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ORIGINAL ARTICLE

"Cladus" and clade: a taxonomic odyssey

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Abstract
The fate of "clade," both as concept and word, is reconstructed here beginning with its first appearance in 1866 as "Cladus," in Haeckel's *Generelle Morphologie*, continuing up to the present. Although central to phylogenetics, the concept of clade is paradoxical since it has been ambiguously understood or even misunderstood by its own promoters. Writings by Ernst Haeckel, Lucien Cuénot, and Julian Huxley, the three authors who discussed the notion of clade at length, are analyzed here in detail as a means of exploring this paradox. First conceived as a rank for a higher-level category, and later as a taxon, the clade is understood today in connection with Hennig's definition of a monophyletic group rather than through Huxley's successful but somehow ambiguous formalization. The inability of these authors to formulate a clear-cut exposition of the concept is considered here within three contexts: firstly, the burden of pre-Darwinian classifications based on similarity; secondly, the underestimation of Darwin's description of a genealogical group; and thirdly, the predominance of thinking in process (vs thinking in pattern), which was the basis of evolutionary systematics in the mid-twentieth century.

Keywords Clade · Category · Rank · Taxon · Darwin · Haeckel · Cuénot · Huxley

With 250 years of history, there are many changes in the vocabulary of systematics, changes with new words for new concepts, and changes with new meanings of old words. Most biologists outside systematics expect taxonomy and its language to remain the same throughout time. They will not bother to learn what was meant years ago, and what the context was. Yet, it is important to know the meaning of a word in the day it was written, how it was used throughout time, and why it was used with contradictory meanings. For example, if you challenge a molecular geneticist to define the word "gene" for important literature, for all time, he should write a long review that includes many different concepts. The geneticist may finish his review of "gene" equivocally, saying that we are still learning about this. We can do better with the critically important word "clade" because we know where the concept should finish.

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As is well known, the words phylogeny ("Phylogenie," "Phylogenese") and monophyly—more precisely the adjective monophyletic ("monophyletisch")—appear in Haeckel's (1866) *Generelle Morphologie der Organismen*. In this book, Haeckel also uses the word "Cladus" which will become prominent in mid-twentieth century literature with the same spelling in both English and French: "clade."

Today, monophyly and clade are closely related concepts that form the basis of the language of phylogenetics. This was not the case in the beginning. Although rooted in Darwin's conception of systematics, initially these concepts were ambiguously defined for whatever reason. The main reason being the difficulties of erecting a methodology connected to the notion of relationships and not to these of overall resemblance and amount of differences which were the basis of pre-Darwinian classifications.

Darwin's conception of monophyly is implicit in his *On the Origin of species*: according to him a genealogical group should include "all the modified descendants from a common and widely-diffused species" (Darwin 1859 cited 1964: 119). This is the first occurrence of the Darwin's understanding of his concept of "community of descent" from an ancestral form (Darwin 1859 cited 1964: 425), defined in this article as a group which is an entire line of descent, that is, where phylogenetic pattern includes all the descendants

of one putative ancestral species. A few years later, Darwin is even more explicit and delineates the structure of genealogical groups within a genealogical system: "this system, it is now generally admitted, must be, as far as possible, genealogical in arrangement,—that is, the co-descendants of the same form must be kept together in one group, separate from the co-descendants of any other form" (Darwin 1871: 188). That is, all of the "co-descendants," not only *some* of them. Since Darwin generally uses "form" for species or varieties, this statement is equivalent to the concept of monophyletic group or clade in its modern sense. Moreover, within the schema published in *On the Origin of species*, Darwin opens a field for methodological thinking and graph-theory that Haeckel—and his followers—did not fully understand when they formalized the concepts of monophyletic group and clade. Darwin's descriptions of his diagram clearly separate resemblance and relationships among members of a community of descent. These descriptions and explanations will not be quoted by the successive students who define the concept of clade. When the reader of *On the Origin of Species* follows the history of the descendants of one ancestral form on Darwin's diagram, he reads that « forms which …diverged in character during the successive generations, will have come to differ largely, but perhaps unequally, from each other and from their common parent» (Darwin 1859: 120 cited 1964), although «all these modified descendants are represented as related in blood or descent to the same degree» (Darwin 1859: 420—cited 1964).

