



Review

# Disciplinary Fields in the Life Sciences: Evolving Divides and Anchor Concepts

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**Abstract:** Recent and ongoing debates in biology and in the philosophy of biology reveal widespread dissatisfaction with the current definitions or circumscriptions, which are often vague or controversial, of key concepts such as the gene, individual, species, and homology, and even of whole disciplinary fields within the life sciences. To some extent, the long growing awareness of these conceptual issues and the contrasting views defended in their regard can be construed as a symptom of the need to revisit traditional unchallenged partitions between the specialist disciplines within the life sciences. I argue here that the current relationships between anchor disciplines (e.g., developmental biology, evolutionary biology, biology of reproduction) and nomadic concepts wandering between them is worth being explored from a reciprocal perspective, by selecting suitable anchor concepts around which disciplinary fields can flexibly move. Three examples are offered, focusing on generalized anchor concepts of generation (redefined in a way that suggests new perspectives on development and reproduction), organizational module (with a wide-ranging domain of application in comparative morphology, developmental biology, and evolutionary biology) and species as unit of representation of biological diversity (suggesting a taxonomic pluralism that must be managed with suitable adjustments of current nomenclature rules).

**Keywords:** nomadic concept; nomadic discipline; anchor concept; anchor discipline; life cycle; generation; organizational module; species

## 1. Introduction

The traditional articulation of biology into main research domains is not always satisfactory. For example, delimiting reproduction from other biological processes is not as easy as it might seem [1]. Let us focus on a strawberry plant. This produces runners that elongate horizontally on the ground, behaving like the branches of a growing plant, but after some time roots and leaves sprout on their lower face: a new plant takes shape, which ends up separating from the parent when the runner connecting them dries up. To use the terms introduced by John L. Harper and James White [2], even in the presence of a single *genet* (genetic individual), the production of runners leads to the formation of a new *ramet*, an anatomically separate individual, which therefore is the outcome of a reproductive event. Is this thus growth, or reproduction, or both?

Another difficult border separates developmental biology from some chapters of physiology, for example the physiology of nutrition or metabolism. In large snakes, e.g., pythons, in conditions of prolonged fasting the intestine undergoes a morphological and functional regression [3]; after a meal, cell proliferation reactivates the intestinal epithelium, which resumes its organization and functionality. This is accompanied by a rapid change in gene expression [4]. In terms of the mechanism, this is development; in terms of the function, this concerns the physiology of nutrition.

Cellular metabolites can modulate the activity of epigenetic factors that establish functional links between nutrition and gene expression [5,6]. More generally, intricate connections between anabolic processes and developmental transitions have been discovered [7,8].

As discussed below, recent and ongoing debates in biology and in the philosophy of biology reveal widespread dissatisfaction with the current definitions or circumscriptions, often vague or controversial, of key concepts such as gene, individual, species, and homology, and even of whole disciplinary fields within the life sciences. To some extent, the long growing awareness of these conceptual issues and the contrasting views defended in their regard can be construed as a symptom of the need to revisit traditional, unchallenged partitions between the specialist disciplines within the life sciences.

The problems deriving from an inadequately critical attitude towards the disciplinary partitions affect biology as a whole because of the unique diversity of the biological phenomena and the ubiquitous contrast between the inertial tendency to defend traditional disciplinary areas and a lively and often aggressive tendency to promote new or newly characterized and newly named research fields. The present paper is intended to contribute to a refreshment of this conceptual area. I articulate my argument as follows.

In the next Section, I focus on concepts as units of scientific knowledge that “continuously undergo transformation, and [ . . . ] function by *guiding ongoing scientific practice*. A biology concept can motivate *future* scientific efforts, and it can also provide a scaffold to direct the generation of new knowledge and the organization of complex knowledge.” [9] (p. 82, italics as in the original). I offer examples of concepts that change meaning according to the disciplinary context in which they are discussed and disciplined, including intentionally created ‘hybrids’ [10].

In Section 3, I suggest one of the possible strategies we could adopt in revising the disciplinary structure of biology. The current relationships between the traditional disciplines and a number of core concepts that change meaning while used in widely different disciplinary contexts is worth being explored from a reciprocal perspective, by selecting suitable *anchor concepts* around which disciplinary fields can flexibly move. Three tentative examples are offered. The first example suggests *redefined concepts of generation* as units in a periodization of the life cycles that opens new perspectives on both development and reproduction, and their evolution. The second example focuses on a notion of *organizational module* flexible enough as to be equally of use in comparative morphology, developmental biology and evolutionary biology, without the requirement for morphological, developmental and evolutionary modules to be overlapping or hierarchically nested. The third example suggests adopting a similarly flexible notion of *species as unit of representation of biological diversity*, as anchor species within which the different species notions can be accommodated in a disciplined form of pluralism.

