

PRACTICAL METHODS FOR THE MORPHOLOGICAL RECOGNITION AND DEFINITION OF GENERA, WITH A COMMENT ON POLYCHAETES (ANNELIDA)

✓ SERGIO I. SALAZAR-VALLEJO
Depto. Sistemática y Ecología Acuática
El Colegio de la Frontera Sur, Chetumal, México
savs551216@hotmail.com

ABSTRACT

There are very few publications dealing with methods for the morphological recognition of genera, and how they can be defined, in comparison to those available dealing with species issues. My objective is to provide a historical review, synthesize and discuss some ideas or practical procedures about this problem. Genera are recognized because member species depict a general morphological pattern, and usually one or a few diagnostic characters separate each genus from other similar genera. Human mind detects patterns by comparative morphology and this explains why experience is extremely important in taxonomy. Analogy is also involved, because by understanding how character patterns help recognizing taxonomic groups, these patterns can be extrapolated in less well-known groups. From an historical perspective, botanists and zoologists perceived or defined genera differently with some common considerations and procedures. Genera are natural groups, size-variable and shape-conservative, that are recognized by different cultures.

As explanatory hypothesis, genera are unstable and difficult to define because their contents are modified after the study of species from different localities; once planetary revisions are made, the resulting delineation is improved because variations are better understood or assimilated into current definitions.

A necessary step for this improvement is the standardization of the terminology for morphologic features, but planetary revisions are the only means to reach this goal. As in other fields in systematic zoology, the recognition of genera among marine annelids (polychaetes) relied in a comparative approach, after the standardization of the terminology for body appendages. The study of larger collections with specimens from distant localities helped to clarify the morphological patterns, but their evaluation sometimes drove to contradictory conclusions, such as a widespread acceptance of cosmopolitan species. Although there are several pending issues, there has been a progressive improvement, especially after the inclusion of additional methods, but more efforts are needed for taxonomic training, and for improving the job market.

“THIS ESSAY IS CONTRIBUTED IN THE HOPE THAT, EVEN IF ITS OWN ARGUMENTS ARE OF LITTLE VALUE, IT MAY, AT LEAST, INDUCE OTHERS TO INVESTIGATE THE SUBJECT ON MORE CORRECT PRINCIPLES THAN HAVE HITHERTO BEEN FOLLOWED.”

HUGH E. STRICKLAND, 1841



Keywords: natural groups, comparative morphology, experience, revisions.

Disclaimer. This review will not focus on philosophical or logical aspects; these issues have been included in several contributions such as Rogers (1958), Lubischew (1969), Callebaut (2005), Pavlinov (2011), Varma (2013), Nicholson & Gawne (2015), or the many contributions by Kirk Fitzhugh (<https://rancholabrea.academia.edu/KirkFitzhugh/Papers>).

INTRODUCTION

How to define a genus has remained a difficult question during at least the last 100 yr. One of the reasons for this is that in comparison with what has been written about species, or about how to proceed for describing species (Dubois, 2010), there are very few publications dealing with procedures regarding genera, how they can be recognized or defined (Dubois, 1988; Winston, 1999; Páll-Gergely, 2017). This historical review tries to fulfill this need and throughout it, statements are translated from the original language (mostly French).

This review starts by taking a look at the synthesis and proposal by Constant Duméril (1805) on the use of comparative methods. It is now easily available, and should be read by anyone interested in the subject (see below). His two main ideas were: 1) "When we think about the means how we acquire and develop knowledge, we note it is always as a consequence of a comparison" (p. vii), and 2) "The natural method ... by arranging the organisms in a most convenient series after their characters, could not establish this comparison, but by choosing between two propositions, becomes the main merit for the classification" (p. ix).

During many years, practicing taxonomists have followed precedent works or keys and apparently undeclared traditions (Agassiz, 1859:208), in a scenario that sometimes rendered contradictory conclusions. Not surprisingly, there are some unpleasant perspectives referring to the unstable delineation of genera (McGregor, 1921), or other ones pointing out to the relevance of taxonomists' expertise to define what a species or a genus could be (Regan, 1926:75). Consequently, these ideas stressed that taxonomic decisions were subjective or arbitrary, and even the reliance on experience was regarded as cynicism (Kitcher, 1984:308). This type of ideas or interpretations were probably due to inadequate means to overcome argumentations, combined with the fact that traditional procedures were not easily available, or that taxonomists failed to be explicit enough regarding his own methods, such that they cannot be easily followed or understood.

This lack of formal explanation generated some critics during the last century. For example, Anderson *et al.* (1923) expressed concern because "the value of the genus has been consistently and progressively lowered since it was first established ... tomorrow it promises to be but little more than a species." Ridgway (1923:371) regarded genera as natural, and that they were scientifically characterized; however, "many of the current genera are, in their composition, really not natural genera at all, but more or less heterogeneous lots of species which resemble one another ..." (Ridgway, 1923:373), and that "evolution of the genus concept is directly the result of progressively increasing knowledge resulting from continual additions to the material studied" (Ridgway, 1923:374) something that was anticipated by Macleay (1821:89). Some of these approaches can be explained because Linnaeus proposals were not easily available; however, a brief

synthesis about his methods was available in English and that, despite some contrary opinions, he indicated that genera were natural (Ramsbottom, 1938:197).

Rogers & Appan (1969:614) concluded: "the ability to perceive patterns is the most significant quality differentiating an inefficient taxonomist from a competent one." However, how to become a competent taxonomist was not explained, although it can be understood by studying precedent publications and especially about the means to proceed in large taxonomic efforts. Some abridged ideas for coping with genera in Botany can be found in Sivarajan & Robson (1991:107 ff), and Stuessy (2009a:163 ff). The following sections include information about genera in Botany as a means to provide a general framework, or to emphasize some ideas; these inclusions are by no means exhaustive, but selective. There seems to be no similar efforts for zoology, despite some excellent synthesis (Panchen, 1992), and this explains why there follows a larger section on this field.

In this contribution, Kemp's (2016) hypothesis about taxa are followed. They are: 1) organisms fall into discrete clusters of similar morphology that differ from other clusters, despite the environmental continuum they inhabit; 2) these morphospace units include all characters representing groups of species; 3) groupings are determined by closely similar ecological niches; and 4) "correlated progression is the most important mechanism for maintaining integration while permitting major evolutionary transitions."

Definition (<https://en.wikipedia.org/wiki/Definition>) is a statement of the meaning of a term; definitions can be intensional if they provide the essence of a term, or extensional if they list the objects that a term describes. In this review, definitions are regarded as intensional. When definitions try to encompass genera, they become diagnosis. In this review, Hamilton & Wheeler (2008:339) are followed by recognizing that although "species are not infrequently described by reference to a single trait when more diagnostic traits are unavailable (footnote) ... taxon definition, description, and diagnosis are usually made by more than one (kind of) character." See Dubois (2017) for an extensive analysis of the use of description, definition and diagnosis.

Further, a critical evaluation about the perceptions and procedure to recognize and define genera will be presented. The main objective, however, will be on zoological genera with some examples taken from marine annelids or polychaetes, a group that has caught my interest during the last 40 years. This is because their affinities have been problematic, not only for generic delimitations, but for matching traditional supra-generic groupings with those resulting from modern analytical methods. Further, there will be an opening section on pattern detection, followed by a review about relevant historical achievements, to show there were indications about how to deal with genera, but they were overlooked or rejected, probably after a superficial reading or understanding. I agree with Mary Winsor (2009:43) that "for the sake of taxonomy's reputation ...

its past achievements should be accurately understood and appreciated." A different, recent perspective is available elsewhere (Cambefort, 2016).

PATTERN DETECTION

There are many studies on how the human mind can detect patterns in nature and how this capability has helped us during evolution (Raven *et al.*, 1971:1210). Some of the easier to find are Sinha (2002), or di Carlo *et al.* (2012), and the successful books by Kahneman (2011), or Kurzweil (2012) are worthy readings. There is a lot of information available in internet but at least a couple of blogs will help improve its understanding (see Wadhawan 2014). It should be no surprise that in an experiment on identification of foreign plants, three taxonomists working independently, agreed upon the differences between genera and species (Anderson, 1957:261), or between crabs and lobsters among experts and naïve non-experts (Reindl *et al.*, 2015:33). De Hoog (1981: 780) indicated that "the human mind ... has the ability to intuitively produce classification by holistically sensing a 'Gestalt'" because intuition "is effective from the first view of the organisms, and evolves during the entire data collection."

A short overview about pattern recognition is now needed. Recognition means to know again and this repeated identification or knowledge depends on our perception, which means how the inputs we receive become meaningful. How we perceive depends on two issues (<http://www.s-cool.co.uk/a-level/psychology/attention/revise-it/pattern-recognition>): template matching hypothesis and feature detection model. In the first, incoming stimuli are compared against templates in our long term memory; if there is a match, the stimulus is identified. In the second, however, stimuli are broken down into their component parts for identification, and it allows a degree of variation in the stimuli.

This is partially explained because of feature detectors. These are brain cortex cells devoted to visual information, and are sensitive to the orientation of contour lines. This is a biological explanation but they cannot account for the effect of context on perception. The other explanation must include the fact that our perception of patterns is modified by our expectations, or knowledge, and this is a top-down processing, whereas perception based upon features of the stimuli are rather bottom-up processes. Some additional ideas are available elsewhere (Salazar-Vallejo, 2019).

Bartlett (1940:349) indicated that two processes operate for distinguishing genera: Analysis and Synthesis. The analysis stems from the fact that as people gathers more experience make finer distinctions such that different names are needed "for newly distinguished entities which have previously been called by the same original name. The original name becomes generic in its application; variously qualified it provides the basis for specific names." On the contrary, genera are set up by synthesis "as language becomes clumsily rich in separate names for closely

similar things, there is a tendency toward grouping or classification under the same name on the basis of newly perceived similarities."

Despite some computational or refined techniques for analysis of morphological similarity, no consensus has been reached on this ground, and even some recent publications have pointed out persistent problems with the available methods for analyzing phylogenetic affinities (Fitzhugh, 2012; Fitzhugh *et al.*, 2015:691-692).

FROM LINNAEUS TO WALLACE

As indicated above, the contributions by Linnaeus (Fig. 1) were misunderstood for a long time, despite some timely critical synthesis or translations trying to clarify his methods (Rose, 1775; Palàu y Verdèra, 1778; Svenson, 1945). Among others, Stevens (2002), Winsor (2003, 2006), Müller-Wille (2005, 2007, 2013), Barsanti (2011), Müller-Wille & Charmantier (2012), have shown that Linnaean methods were not essentialist and that his genera and species concepts were descriptive and polytypic, nor following logical divisions but tried to find natural groups by induction, and based upon empirical methods including making systematic comparisons (collation).

The Linnaean taxonomic method was briefly explained as an introduction (*Ratio operis*) to the first edition of *Genera Plantarum* (Linnaeus, 1737), and it was later expanded in his *Philosophia Botanica* (Linnaeus, 1751), which was translated at least to English (Rose, 1775) and Spanish (Palàu y Verdèra, 1778). As emphasized by Müller-Wille (2005:60), this *Ratio operis* had been completely ignored by historians of Biology. There are three recent translations available, one in French (Hoquet, 2005), and two others in English (Müller-Wille & Reeds, 2007; Cambefort, 2016), and by following the original sequence and numbering, the main Linnaean aphorisms related to genera can be synthesized as follows (mostly after Müller-Wille & Reeds, 2007):

1. All our knowledge depends on a comparative method (collation).
6. Genera and species are natural (repeated in aphorism 8). "We have to study the limits of genera with attentive and diligent observation, since it is very difficult to determine them *a priori*, even though this work takes effort."
8. "According to our own understanding, (we) must submit ourselves to the laws of nature and, with diligent study, learn to read the features."
10. "Each genus is circumscribed by true limits and terms, which we call generic characters."
15. Generic characters can be artificial, essential and natural.
16. Artificial characters are imposed on a genus to facilitate its identification.
17. Essential characters supply the genera with a single and most characteristic feature.
18. "I therefore propose natural characters ... which exhibit all obvious and common features in fructification" such as flower's calyx, corolla, stamens, pistils, or fruits.

19. Four mechanical principles must be also incorporated: number, shape, situation and proportion.

Before leaving Müller-Wille & Reeds (2007) translation, let me emphasize an aphorism (25) which is especially relevant for scientific communication: Express your ideas with “as few words as possible” and prefer weighty words instead of pompous, eloquent phrases.

On the other hand, it must be indicated the relevance of Pitton Tournefort (Fig. 1) for the Linnaean *Ratio operis*. Tournefort provided definitions for 700 genera and 9000 species (; Leroy 1956:351), integrated into 22 classes, and by explaining his method he stated (Tournefort, 1694: 20): “the distribution of species under their true genera is not arbitrary ... the author of Nature ... has imprinted a common character in each of its species which will help us guide arranging them in their natural setting.”