During the second half of the nineteenth century and the first half of the twentieth century, only a few taxonomists use the word and concept of clade, namely Haeckel, Hatschek, Robben, Cuénot, and Julian Huxley. In this article, we are trying to identify the difficulties that they encountered when delineating a genealogical group and categorizing it in the tree of life. In order to establish a rational explanation for the failure of prominent evolutionists such as Cuénot in the 1940s and Huxley in the 1950s, here we will examine their writings for the lack of graph-theory logics, misunderstandings of Darwin's scheme in the *Origin of Species*, and the influence of a progressive view of evolution burdened by traditional evolutionary trees that depict groups rooted within groups. Finally, when Hennig coined the expression "paraphyletic group" in a paper published in 1962 (see Williams and Ebach 2009: 261; Schmitt 2013: 137; Willmann 2016: 143) and used it regularly thereafter (e.g. Hennig 1966) the ambiguities cease among systematists, nearly one century after Haeckel's initial efforts. The inefficiency of nonmonophyletic groups, such as paraphyletic groups, is explored by Hayden (2020).

Haeckel's "Cladus"

Phylogenetic background

Williams and Ebach (2009, note 1 p. 257) explain that Haeckel used the word "Cladus" as a category of classification (that is, a rank) and in fact, "only as a category in classification." This straightforward conclusion merits some comments.

The word "Cladus" appears on p. xxxviii under the classification of living beings, which is the introductory section to the second volume of *Generelle Morphologie der Organismen*. There, "Cladus" is a rank between the "Phylum" and the "Classis." Chapter 24 of this volume, titled "The natural system as genealogical tree (principles of classification)" (*Das natürliche System als Stammbaum (Principien der Classification)*—all translations from the German and the French are ours, except when indicated), includes a table on p. 400 illustrating the concept of "Cladus" and "Subcladus." This table is part of section VI of this chapter, "Graduated levels of subordinate categories (= ranks)" (*Stufenleiter der subordinierten Kategorien*), which follows a long discussion of the signification of the nomenclatural categories for classification. The title of chapter 24 clearly demonstrates that tree and classification are the same thing in Haeckel's mind. The title of the second section implies that the ranking is just as important as the arrangement, that is, the genealogical tree.

Haeckel (1866, vol. 2: 365) defines his conception of the development of phyla, basing his discussion largely on a process approach. "Phylogeny is paleontological development, and this development is purely a physiological process" (*Die Phylogenese oder paläontologische Entwickelung (…) ist ein physiologischer Process*). Previously (Ibid: 303), phylogeny had been more generally understood as "the historical development of organic phyla" (*Phylogenie oder Entwickelungs-geschichte der organischen Stämme*), where the concept of relationship is prominent; each phylum is composed of "successive and coexisting blood-related members" (*successive and coexistente blutsverwandte Glieder jeden Stamm zusammensetzen*). Within these descriptions of phylogenesis and phylogeny, one can infer the respective process and pattern approaches. Yet in the process, the "divergence of blood-related groups" (: 365) (*Divergenz der blutsverwandten Formen*) takes on major importance. These divergences produce connected, subordinate so-called form-groups, as well as ordered categories, or ranks ("System von subordinirten Formengruppen verbindet… (und)… geordnete Gruppen oder Kategorien": 369–370). This means that form-groups (blood-related groups) are conceived without reference to categories (ranks), even if ordered categories

are applied to these subordinate form-groups. But one may wonder whether within Haeckel's logical system the subordination of categories inherited from Linnaeus in fact precedes that of groups, or not. Haeckel does not seem to go further into this question since he always confuses grouping and ranking (although Dupuis (1988) supports the idea that Haeckel clearly distinguishes groups and categories (ranks)—see below).

Haeckel (1866) ends chapter 24 with a discussion on the method of grouping and ordering, which consists entirely of Agassiz's threefold parallelism—comparative anatomy, paleontology and embryology are the sources of classification—(Agassiz 1857, cited 1962) with a simple shift from a classificatory purpose (natural groups) toward a phylogenetic one (groups of descent). As such, the method somehow misses the major task. Once characters have been identified based on comparative anatomy, ontogeny, and paleontology, then how should the congruence between all of these characters be organized? The importance of characters for ranked groups as phyla, families, genera and so on, is largely the continuation of Jussieu's concept of the subordination of characters—with more general characters and less general characters—(Jussieu 1789; see Tassy 1996).

"Cladus" and "Subcladus"

Chapter 24 of *Generelle Morphologie der Organismen* is largely devoted to the use of categories and the relation between categories and the degrees of structural differences, bauplans, and the importance of hiatuses. This chapter is largely based on Agassiz's *Essay on Classification* (1857 cited 1962), and only slightly amended by Haeckel, especially at the end of the chapter (see below).