## 2. Questionable Boundaries between Biological Disciplines

### 2.1. Multidisciplinary or Interdisciplinary?

In biology, as in other sciences, interdisciplinarity has been steadily increasing in the last decades, but with a diversity of levels, intensity and outcome. The transfer of concepts, problems, and tools between disciplines is often strongly polarized, with the receiving discipline adopting them from a donating discipline [11], but often it is a two-way affair. In this case we can characterize the process as one of integration, either epistemic or organizational, or both [11]. Moreover, it is an accepted notion that in modern science many key concepts are shared by traditionally separate disciplines, and these are often concepts that do not lend themselves to precise definitions [12].

The biological concepts whose definition has proved more problematic and is still controversial are probably those of species, homology, gene, and individual. In the first case the controversy is particularly strong within the single biological discipline of systematics [13]; in the second case it involves different disciplines (morphology, phylogenetics etc.), mostly insofar as that these are united by the adoption of the comparative method [14]; see [15] for a broader perspective on these cases. The definition of gene has an overt transdisciplinary value, involving genetics in its various

declinations, evolutionary biology, developmental biology, and the philosophy of biology [16–19]; the same applies for the definition of individual [20–25].

The need to address seriously, in a flexible and pluralistic way, the problem of a re-determination of the boundaries between biological disciplines is demonstrated by the number of concepts that in recent decades have assumed the value of nomadic concepts [26,27]. This term was proposed to describe concepts for which the meaning and domain of application changes with the new contexts into which they migrate. This has soon proved true also of the very notion of the nomadic concept [28–30]. I will use it to describe concepts that seems to be flexible enough to serve an epistemic role in different disciplinary contexts, but risk taking ever changing and not necessarily overlapping meanings.

It is legitimate to think that the lack of shareable definitions for the terms listed in the penultimate paragraph is not only a consequence of progress in the disciplines in which each of them originated, but also evidence of the disputable delimitation of biological disciplines. Eventually, we must acknowledge the historical specificity of individual disciplines, and possibly also the historical specificity of our own concepts of discipline [31] (p. 51).

## 2.2. Hybrid Disciplines—The Case of Evolutionary Developmental Biology

Gross conceptual rearrangements may be required by the emergence of a new hybrid discipline. This happened, in the last two decades of the 20th century, at the interface between evolutionary biology and developmental biology.

Interestingly, these two disciplines had been diverging more and more during most of the century. In the mind of authoritative evolutionary biologists, development was a black box between genotype and phenotype whose content could be ignored [32]. On the other hand, the transition from the descriptive embryology of the 19th century (which had provided valuable contributions to the understanding of phylogenetic relationships) to the experimental embryology of the following century had seen a progressive loss of interest in the comparative aspects of developmental processes and a growing focus on experimental work restricted to a very small number of model species [33,34]. Eventually, however, formidable technical advances in the second half of the 20th century made it possible to implement a developmental genetics program. One of the most sensational results was the discovery of the involvement of homologous genes in the development of such different organisms as mouse and fruit fly. The increasingly accessible contents of the black box between genotype and phenotype proved to be of utmost interest not only for development biologists, but also for evolutionary biologists. The emergence of a new research field in this interface area is conventionally fixed by two books whose publication dates and titles respectively mark the completion of the maturation phase and the first full expression of the new discipline. In 1983, Rudy Raff and Thomas Kaufman published a book [35], the title of which (*Embryos, Genes, and Evolution*) clearly identified the subject, approach, and problems of this discipline, while *Evolutionary Developmental Biology*, the title of the book published nine years later by Brian K. Hall [36], provided the name (often abbreviated as evo-devo) by which the latter was definitively identified [37,38].

Gilbert and Burian's early summary [39] that evo-devo "is both a synthesis between evolutionary biology and developmental biology and an ongoing negotiation between these two disciplines" (p. 61) is still up-to-date [40]. Winther [41] proposed to characterize evolutionary developmental biology as a *trading zone*, a catching term introduced by Galison [42] to indicate those interdisciplinary areas in which specific adoption and redefinition of both the concepts and the environment where they are implemented allow successful conceptual transfers [12,30].