Tournefort also indicated the three main methodological questions (pp 23-25): 1) “For establishing genera, to know if the needed characters should be found in the five ordinary plant parts ... or if it is enough to have such characters in four of them, in three, in two, or in a single part;” 2) “If we should regard in all genera the same parts, and to the same number of parts; or if it is allowed in certain genera to rely indistinctly over some of them over the other (parts);” 3) (unnumbered) “The parts of the plant must be examined one after the other.” In summary (p. 28) he indicated that his method: 1) relies on flowers and fruits (emphasized as absolutely needed in p. 30), 2) seasonal observations are needed to confirm their characters, and 3) some other characters are supplementary, if already employed to separate genera.

Vasilyeva & Stephenson (2012:26) made some additional remarks relevant for delineating genera from Linnaeus’ *Philosophia Botanica*: “*Essentialis character unica idea distinguit Genus a congeneribus sub eodem ordine naturali*” (Linnaeus, 1751:128, Sect. 187), which they translated as: The essential character as a *unique idea* distinguishes a genus from those of the same kind included in the same natural order. Vasilyeva & Stephenson further explained that by *unique idea*, Linnaeus referred to “all genera that are distinguished simultaneously and somehow serves as a cohesive agent at the generic level.” And that this means that genera “are comparable in level only when they are distinguished by states of the *same character set*,” and these characters should be fundamental for delimiting genera.

In order to have a more complete perspective of Linnaean ideas, two other aphorisms, already discussed by Barsanti (2011), deserve to be repeated here.: Aphorism 77 in *Philosophia Botanica* (Linnaeus, 1751): Plant affinities can be shown as a landscape in an orographic map; and 2) in pages of his Inquiry on Plant Sex (Linnaeus 1790:127-128; transl. by Barsanti, 2011): “it cannot be doubted that new species appear through hybridization. From this we learn that the hybrid is, for the medullary substance, the internal parts of

the plant and the reproductive organs, an exact image of the mother but, for the leaves and other external parts, an image of the father. These considerations give new bases for the study of nature ... In fact, it seems to follow that the various species of plants belonging to the same genus were, originally, a single plant, and arose from it by hybrid generation... The botanist should think that the species of each genus are only as many different plants as there were associations with the flowers of a single species and that, therefore, a genus is nothing but a certain number of plants derived from the same mother by the work of different fathers.”

Michel Adanson (Fig. 1) was a French naturalist with an interest for plants, and made five trips to Senegal where he collected many specimens and, at the same time, amassed an interesting collection of mollusks that helped him propose a different approach to taxonomy (Adanson, 1757). His volume included two parts, being the first one a chronological history about his trips, and the second a critique of the state of mollusk taxonomy, which deserves some comments because he made relevant recommendations. For example, for characters he stated (Adanson, 1757, 2:xx): “I have not assigned particular characters to each genus that I propose, because they are arbitrary, sometimes vary, and are often equivocal once new species are discovered; I have provided an exact and complete description; this will contain the best characters, once they are assembled together, those that are arbitrary and those that are real.”

Regarding molluscs and to improve the observation of as many details as possible, he introduced dorsal and ventral views of each gastropod shell, and recommended illustrating gastropod shells as in living condition, not upside down (Adanson, 1757, 2:xxvi). He then presented a detailed account of shell and body parts and tried to standardize the terminology for the corresponding structures regarding variations due to size, age or sex.

Five years later he finished the study of the Senegalese plants he had collected, and made a complete catalogue of plant families (Adanson, 1763). The monograph has four parts: a) Historical methods and systems in Botany; b) Current state of Botany; c) Proposed families; and d) How to improve Botany. In the first part he divided previous classification methods into universal or general, and referred to them later as artificial and natural (Adanson, 1763:xciv), as has been done before, whenever they include all known species, or only those present in a certain region or country. In the historical account, he praises Tournefort (Adanson 1763:xxx) because Tournefort “has introduced in Botany order, purity and precision, by proposing very smart and certain principles to establish genera and species, and by founding on these principles the so-far easiest and most precise method.” On the contrary, he regarded Linnaeus method as problematic, artificial and restricted to plant fructifications (flower and fruits), and presented some critics along several pages (Adanson, 1763:xxxix-xxvii).

It is interesting to note that in the second part, Adanson (1763:civ) praised Tournefort because he was "the first who assigned, in 1694, satisfactory generic characters common to many plant species, based upon the fructification parts, and provided the rules ... to fix the limits."

Adanson (1763:civ-civi) further defined Tournefort's plant genera as: "an assemblage of many species resembling each other in all parts of fructification or only on those essential features after Tournefort, and by all six parts of fructification after Linnaeus."

He also (Adanson, 1763:cxxiii) regarded that a hierarchy of characters was false, such that for classes there are some characters of fructification (flowers and fruits), for genera all or most essential characters of fructification, and for species those other characters not belonging to fructifications. He recommended instead, regarding all parts of the plant for defining the characters (extended from page clv). Adanson also noted that plants could be recognized by name, by definition or by description. For definition (or diagnosis) he stated that: "the definition is a short note, an abridged table with the main characters of an object compared to (or not at all) another one," whereas: "The description is a detailed account of all parts and qualities of an object compared to (or not at all) to another one! (Adanson, 1763:cxxiv). It is remarkable and regretful this distinction has not been properly understood, even by some contemporary authors (Cifelli & Kielan-Jaworowska, 2005).

Nevertheless, and quite contradictory, for the third part of his monograph Adanson explained his own method. His three main points were that (Adanson, 1763:cliv-clivi):

1. All methods are defective and cannot be natural because they are based upon a single part or a small number of plant parts.
2. Genera or species are not static.
3. Characters that have been regarded as natural are not at all.

He then argued for regarding all plant parts as the only means to reach a natural method, that this idea was proposed by Buffon, and that he reached this conclusion after the study of Senegalese materials. He later presented the 58 (65 actually) different arrangements of families based upon single characters (Adanson, 1763:ccii-cccvi).

Johan Christian Fabricius (Fig. 1) made a significant modification to the Linnean system for insects, because Linnaeus used wings to separate his classes. Fabricius, however, relied upon the feeding appendages (Fabricius, 1775, Prolegomena, 5th page): "Such that a new idea to use the feeding appendages as characters for classes and genera was tested. They were constant and sufficient and genera became more natural."

For his monograph on insect genera, Fabricius provided some additional brief explanations (Fabricius,

1776, Prolegomena, pp 9th to 10th) emphasizing the relevance of the feeding appendages together with other characters such as antennae for lepidopterans (page 6th), and metamorphosis, larvae or pupa features (page 7th), and habitat (page 8th) for other groups. Other contributions by Fabricius are detailed elsewhere (Tuxen, 1967). Macleay (1821:490-494) reviewed several Linnean or Fabrician taxonomic principles regarding some beetle genera, and rejected the selection of single morphological features to define them.

Jean-Baptiste Lamarck (Fig. 1) proposed a slightly different approach. He also believed that genera were not natural groups, but defined by taxonomists; in his contribution to the *Encyclopédie Méthodique*, he indicated that plant genera were "one type of division established among plants to facilitate their knowledge, and that result from particular species assemblages under a common feature" (Lamarck, 1786b:630). He also indicated that it was Caspar Bauhin the first to propose generic names based upon shared characters, but Tournefort improved this procedure by using floral and fruit characters, and that the method was later refined by Linnaeus by using calyx, corolla, stamens, pistil, pericarp and seeds (Lamarck, 1786b:630-631). After giving an extensive account of some Linnean problematic genera, Lamarck proposed some guidelines for establishing them (Lamarck, 1786b:634) and two of them were: 1) Genera should not have too many species and be based upon constant and well-defined characters; 2) Genera should not be too reduced.

Antoine-Laurent de Jussieu (Fig. 1) belonged to a family of French botanists working in the Royal Botanical Garden in Paris (Williams, 2001). This explains part of the long name of his monograph (de Jussieu, 1789), which unlike Lamarck's *Flora of France*, who wrote in French, it was written in Latin. de Jussieu (1789:lx-lxi) concluded that characters have different relevance. He thought that characters should be weighted or calculated, such that a constant feature would be equivalent to some variable ones. Consequently, characters were regarded as belonging to one of three types: a) primary uniform, or essential because they were constant and uniform whenever they are present; b) secondary subuniform or general, which are uniform but can exceptionally vary; and c) tertiary semi-uniform or variable. Further, genera belonging to the same family must be recognized by the presence of essential characters, although sometimes they can be recognized by using general or variable features, and this is made after a comparison within the same family, and after making a hierarchy of characters.

André Marie Constant Duméril (Fig. 2), as indicated above, explained he used a comparative method and dealt with the animals for which he listed 976 genera and introduced many names; for example, *Nomenclator Zoologicus* lists 106 genera attributed to him (although they have 1806 as their date instead of the correct one of 1805). Duméril's method was explained in the preface (pp vii-xxiv) and besides those



Figura 1. Personajes y fuentes. Tournefort <https://www.sciencephoto.com/media/77897/view/joseph-de-tournefort-french-botanist>, Linnaeus https://en.wikipedia.org/wiki/File:Carolus_Linnaeus_by_Hendrik_Hollander_1853.jpg, Adanson <http://www.bihrmann.com/caudiciforms/div/hist2.asp>, Fabricius https://en.wikipedia.org/wiki/Johan_Christian_Fabricius, Lamarck <https://www.biografiasyvidas.com/biografia/l/lamarck.htm>, de Jussieu <https://wellcomecollection.org/works/jauwc4uq>.

ideas indicated above, some other ones are worth repeating:

- a. (p. ix) "The natural method indicates us the families and the respective disposition of genera, whereas the system, by using different means, establishes the needed inversions, continually provides us the most developed objects, under some features, those absolutely opposed conforming particularities."
- b. (p. ix) "The study methods of Botany, so productive to determine species, have served as a model to this work."
- c. (p. xiv) "While granting that for every class the character lies in an essential and important organ, whose modifications would also sustain the proposal of orders and genera, the only evidently resulting advantage is that descriptions will be always short and comparative."
- d. (p. xvii) "The general disposition of this work will be appreciated once it is known its arrangement is as a large synoptic table where, in a series of twin, successive branches, all known animal genera are exposed."

- e. (p. xviii) "The synoptic tables drive to the names of genera whose essential character often lies in a simple indicative note, but always constant and easy to be detected. These divisions and subdivision are so arranged, to its surplus, such that it is rare that for determining a genus more than eight consecutive observations are needed ..."

The objective of Alphonse de Candolle's (Fig. 2) for his *Elementary Theory of Botany* was that " (1815:77) "it became necessary to compile the principles of the natural method, not to follow this or that author, but to take advantage of all recent observations." This is especially relevant because: (p. 77) "What can be learnt is reduced to some general ideas, that the First-Class Botanists exposed in their conversations rather than in their books, and that are even a number of opinions that Bacon called floating, because they were never exposed with a method, and they have never been seriously discussed."

De Candolle's book has an introduction and three other parts: 1) Plant taxonomy or theory of classifications, 2)

Phytogeography or theory of descriptive Botany, and 3) Botanical glossary, or knowing the terms. By combining the Greek words for order (*taxis*) and for law or rule (*nomos*), he coined taxonomy (p. 19). He indicated that "the theory of natural classification essentially includes three parts: 1) the estimation of the relative importance that must be given to the organs compared against each other; 2) the knowledge of those instances that could mislead us regarding the true nature of organs; 3) the evaluation of the importance that must be given to each perspective under which an organ is regarded" (de Candolle, 1815:78).

A species was defined (de Candolle, 1815:157) as "the collection of all organisms that resemble more to each other than to other organisms, that by reciprocal fecundation, can produce fertile offspring, and that they reproduce in such a way that we can, by analogy, regard that all of them have resulted from a single organism." In turn, a genus was defined as (de Candolle, 1815:183): "the collection of species that have a remarkable similarity in the arrangement of their organs." He added that genera (p. 184) "cannot be regarded but as aggregations of similar species united by a shared character."

De Candolle (1815:186) emphasized that "genera should be proposed upon characters that, compared between them, have had the same relevance; as a consequence, in a family, any character that has been used to separate some genera, should retain the same importance in all similar cases." And that (p. 189) "genera must always be based upon the importance of the characters, and not on the number of included species".

De Candolle (1815:201) indicated, about how to display the arrangement of organisms, that "Linnaeus was the first, with his usual sagacity, to compare the plant kingdom to a map." de Candolle (1815:203) added that "In nature there are no continuous series, the organisms group along very unequal distances, such that it is impossible to display their true characters along a linear order, and that it is only through tables (keys), being general or partial, that one can grasp an idea about the general pattern of nature."

For de Candolle (1815:259) a character is "the particular feature upon which we can distinguish an organism or a collection of organisms. A character is specific, generic, ordinal, or classical, if it can distinguish a species, a genus, an order, or a class."