Hence "Cladus" and "Subcladus" appear as categories between phylum and class ("Phylum" and "Classis") in the table on p. 400, ranks that are applied to blood-related form-groups. Indeed, here the clade is a category, but the concept is connected to the phylogenetic nature of the groups (community of descent). According to Haeckel, the vernacular German words for "Cladus" and "Subcladus" are "Stammast" (primary branch) and "Unterast" (secondary branch); the "Phylum" is the "Stamm" = main branch or trunk, or even the stem as well, which can be confusing; the "Classis" is the "Classe" = class). Clearly, for Haeckel blood-related form groups are identified by their arrangement, and the ranking follows.

In the last section on the "differences in characters of subordinate groups" (*Charakter-Differenzen der subordinirten Gruppen*), Haeckel (1866: 402) emphasizes that the subordination of groups is tied to their respective ages: a species is younger than a genus, an order is younger than a class. Thus, even if the choice of characters for defining and diagnosing subordinate groups depends on differences in characters due to the course of phylogeny, this course applies to ranked groups. Classification precedes phylogeny reconstruction. The quest for phylogenetic characters is not devoid of circular reasoning in the nineteenth century.

Clearly, what is lacking here is a concept independent of that of rank (= category), that is, the concept of taxon. Today the species is both a taxon and a rank, but no taxonomist makes the confusion between the two. In the nineteenth century, Haeckel approaches the concept of taxon when he speaks about "groups" and "groupings" conceived only in terms of their genealogical structure. According to this conception, derived directly from Darwin's descent with modification and his "community of descent", groups are parts of the genealogical tree. Yet, Haeckel does not clearly define these parts, that is, how the shape of the genealogical tree distinguishes among a main branch, a branch, and a lesser branch. He emphasizes that the groups are necessarily subordinated, but in respect to the details of the multiple branching the reader is left with a rather vague procedure. The modern reading of *Generelle Morphologie der Organismen* implies that these groups are monophyletic. Haeckel seldom applies his own conception. For him monophyly is the unique origin of the tree of life according to his famous plate which caption reads: "Monophyletischer Stammbaum der Organismen" (Haeckel 1866, table I). In the text (Haeckel 1866, vol 2, footnote p. 417), the only explanation of "monophyletisch" is given as the "hypothesis of the unitary descent of all organisms" (*Hypothese von der einheitlichen Abstammung sämmtlicher Organismen*). All cladists interpret this sentence and the notion of entirety ("all organisms") as defining genealogical groups, communities of descent. Hence, phylogenetic groups are monophyletic (e.g. Dupuis 1988: 84, "by definition, a monophyletic group thus includes the entire line of descent" (*par définition, un groupe monophylétique comprend donc la* totalité *d'une lignée de descendance*); see also Dupuis 1986: 221). As we know, the question of monophyly was one of the hottest debates in the early days of cladistics, as recalled by Farris (2018).

But in *Generelle Morphologie der Organismen*, most of the time the discussion of subordinated groups is connected to the ranking of these groups. Moreover, it seems that for Haeckel, some groups, for instance the vertebrates, are clearly a "Phylum," so that there is no need to separate what is classified in the "Phylum" from the category itself. Indeed, the only instances where Haeckel again stresses the concept of community of descent appear in the discussion about the "Phylum," as a higher rank rather than a lineage of any kind: "the entirety of all currently existing or already extinct organisms derive their origin from one and the same common stem form" [translation by Schmitt (2013: 131) of "*die Gesammtheit aller jetzt noch existirenden oder bereits ausgestorbenen Organismen, welche sich von einer und derselben gemeinsamen Stammform ihre Herkunft ableiten*"—see

also Rieppel (2016: 45)]. Here the group is understood as a community of descent which includes the co-descendants of one putative ancestor, that is, a monophyletic group or clade in modern sense. Haeckel is on the verge of defining groups within a phylogenetic content, that is, of establishing a general rule, but he restricts it to the "Phylum." We are not arguing that Haeckel did not care about monophyly and constantly confounds group and category. However, there is some confusion in the use of these concepts. For Dupuis (1988: 53) when Haeckel confounds "groups and categories" (*Gruppen oder Kategorien*) it appears to be simply inadvertent, but perhaps it is more significant than that.

First variations

Williams and Ebach (2009) cite several of Haeckel's books and editions from 1876 up to 1894, all subsequent to Darwin's (1871) explanation of the structure of a genealogical group. If the fate of the word "Cladus" is blurred by Haeckel himself, this was not in response to Darwin. "Cladus," and the new word "Cladoma" (translated in English as "clade" and "cladome") are the same rank. In his last phylogenetic synthesis, *Systematische Phylogenie*, Haeckel (1894–1896) uses the word "Cladoma," as well as "Cladom," in volume 2 (dated 1896). As for "Cladus," "Cladoma" is a category ranked between the phylum and the class: this is Haeckel's original (1866) usage.

