent” is unclear in this context. It cannot mean the absence of etho-ecological interactions, as these are frequent between sympatric *specions*, especially when they have the same origin, and it must therefore mean that there are no *genetic* interactions between individuals belonging to distinct *specions* – which in return means that such interactions do exist *within* a *specion*. Then, if this is indeed the case for *mayrons*, it is not true for *klonons*. In the latter, the only genetic link is vertically from parent to offspring, but never horizontally between individuals of the same generation. In these conditions, what should be considered to constitute an “independent lineage”? Is this the group of all individuals having the same genome, before mutations have appeared? Such an interpretation would be a return to an essentialistic, typological conception of lineages and of taxonomy. If the *specion* is understood literally as an independent lineage, any distinct founder event must be interpreted as the origin of a new lineage, and therefore as a distinct taxon. From a purely formal point of view, every time a female gives birth by parthenogenesis to two daughters, at least one new lineage appears, independent from the other parallel lineage, even if it possesses exactly the same genome. Should we then recognize each of these lineages as a distinct *specion*? As it would doubtless appear absurd to recognize then two “species”, even the supporters of the “unified species concept” acknowledge that in this case the two “sub-lineages” must be considered to belong in the same taxon, but then they are obliged to modify their definition of “independent evolutionary lineage” and to write such vague statements as: “*species-level lineages in asexual organisms, if they exist at all, must result from processes other than reproduction*” (de Queiroz, 1998).

The solution to this problem requires one to take in consideration the founder event of the parthenogenetic lineage. Of course, a single founder event may be enough to start a *klonon*, but in cases of contact between two *mayrons* in a rather wide zone, it is not rare to observe several distinct events of hybridization. The different parthenogenetic lineages thus initiated are definitely isolated from each other from a genetic point of view. However, it would be fully irrelevant and impracticable to recognize each of

them as a distinct taxon. Such a hyper-analytical approach would not bring an appropriate tool to all users of taxonomic data, many of whom are neither taxonomists, nor phylogeneticists, nor geneticists. Although some “purists” of evolutionary or cladistic thinking tend sometimes to forget it, taxonomy is not meant only for themselves, but has among its main functions that of providing a tool to all biologists interested in biodiversity. This tool must be efficient and rigorous, but of clear and easy use. To recognize in a purely formal way such countless taxa, virtually identical in most respects, for the only sake of respecting an a priori theoretical decision, would not do a service to these users and would contribute to a bad image of taxonomy among biological sciences. The genomes of all individuals of the different parthenogenetic lineages resulting from distinct phenomena of hybridization between the same two parental *mayrons* result from different combinations of genomes originating from the same two initial gene pools. These individuals therefore share the same global genetic pool, and they have most similar behaviours, ecologies and habitats. Although they do not recombine their genomes to produce a common descent, they belong in a single evolutionary entity, which occupies a peculiar ecological niche in the ecosystem, and they must be referred to the same *klonon*.

A similar situation exists in viruses, in which genetic transmission is also clonal and all individuals genetically very similar, although not identical, because of the frequent occurrence of new mutations. The definition of the species category in virology adopted by the International Committee on Taxonomy of Viruses reads as follows: “a virus species is a polythetic class of viruses that constitute a replicating lineage and occupy a particular ecological niche” (Pringle, 1991; Van Regenmortel, 2007, 2010). This concept is equivalent to that of *klonon* as recognized here for parthenogenetic animals, although different in the details due to the many differences between viruses and metazoa.

The second reason why the generalisation of the use of the concept of *simpson* to all species results in an important loss of information is that it discourages taxonomists to pay close attention to the fine particularities of the evolutionary situations surrounding speciation in the cases of hybrid zones. Whereas during the 20th century many evolutionary biologists had worked on the characterisation of these situations, to the elaboration of concepts and criteria allowing their detailed eidonomic treatment, the “all-cladistic” approach currently dominating invites taxonomists to abandon these fine analyses, to replace them by brutal and schematic affirmations such as “as soon as there are hybrids, we are inside the same species” (Samadi and Barberousse, 2006) or “as soon as two groups of individuals are geographically separated, they are distinct species” (de Queiroz, 1998). Such rigid and purely formal approaches are at variance with the whole tradition of zootaxonomy and “redefine” drastically the terms “hybrid” and “species” in a very confusing way. They do not encourage biologists to study the concrete features of the situations of speciation, although these constitute an irreplaceable mine of information on the reality of speciation and on evolution in progress (Dubois, 2008b). This reality is more complex and difficult to analyse, understand

and translate in taxonomic terms than as suggested by these reductionist approaches. The taxonomic categories presented above, even if they are more complex than any “unified species concept”, remain nevertheless simplifications and generalisations, particularly as concerns all the situations here gathered in a partly artificial manner in the heterogeneous category of *kyon*.