Between de Candolle and de Mirbel (Fig. 2), the contributions by Henri Cassini must be summarized (Stevens, 2009, citations therein). Cassini proposed 324 genera and hundreds of new species, and preferred to see nature as a three dimensional network, which is more complex than a map. Stevens (2009:36) concluded this is the 'substitution of the linear by the reticulate method.' Cassini also concluded that 'hypotheses were indispensable when talking about analogies, and to make the natural relationships of things clear' (Stevens, 2009:37).

Charles-François de Mirbel (1832:472) regarded positive characters as constant or variable, and emphasized the use of positive, constant characters to unite different groups; he also noted that some of these characters are present singly, or forming groups (p. 473). For genera, he indicated (p. 477): "Since genera result from very real organic analogies, the adopted generic classification by botanists is based upon nature." Regarding the hierarchical nature of characters, he concluded (p. 481) "It is also evident that usually most family characters would be useless for distinguishing genera, because they must be found in all genera in the family ... and it follows that each organism in any family has three types of characters: the family characters, the genus characters, and the species characters."

In the American continent, Constantine Rafinesque (Fig. 2) provided some interesting perspectives. After 40 yr of experience he had proposed about 500 genera, which eventually grew up to 2700, and 6,700 species in over 1,000 books and publications (Chambers, 1992:6; Warren, 2004:159). Rafinesque insisted that "no proper genus can exist without a character applying to all the species it contains." For distinguishing them it would be mandatory "to frame none but *positive* and *exclusive* characters of a permanent nature in contrast - and besides to shorten long descriptions by avoiding repetitions, or merely stating how a genus may differ from another, which always implies that they agree in everything else." (p. 10). Rafinesque (1836:39) also pointed out that "genera are the collective groups of species, that agree in the characters of the fructification. No species belongs to a genus unless it agrees with all the others therein included." He also indicated that genera are natural groups (repeated in page 95). He proposed 50 rules of nomenclature by 1814, and revised them later (Rafinesque, 1836:81). Several referred to genera and their definition are interesting. For example, his rule 1: "all species united by some essential definite characters must form a genus" (rewritten as 4: all plants "possessing similar characters must form a genus, and bear the same name"), and 7: "if a genus has been made upon erroneous characters, it must be annulled, and united to the genus that bears the real character."

Rafinesque also concluded that (1836:93-94): "... the importance of floral organs stands in the following order: 1) Pistil and fruit ... 2) Stamens (and their insertion) ... 3) Perigone or floral covering ... 4) Fruits and seeds ... 5) Accessory parts..." And that "it is very important neither to invert this order of values, nor to ascribe more power to any than really can be ascertained." Regretfully, most Rafinesque's ideas and proposals faced rejection or ignorance by his peers, but his contributions are now better understood and appreciated (Mosquin, 2012).

In Zoology there were two contributions where Hugh Strickland (Fig. 2) was involved. In the first, Strickland (1841) explained the true method for discovering natural systems and rejected some proposal based upon the then popular ideas of symmetry of the natural world. He indicated (p. 184) that the natural system was "the arrangement of species according to the degree



Figura 2. Personajes y fuentes: Dumeril <https://pixels.com/featured/andre-marie-constant-dumeril-french-mary-evans-picture-library.html>, de Candolle <https://www.pictorialpress.com/timeline/pre-1900/alphonse-de-candolle/>, Mirbel <http://dicci-eponimos.blogspot.com/2010/01/mirbel-charles-francois-brisseau.html>, Rafinesque <https://dailyjstor.org/the-raffish-and-radical-constantine-samuel-rafinesque/>, Strickland https://es.wikipedia.org/wiki/Hugh_Edwin_Strickland, Agassiz https://es.wikipedia.org/wiki/Louis_Agassiz#/media/Archivo:Louis_Agassiz.jpg.

of resemblance in their essential characters" and that "for the degree in which one species resembles another must not be estimated merely by the conspicuousness or numerical amount of the points of agreement, but also by the physiological importance of these characters to the existence of the species." And inadvertently repeated de Candolle's (1815) idea on distance, and anticipating Mayr's ideas on discontinuities or gaps (see below), Strickland indicated that species should be arranged "at greater or less distance from each other, in proportion to the degree of resemblance." For Strickland, this process resembled that of a geographical survey (p. 189), and that (p. 190) "the natural system may, perhaps, be most truly compared to an irregularly branching tree, or rather to an assemblage of detached trees and shrubs of various sizes and modes of growth." Such that "may the natural system be drawn on a map, and its several parts shown in greater detail on a series of maps." He concluded (p. 192, Fig. 3) "no linear arrangement, whether adopted in a museum, a catalogue, or a descriptive work, ever can express the true succession of affinities: such an arrangement, therefore, is necessarily in great measure artificial, and, if sanctioned by custom, may still be adhered to. The true order of affinities can only be exhibited (if at all) by a pictorial representation on a surface, and the time

may come when our works on natural history may all be illustrated by a series of maps ..."

The other contribution had a wider nomenclatural perspective. The Strickland committee (Strickland et al., 1843:263) dealt with some practical issues, and provided some indirect recommendations. For example, in the comments for article 3 they indicated that "when a genus is subdivided into other genera, the original name should be retained for that portion of it which exhibits in the greatest degree its essential characters as first defined." Further, in the remarks for article 11 (p. 267) they indicated: "Two things are necessary before a zoological term can acquire any authority, viz. *definition* and *publication*. Definition properly implies a distinct exposition of essential characters, and in all cases we conceive this to be indispensable, although some authors maintain that a mere enumeration of the component species, or even of a single type, is sufficient to authenticate a genus." The recommendations of the Strickland Committee were not followed with enthusiasm. On the contrary, Agassiz (1871:23, footnote) regarded them 'by no means satisfactory' and that "the recent revision of these rules shows how impossible it is to lay down general instructions intended to be retrospective and prospective; to apply

them to times of which the scientific spirit was so totally different from our own".

Louis Agassiz (Fig. 2) undertook a titanic effort for his Contributions to the Natural History of the United States; the first volume included a thorough study about classification, which was published separately as well. He was already well-known by his monographs on fossil fishes and by preparing the *Nomenclator Zoologicus*. Agassiz emphasized that despite many discrepancies, and contra Lamarck (1809) all taxonomic groups were natural, and tried to provide means to define them; he defined genera (Agassiz, 1859:249) as "natural groups of a peculiar kind; and their special distinction

rests upon the ultimate details of their structure". A few lines above, he indicated that his definition has been taken from Latreille, whom he regarded as the most prolific author on the subject of genera. It must be indicated that Latreille's monographs were systematic arrangements of crustaceans and insects (Latreille, 1796, 1806; Dupuis, 1974), but the means he followed for defining his genera were not explained, beyond an indication that he was following Fabricius, his mentor (Latreille 1808). This was implicit in the standardized presentation of characters for each genus.

Charles Darwin (Fig. 3) has a widespread influence in many issues in Biology, and made a large taxonomic

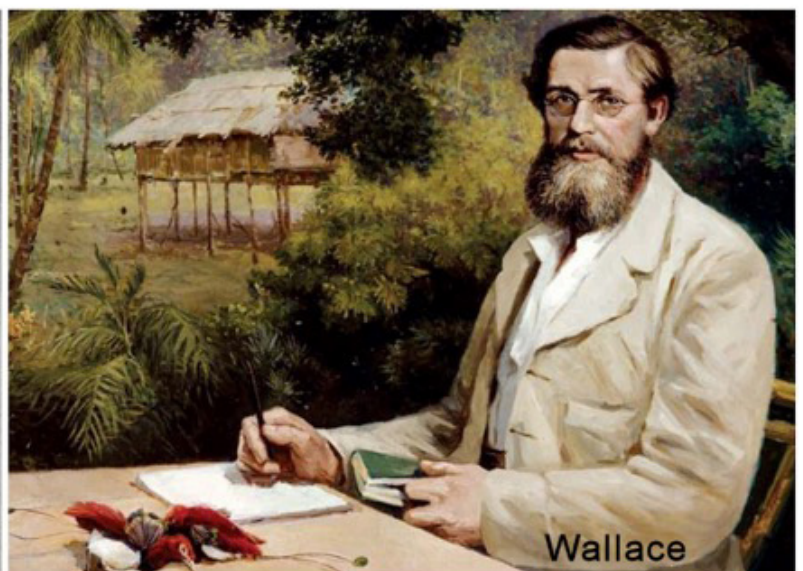
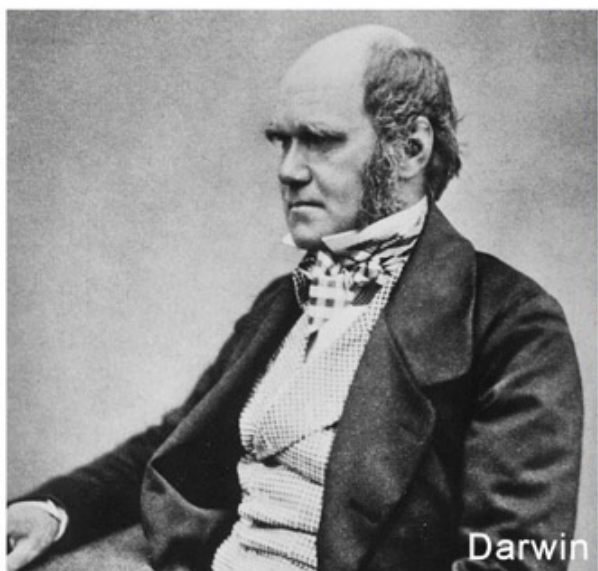
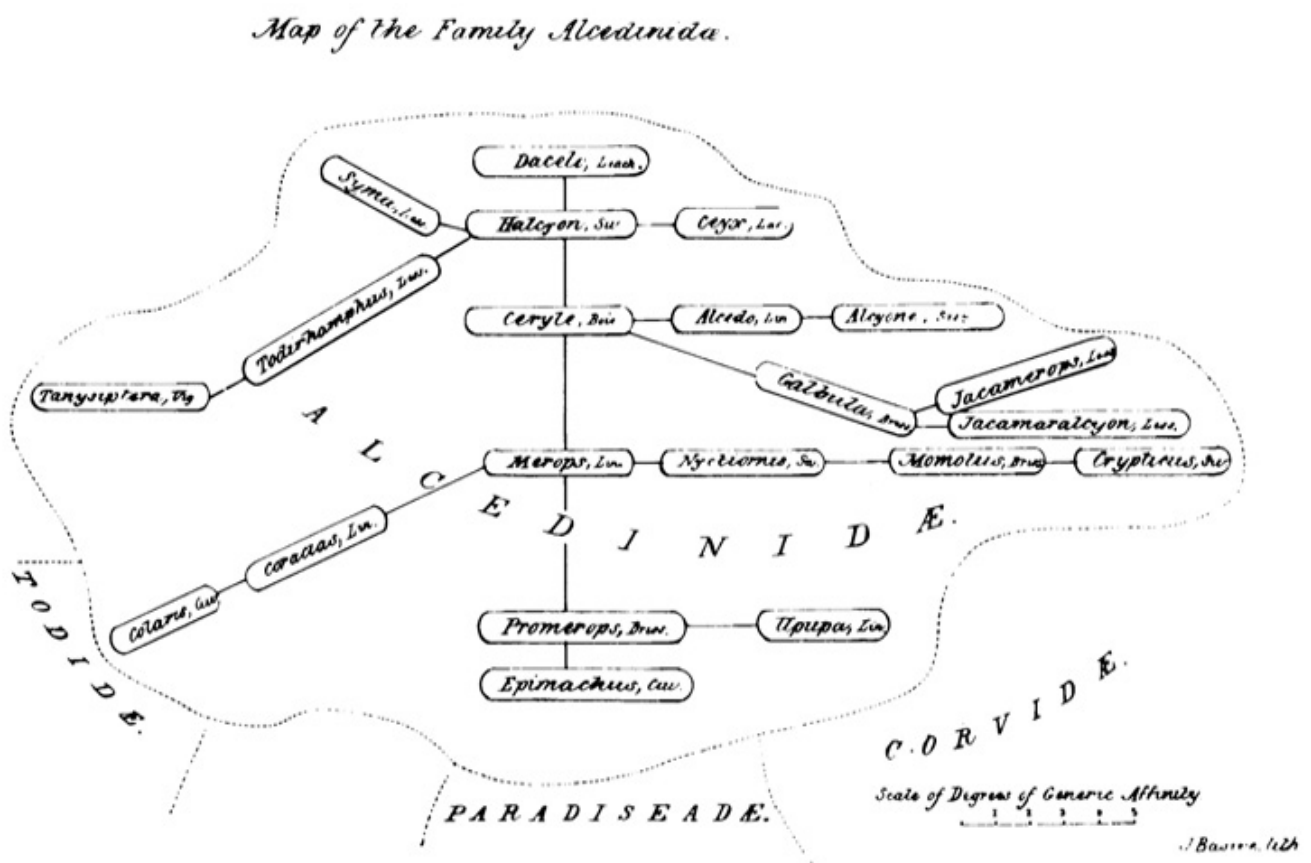


Figura 3. Mapa de afinidades genéricas según Strickland (1841), Darwin https://en.wikipedia.org/wiki/Charles_Darwin#/media/File:Charles_Darwin_seated_crop.jpg, Wallace <https://www.newscientist.com/article/mg22029421-100-alfred-russel-wallace-a-very-rare-specimen/>

effort by revising the *Cirripedia*. In the *Origin* (Darwin, 1859, chapter 13) he referred to classification and other relevant concepts. He said that (p. 413-414) "propinquity of descent, - the only known cause of the similarity of organic beings, - is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications." And a few pages expanded it twice; first (p. 420): "the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking." And second (p. 423): "the principle of inheritance would keep the forms together which were allied in the greatest number of points."