Between Haeckel (1866) and Huxley (1957) the few users of the concept and word clade mix the arrangement and the ranking of groups. In Hatschek (1888: 39, 304) "Cladus," as well as "Subcladus," appears as categories following Haeckel's sense, between phylum and class.

The category appears again in the same way, with the spelling "Kladus," in Grobben (1909: 495) where the monophyly of the group classified as "Kladus" is necessary according to Grobben. For example, "the clade of arthropods refers to a monophyletic origin" (*Arthropodenkladus im Sinne einer monophyletischen Abstammung*). This is an improvement. Even if monophyletic origin is not necessarily synonymous with community of descent as seen above, it nevertheless tends to be. Indeed, Grobben contrasts theories of monophyletic origin and the "heterophyletic origin of arthropods" (*eines heterophyletischen Ursprunges der Arthropoden*). It becomes synonymous in 1917 with Naef: "a systematic category [taxon] is the entirety of species which are believed to have developed from one stem form" (citation, translation, and bracketed insertion by Willmann 2016: 159). Finally, in his discussion on higher taxa, Chitwood (1958: 870, 874, table p. 888) cites Haeckel's "Cladus" and "Cladom" as categories, but he does not endorse them in his final synthesis (Chitwood, table p. 888) where neither "Cladus" nor "Cladom" appears between phylum and class (instead there are five categories, supersubphylum, subphylum, supersuperclass, subsuperclass, superclass).

In 1926 Meyer-Abich had coined the word "taxon" (plural taxa), a major concept in the history of systematics. One may infer that taxa are more or less equivalent to Haeckel's subordinated groupings, which are blood-related form-groups—a concept we see as the embryo of the concept of clade as a monophyletic taxon. But Meyer-Abich (1926: 273) proposes two terms, the terms "taxon" for systematic (classified) groups, and "phylon" or "phylotaxon" for phylogenetic groups. This is a logical but unfortunate choice since, once again, phylum and *phylon* for either a category of high rank (generally), and for a lineage of any kind had already been used by Haeckel (1866). "Phylotaxon" was ignored but appears to be a senior synonym of clade. This practice is still current today. Taxon, as a concept (a group independent of its rank in classification), appeared in botany in 1950 (Lam 1950) and in zoology in 1953 (Mayr et al. 1953); this is a significantly protracted period for the concept to develop, since it was long confused with category (Dupuis 1988). Even today confusion between arrangement and rank persists, for instance when one reads of the definition of taxon as being both "a taxonomic unit and a category" (Meyer 2016).

Cuénot's clade

In the first half of the twentieth century, in France the biologist Lucien Cuénot is one of the very few to consider the concept of the phylogenetic tree favorably, although he was essentially interested in genetics. For him, higher-level systematics is not a side issue (Tassy and Barriel 1996).

Throughout four more or less connected essays, Cuénot (1939, 1940a, b, c) discusses the tree of life and the concept of genealogical trees, arguing for the idea that although such trees are considered "old-fashioned" (*périmés*), we "cannot carry out biology without phylogenetic constructions" (*on ne saurait se passer de constructions phylogénétiques*) (Cuénot 1939: 736). In three of these essays, Cuénot (1940a, b, c) introduces and defines the "new word clade from the Greek *clados*, branch" [*terme nouveau de* clade *(du grec clados, branche)*) Cuénot (1940a: 24)]. It is clear that Cuénot thought that he had invented the word and the concept at this point. Later Cuénot (1940c: 225), in reference to Kükenthal's previous use of "Cladus" (in fact Hatschek's), recognizes that the word "clade" is not new but nevertheless "useful" (*commode*). It appears that the geneticist Cuénot seems to not be fully conversant with phylogenetic literature. He believes that the first tree of life ever published dated to 1868 (in *Natürliche Schöpfungsgeschichte*), which he describes as a "very premature and unclear essay" (*essai très prématuré et très confus*) (Cuénot (1940c: 222). This means

that Cuénot probably had not read *Generelle Morphologie*. Moreover, nearly 70 years after Haeckel's essay, Cuénot's conception of the phylogenetic tree and his taxonomic ambiguities remain nearly the same as Haeckel's.