For sure, conflicts cannot be avoided even in the best trading zones. In the case of evolutionary developmental biology, Love [43] has pointed to a hardly erasable tension between the two 'souls'. Repeatability of experimental results requires the highest possible uniformity in the strains (often long inbred laboratory lines) used in the tests. But this choice potentially deletes all the intraspecific variation on which evolution is deemed to happen. In this tug of war between developmental biology and evolutionary biology, it is not surprising that studies effectively coupling developmental genetics and

population genetics (devgen-popgen [44]) are still few, despite a few excellent examples such as the already classic studies on the beaks of Darwin's finches revisited from an evo-devo perspective [45,46]).

### 2.3. Beyond Hierarchies and Facile Interdisciplinary Transfers

In these years that witness so much talk about the need to broaden the traditional neo-Darwinian vision of evolution to move towards an extended synthesis [47–49] it is necessary, in my opinion, to make an even more generous and adventurous effort and to seek, in an ever wider trading zone, to refresh the relationships between biological disciplines.

An overarching question is the relationship between the disciplinary articulation of the natural sciences and a hierarchical vision of nature structured into levels of organization.

The starting point of a debate that continues to this day [50,51], with an unceasing renewal of points of view and arguments, is a 1958 article by Oppenheim and Putnam [52] postulating both an articulation of nature in terms of levels of organization, and a close reciprocal correspondence between levels of organization in nature and the sciences that describe their components and develop theories on the relationships between them [53]. From these premises, Oppenheim and Putnam derived an entire reductionist program.

A description of reality in terms of levels of organization seemed useful even to those who were ready to recognize that theories are not always “limited to single levels, that levels are always well defined, or that two or more entities can always be unambiguously ordered with respect to level” [54] (p. 215). But in more recent times, the progressive move away from the reductionist program of Oppenheim and Putnam was one of the reasons for the decreasing favor of the very notion of levels of organization [55–57], until its total rejection by some authors [58]. Others have brought their arguments against these dismissory positions, while nevertheless proposing new interpretations (and new epistemic roles) for the notion of organizational levels. While rejecting an ontological interpretation according to which the world would be structured by levels of organization, Brooks and Eronen [59]; see also [60,61] nevertheless save this notion as useful in the abstract description of systems and as a guide in the search for new areas of investigation to be explored. On the other hand, DiFrisco [62,63] rejects the criteria thus far used in identifying organization levels, in terms of compositional relationships or spatial scale, and suggests a dynamic approach that recognizes levels defined on the basis of rates or time scales of processes. Baedke [64] challenges the general acceptance of a never changing existence of levels of organization such as cells, tissues, organs, and individual organisms and points to the necessity of addressing their dynamical nature over developmental time and in evolution.

An overlooked consequence of the generalized acceptance of a vision of the living world in terms of compositional levels organized in part-whole relations [65] is the creation of disciplines through a copy-and-paste process. If in the study of humans and, more generally, of animals, it has proved useful to recognize a science of cells (cytology), a science of tissues (histology), a science of embryonic development (embryology) etc., this disciplinary articulation was accepted as sensible for all animals and even for multicellular organisms at large and corresponding disciplines were created for plants. Many biologists may take for granted, for example, the legitimacy of a plant embryology, but this should be resisted. In plant science, the use of the term *embryo* for the future seedling still enclosed within the seed casings was virtually unknown until 1788, when Gaertner [66] successfully introduced it in his treatise *De fructibus et seminibus plantarum* (On Plant Fruits and Seeds). Gaertner borrowed a number of terms and concepts from animal embryology. Some of these terms have remained in use for both plants and animals, but nobody would venture today to say, for example, that the placenta of plants is homologous to the placenta of mammals. Unfortunately, instead, the idea of an equivalence between what is called an embryo in either kingdom is still widespread, even among professionals [67].

### 3. Moving Ahead—Nomadic Concepts or Nomadic Disciplines?

I mentioned above that several core concepts of the life sciences have been taking continuously new meanings as long as their domain of application has been shifting from one biological discipline to another. Other adjustments to the meaning of concepts have accompanied the emergence of new subdisciplines within an older research area in which the concept was already in use, but with a different meaning. In a dialectic relationship between concepts and disciplines, the former have been continuing their *nomadic* existence, taking different meanings as a consequence of their changing association with disciplines, each of which acts as a semantic *anchor context*.