He later added (p. 415) that "almost all naturalists lay the greatest stress on resemblances in organs of high vital or physiological importance ... But their importance for classification, I believe, depends on their greater constancy throughout larger groups of species; and this constancy depend on such organs having generally been subjected to less change in the adaptation of the species to their conditions of life."

Regarding characters, Darwin emphasized that (p. 417) "The importance, for classification, of trifling characters, mainly depends on their being correlated with several other characters of more or less importance" and probably thinking about Aristotle's ideas that "a classification founded on any single character, however important that may be, has always failed; for no part of the organization is universally constant." He later commented on the work of other naturalists doing classifications, including Augustus St. Hilaire, that (p. 418) "If they find a character nearly uniform, and common to a great number of forms, and not common to others, they use it as one of high value; if common to some lesser number, they use it as of subordinate value." Further, Darwin added (p.426): "when several characters ... occur together throughout a large group of beings having different habits, we may feel almost sure, on the theory of descent, that these characters have been inherited from a common ancestor. And we know that such correlated or aggregated characters have especial value in classification."

Quite interestingly, he cited de Saint-Hilaire, and only cited him for the whole chapter, but failed to read his advertisement (de Saint-Hilaire, 1840): "Every time that I have published any special work, I have scrupulously cited the authors to whom I have borrowed anything."

Darwin further explains his perspective (p. 434): "We have seen that the members of the same class, independently of their habits of life, resemble each other in the general plan of their organization. This resemblance is often expressed by the term 'unity of type;' or by saying that the several parts and organs in the different species of the class are homologous." Di Gregorio (1982) made a compilation about zoological

classification in Victorian Britain, and his paper is relevant to those interested in these features and their development in the United Kingdom.

A couple of definitions by Alfred Russel Wallace (Fig. 3) deserve to be included here: A species "is a group of living organisms, separated from all other such groups by a set of distinctive characters, having relations to the environment not identical with those of any other group of organisms, and having the power of continuously reproducing its like. Genera are merely assemblages of a number of these species which have a closer resemblance to each other in certain important and often prominent characters than they have to any other species" (Wallace, 1895:441).

XX CENTURY

In the dawn of the New Systematics, which tried to combine genetics and taxonomy, there were three meetings in the United States. They are presented separately because they were part of botanical or zoological conferences, and because their conclusions were slightly different. Further, unlike their XIX-century predecessors, modern taxonomists tended to be more specialized in their research efforts, and consequently reading or incorporating ideas or methods from different fields became a rather uncommon practice. However, it must be indicated that after 260 yr of taxonomic studies, no paradigm shift seems to have ever happened (Stuessy, 2009b), but a chronological presentation might help understand how we get where we are.

BOTANY

There were two major scientific meetings organized jointly by the Botanical Society of America and the American Society of Plant Taxonomists in 1937 and in 1952; they resulted in two series of contributions. The first meeting produced five contributions, although an early critique about the instability of genera had been made by Hitchcock (1921:251), and species had been declared as non-existent (Bessey, 1908:218). Harley Bartlett (1940) provided the historical development of the genus concept, and showed it was an important component in many cultures (see Atran, 1987 for an impressive revision); he also indicated that for Linnaeus the genus was a natural entity, comprising species morphologically similar because of a "real genetic relationship" (Bartlett, 1940:362).

Edgar Anderson (1940) made a questionnaire for taxonomists trying to find out what were the major ideas around the genus concept. From 50 taxonomists, 26 indicated genus was the more natural unit (than species), and 31 indicated that genera originate in the same way as species (Anderson, 1940:366; Barraclough, 2010:1810). He also noticed that "there is a very strong correlation between monographic experience (as opposed to floristic one, *mih*) and a trend to emphasize that genera are more natural groups than species ..." (Anderson, 1940:368). It is noteworthy that

trying to help improve decision making, Ronald Fisher took some of Anderson's data and developed his method of discriminant functions, which relied upon statistics for quantitative characters and tell apart different populations; regretfully, the method was not followed by Anderson himself (Hagen, 2003:361).

Greenman (1940) provided a perspective from Morphology. It is no surprise that for him "our present system of classification is ... the result of the experience of many generations; and it rests primarily on comparative morphology" (Greenman, 1940:371). In reference to the effect of revisions he confirmed previous conclusions (Hitchcock, 1921:251) and indicated that "many genera, as now delimited in literature, have been greatly altered from the original interpretation... It not infrequently happens that generic names, which have been reduced to synonymy, upon a more intensive study have to be revived and given coordinate generic rank" (Greenman, 1940:372). He further suggested (p. 373) that for formulating our concept of a genus we should "take into consideration not only comparative morphology, but also geographical relationships." A formal method was recently proposed to address this type of analysis (Zapata & Jiménez, 2012).

Earl Sherff (1940) tried to provide some means for delimiting genera. First, he emphasized the need for planetary or monographic revisions and for a corresponding perspective (Sherff, 1940:376, 377), which was right, indeed, and continues to be a pressing need (Kocielek & Williams 2015). Second, however, he disliked splitting of genera "solely upon the presence or absence of one or more supposedly diagnostic characters" (p. 378), which is interesting. Third, he rejected the pressure to "turn to experimental taxonomy, especially in its ecological and genetical aspects" (Sherff, 1940:380). This anticipated a pressure over taxonomists to become 'more modern,' or more involved with other environmental scientists, which has been slightly modified nowadays, if any at all (Wheeler, 2008).

The last contribution dealt with changing generic concepts (Camp, 1940). Camp regarded the genus (p. 381) as "a unit expressive of close phyletic relationship." However (p. 382) "there is no equality in the standard delimitation; that in one group of plants, those characters which scarcely constitute specific differences, in another may be sufficient to separate the genera." This, as indicated above, has been already anticipated by Adanson (1763:cxxii). On the need to incorporate or generate other sources of information, Camp concluded that (p. 387) "... we as taxonomists must face the issue. Either we must take our place with those who are attacking the fundamental problems of biology, or we will degenerate into mere namers of specimens. We must either confine ourselves to the grinding out of a few lines of miserably inadequate Latin with *sp. nov.* and our names hooked onto it, or be biologists." And (p. 388): "are we, the taxonomists, then, to be stuck forever with concepts of the limits of genera as defined by Linnaeus, by Bentham, or even Asa Gray?"

Turrill (1942a-c) made an interesting historical account of botanical taxonomy and phylogeny in three major

contributions. In the first part, the historical development is presented and it is remarkable that French and German quotes were not translated; botanists should be very fluent in those languages, indeed. The second part dealt with taxonomic and phylogenetic concepts and criteria, and with the data used in classification and phylogeny. The third and last part dealt with the classification and phylogeny in major groups, an analysis of the logical against phylogenetic classifications, as they were defined in those times, and phylogenetic diagrams.

Rogers McVaugh (1945:15-17) made eight recommendations for recognizing genera and indicated that (page 15) "most of the suggested procedures are fairly obvious, but I am not aware of any previous attempt to evaluate and integrate them." The original wording was repeated elsewhere (Gillis, 1971:89; Grasshoff, 1975:71-72), and the recommendations can be synthesized as:

1. Characters. Prefer qualitative morphological characters ("nature of plant-parts, or the presence or absence of some distinctive attribute") rather than weaker characters ("changes in number, shape, position or attachment of parts"); weighting characters was assessed and recommended by McNeill (1972).
2. Homogeneity. The most important generic criterion is the homogeneity in many characters of its member species.
3. Standards and boundaries. Proposals must be framed by the "diagnostic features of the more inclusive genera" and "any segregate genus should be sharply delimited."
4. Stability. The "... position of any genus increases rapidly in proportion to the number of differentiating characters..." and "... if it comprises two or more species, ... if the group have (sic) a distinctive geographical range..."

The second botanical meeting indicated above produced six contributions and included an invited essay (Lawrence *et al.*, 1953). Just (1953:103) proposed large scale generic diagnosis, and international cooperation. He also indicated that 'the genus is admittedly the most workable and comprehensive taxonomic unit' and that 'most genera represent well defined natural units.' He then repeated the then new definition by Buxbaum (Just, 1953:105): 'the genus is the sum total of species belonging to a phylogenetic unit recognized as such by the unity of its morphological type (generic types).'

Bailey (1953) and Eames (1953) emphasized the study of anatomy for revising families, with the latter focusing in flowers. Rollins (1953) proposed cytogenetic studies and noted that during the previous symposium, a negative perspective had been presented. Cave (1953) incorporated some approaches of cytology and embryology for delimiting genera.

Lawrence (1953) proposed some means to attain integrative definitions of genera, especially in difficult

families, for incorporating anatomical, embryological, or other type of data. His recommendations included promoting specific areas of research, to collaborate with specialists in those fields, to publicize the fulfilling of these missing details, and to gather materials to be sent to specialists for approaching these research needs.

Mason (1953) revised the relevance of plant geography to plant taxonomy. He indicated that (p. 155): "the greatest value of plant geography to the taxonomist is in the utility of its principles as a set of limitations to theory and as a foundation for the logic of his interpretations". He then moved to criticize the studies on areography by recalling his previous conclusions that "the most significant aspect of the area of any interbreeding population is the set of environmental conditions that prevail and to which members of the population are preadapted" and for discontinuous distributions, he added "we must think of distributional problems in terms of the dynamics of divergence".

De Hoog (1981:780) stated that "the most accepted axiom of taxonomy is that order exists and is expressed in character correlation. The main criterion of goodness of a given classification, predictivity, is based on this axiom." Some other issues related to defining genera, species and varieties in diatoms (Round, 1997), or plants in general (Malik 2017) deserve a further analysis for interested parties.

ZOOLOGY

The zoological perspective came out a few decades later of the first Botanical meeting indicated in the preceding paragraphs. The New York Academy of Sciences organized a special issue dealing with the definition of genera, species and subspecies in vertebrates (Bogert, 1943). For genera, Bogert (1943:108) indicated that "criteria for genera cannot be defined on any grounds ..." Let's start with some of the contributions for this issue, and then proceed as the idea has been modified as taxonomic methods were progressing.

Dunn (1943:123) dealt with amphibians and reptiles. He indicated that "genera are matters of opinion, personal arrangements of species," and that for distinguishing them the characters "are all of the same status. There is no distinction between individual, varietal, subspecific, specific and generic characters." However, in the following pages he modified his perspective (Dunn, 1943:129): "The arrangement of ... (species) into higher categories is done on a basis of morphological similarity. The original purpose was to afford a convenient classificatory basis as an aid in identification and in reference. Therefore, the criteria for genera are convenience and relationship." He later added (Dunn, 1943:130) that because ecological divergence is usually correlated with morphological change, the genus is based upon morphology and ecology. This is especially important because, for example, there is a positive correlation between latitudinal range of bivalve genera and its species content, both globally and within regions (Krug *et al.*, 2008).

Next came Carl Hubbs, an ichthyologist with an impressive experience on freshwater fishes (after the study of over one million specimens), and who mainly focused on subspecies, varieties and introgressions. Hubbs (1943:110) indicated that "systematic characters must have a genetic basis", that for ranking organisms as subspecies or genera, "we must be arbitrary", and that "it is bad science to deny that decisions are arbitrary". His final statement was that there are "no objective criteria for genera" (p. 121).

Ernst Mayr discussed the criteria for birds. He defined the genus (Mayr, 1943:138; Mayr & Ashlock, 1991:135) in opposition to species, which emphasize distinctness, as being collective and emphasize similarity or relationship. However, he insisted: "nobody has ever found an objective criterion for the genus" and that he preferred one admitting its subjective nature. He even proposed a definition (p. 139): "A genus is a systematic unit including one species or a group of species, presumably of common phylogenetic origin, which is separated from other similar units by a decided gap." The size of this gap was expected to "be in inverse relation to the size of the unit", which was proposed to avoid recognizing many monotypic genera (see below).

Mayr also pointed out some important facts for genera: 1) species are arranged in groups separated by small or large gaps; and 2) this is a natural phenomenon. However, there are no taxonomic characters "that prove generic distinctness" (p. 139). There was a similar perspective among mammals (Hall, 1943), and the definition for genera was later modified by Mayr *et al.* (1953:50) into "the essential property of genera is morphological distinctness (usually correlated with the occupation of distinctly different ecological niches)."