For Cuénot, as for Haeckel, the clade has a phylogenetic dimension. It is an "autonomous, closed leaf" (*feuille autonome*) of the tree (Cuénot 1940a: 24, 1940c: 225). This definition is that of a monophyletic taxon. But Cuénot (1940a: 24, 1940c: 225) adds that the leaf is recognized by a "structurally defined type" (*type défini de structure*), that is, by a group ranked as "phylum" (French word: *embranchement*). As a consequence, the clade is also presented as a high rank suited for major lines (according to Cuénot, thirty lines such as arthropods, cnidarians, ctenarians, echinoderms, echiurians, ectoprocts, entoprocts, pterobranchs, sipunculans, vertebrates, and so on), thus replacing the category of phylum, which can then be subdivided into class, order, family, tribe, and genus (Cuénot 1940c: 225). In other words, the clade as a leaf is, in principle, of any size and order but, in fact, if considered as a major line, then it is synonymous with the category phylum. The only difference with Haeckel's treatment is that for Haeckel clade is a category subordinated to the phylum. Indeed, Cuénot (1940b: 197) also writes that we should "group species into scaled categories, and that each of them indicates or should indicate a point within evolutionary branching: genus, tribe, family, order, class, and finally clade" (*nous groupons les espèces en categories étagées, dont chacune marque ou devrait marquer un point de bifurcation évolutive: genre, tribu, famille, ordre, classe et finalement clade*).

Cuénot's leaf, that is, the clade as a taxon (although he does not use the word), or an evolutionary closed group (he could have written Darwin's words "a line of descent" or "a community of descent" but he did not), cannot derive from another leaf. This important advance has consequences that Cuénot (1940c: 225) explains as follows: if two leaves are connected it can only be "by their common stem" (*par leur base commune*). This connection describes two sister groups of modern systematics. Yet Cuénot does not draw a general conclusion from this, because at the same time he considers the clade as a high-ranking category. Hence, a clade includes only the major branches of the tree recognized by their structural type, which is a typological concept.

Even the concept of a common stem is not devoid of ambiguity. When Cuénot describes the tree of life, he uses the same kind of image that Haeckel did for the subordination of major groups. For Cuénot (1940a: 25), the tree is "an axis with few branches, which laterally bears clades" (*un axe peu ramifié… qui porte latéralement des clades*), and further, "clades are connected on axes as successive buds on a branch" (*clades … insérés sur des axes comme des bourgeons successifs sur une branche*). One may conclude that in Cuénot's mind, the common stem is an axis, so that the pattern of the tree does not anticipate that of the cladist's cladogram nor recalls that of Darwin' diagram. In Haeckel (1866) the clade (group) is recognized by sharp differences in structure (bauplan) more or less synonymous with Cuénot's closed leaf. Yet, in describing the tree of animals, Haeckel (1868) makes comparative discussions of the four major lines, phyla (also called "types") echinoderms, arthropods, mollusks and vertebrates, connected to the worms (Vermes), which grew like isolated buds on four distinct points of the stem (the worms). The group named Vermes, the ancestor of four phyla that still exists as a fifth phylum, is a perfect paraphyletic group.

For Cuénot, the concept of stem is close to that of "transitory forms" (*formes de passage… espèce de transition*) (Cuénot 1940c: 224). Cuénot does not cite Gaudry who was the first paleontologist to draw Darwinian trees with connections between extant and extinct species based on Darwin's (1859) diagram (Gaudry 1866; see Tassy 2006, 2020). But his reasoning and examples are the same and lead to paraphyly. Gaudry (1873: 40) chooses the example of horses (Pernègre and Tassy 2014: 632), but Cuénot chooses a theoretical example. Let us take two successive groups **A** and **B**. A transitory form is a form that has many characters of **A** and a few characters of **B**. If the characters of **B** are not numerous or are unimportant from a physiological viewpoint, then the transitory form is kept in group **A**. In the reverse situation, the transitory form belongs to **B**. The arbitrariness of these kinds of decisions about important and unimportant characters is acknowledged by Cuénot in a Simpsonian way, where taste and feeling are crucial. As an example, Cuénot (1940c: 224) cites the extinct genus *Tritylodon* classified by authors as either reptile or mammal (the second choice is more appropriate, Cuénot adds correctly, on the verge of phylogenetic systematics): the concept of the primacy of derived characters and its relevance to monophyletic groups is not yet mature.

Evidently the concepts of bauplan and type—referred to by Darwin as the "amount of modifications"—have several consequences, for they: (1) pervade the conception of the monophyletic "Stammbaum;" (2) fail to apply Darwin's conception of a genealogical group derived from his description of the process of evolution and his definition of the phylogenetic system; (3) confuse the notions of clade as a taxon and clade as a category; (4) misinterpret Darwin's famous sketch of "descent with modification" in his *On the Origin of Species*, which does not show any axis.