A final difficulty with the *simpson* concept as an “independent lineage” is that it does not provide any clue for distinguishing *simpsons* from all other more inclusive taxa or “clades”, which are also cladistically defined as “independent lineages”. The idea that the latter would be “multiple lineages” and the former “single lineages” (de Queiroz, 1998) does not hold, because no clear and operational definition of “multiple lineage” is available, as we have seen above in the case of *klonons*.

The concept of *mayron* doubtless corresponds to a real situation in nature, but concretely, in many cases, the data are insufficient to identify *mayrons* with certainty, and the operational difficulties of the concept are real. Although theoretically well supported, it poses real problems of implementation in many concrete situations, as it can be tested only within a unit of time and place. It is a strong stimulation for the deepening of works on the structure and dynamics of hybrid zones or on the study of the status of allopatric entities deriving from a single ancestral species, for which it is often impossible to know whether in nature a reciprocal gene flow would establish if they came in contact again.

Two entities, which never breed together in nature can do it in captivity or in perturbed ecological conditions. The situation can then be clearly interpreted only in one case, when repeated crosses between the two entities have proved sterile: then, it can be quite safely concluded that the two entities are two distinct *mayrons*. But the reverse is not true, as this *relational criterion* (Dubois, 1988) or *relacter* (Dubois, 2004) is not symmetrical (Dubois, 1977, 1988, 1998). If artificial crosses produce viable and fertile offspring, other criteria will have to be used, as the *mayron* concept is a *naturalist concept*, which applies and is meaningful only in nature. From the viewpoint of the *mayron* concept, it is only the dynamic reply in nature to the restoration of the contact between the two entities which allows a clear interpretation. What happens then in a contact zone is directly correlated neither with morphological resemblance nor with genetic similarity. The so-called “genetic distances”, either measured by the traditional methods of protein electrophoresis or through nucleic acid sequencing (including through “barcode” approaches), do not allow to predict what would occur in case of restored parapatry or sympatry. In all cases where we observe in nature isolated hybrids or hybrid zones between two entities, the relevant question is whether there exists a reciprocal gene flow between them or whether this gene flow is unidirectional, towards the hybrid zone where it “falls” like in a “black hole” from which no gene flow returns towards the two parental entities. In many cases, reliable replies to these questions are difficult to obtain for lack of data.

Because of the difficulties in the use of the *mayron* concept in allopatry, it is often necessary in such cases to do

with a default solution. A usual practice (e.g., in “barcode” approaches) is to call on *inference*, i.e., on comparisons. If entities separated by a certain degree of divergence behave in sympatry as distinct *mayrons* (absence of significant gene flow between them), it is acceptable, in the absence of contradictory evidence, to consider that other entities in the same taxonomic group showing a similar degree of divergence are also distinct *mayrons*. Another solution may be through the “temporary” use (that in some cases may last long) of other concepts of *specion*, particularly that of *simpson*, which is of simple use although it has a limited biological meaning.

Such solutions are certainly not “ideal”. Should these difficulties lead us to reject the concept of *mayron* as “non-operational”? Certainly not. Science does not always progress in a straight line, from certainties to certainties. In many cases, leaving some questions open, instead of closing them artificially by declaring that they do not exist, may be an important stimulating factor for a deepening and improvement of research. The differentiated use of more or less “precise” concepts according to the available information is rather frequent in science and has nothing shocking. Let us consider another example. Nowadays, the phylogeny and higher taxonomy of vertebrates is more and more based on phylogenetic analyses relying on nucleic acid sequences, combined with studies bearing on large numbers of characters obtained from morphology, cytogenetics, etc. But when one turns to fossil vertebrates, almost none of these pieces of information is available: we cannot study their soft parts, their chromosomes, their behaviour or, except in rare cases, their nucleic acids, so that most of the taxonomy of these organisms must rely on information obtained from the study of their skeleton. In order to build a “unified taxonomy” of all vertebrates, including both fossil and living taxa, should we then use their “smallest common denominator”, that is, should we base all the systematics of vertebrates on the characters of their most often fossilised parts, their skeleton? This would be absurd. We use as much information as available in all cases, and when information is missing we do what we can with the available data.