The most cited contribution in the issue was by George G. Simpson. He was a paleontologist, working especially on mammals, and made several important contributions to taxonomy (Olson, 1991). For understanding and defining genera, Simpson (1943:154) proposed: "if the subgroups do not intergrade in one well-marked character, or preferably in several characters, it is proper to infer that the subgroups are species and the group a genus." Further, by analyzing how to proceed, he indicated (Simpson, 1943:155) "every working taxonomist knows that some morphological differences do tend to be diagnostic of certain levels of classification, but the problem of determining this correspondence is essentially empirical and the values are properly assigned only *a posteriori*. Once so determined, there may be a degree of probability, not certainty that similar values can be assigned *a priori* in studying allied forms." A lengthy explanation was provided elsewhere (Simpson 1945), but as indicated by Vasilyeva & Stephenson (2012:28), this *a posteriori* determination has been already indicated by Linnaeus himself (Linnaeus, 1751:100, Stat. 159).

Simpson was especially influential during 30 yr because of the two editions (1939, 1960) of his *Quantitative Zoology* (Hagen, 2003:356); the second edition was

completely revised by Richard Lewontin, who promoted that uniting statistics and biology “was a common commitment to hypothesis-testing and probabilistic thinking” and he included a chapter on analysis of variance (Hagen, 2003:365).

These contributions in Botany or Zoology overlooked an important paper by Vavilov (1922), now famous because of his ideas about the center of origin of cultivated plants; he lost against Russian genetist Lysenko and died of starvation in prison. However, his publication was ignored probably because it was based upon variations or polymorphism in cultivated plants, despite its catchy title as “*The law of homologous series in variation*.” The paper runs through 45 printed pages providing plenty of details and analysis of several issues that helped him reach relevant conclusions, and were inadvertently incorporated as a means to understand morphological patterns and their regularities. Thus, he concluded (Vavilov, 1922:75): 1) genera “more or less nearly related to each other are characterized by similar series of variation with such a regularity that, knowing a succession of varieties in one genus ..., one can forecast the existence of similar forms and even similar ... differences in other genera.” 2) “whole botanical families in general are characterized by a definite cycle (series) of variability which goes similarly through all genera of the family”, and trying to explain the differences he added (Vavilov, 1922:76): 3) “genera consequently differ ... by their specific complexes of morphological and physiological nature. These differences we shall call radicals. There might be radicals for ... genera, and whole families too.” He also made some comments extending these ideas to animals (Ivanov, 1922:84): “Exterior characters of many animals show an evident subordination to the law of homologous variation ... The systematical division of many genera ..., shows in some cases a clear series of homologous variation.”

It is noteworthy that a precedent was long established among French zoologists and was called parallel variation (Portères, 1950), which was originally proposed, albeit briefly, by Isidore Saint-Hilaire (1832:380-381, footnotes): “The species in a genus, the genera in a family, the families in an order, and even the orders in a class ... form almost constantly ... parallel series with those preceding and those following ...”

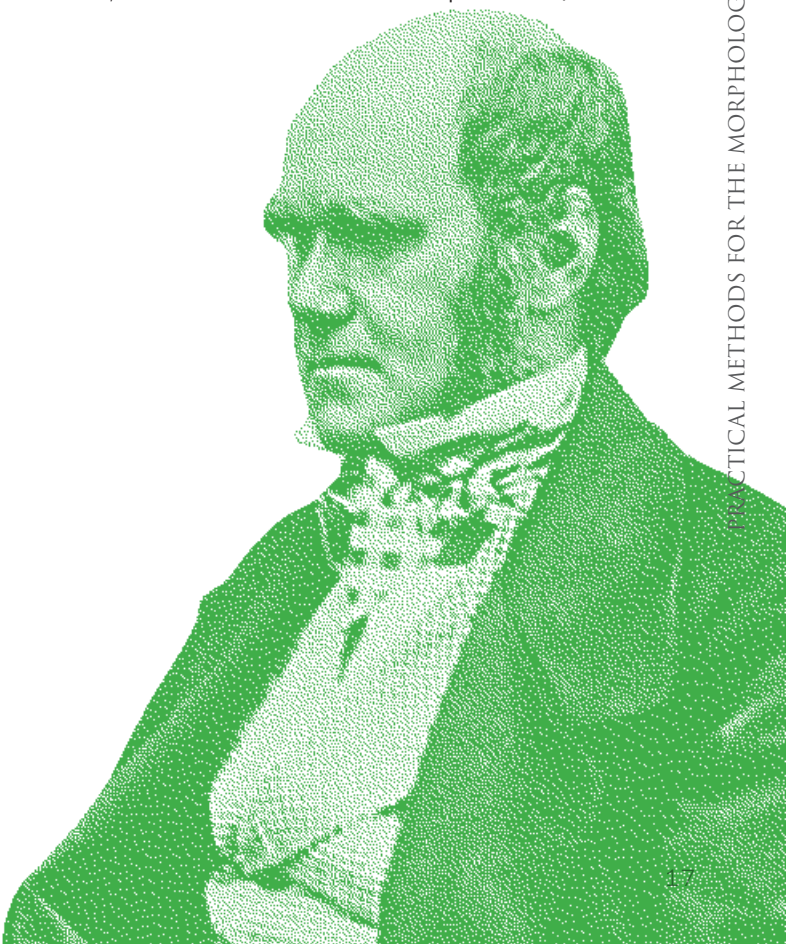
Folta (2015) assessed molecular-genetic extensions of these ideas, and found partial support; for those traits controlled by single genes, it works fine, whereas in multigenetic traits, it is less precise. Further, Vasilyeva (1999) and Vasilyeva & Stephenson (2010) have been enthusiastically promoting a more widespread use of Vavilov principles in the taxonomy of fungi. In particular, their recommendation for a critical evaluation of character hierarchy, and then by generating a table for a combinational analysis of the main diagnostic features, filling the cells with matching taxa, helps finding out which could be synonyms or deserving independent generic status (Vasilyeva & Stephenson, 2010:49, Fig. 2; Salazar-Vallejo, 2020).

SPECIES PER GENUS

One means to explore if genera are natural units is to analyze how species are distributed among genera, and if there is a common pattern. It has been shown that the number of species per genus relationships in plants or animals show a striking similarity that can be explained by power laws or as fractals (Bock & Farrand, 1980; Burlando, 1990, 1993; Minelli et al., 1991; Newman, 2005; Krug et al., 2008; Strand & Panova 2015; Sigwart et al., 2018).

Genera having one or a few species are more abundant than those having many species; this pattern is confirmed from classifications made by different taxonomists, working on different character sets, and on different groups of organisms. Williams (1951:171) concluded that “there must be some corresponding order in the natural relations of species and genera.” Another interpretation is that this numerical pattern may also reflect the development of the taxonomic knowledge for a certain group; since taxonomists look for patterns and for their anomalies, and once the latter are detected, they would be named and frequently set into distinct, separate genera.

Other taxonomists could have reached similar conclusions and introduced different names for other monotypic genera. It is after revisionary works that this type of problem is detected and hopefully solved. Nevertheless, some genera could remain monotypic just because of their unique combination of characters (Strand & Panova, 2015); on the other hand, taxon age and ecological diversification can explain species richness (Stadler et al., 2014) and species per genus distributions have a real potential to reveal diversification dynamics (Foote, 2012:135; see Stevens, 1997 for an alternative explanation).



These species:genus numerical proportions also fit a logarithmic series (Williams, 1951:172). However, because more than a single series could be used, no classification is necessarily better, but all may be correct (Williams, 1951:175), and “the relative relationships that we call species, genera, etc., are real - but the point at which we draw the line is a question of personal opinion.” Clayton (1972) supported the same perspective.

Without any attempt to deal with the long debate about what a species is, let's refer to Arthur Cronquist (1978) interesting critique of the biological species concept, and his operational approach, later known as the morphological species concept: “the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.” It is interesting that Seifert (2014) reached a similar conclusion for his pragmatic species concept: “a species is a cluster of organisms which passed a threshold of evolutionary divergence. Divergence is determined by one or several operational criteria described with adequate numerics. A single conclusive operational criterion is sufficient. Conflicts between operational criteria require an evolutionary explanation. Thresholds for each operational criterion are fixed by consensus among the experts of a discipline under the principle of avoiding over-splitting.”

ZOOLOGICAL GENERA

After the proposal by Willi Hennig (1966), all taxa should be monophyletic in a phylogenetic classification. This was a proposal for refinement of taxonomic practice to deal with the problem of grouping similar species, or species groups, that have also improved our understanding of evolutionary relationships among organisms (de Queiroz & Gauthier, 1992). However, because there are many different options to group similar taxa, the Linnean hierarchy was regarded as inadequate and there were proposals for abandoning it, whereas some others have pointed out some means to improve the Linnean hierarchies and to retain them. Other perspectives are the recognition of holophyletic instead of monophyletic groups, and that paraphyletic units are common and widespread, together with several different options for speciation (Hörandl & Stuessy, 2010). The essential difference is between process and pattern and a refinement of their formulation, or at least a better understanding, should be mandatory (Envall, 2008).

A.J. Cain was uncomfortable with the Linnean system and criticized it from his own perspective about Aristotle, although later in life he modified his approach (Winsor, 2001). Cain (1956:107) indicated “most of our genera are not natural units but merely represent a stage of classification above that of the species, in the sense that many are merely easily keyed-out groups and thus artificial ...” He then added (Cain, 1956:108) “...the genus cannot now be regarded as a naturally discrete group either in relation to its ancestors and descendants, or at any one time. It is not necessarily definable by one single peculiar attribute, nor are its constituents monotypic, equivalent, essentially merely subdivisions of it, or themselves wholly discrete. It

is monophyletic, but purely positional in rank, and a collection of phyletic lines, not an entity subdivisible into species.”

He made some other criticisms from a logical perspective (Cain, 1958). For example, he indicated that for defining genera, Linnaeus (Cain, 1958:148) stated: “The *essential character* of a genus is that which gives some characteristic peculiar to it, if there is one such, which will instantly serve to distinguish it from all others ...the *factitious character* is one that distinguishes a genus from all others in an artificial order and is used only as a succedaneum until the natural classification can be discerned.” From a practical perspective, he added (Cain, 1958:150): “... the overworked taxonomist, required to get out such a classification, will inevitably use the most striking characters as basis for his “definitions” because *they will be the most easily described in words*, and they may then assume a wholly disproportionate importance to his classification.” Returning to definition of genera by Linnaeus, Cain indicated that (Cain, 1958:158): “... each genus differs in (at least) one particular attribute from its nearest relatives (in accordance with Logical Division) and must be the smallest group of species.”

Robert Inger made an extensive study of Philippine amphibians and then tackled the problem of defining genera (Inger, 1958). He indicated that genera have been regarded as a difficult taxonomic category, probably because the genus is a synthetic group, whereas the species is an analytic one, and that taxonomists have delimited genera on morphological grounds, disregarding the function for the observed structures (Inger, 1958:371). The alternative method must take into account the functionality and adaptive value of characters, already indicated by Strickland (1841:184), in terms of genetics, biomechanics, and natural selection, and this implies that characters have different relevance for adaptation, and because of this difference, they should not be treated as equal to each other (Inger, 1958:373 ff). He concluded (p. 383) that there were three advantages by defining genera upon complex adaptive features: 1) such that each genus represents “the same kind of entity: a distinct mode of life and a distinct evolutionary shift”; 2) they would allow “predictions of habits and ecology that test taxonomic conclusions”; and 3) “species interrelationship is maximized.”

Probably inspired by a growing trend in quantitative biology led by, among others Hutchinson (1957), Legendre & Vaillancourt (1969) proposed a mathematical model for defining genera and species. Their definition for genus was (page 247): “a category including only species that are naturally related by monophyletism (genetic concept); this category may also be arbitrarily delimited so as to correspond to the intuitive idea that one has of an evolutionary peak that is distinct from any other closely related peak (evolutionary concept).” They then introduced a mathematical model emphasizing distance methods but without an empirical test of it. Despite other contributions on the same argument (Legendre, 1971, 1972), the proposal has not been followed at all. In fact, it has been shown that taxonomic decisions can rely upon univariate or multivariate analysis (Ohler & Dubois, 1999), such

that further refinements are not really better than simpler methods.

Clayton (1983:150) tried to clarify the use of the genus concept. First, he indicated that the “morphological evidence for the existence of species clusters is sufficiently compelling to ensure the(ir) universal acceptance” and that the “morphological relationships are judged by estimating the degree of overall similarity between species, similarity being expressed in terms of shared character states.” He further added that “despite our failure to find an objective criterion ... species clusters of varying distinctness exist in nature.” Clayton’s (1983:151-152) operational rules for defining genera were:

1. Characters are ranked, albeit subjectively, to recognize species clusters;
2. These species clusters must be relatively distant to each other, but there is no way to define the distance;
3. Genera must be marginally well-cut, but there are always some intermediate forms;
4. Size of cluster depends on convenience; and
5. Species tend to be densely packed and analogy is important to define how densely species will be grouped.