In his last synthesis, Cuénot extends his discussion on the genealogical tree and the history of the word clade (Cuénot and Tétry 1951). He also cites the word "cladoma" (but incorrectly refers to Haeckel (1866)). He outlines a notion that he had briefly introduced earlier (Cuénot 1940c: 226) on the nodal group, that is, the stem group ("groupe nodal") that gives rise to diverse specialized orders ("divers ordres

spécialisés"). For Cuénot and Tétry (1951: 21), this group is basically "a species, a founding or nodal species, or archetype, from which all of the extinct and extant forms forming the clade under consideration may be soundly derived" ("*espèce primordiale, fondatrice ou nodale, ou encore* archétype*, de laquelle il est intelligible de faire deriver toutes les forms éteintes et actuelles qui composent le clade considéré*"). This "archetype" is defined as the "reconstruction of a species that in fact once lived" (*reconstitution d'une espèce qui a réellement vécu*) (Cuénot and Tétry 1951: note 1 p. 21). As a "reconstruction" this archetype is close to the concept of Hennig's *Grundplan* (or hypothetical ancestral morphotype). The «archetype is the leafstalk» (*L'archétype est le pétiole de la feuille cladique*) (Ibid.). In other words, the archetype is the connection. As such, this archetype is an alternate interpretation of the axis that is so pregnant with meaning in Cuénot (1940c), a step towards monophyly and sister group relationships. In any case, the clade is still an elusive concept. Fixed and standardized views and definitions will come with Huxley (see below).

To conclude, Cuénot, like Haeckel, did not fully understand Darwin's description of a genealogical group.

Huxley's grades and clades

Bernard Rensch's (1959) *Evolution Above the Species Level* (a translation of the 1954 edition of *Neuere Probleme der Abstammungslehre*) is a study of the process that yields both grades and clades (in the modern sense). Evolution as understood by Rensch has two sides: phylogenetic branching and progressive evolution or, respectively, cladogenesis and anagenesis (although no taxonomic outcome of these concepts is discussed by Rensch). This is endorsed by Julian Huxley, a theoretician of biological progress (Huxley 1923, 1942) who adds a third process, stasigenesis.

The three processes are defined in three articles by Huxley (1957, 1958, 1959). Huxley (1958: 21) cites Darwin's *On the Origin of species*, neither for the definition of genealogical group, nor for the concept of co-descendants (that is, the embryo of the concept of monophyletic group), but rather for having perceived the existence of the three main types of process leading to diversification.

Huxley (1957: 454) writes: "*Cladogenesis* I have taken over directly from Rensch to denote all splitting, from subspeciation through adaptive radiation to the divergence of phyla and kingdoms… Rensch has used *anagenesis* to denote advance in general organization or perfection of some major function: I propose to generalize it to cover all types or degrees of biological improvement, from detailed adaptation to general organizational advance…. I therefore propose the term *stasigenesis* to cover all processes leading to stabilization and persistence of types and of patterns of organization, from species up to phyla." These processes result in the taxonomic entities introduced by Huxley in the same three articles: "Cladogenesis results in the formation of delimitable monophyletic units, which may be called *clades*; and anagenesis results in trends in improvement… Finally stasigenesis results in the formation of delimitable and persistent anagenetic units, or *grades*" (Huxley 1957: 455).

These definitions were new, even if the words were not. Even grade ("Grad") appears in Haeckel (1866) as Dupuis remarks (1988: note 5 p. 54). However, Haeckel's use of this term following that of von Baer applies to ontogeny: "type and degree of individual development" (*Typus und Grad der individuellen Entwickelung*) (Haeckel 1866: 10). A grade is a "level of the formation of organs" (*dem Grade der Ausbildung*). In both cases, evolution and ontogeny, it is a level, that is a comparable concept. In regard to grades as well as clades, Huxley does not rely on any previous papers. As a consequence, he does not mention Haeckel's original concept of clade. Moreover, one may ask if Huxley, like Cuénot before him, was only aware that the concept of clade had been discussed through fluctuating definitions and approximations.