Traditionally, disciplines are taken for granted, as *anchor disciplines*, and concepts may nomadically wander from one to another. My suggestion here is, that a reversed relationship between disciplines and core concepts may prove useful, at least as an epistemic tool to be used to refresh the traditional divides separating a number of biological disciplines. I am suggesting indeed that we should perhaps move from a few *anchor concepts* around which *nomadic disciplines* may continuously evolve.

In this reversed perspective, a suitably chosen concept becomes the anchor around which important problems agendas in a number of traditional disciplines can nomadically move. To be sure, within the general framework I am suggesting, one of disciplinary flexibility, no anchor concept shall be regarded as definitely fixed, but it may be worth exploring for a while its possible epistemic usefulness. I will offer here three examples.

#### 3.1. Anchor Concept 1—Nomadic Disciplines in the Study of the Life Cycle

Much of biology deals with objects, processes, and concepts about reproduction, development, or evolution. A great many problems have been successfully addressed by restricting attention to one or another of these main themes and often accepting—operationally at least—variously restrictive and partial notions of reproduction, development, or evolution. These partitions, however, limit the formulation of potentially interesting questions and thus constrain progress both in the life sciences and in the philosophy of biology. Therefore, it may be sensible to explore in a free, innovative way the notoriously difficult and therefore challenging border areas between development and reproduction, and those between development and evolution. As mentioned above, the latter frontier came into the spotlight at the end of the last century and has been generally managed by making room for a new discipline, evolutionary developmental biology, within which new key concepts have emerged such as evolvability [68,69], modularity [70] and innovation [15,71–73]. However, a small number of scholars prefer a different path, suggesting a much closer integration between the two traditional disciplines [74,75].

The other boundary, the one between reproduction and development, may deserve a conceptual re-organization by treating these two chapters of biology as *nomadic disciplines* whose core problems vary according to their various association with a small number of *anchor core concepts*.

To the best of my knowledge, this reversal of perspective has not been formalized before; however, to see how this may operate, we can get advice from the literature. Let us start by comparing the complementary approaches of Paul E. Griffiths, Karola Stotz, and James Griesemer to the relationships between reproduction and development. On the one hand, Griffiths and Stotz take development as the core process, and reproduction as the linking one: “It is the developmental process that replicates itself across the generations” [76] (p. 227). A complementary proposal, centered instead on reproduction, comes from Griesemer, who takes reproducers as the units of multiplication, hereditary variation, and development: by reproduction, a parent generates an offspring that is able to develop so as to generate its own offspring [77]. Both perspectives have their merits and can suggest new, original research programs. In this context, it is fitting to remark that “Dobzhansky’s declaration (1973) [78] that nothing in biology makes sense except in the light of evolution notwithstanding, it is equally clear that evolution does not make sense except in the light of the rest of biology [79]. So, it is a toss-up which concepts must “come first” in order to understand “the rest”” [80] (p. 140).

By introducing unprecedented perspectives on reproduction and development, these proposals contribute to the debates on the notion of the individual [22–27], the nature of development [81–83], and the diversity of hereditary mechanisms, which include Mendelian ones but are not limited to these [84–90]. These theoretical approaches put center stage the *biological cycle*, rather than the individual organism, both in ontogenetic and evolutionary perspectives [91–93].

Largely overlooked, however, is the problem of a segmentation (periodization) of biological cycles suitable for comparisons across the different branches of the tree of life. Current textbook descriptions do not help much [1]. For example, it is taken for granted that the biological cycle of most animals is monogenerational. Two generations are recognized only in particular instances, for example in those cnidarians in which an asexually reproducing polyp alternates with a sexually reproducing medusa. In plants, the haploid cells that derive from meiosis do not behave like gametes. Instead, each of them (a spore) gives rise to a multicellular organism. Two generations are also recognized in plants, a diploid sporophyte alternating with a haploid gametophyte. In the flowering plants, the sporophyte is the conventional individual plant, while the gametophyte is much less conspicuous: in the male version, the gametophyte is the pollen grain, made up of only three cells; in the female version, it is the complex of an egg plus an embryo sac of six cells.