Stevens (1985:460) recommended that “when groups are being compared, the comparison should be between characters of the basal lineage of the groups, not between all characters occurring somewhere in them.”

Lemen & Freeman (1984:1219) were “fascinated by the apparent tendency of members of a genus to have the same shape (body pattern, *mihi*) in contrast to the great differences in shape among genera at the family level.” They also noted that “the high morphological similarity of congeneric species would reflect the ecological pressures of adaptive zones, *sensu* Simpson (1944; Dumont *et al.*, 2012), to confine morphological divergence” (Lemen & Freeman, 1984:1221). Trying to explain this, they used the information about size and shape of three families of bats and subjected them to three different evolutionary models. This is relevant because body size has an extremely high adaptive importance, by indicating the operation of environmental conditions (Maurer *et al.*, 1992:951; Barraclough *et al.*, 1998:752). These models were defined as uni-modal, size-coupled/size-decoupled, and saltational. In the first, changes in morphology through time have a normal distribution; the second is a complex combination between some size-dependent changes, where all characters have a similar direction of change, and size-decoupled changes, where characters become decoupled and change independently. The saltational model resembles the size-coupled change, but differs by having a larger magnitude of change. Lemen & Freeman (1984:1234) concluded that genera are size variable and shape conservative and that the decoupled/adaptive zone model explains these groups. Further, they think that “evolution proceeds as a two-step process: one, diversification in size within one shape group, and two, decoupling of correlated

characters to form new shape groups that may in turn diversify in size.” They listed some relevant properties (Lemen & Freeman, 1984:1236):

1. Decoupled or adaptive zone groups (genera) will differ in size along an allometric curve;
2. Genera will be shape conservative but not always monophyletic;
3. Genera may overlap, especially if divergence jumps are small; and
4. Rates of coupled and decoupled events determine both number of species per genus, and the shape diversity in each family.

Alain Dubois (1982, 1988) extended the biological species concept to genera, defined genera as evolutionary units, and indicated that the defining criterion for genera was the interbreeding of its species. This sounds interesting but likewise the biological species concept, it applies only to those organisms whose reproduction and descendants can be detected and evaluated. This is hardly usable among marine invertebrates, where colonial corals are probably among the best studied species, but most others are barely known after their original description, or those available as preserved museum specimens.

Armand Maggenti (1989) commented upon genera and families as natural groups. For genera, he followed Mayr’s definition emphasizing gaps between groups of species and that (p. 4): “a genus will have common features that facilitate recognition” and that: “as a phylogenetic unit, the genus differs from similar and related assemblages by reflecting an ecological unit that is adapted to a particular mode of life.”

Warren Allmon (1992) listed three working definitions for genera: 1) phylogenetic, 2) phenetic, and 3) hybridization. The latter has been proposed by Dubois (1982) and, as indicated above, cannot apply to fossils or preserved organisms. The phylogenetic definition regard genera as monophyletic clades which can be separated by at least one distinct, derived character or synapomorphy (Fransen 2002); this approach has been shown to be relevant in many retrospective studies of generic classifications (Kawano 2000). The phenetic definition regards genera as clusters in morphological space, separated from other clusters by many differences as already indicated by Mayr. Allmon (1992:151) added that “the phenetic concept of genera expresses the common definition of many taxonomists and field naturalists (...): different genera look different, and are usually readily distinguishable by relatively unsophisticated hand examination.”

For lucanid beetles, on the other hand, Kawano (2000) concluded that genera are quantitatively describable biological entities regarding mandible allometry and dimorphism. This evolutionary trend involving allometry of ornaments or weapons is also present in other animal groups (Kodric-Brown *et al.*, 2006). Vinarski (2013:45) recently compiled the available

information and concluded that a synthetic concept for genera should include morphological similarity, phylogenetic affinities, and ecological occupation of an adaptive zone. A more traditional study involved the assessment of morphological features for inferring phylogenies (Clarke, 2011), and the main conclusion is that morphologic characters are relevant, especially because for most species molecular data would be very difficult or impossible to obtain. Some of these morphological characters might become key innovations causing faster diversification rates (Barracough, 2010; Garbino, 2015).

Maruvka et al. (2013: abstract, box) have developed a SEO (speciation-extinction-origination) model which "supports the consistency of generic boundaries based on morphological differences between species" and that "although taxonomic groupings are manmade, they nonetheless reflect natural evolutionary processes." On this same ground, Eronen et al. (2010) concluded that morphological "traits are the means by which organisms interact with their environment." More recently, Ezard et al. (2016:3) would add that genera are: "in one sense, a crude index of morphological disparity through time."

POLYCHAETE GENERA

In the following abridged historical account for polychaete genera, the contributions of Grube and three French taxonomists must be analyzed. Lamarck, Savigny and de Quatrefages made several contributions in invertebrate zoology and only Savigny attained widespread recognition during his life, whereas the two others faced indifference or open rejection because of their ideas. Unlike the French trio which dealt with several taxonomic groups, Grube concentrated on annelids and tried to cover all families (Roemer, 1880; Zaddach, 1880).

After Linnaeus (1758), Lamarck (1818) and later Savigny (1822) proposed several groups of annelids, including genera, based upon both comparative morphology and standardized terminology for body appendages. De Blainville (1828:422) indicated how to proceed: "The proposal of genera is supported by considering different organs in each order and family; but it is in general by the particular arrangement of cephalic appendages, pharynx armature, parapodial appendages and of those at the end of body."

It might seem enigmatic how Lamarck moved from being a botanist to become the founder of invertebrate zoology. His achievements in evolutionary theory are also very important. On this ground, he was also capable to refine his ideas and change his mind about species and major groups' relationships (Gould, 2000). Because Lamarck made some contributions in hydrology and meteorology, he had a cosmic approach (Stafleu, 1971) and his life achievements are really impressive. For example, he was a bank employee while preparing the *Flore Française* (publ. 1778), then botanist in the *Jardin des Plantes* for 15 years, and from 1793 he became a professor of zoology, when he was 49, in the *Muséum d'Histoire Naturelle, Paris*.

The three volumes of the *Flora of France* were written in French, as indicated above, and all species were arranged in dichotomous or almost always dichotomous keys, which made it a very successful contribution and strengthen a tradition in taxonomic works. It must be emphasized that keys usually follow the Aristotelian principle of the 'Excluded Middle' such that only extreme conditions are used (Stearn, 1959:16), and that the charactes included, since Linnaeus, are either essential or synoptic. Stearn (1959:18) stated that "an essential character (*nomen specificum essentiale*) is a single character enabling the species to be recognized by it alone", whereas "a synoptic character (*nomen specificum legitimum*) mentions several features which are diagnostic when associated but not so when taken singly." There were some earlier dichotomous keys published about 100 yr before (Griffing, 2011; Voss, 1952), but they did not have the same impact and widespread use as those made by Lamarck.

The transformation of Lamarck into a zoologist was through the study of mollusks. He had been an avid collector and made two contributions about mollusks for the *Encyclopédie Méthodique*, and another one about the classification of shells in 1798 and 1799, respectively. His series of publications on other invertebrates started in 1801, when he introduced the theory of biological transformism. Stafleu (1971:401) thought that Lamarck arrived to this level of synthesis because he had a good understanding about geology and how relevant was the changing earth surface, and by understanding that by extension, these changes might also be present in living organisms.

After Stafleu (1971:410) the development of Lamarck's contributions to taxonomy were also presented in the *Encyclopédie*; for species, he wrote: "In Botany as in Zoology, the species is necessarily made by the assemblage of similar organisms, which are perpetuated by reproduction" (Lamarck, 1786a:395). This stems from earlier ideas by Buffon (1753, 4:384-385), and even farther back to Cesalpino who made a similar proposal in 1583 (Atran, 1987:202); these ideas would fit into what is now known as Mayr's biological species criterion. However, as indicated above, Lamarck regarded genera as "perfectly artificial, generated by the human mind". It must be indicated that Henri Milne-Edwards, for the second edition of Lamarck's invertebrates *opus magna*, continued using Latin diagnoses for each genus and introduced tabular or key formats for major groups, but not for all genera, as he had done, albeit quite roughly, for the crustaceans section in the same volume (Milne-Edwards, 1838).

Unlike Lamarck, who was rejected for his ideas on evolution, Savigny was widely acknowledged as a very good naturalist during his life. He participated in the French Expedition to Egypt and worked on several invertebrate and vertebrate groups; for example, he made a careful study of insect mouth parts and showed their homologies, what was later known as the Savigny Theory (Kellog, 1902; des Cilleuls & Girard, 1968:31). Regretfully, a serious disease made him abandon his research activities quite early, but he was recognized by the high quality of his contributions.

By the way, there are some problems trying to define the publication date of the corresponding part of annelids. It was apparently finished and available in 1809 (Ehlers, 1864:12; des Cilleuls & Girard, 1968:30), and was certainly circulating in 1812 (de Blainville, 1828:622; Grube, 1851:158), but it was presented to the Académie des Sciences on either 19 June (de Blainville, 1828:380), or 14 July, 1817 (Pallary, 1931:716). However, Sherborn (1897:287) by following a review dated 1827, probably based upon the second edition (available in Gallica, digital library from France, and dated 1826), concluded that 1822 should be the publication date. This was later confirmed and ruled out (Tollit, 1986, ICZN 1987); therefore, the annelid part should be cited as Savigny (1822).

Savigny (1822:3-4) indicated that annelids should be characterized after a standardization of the terminology for body appendages, especially cephalic, pharyngeal and parapodial features, such that their modifications can be better understood. Consequently, he defined his orders, families, genera and species by the combination of external features, such as the presence of palps, antennae, and eyes, together with parapodial features (cirri, branchiae, chaetae and aciculae), internal modifications in the pharynx and even the presence of enteric diverticula. However, Savigny did not use dichotomous or polytomous keys but rather listed his groups into a tabular fashion. For the species, he combined his material from the Egypt expedition with other specimens deposited in the Paris museum, or previously published by others from different localities. Polychaetae chaetae have many different patterns; they are useful for sensing the environment, moving and anchoring to the sediment or tube where the animals live, and traditionally have been used for taxonomic purposes (Merz & Woodin, 2006).

Two papers by Grube are especially significant because he proposed a new arrangement for annelids, listed all available family names, proposed some new ones, listed all known genera and species, and introduced keys as synoptic tables; first for families (Grube, 1850, foldout on page 281), and later for genera and species (Grube, 1851). This second part was really innovative and useful, but because it did not appear in an academic journal, its widespread use was likely limited. Further, probably derived from the size of the task, by defining genera Grube had an irregular perspective and some of his genera or species were apparently not separated after standard approaches or delineations, but rather after his own experience.

Enter Armand de Quatrefages (Fig. 4). Because he had made doctoral studies on mathematics, medicine and natural sciences, he divided his efforts into the study of annelids and anthropology (Hamy, 1892). His main interests on zoology are indicated by the fact that he published 84 papers in 12 years (1840-1852), a high number even for XXI-century authors, which included results of field trips and observations of living specimens in the lab (Hamy 1892:10).

However, his monograph *Histoire Naturelle des Annélés Marins et d'Eau Douce* (de Quatrefages, 1866) was the

most relevant work for this topic. Trying to find a natural order for annelids, he followed de Jussieu comparative approach regarding characters (de Quatrefages, 1866; l:169): "the most essential character must be the one present among the largest number of species and groups." This corroborates that trying to find a natural order, de Jussieu gave different weight to characters (Stevens, 1994:34-35).

Among other things, de Quatrefages provided synoptic tables for orders, suborders, and families, and then for genera in each family. For this, he went further into a stricter, standardized approach and, as a result, the number of genera was markedly increased. In the table below it can be seen that de Quatrefages almost tripled the number of known genera in about five years, reaching almost 250 (50 genera/year), whereas it took about 90 yr to increase it seven times to 1513 (Fauchald, 1977; 13 genera/year). By the way, Kinberg proposed 54 genera in a series of small papers based upon the specimens collected during the expedition of the Swedish Frigate Ship Eugenie (Kinberg, 1857-1910).

Kristian Fauchald's Pink Book (Fauchald, 1977) is the last thorough compilation of most polychaete taxa and besides preparing dichotomous keys, he provided standardized diagnoses for each order, family and genus. During 40 yr (1961-2002), Fauchald made 72 publications including proposals of three families, 34 genera and described 256 new species (Ward, 2005).