For Huxley, a grade is an anagenetic unit, that is, a certain level of progressive evolution (Huxley 1957: 455, 1958: 24, 27). When anagenesis stops and stasigenesis allows the evolutionary level to persist, then the grade is evident. Yet, organisms which share this level can form a polyphyletic pattern of descent. According to Huxley (1957: 455, 1958: 27) the grade Homotherma (birds and mammals) is "certainly" polyphyletic ("diphyletic"), while the grades Reptilia and Amphibia "possibly" are. On the contrary, a clade is a monophyletic unit of any classificatory level (Huxley 1957: 455, 1958: 27). Curiously, the burden of pre-Darwinian classification is at work in Huxley's drawings of the relations between grades and clades. In each of his papers devoted to grades and clades Huxley is more interested by grades. These illustrations explicitly display direct ancestor–descendant relations between grades, such as the vertebrate traditional classes: Agnatha, Placoderma (conceived by Huxley as extinct ancestors of Osteichthyes), Osteichthyes, Amphibia, Reptilia, up to Homotherma (Aves and Mammalia) (Huxley 1957, Fig. 2 p. 455, 1958, Fig. 5 p. 28). As such, they are all paraphyletic, except Aves and Mammalia. In any case, according to Huxley, these grades originated through cladogenesis. Hence, grades (not only clades) somehow originate from cladogenesis, contrary to Huxley's definition ("cladogenesis results in the formation of delimitable monophyletic units, which may be called *clades*"—see above). When Huxley tends to conceive the connection between process (cladogenesis) and pattern (clade), he somehow nullifies the specificity of the product (the clade) since the process produces everything including higher-level groupings based on similarity (grades). Because

Huxley's own evolutionary concepts are influenced by progressive evolution, they are neither entirely clear nor devoid of any confusion, to say the least.

One favorite example chosen by Huxley is that of *Homo sapiens*, classified as a grade in the category rank kingdom (Psychozoa), as well as a clade in the category rank family (Hominidae). As expressed by the title of Huxley's articles (1957, 1958), his reasoning is based on interpretations of evolutionary process, and not character analysis. As we now know, the story that followed is somewhat ironic. Evolutionary systematists will adopt the non-phylogenetic concept of grade to realize Darwin's prediction that: "our classifications will come to be, as far they can be so made, genealogies" (1859: 486). Yet, the introduction to Huxley's third paper is an authoritative phylogenetic statement: "The aim of modern taxonomy as usually formulated is expressly to produce a classification which reflects phylogeny… and in which, therefore, groups are monophyletic" (Huxley 1959: 21). But, as Huxley emphasizes, it is a difficult task because convergence and parallelism are not easy to detect, especially "when the fossil record is poor" (Huxley 1959: 21). What does monophyletic mean? No methodological answer is given. Moreover, Huxley adds that polyphyletic groups (as grades) are "quite 'natural' since they bring together related forms which have all achieved the same grade of organization" (Huxley 1959: 21). What does "quite natural" mean? Huxley's tentative clarification between phylogeny (clade) and evolutionary level (grade) is thus negated. This conception of natural groups recalls that of Thomas Huxley (1880)'s evolution of mammalian orders when the same characters are hypothesized to having been acquired in parallel by the mammalian orders without any phylogenetic connection, that is, without common descent (see Wyss 1987; Tassy 1991).

Within the same collection of essays where Huxley explores his conception of grades and clades, Mayr explains the significance of categories from the species up to the kingdom. Although he conflated the concepts of taxon and category as was common at the time, Mayr (1958: 17–18) nevertheless asserts that common ancestry is the reason for grouping species in higher categories. Darwin (1871: 188–189; 195) had already emphasized that "the amount of modification undergone" (or "strongly marked difference") is perhaps less useful for revealing "true affinity" than the "resemblance in unimportant points," for the latter "reveal the old times of descent." Yet Mayr reaches the opposite conclusion: "Why is there essentially a morphological uniformity within a higher category, but in most cases sharp discontinuity between it and the nearest sister category?" (Mayr 1958: 18). This question relies entirely on the concept of similarity (amount of difference disconnected from relationships). Let us take one example. The Vertebrata (a taxon generally classified as a subphylum, that is, a clade as defined by Haeckel) includes, for example, the hagfish, elephant, and hummingbird. There is no morphological uniformity. And one may argue that the hagfish resembles the lancelet (subphylum Cephalochordata) more than the hummingbird. It is no surprise then that the clade as a monophyletic or genealogical group was ambiguously understood among adherents to the modern synthesis of the early/mid-twentieth century.

Moreover, evolutionary taxonomists felt that the branching pattern was less important than the number of characters departing from the ancestor, so the concept of clade was unimportant. Subsequently, they (Mayr 1974) also heavily criticized Hennig for his clear and unambiguous definition of a monophyletic group, that is, as a clade, in the cladist sense of the word (in fact a word that Hennig never uses).