To identify comparable generational units in the life cycles of organisms belonging to the different evolutionary lines, a suitable periodization is required. Gorelick [94] proposed to recognize the beginning of a new generation every time a sexual phenomenon brings about changes in the chromosomal set. In the typical biological cycle of animals, we should therefore recognize two generations, respectively initiated by meiosis (which leads from diploid to haploid condition) and karyogamy (the fusion of the haploid nuclei of the gametes, which reinstates diploidy). If we accept Gorelick's proposal, eggs and spermatozoa represent a haploid generation distinct from the diploid generation that begins with the zygote.

Gorelick's suggestion is very reasonable, irrespectively of whether or not it is advisable to retain the term generation for each of the two segments of an animal's life cycle. The real problem with this proposal is instead that it does not work for many groups, e.g., plants or ciliate protozoans. The articulation of the biological cycle into a haploid and a diploid generation separated from each other by meiosis and karyogamy works only for diplobiont organisms, i.e., those in which the cells that derive from meiosis are the gametes, and for haplobionts, i.e., those in which the diploid condition is restricted to the zygote, that directly undergoes meiosis, starting a new haploid generation, as in *Volvox* and other green algae [1]. But plants, as said, are haplodiplobiont. To dissect their life cycle into meaningful phases, Gorelick's periodization is insufficient.

To describe the different relationships between sexuality and reproduction in the biological cycle, irrespectively of its haplobiont, diplobiont, or haplodiplobiont nature, I proposed [95] to recognize two kinds of generations (and, correspondingly, two kinds of individuals):

*Demographic generation*: the individuals produced by sexual or asexual reproduction by individuals of a parent generation.

*Genetic generation*: a set B of individuals produced by a set A of individuals (which represents a distinct genetic generation) by a sexual process (sexual reproduction or pure sexuality, i.e., sexuality without reproduction, as in the ciliate protozoans, see below).

Based on these definitions (but also based on Gorelick's proposal), in the life cycle of animals like humans there are two generations. More precisely, the haploid generation (gametes) is a demographic generation, while the diploid generation (the conventional individual organisms) is a genetic generation (beginning with karyogamy), but it is not a new demographic generation (fertilization does not increase population size).

In plants, however, the biological cycle includes three generations, separated either by a reproductive event (production of gametes without meiosis), by a sexual event (karyogamy followed by sporophyte development) or by overlapping sexual and reproductive events (production of spores through meiosis).

The case for ciliate protozoans is very different. In these single-cell organisms, there is no association between sexuality and reproduction. Sexuality consists here of the exchange of nuclei between two cells that retain their somatic identity and resume independent life after the exchange: two ex-conjugants are genetically ‘renewed’, but this has no demographic consequence; reproduction is achieved by simply dividing the diploid cell into two daughter cells, without any genetic change. Therefore, in ciliates, genetic generations separated by meiosis and fertilization do not coincide with the demographic generations punctuated by mitoses.

A periodization of the biological cycle based on the notions of generation defined above opens the way to comparisons between the most diverse groups of living beings and suggests new perspectives, both for developmental biology and reproductive biology. For example, recognizing the meaning of generation (demographic and genetic) in the unicellular phase of a typical animal life cycle legitimizes the description of gametogenesis in terms of developmental biology (and therefore provides an extension of developmental biology to unicellular organisms). At the same time, the distinction between genetic generation and demographic generation leads to recognizing, in the biological cycle of animals, the exclusively genetic nature of the diploid generation, except in the case of polyembryony, that is to say, the production, through a reproductive event not accompanied by sexual phenomena, of two or more embryos (twins) starting from the same zygote [1].

### 3.2. Anchor Concept 2—Organizational Module

Most of research in biology presupposes a sensible decomposition of the complex body architecture of the individual into recognizable parts based on morphological or functional criteria. For example, a textbook tradition made solid by the general acceptance of a hierarchical vision of nature suggests an articulation of the body into organs, each of which is made up of variously differentiated tissues, formed in turn by cells. This hierarchy continues with the subcellular structures, which for simplicity, we can ignore here. For the same reason we will ignore the complications deriving from the interactions between the cells of an animal and those of the prokaryotes forming the associated microbiome [96–100]. Instead, we will address the question, whether it is possible to identify, in the structure of a multicellular organism, fundamental units on which we can focus in the most diverse disciplinary contexts: for example, as structural units in comparative anatomy (homologues), and as largely autonomous elements from the point of view of development or evolution.