Year	Author	Genera
1758, 1767	Linnaeus	5
1822	Savigny	26
1838	Milne-Edwards	49
1851	Grube	86
1857-1867	Kinberg	54
1861	Schmarda	97
1866	de Quatrefages	245
1977	Fauchald	1513

Fauchald started his academic career in polychaete taxonomy with a paper on Norwegian nephtyids (Fauchald, 1963), and five years later and within the same family, he proposed his first genus: *Inermonephtys*. After following a standard protocol by making an analysis of several diagnostic features for nephtyids and, by defining his new genus, he concluded that (Fauchald, 1968:9): "It must be emphasized that no single character can be used to distinguish any genus. A set of three or four characters is necessary and sufficient to describe all known genera." He also included a key and a table to compare diagnostic features for all nephtyid genera; however, he apparently confused diagnosis with description since in his key most genera are diagnosed by single features. Thus, *Micronephtys* is the only genus lacking interrampal cirri, *Nephtys* is the only genus with recurved interrampal cirri, and *Inermonephtys* is the only genus with smooth pharynx (and with one pair of antennae).

It might be interesting to indicate that Olga Hartman, Fauchald's Ph.D. advisor, proposed her first genus in the scale-worm family Polynoidae: *Halosydnella* (Hartman 1938), and separated it from *Halosydna* Kinberg with some features as body shape and size, and pattern of elytra (scales) arrangement along the body. It seems, however, that the most similar genus to *Halosydnella* is *Acholoe* Claparède (Fauchald, 1977:59) and they differ by the type of neurochaetal tips: *Halosydnella* has uni- and bidentate neurochaetae, but *Acholoe* has only unidentate neurochaetae.

A contribution by Ralph Chamberlin (Fig. 4) deserves some comments regarding the importance of keys to understand the segregation of morphological patterns, or to find out parallelisms at different hierarchical levels (Vasilyeva, 1999:164). Chamberlin made a few papers on polychaetes because he devoted most of his time to spiders, centipeds and millipeds; his larger contribution (Chamberlin, 1919) dealt with materials collected during three cruises of the *Albatross* in the Pacific Ocean. He presented a key to families, and then 42 keys to genera in the same number of families, driving to 587 genera, and 54 were newly described. It must be emphasized that he did not study specimens for these keyed-out genera, but followed previous publications, such that his keys became one of the major contributions in the volume.



Figura 4. Personajes y fuentes. De Quatrefages <https://wellcomecollection.org/works/eju7csyf>, Chamberlin <https://en.wikiquote.org/wiki/File:Ralph-V.-Chamberlin.jpg>.

The frequent use of Fauchald's taxonomic keys to families or genera builds up a mental perspective that incorporates family and generic body-patterns. In his keys, characters are arranged in a hierarchical succession, such that their relative relevance is evident, and this hierarchical succession is different for each polychaete family. Further, for some families, having 10 or more genera, these sequences provide an excellent perspective about inter-generic differences and about patterns of generic characters. This explains why, whenever a specimen is observed, a well-trained mind notices if this represents a different or unique morphological pattern; after repeatedly running the keys and observing different worms, one acquires a valuable perspective about body patterns. Then, because "the characters used in keys should be the most clear-cut and distinctive diagnostic characters" (Winston, 1999:370), and because they are presented as "alternative, generally mutually exclusive features" (Tyril,

2010:79), they provide a perspective for body patterns, understood as different combinations of characters. This approach can be set into an analogical context, and then the relative degree of difference observed in a particular specimen can lead us to conclude this particular body pattern should belong to a distinct, probably new genus (Wheeler, 2008:4). Nevertheless, there are taxonomic problems in most polychaete families; usually an imperfect or heterogenous means for making standard comparisons, or some problems to assess homologous structures have resulted in unstable delimitations for many genera (Salazar-Vallejo & Hutchings, 2012).

As indicated above, geographical distribution is very important in recognizing different taxa. Species with restricted geographical distribution have been known for a long time, especially after the results of some major scientific or exploratory expeditions. The first formulation was by Buffon (1761, 9:101). By referring to the mammals of the New World, in comparison to those living in the Old World, he stated: "further, we see that among all animals living or passing by the Northern lands, which could be common to the two worlds ... cannot be found in both places at the same time." This was generalized as "environmentally similar regions but isolated from each other, have different assemblages of mammals and birds", or even further as "different areas have different species." For Nelson (1978:274-275), this is the first biogeographical law. On the basis of these restricted distributions de Candolle (1820) formulated botanical regions, which was later employed for defining ornithological (Sclater 1858), or vertebrate regions (Wallace, 1876; Proches & Ramdhani, 2012; Holt et al., 2013; Kreft & Jetz, 2013).

De Quatrefages published two notes on the geographical distribution of marine annelids, which were later incorporated into his monograph. In the first note (de Quatrefages, 1864) he announced the forthcoming monograph and added that he had studied over 700 preserved lots from the Paris museum, but made the plates based upon living specimens (with the exception of one *Aphrodita* and one *Hermione*). He listed 10 main ideas and two of them deserve comments: 1) annelids live in all the seas and they are cosmopolitan if regarded as orders and even genera, and 2) annelid species have a restricted distribution. He explained (page 173): "The number of common species in two continents, in two hemispheres, to the eastern and western seas in the same continent, etc., if it is not absolutely nil, it will always be excessively reduced ... I have not found a single common species in our (Atlantic) ocean and Mediterranean coasts." The larger paper (de Quatrefages, 1865) was mostly an extended series of explanations about his zoogeographic conclusions.

Regretfully, de Quatrefages ideas on species distributions were rejected by some influential taxonomists, and the ideas of four of them are relevant to clarify this perspective. It must be emphasized that all of these specialists made large reports resulting from faunistic surveys, or from maritime explorations. Pierre Fauvel (1897) regarded one specimen from New Caledonie,

despite some morphological differences, as identical to a species described from Equatorial Western Africa (*Eupolyodontes cornishi* Buchanan, 1894), and in a later publication (Fauvel, 1925) he concluded that cosmopolitanism was very common among polychaete species. His remarks were: 1) "Many exotic species have been described as special to this or that region, but often, if we carefully compare with the species in our coasts, trying to find specimens of similar sizes, we soon conclude that there are only insignificant differences, such as those that can be noticed among specimens from the same locality" (Fauvel, 1925:313), and 2) "Species from the Indian Ocean also live over the western African coast and along both coasts of Tropical America, in the Atlantic and in the Pacific" (Fauvel, 1925:314).

Hermann Augener (1913) in his study of Southwestern Australian polychaetes, indicated that there were many species identical to those found in the Mediterranean Sea, or in other northern localities. Charles Monro made several publications on tropical polychaetes and dealing with those living in Pacific Panama, he concluded (Monro, 1928:75): "The fauna of the Panama coast is tropical, and the forms here studied confirm Prof. P. Fauvel's contention that among the Polychaeta the tropical fauna includes many species common to the Atlantic, the Pacific and the Indian Ocean." The last influential expert was Olga Hartman. She combined her early efforts trying to clarify some nomenclatural issues, revising type material in museums, and studying the Eastern Pacific fauna in general, and especially the Californian species. In an evaluation of endemism (Hartman, 1955:43) she made a very important but little known conclusion: "The list of endemic species is far more considerable and comprises, for California alone, more than 500 species. Fewer than two per cent of the total number are cosmopolitan." In her Atlases for Californian polychaetes (Hartman, 1968, 1969) she changed her mind by regarding 34% of the fauna as made up by cosmopolitan species. However, after several revisions made over different polychaete families or genera, the general conclusion is that cosmopolitan species are very rare. However, there are exceptions including those species living associated with some cultivated marine molluscs, like the giant Japanese oyster that has been the subject of intensive mariculture in many different countries, driven by migratory birds, or being carried in ballast water. If cosmopolitans are real, they should be present along a similar ecological horizon, not along widely different regimes of salinity, temperature, substrate and depth (Salazar-Vallejo *et al.*, 2014).

As far as a simple routine could be desired (Jenyns, 1833), it would be very difficult to provide it for any taxonomic group. However, as a rough synthesis on the means to recognize and delineate genera, a series of steps and experiences will help any practicing taxonomist to discover a new morphological pattern, and then proceed to propose it as a new genus:

Assess characters that have been used in the group by understanding the original descriptions and more recent redescriptions; if available, concentrate especially

on those publications dealing with size-variation, or modifications due to sexual maturity.

Second, study as many specimens as possible, including type and non-type material, and standardize their characterization, making a comparative approach either by comparing specimens against each other or, by using a series of photographs of specimens of similar size; thus, differences could be detected more easily than based upon memories of the specimens. If there is no study about variation, do it on your own for showing how reliable the characters are being independent of body size.

Third, find out new characters or modifications that help define or explain groups, or new means to understand the traditional characters, such that the discovered discontinuities help explain the groups you have detected.

Fourth, for a newly discovered morphological pattern, look for previously junior synonyms because the pattern might have been already noted, and a name proposed for it, although the differences were not fully understood. If so, reinstate the previous name; if not, then propose a new genus-group name for it. In either case, modify the diagnosis to clarify the differences among similar genera, and incorporate a key to help identify the resemblances and differences among genera; this will facilitate understanding the relevance of the discontinuities just discovered.

Fifth, arrange the illustrations by following a similar approach such that diagnostic features are clearly shown; now, proceed to complete the text and figures for preparing the first draft of your publication. Be prepared for some negative evaluations, especially if the new proposal modifies a lot the current paradigm. Take the best of referees recommendations and improve the document as much as possible, such that it can be accepted for publication. Then, look for another challenge.

PERSPECTIVES

Annelid phylogenetics is undergoing an interesting transformation. Most traditional suprageneric or familiar polychaete groupings were not recovered by using modern analytical methods based upon morphological or molecular characters (Zrzavý *et al.*, 2009; Kvist & Siddall, 2013; Purschke *et al.*, 2014). However, a modification of previous data into amino acid sequences of 231 genes resulted in the confirmation of the ancient groups Errantia and Sedentaria, although with some modifications (Struck *et al.*, 2011), such as the inclusion of echiurans and sipunculans within annelids, and recognizing the highly modified Chaetopteridae as a basal group. Later, Struck (2011) named the combination of Errantia and Sedentaria as Pleistoannelida, leaving out, but still within annelids, several other groups such as sipunculans, magelonids, myzostomids, chaetopterids and oweniids, together with some of the formerly called archiannelid families;

this was later improved by detecting paralogous sequences (Struck, 2013). Later refinements include Weigert *et al.* (2014), Andrade *et al.* (2015), and Parry *et al.* (2016), but several details are still unsettled and additional studies are expected in the near future.

DNA barcoding of the COI mitochondrial gene is a powerful method for identifying species, which of course has some limitations (Fitzhugh, 2006; Rubinoff *et al.*, 2006; DeSalle, 2007; Sbordoni, 2010; Collins & Cruickshank, 2013) which must be taken into account. A study on a large number of birds (Hebert *et al.*, 2004) promoted the use of DNA barcodes for recovering generic groups. Further, some studies on marine fishes have involved the use of COI barcoding approaches to define species and genera depending on their relative dissimilarity, as expressed by the so-called Kimura 2-parameter (K2P), such that percentage differences were 0.4% between species, 10% between genera, 15% between families, 22% between orders, and 23% between classes (Ward *et al.*, 2005). Asgharian *et al.* (2011:469, Table 3) indicated that in seven different projects dealing with marine fishes, the average distances were 0.30 (range: 0.17-0.47) for members of the same species, 11.4 (range: 3.70-16.05) for members of the same genus, and 17.9 (range: 13.92-20.72) for members of the same family. Another study (Jaafar *et al.*, 2012) concluded that the K2P distances were overlapped: "... in accordance with expectations based on taxonomic hierarchy: 0% to 4.82% between individuals within species, 0% to 16.4% between species within genera, and 8.64% to 25.39% between genera within families."

On the other hand, there are some other problems when trying to cope with separating species (or genera) by using COI barcoding among polychaetes. Kvist (2016:2244, Table 2) has shown that for polychaetes there is a very wide variation in published data, being the average data of about 29% for interspecific, and up to 10% for intraspecific distances. He explains this, not surprisingly, because "... the taxonomic labels associated with the sequences are incorrect" (Kvist, 2016:2249). This has been early noticed by Stoeckle (2003) and by Pleijel *et al.* (2008) but there is no means to solve the earlier problematic identifications, but additional sequences must rely on better taxonomic procedures. Identifications, by the way, can be very problematic in some little studied areas like deep-sea polymetallic nodule fields such that a reverse taxonomic approach—first sequencing, then identifying—was regarded as the only option available (Janssen *et al.*, 2015).

For polychaetes, there are fewer large-scale studies than in other large marine invertebrate groups (Radulovici *et al.*, 2010), and one deserving mention was made by Carr *et al.* (2011), where the affinities of Canadian polychaetes living in three oceans was assessed. They concluded that average K2P distances for members of the same species was 0.38, whereas for genera it was 16.50; this somehow resemble what has been found among fishes.

Defining polychaete genera by using morphological features after thorough analyses has resulted into

different perspectives; in some studies (Carrera-Parra, 2006), lumbrinerid genera were well defined, whereas for nereidid genera provided with paragnaths (Bakken & Wilson, 2005), or for polycirrids (Fitzhugh *et al.*, 2015), many genera could not be defined because of large polytomies. Although there is relevant information on morphological features, taxonomic studies should include molecular methods and there has been some interesting results in other taxonomic groups (Padial & de la Riva, 2007).