The cladist's clade

Between 1926 (the year the word "taxon" was coined) and 1957 (the year that Huxley defined grade and clade), few evolutionary systematists had read Zimmermann's and Hennig's analyses of relationships, phylogenetic ordering, and monophyly, which were partly inherited from Naef (e.g. Zimmermann 1931; Hennig 1947, 1950; for Zimmermann and the lineage Naef-Zimmermann-Hennig, see Donoghue and Kadereit 1992; Williams and Ebach 2009; Willmann 2003, 2016). Not only Zimmermann's phylogenetic discussions were neglected (or ignored), but largely all of his major works in evolutionary biology published from the late 1920s up to 1943 (except perhaps the telome theory, see Beerling and Fleming 2007; see Simpson 1949). Yet, according to Reif et al. (2000: 67), "in a way Zimmermann singlehanded [sic] accomplished a synthesis many years before other synthesists."

Zimmermann and Hennig's phylogenetic renditions are based more on logics and graphs than on inductive scenarios compatible with a progressive view of evolution (logics is certainly not a side issue—see Farris 1983): a possible explanation for early misunderstandings or ignorance. Rather, the success of Huxley's grade and clade is due to the fact that most biologists and paleontologists believed that, as a co-founder of paradigmatic modern synthesis, Huxley could neither be wrong nor be improved upon. Mayr's conceptions are somewhat more problematic. In his introduction to *On the Origin of Species*, Mayr assures the reader that, "Darwin's conceptual framework is, indeed, a new philosophical system," devoid of a kind of "typological thinking [that], no doubt, had its roots in the earliest efforts of primitive man to classify the bewildering diversity into categories" (Mayr *in* Darwin 1964: xviii–xix). At the same time, Mayr (1974) argues continuously for ranking paraphyletic

reptiles as a grade in the category Class Reptilia; this option was criticized by Hennig (1974) as "typological thinking."

For us it is clear that Hennig's quest for subordinated monophyletic groups, hypothetical ancestral morphotypes, and hypotheses of synapomorphy, represents both pattern and process approaches. This is why evolutionary systematists who largely discard pattern approaches see evolution as a biological progress supported grades and paraphyly, and in the beginning underrated Hennig's (1966) contribution. Yet because of Huxley, the clade as a taxon became a major concept of phylogenetics, perhaps *the* major concept once its monophyletic definition had been agreed upon among biologists. This is a major concept, yet it is sometimes distorted, probably inadvertently, as in the case of the expression, "non-monophyletic clade" (Tavares et al. 2009: 272).

As far as we know, the last occurrence of the term clade as a category within systematic literature is found in Dubois (2006), who actually promotes an alternative to the *PhyloCode* by providing a historical list of category names of higher ranks. Haeckel's "Cladus" and "Cladoma" are listed in Dubois' "CS05" rank (= between phylum and class) (Dubois 2006: 212). But for rank CS05, Dubois selects the earlier name "circulus" (dated 1843), and discards the term "Cladus," "because it has often been used to designate any holophyletic [= monophyletic] group, whatever its taxonomic rank" (Dubois 2006: 218–219). This means that the cladistic usage superseded the earlier understanding of clade as a rank: the clade, when understood as a community of descent, is definitively conceived of by the scientific community as a taxon, not a rank. Moreover, many readers of Dubois (2006) and Williams and Ebach (2009) subsequently discovered that in the beginning the clade was one among the various ranked categories of classification: a large part of the clade history was unnoticed or underestimated.

Our conclusion is that the odyssey of the clade is a long-time research trying to find an answer to a basic question in the realm of evolutionary biology as well of systematics: what means phylogenetic content? From Darwin's community of descent up to the cladistic definition of the monophyletic group, this quest has been a painstaking task. The clade, as concept and word, was independently conceived three times: by Haeckel in 1866, Cuénot in 1939 and Huxley in 1957 with the same flaws. What may be learned through the years is the confusion between the two sides of phylogeny: the narrative or «story telling» of phylogeny understood as the history of the living beings, and the pattern of phylogeny understood as a hypothesis of relationships between the living beings. Confusion only stopped, at least in theory, during the second half of the twentieth century. It could have been much earlier. The roots of graph-theory go back to the eighteenth century with Leonhard Euler. Few exchanges if any can be found between mathematicians and naturalists during these remote times. Yet the concept of relationships was put by Darwin within a diagram where connections between species were approached together with the notion of propinquity of descent and a prefiguration of sister species relationships. This aspect of Darwin's descent with modification was underestimated. Haeckel, Cuénot, Huxley (and even Hennig) never explicitly rooted their conceptions of the clade or monophyletic taxon in Darwin's drawing of community of descent. This is perhaps the explanation of one century of difficulties and ambiguities.

History, as well as phylogeny, has to be reconstructed all of the time.

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