A good starting point is Günter Wagner’s revisitiation, first formulated towards the end of the last century, of the concept of homology: “Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype.” [101] (p. 62). Subsequently, shifting the focus from development to evolution, Wagner stated that “homologues can be understood as modular units of evolutionary transformation” [102] (p. 36).

In the same years the use of ‘module’ as a neutral term (in a disciplinary sense) began to spread, to the point that Borja Esteve–Altava could affirm that “The study of modularity is commonplace in all biological disciplines” [103]. However, difficulties in reaching agreement on a definition of module did not take long to emerge [70,104,105].

A basic issue is the distinction between variational modules [106–110] vs. organizational modules [103]. A *variational module* is a set of traits that vary in a coordinated manner, in some way independent of other groups of traits within a given system, for example, within the same individual organism. These patterns of (co)variation can be useful for recognizing units worth focusing on, but this module concept is arguably too vague to serve as a useful anchor concept. More promising are the *organizational modules*. These can be defined as groups of elements that establish more and/or stronger interactions within the group than outside it. In this deliberately abstract definition, the nature of the interactions that define a module is not specified. The concept is therefore applicable, within biology, to the units on which the most diverse disciplines focus, facilitating comparisons and exchanges between them [103,106]. Organizational modules are, for example, the parts of the body recognized by

the morphologist, based for example on relationships of contiguity and connection, or on the gene regulatory networks of developmental genetics, or on the developmental modules on which Wagner's biological notion of homology is based, or on the morphofunctional units (e.g., the circulatory system, heart, and brain) which the physiologist deals with, or on sets of traits that evolve in a coordinated way, whatever the cause, such as selection or concerted evolution [101–113].

Units defined from different perspectives do not necessarily overlap [114]. The correspondence between developmental modules and evolutionary modules is a big problem for which we do not have any general solution [8]. Characteristically, organs such as heart or brain are obvious morphological and functional units, but are not modules from a morphogenetic point of view: in other terms, there are, for example, hearts as modular organs, but not a 'cardiogenesis' as a correspondingly integrated and largely autonomous developmental process [115–117].

### 3.3. Anchor Concept 3—Species as Unit of Representation of Biological Diversity

Few of the most important concepts in biology have taken on the character of nomadic concepts for as long as the concept of species, to the point that the topic already turned into a 'species problem' more than a hundred years ago. When this expression appeared for the first time in the title of a book [118], the species problem had already been the subject of numerous articles, some of which date back to the early years of the last century [119–121]. An article in *Nature* that highlighted the importance of that book reported an impressive example of the consequences of the plurality of alternative species concepts supported by taxonomists at the time: "Some years ago [ . . . ] I endeavored to get from my colleagues at the Museum [=The British Museum (Natural History), as it was called at the time] estimates of the numbers of species in the various groups with which they were specially conversant. Some of the answers obtained were very interesting. With regard to mammals I was told "anything from 3000 to 20,000, according to the view you take as to what constitutes a species"" [122] (p. 440).

Ninety years later, we are still witnessing an endless evolution of the species concept, as tagged in the title of a recent article [123]. More or less formally, no less than 30 different notions of species have been proposed to date [13,124].

Ironically, perhaps, it is precisely the substantial intractability of the 'species problem' the strongest stimulus to adopt a 'radical solution' that may turn the species into a veritable anchor concept. The way forward was suggested by Robert O'Hara towards the end of the last century: "Perhaps the species problem is not something that needs to be solved, but rather something that [...] needs to be gotten over" [125] (p. 232). In addressing the 'species problem', we do not face a problem of fact, but rather as a problem of systematic representation [125]. Indeed, in agreement with Robert O'Hara's revisitation (and eventual dismissal) of the 'species problem,' I suggest here that, rather than accepting the species concept as incurably nomadic, we can fix it by divesting it of all the special qualities that differentiate its all too many notions, to fix it simply as a *unit of systematic representation* of biological diversity. This simplified concept returns to the different disciplinary domains in which the term 'species' is used the burden to customize it as required, whereas taxonomy continues to accommodate all the taxonomic units that biology requires without introjecting the controversies about species concepts, their legitimacy, and the priorities, conflicts, and compatibilities among them.