The same applies to eidonomy. Like in all other scientific domains, the use of the “smallest common denominator” would entail a loss, sometimes gigantic, of information. In concrete science, eidonomists make use of as much information as possible, i.e., more or less according to the situation. It is sometimes possible, when reliable and detailed data are available on a bisexual entity, to use correctly the category of *mayron*. In other cases, data are wanting and this is impossible. It is then appropriate, at least in a provisional way, to use inference approximations, or to appeal to the category of *simpson*, even if this interpretation may later have to change when new data are obtained. The same applies when biologists discover in nature an entity having abnormal biological characteristics, such as being constituted only of females. This information, if it is reliable, shows that this entity cannot be a *mayron*, but does not tell us, by itself, if it is a *klonon* or a *klepton*. As long as complementary data are unavailable, it is advisable to treat this entity simply as a *kyon*.

The arguments presented above against the “unified species concept” apply only, let us stress it again, to the concept of “species as a taxonomic category” or *specion*, but not to the nomenclatural rank *species*. In order to play fully its function of universal communication about living organisms, usable both within biology and outside of it, it is indispensable that a single nomenclatural hierarchy be used for the whole animal kingdom, independently from the taxonomic theories adopted by the authors (Dubois, 2005, 2007, 2008a). The nomenclatural rank *species* is crucial for the whole biology, and each living organism must be referable to a taxon at this rank, designated by a Latin *binomen*. This operation is distinct and independent from the allocation of this taxon to one of the taxonomic categories discussed above. In order for us to be able to communicate about them, all taxa must bear *nomina*. *Kyons*, just like *mayrons*, must be referred to by Latin *binomina* governed by the international nomenclatural rules of the *Code*, and not by any other system of numbers, letters, codes, abbreviations or plurinomial designations that are not real *nomina* (Avisé, 2008; Bogart et al., 2007; Schultz, 1961, 1966, 1967, 1969). When what is at stake is simply to mention these taxa in official lists, in publications of physiology or in the medias, it is often enough to mention the two terms of the *binomen*, substantive and epithet. In contrast, in more specialised publications, intended for taxonomists or evolution biologists, it may be useful to indicate briefly, by a symbol placed between the generic and specific *nomina*, to which taxonomic category the taxon designated by this *binomen* belongs (see Table 1). It is thus possible to combine the indication of the nomenclatural rank *species* of these taxa (through their Latin *binomen*) and that of their fine eidonomic category (through the possible presence of symbols), the latter only providing information on the evolutionary peculiarities of the organisms and entities at stake.

In the light of all the facts presented above, the traditional representation of evolution traditionally credited to Darwin as a *tree* appears to be an inexact oversimplification. This is not only because this image carries a teleological connotation and that Darwin himself possibly favoured rather that of the coral (Bredenkamp, 2003). This is mostly because some of the branches of this tree may, long after their separation, unite again to produce new branches. Even if it may appear shocking in regard of the current “dogma” of the “universal tree of life”, this phenomenon is not “exceptional” or “trivial” regarding the general pattern of evolution. It would be desirable to replace the image of the tree by that of the *network*. More than a tree, the branches of which always go irreversibly away from each other, the evolution of organisms reminds a network like those of some large tropical rivers, the arms of which split and then meet again, or the anastomoses of biological circulatory systems. This reticulate nature of biological evolution is a most general fact. Besides the phenomena of lateral gene transfer in prokaryotes, the importance of which starts only being understood (Doolittle, 1999), those of interpecific hybridization among complex organisms like metazoa are now known to be very widespread and to have played a major role in evolution, even in unexpected cases (Patterson et al., 2006). The image of the tree

is misleading regarding evolution and has no operational universality regarding taxonomy (Doolittle, 1999; Dubois, 2005), so it should be abandoned.

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