In principle, within one and the same set of organisms we can recognize groups on the basis of the most diverse criteria, which may correspond to different concepts of species, e.g., biological species, on the basis of reproductive isolation; morphological species, based on structural similarities, and so on. In different contexts, one choice may be preferable to another, while the claim to recognize a criterion of absolute validity appears unsustainable. Among others, Mishler and Donoghue [126] consequently defended a certain degree of pluralism in biological classification. Among the positions expressed in the last three decades, some authors (for example, [127–130]) support pluralism, others (for example, [131,132]) reject it. Despite the intentions and efforts of many taxonomists, current taxonomic practice is already remarkably pluralistic [133]. This choice, however, can be

sustained only if the various species concepts adopted in the different instances are stated explicitly or are at least evident from the context [134].

Moreover, this pluralism may require adjustments in nomenclature [127]. Changes in a group's taxonomy are in fact a source of ambiguity in the meaning of species names. For example, until a few years ago, almost all authors classified African elephants as belonging to a single species (*Loxodonta africana*); at most, some zoologists distinguished the forest elephant as a subspecies (*Loxodonta africana cyclotis*) distinct from the savannah elephant (*Loxodonta africana africana*). However, recent studies [135] have led to classifying the two forms as two distinct species, in which case the savannah elephant retains the name *Loxodonta africana*, while the forest elephant takes the name *Loxodonta cyclotis*.

Diverging (or renewed) opinions about the taxonomic treatment of a group (for example, how many species, and which ones, are best recognized within a genus) are current in zoology as well as in botany. This circumstance, combined with the (otherwise sensible) rules of the international codes of nomenclature [136,137] causes the names attributed to the species to become semantically unstable. To avoid misunderstandings, it is sometimes necessary to specify the *taxonomic concept* [138], that is, the precise meaning of the name as used in a particular work. For example, in the case of African elephants, *Loxodonta africana* as used by [135], where the name is applied to the savannah elephant only, is different from *Loxodonta africana* as used by [139], which refers to all African elephants, treated as a single species: the latter taxonomic concept includes the former, but it is not identical to it [127,133]. The number of different taxonomic concepts that can correspond to a single Linnaean name is sometimes impressive. Precise data are available regarding birds, where for approximately 10,000 species and 22,000 subspecies that are currently recognized, over 1.5 million taxonomic concepts are available in the literature [140,141].

#### 4. Summary and Conclusions

Until well into the second half of the 20th century, biology was accorded a status dramatically lower than other sciences, physics in particular. Similarly, the philosophy of science of the time largely disregarded the life sciences, to concentrate instead on those more mathematized and more rich in theory. Things changed dramatically in recent decades. In the meantime, however, advances in scientific knowledge have fragmented biology into an ever-growing plurality of disciplines, each of which, at least for a time, has consolidated around more promising or more successful research agendas. Only in exceptional cases, such as at the interface between developmental biology and evolutionary biology, has a new discipline (evolutionary developmental biology) taken shape in which a debate around the founding concepts is still in progress.

Today, the life sciences are extensively populated by nomadic concepts that take on the most diverse meanings depending on the contexts in which they are recognized and used. This is possibly attractive for the philosopher of science, but problematic and potentially dangerous for the scientist.

It is legitimate to ask whether in our day, it is still useful and appropriate to address the conceptual problems of biology with the breadth of horizons of what two centuries ago took shape under the name of biology. Today, in fact, this name often identifies only a large container, in front of which it is not regarded necessary or useful to address critically and flexibly the possible relations between its contents. This situation is arguably acceptable to many, or most, practicing biologists. However, it is not so for the philosophy of biology, which up to now has taken into consideration only a part of the concepts and problems faced by the life sciences.

Eventually, both biology and philosophy need a refreshment of the reciprocal relations between the different disciplines recognizable in this field.

In the previous pages, I have suggested one of the possible strategies we could adopt in revising the disciplinary structure of biology. The current relationships between anchor disciplines such as comparative morphology, systematics, evolutionary biology, developmental biology, biology of reproduction, and nomadic concepts wandering between them is worth being explored from a

reciprocal perspective, etc., by selecting suitable anchor concepts around which disciplinary fields can flexibly move.

Advantages and shortcomings of a re-organization of biology as a set of nomadic disciplines revolving around a small number of anchor concepts is a challenge whose results deserve careful evaluation. As suggested by a referee, another nomadic concept that may deserve being re-refined in such a way as to fix it as anchor concept is the concept of environment. This being already at the boundary between biology and many other sciences, and largely beyond my own field on enquiry, I must leave it to others to explore the heuristic potential of this attractive suggestion.

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