Comparing chromosome numbers is a promising field but there are some problems for linking their diploid numbers, or chromosomal shape, to taxonomic categories. For example, most nereidids, including *Platynereis* and *Perinereis*, have a diploid number of 28 chromosomes (Ipucha *et al.*, 2007), but *Laeonereis* has 38 (Leitão *et al.*, 2010). Because the chromosome number is highly conservative, it could not be diagnostic. However, Grassle *et al.* (1987) found 14, 20 and 26 chromosomes in sibling *Capitella* species. Further, in four species of *Neanthes*, Reish *et al.* (2014) indicated that there were 18, 22, or 28 chromosomes. On the other hand, Pesch & Mueller (1988) found that what has been regarded as allopatric populations for the same species (*Neanthes arenaceodentata*), were actually two different species with chromosomes having different number and shape, one with 18, the other with 24.

PENDING ISSUES

There are several pending problems or challenges for taxonomic practice and evolutionary studies in the near future; for some interesting philosophical issues see Hołyński (2005), Wilkins & Ebach (2014), and Minelli (2014) or the first issue of Megataxa. Morphologically defined genera are usually reflected in molecular phylogenies, indicating that morphological approaches are not overdue (Kawano, 2000; Jablonski & Finarelli, 2009; Filatov *et al.*, 2013; Lee & Palci, 2015), despite the fact they might look anachronistic from a molecular perspective.

There is a lack of consistency between Linnean taxonomic ranks such as family, genera or species, when different groups of organisms are taken into account, because they evolved or have spanned along different time scales (Johns & Avise, 1998), as Hennig had noticed already (1966:72), and early anticipated by Agassiz (1859:233). Avise & Liu (2011) have emphasized the large discrepancies between vertebrates, which might be roughly arranged in a chronological fashion as amphibians, then reptiles, birds and mammals. However, invertebrate groups are older; for example, decapod crustaceans tend to be twice as old as amphibians. Avise & Liu (2011:712) suggested that the date of origin could be appended to taxonomic ranks but the proposal has not been incorporated into current taxonomic practice; however, some invertebrates are older than decapods, but their fossil record is scarcer such that setting their first appearance is not straightforward.

Cavalier-Smith (2010) has pointed out that the influence of Hennigian cladistics must be reduced by incorporating some evolutionary processes for phylogenetic analysis such as stasis, cell merging, allopolyploidy, and lateral gene transfer, together with a reappraisal of paraphyletic taxa. There might be a need (Zander, 2013:1) for pluralistic approaches “to correct the difficulties in which modern systematics has found itself.” Phylogenetic analysis need some improvements (Ebach *et al.*, 2013; Vasilyeva & Stephenson, 2013), not only for considering the above evolutionary processes but a better understanding of how the computer algorithms work (Brazeau, 2011). Further, in some problematic groups, more than one solution is possible and none should be rejected *a priori* such that they can coexist (Vinarski, 2013), and especially for those groups capable of hybridize and undergo introgression (Zakharov *et al.*, 2009). Another critique and evaluation of cladistics was made by Aubert (2015) and his interesting and useful recommendations should be taken into account for future studies.

EPILOGUE

Despite the fact we currently have plenty of analytical sophistication, including molecular indicators, together with many statistical and computer software for image comparison, morphological taxonomy must be strengthened. Otherwise, the current bottle-neck of having many discovered species by molecular methods, but still waiting for being formally (or even turbo-) described will not be solved. Further, most taxonomists have been following a long tradition for

pattern recognition and undertaking revisionary studies, but we have seldom been explicit enough about how to proceed. Younger colleagues must understand that it takes several years to fully understand a group of species, their variations and affinities. At the same time, older colleagues must keep in mind these needs and do their best to encourage and accelerate the formation of a much needed batch of new taxonomists. Of course, it will also help we push our authorities and politicians into promoting new permanent positions concentrated on morphological studies. No one else will do these activities for us, or for the forthcoming colleagues (Salazar-Vallejo & González, 2016).

ACKNOWLEDGMENTS

This revision was encouraged by my former and current students of polychaete taxonomy, and as a position paper for my seminar on advanced systematics. Eduardo Suárez-Morales and Jacobo Schmitter-Soto, both from Ecosur, as well as Kirk Fitzhugh (LACM), Pat Hutchings (AM), and J. Rolando Bastida-Zavala, carefully read earlier drafts and their recommendations improved this contribution. The availability of classical papers in the Biodiversity Heritage Library, Digital Library of the American Museum of Natural History, Gallica, InternetArchive, Persée, or Smithsonian Libraries, together with the kind help of ECOSUR librarians, especially José Santos Gómez, made easy the finding and reading of what used to be very difficult to find documents. Of course, institutional subscriptions were really useful and are highly acknowledged. 🌸



REFERENCES

- Adanson, M. 1757. *Histoire naturelle du Sénégal. Coquillages*. C.J.B. Pauche, Paris, 190+xciv+275 pp, 19 Pls. <http://www.biodiversitylibrary.org/bibliography/11585/#summary>
- Adanson, M. 1763. *Familles des Plantes*. Vincent, Paris, 1186 pp. <http://www.biodiversitylibrary.org/bibliography/271/#summary>
- Agassiz, A. 1871. Systematic zoology and nomenclature. *American Naturalist*. 5: 353-356 <http://www.jstor.org/stable/2447062>
- Agassiz, L. 1859. *An Essay on Classification*. Longman, Brown, Green, Longmans & Roberts, London, 381 pp. <http://www.biodiversitylibrary.org/bibliography/1831/#summary>
- Allmon, W.D. 1992. Genera in Paleontology: Definition and significance. *Historical Biology*. 6: 149-158. http://www.museumoftheearth.org/files/research/pubs/51_Allmon_%281992%29_Genera_in_Paleontology_Definition_and_Significance_Historical_Biology_6_%28149-158%29.pdf
- Anderson, E. 1940. The concept of the genus, 2. A survey of modern opinion. *Bulletin of the Torrey Botanical Club*. 67: 363-369 http://www.jstor.org/stable/2481069?seq=1#page_scan_tab_contents
- Anderson, E. 1957. An experimental investigation of judgements concerning genera and species. *Evolution*. 11: 260-263. <https://www.jstor.org/stable/2406055>
- Anderson, R.M. (+ 27 coauthors). 1923 The genus debased. *Auk*. 40: 179-180. <https://sora.unm.edu/node/12896>
- Andrade, S.C.S., Novo, M., Kawauchi, G.Y., Worsaae, K., Pleijel, F., Gorobet, G. & Rouse, G.W. 2015. Articulating "archiannelids": Phylogenomics and annelid relationships, with emphasis on meiofaunal taxa. *Molecular Biology and Evolution*. 32: 2860-2875. <https://academic.oup.com/mbe/article-lookup/doi/10.1093/molbev/msv157>
- Asgharian, H., Sahafi, H.Y.H.A., Ardalan, A., Shekarriz, S. & Elahi, E. 2011. Cytochrome c oxidase subunit 1 barcode data of fish of the Nayband National Park in the Persian Gulf and analysis using meta-data flag several cryptic species. *Molecular Ecology Resources*. 11: 461-472. <http://onlinelibrary.wiley.com/doi/10.1111/j.1755-0998.2011.02989.stract;jsessionid=833CFD4C26EFE25552BADAAF28D0B7B6.f02t03?userIsAuthenticated=false&deniedAccessCustomisedMessage=>
- Atran, S. 1987. Origin of the species and genus concepts: An anthropological perspective. *Journal of the History of Biology*. 20: 195-279. <http://link.springer.com/article/10.1007%2FBF00138437#page-1>
- Aubert, D. 2015. A formal analysis of phylogenetic terminology: Towards a reconsideration of the current paradigm in Systematics. *Phytoneuron*. 2015-66: 1-54. <http://www.phytoneuron.net/2015Phytoneuron/66PhytoN-PhylogeneticTerminology-pdf>
- Augener, H. 1913. Polychaeta 1. Errantia. *Fauna Südwest-Australiens, Ergebnisse der Hamburger südwest-australischen Forschungreise 1905*. 4: 64-304. <http://www.biodiversitylibrary.org/item/31515#page/3/mode/1up>
- Avise, J.C. & Liu, J.-X. 2011. On the temporal inconsistencies of Linnean taxonomic ranks. *Biological Journal of the Linnean Society*. 102: 707-714. <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.2011.01624.x/pdf>
- Bailey, I.W. 1953. The anatomical approach to the study of genera. *Chronica Botanica*. 14(3/4): 121-125.
- Bakken, T. & Wilson, R.S. 2005. Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. *Zoologica Scripta*. 34: 507-547. <http://onlinelibrary.wiley.com/doi/10.1111/j.1463-6409.2005.00200.x/abstract>
- Barracough, T.G. 2010. Evolving entities: towards a unified framework for understanding diversity at the species and higher levels. *Philosophical Transactions of the Royal Society, B*. 365: 1801-1813. <http://rstb.royalsocietypublishing.org/content/365/1547/1801>
- Barracough, T.G., Nee, S. & Harvey, P.H. 1998. Sister-group analysis in identifying correlates of diversification. *Evolutionary Ecology*. 12: 751-754. <http://link.springer.com/article/10.1023%2FA%3A1017125317840>
- Barsanti, G. 2011. Linnaeus: The order of nature, the nature of man, and evolution. *Journal of the Siena Academy of Sciences*. 3: 61-65. <ftp.fadoi.org/index.php/jsas/article/download/jsas.2011.61/344>
- Bartlett, H.H. 1940. The concept of the genus, 1. History of the generic concept in Botany. *Bulletin of the Torrey Botanical Club*. 67: 349-362. http://www.jstor.org/stable/2481068?seq=1#page_scan_tab_contents
- Bessey, C.E. 1908 The taxonomic aspect of the species question. *American Naturalist*. 42: 218-224. <http://www.jstor.org/stable/2455533>

- Bock, W.J. & Farrand, J. 1980. The number of species and genera of Recent birds: A contribution to comparative systematics. *American Museum Novitates*. 2703: 1-29. <http://digitalibrary.amnh.org/handle/2246/5389>
- Bogert, C.M. 1943. Introduction. *Annals of the New York Academy of Sciences*. 44: 107-108. <http://onlinelibrary.wiley.com/doi/10.1111/j.1749-6632.1943.tb31296.x/abstract>
- Brazeau, M.D. 2011. Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society*. 104: 489-498. <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.2011.01755.x/full>
- Buffon, G.L.L. 1749-1768. *Histoire naturelle Générale et Particulière, avec la Description du Cabinet du Roi*. 15 vols. Imprimerie Royal, Paris (<http://www.buffon.cnrs.fr>).
- Burlando, B. 1990. The fractal dimension of taxonomic systems. *Journal of Theoretical Biology*. 146: 99-114. [http://dx.doi.org/10.1016/S0022-5193\(05\)80046-3](http://dx.doi.org/10.1016/S0022-5193(05)80046-3)
- Burlando, B. 1993. The fractal geometry of evolution. *Journal of Theoretical Biology*. 163: 161-172. <http://dx.doi.org/10.1006/jtbi.1993.1114>
- Cain, A.J. 1956. The genus in evolutionary taxonomy. *Systematic Zoology*. 5: 97-109. <http://sysbio.oxfordjournals.org/content/5/3/97.extract>
- Cain, A.J. 1958. Logic and memory in Linnaeus' system of Taxonomy. *Proceedings of the Linnean Society of London*. 169: 144-163. <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.1958.tb00819.x/abstract>
- Callebaut, W. 2005. Again, what the philosophy of Biology is not. *Acta Biotheoretica*. 53: 93-122. <http://link.springer.com/article/10.1007/s10441-005-5352-7>
- Cambeftort, Y. 2016. How general are genera? The genus in systematic zoology. In: Chemla, K., Chorlay, R. & Rabouin, D. (Eds), *The Oxford Handbook of Generality in Mathematics and the Sciences*. Oxford University Press, Oxford, 257-284.
- Camp, W.H. 1940. The concept of the genus, 5. Our changing generic concepts. *Bulletin of the Torrey Botanical Club*. 67: 381-389. http://www.jstor.org/stable/2481072?seq=1#page_scan_tab_contents
- Carr, C.M., Hardy, S.M., Brown, T.M., McDonald, T.A. & Hebert, P.D.N. 2011. A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLoS ONE*. 6(7), e22232, 12 pp. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0022232>
- Carrera-Parra, L. 2006. Phylogenetic analysis of Lumbrineridae Schmarda, 1861 (Annelida: Polychaeta). *Zootaxa*. 1332: 1-36. <http://www.mapress.com/zootaxa/2006f/z01332p036f.pdf>
- Cavalier-Smith, T. 2010. Deep phylogeny, ancestral groups and the four ages of life. *Philosophical Transactions of the Royal Society, B*. 365: 111-132. <http://rsta.royalsocietypublishing.org/content/365/1537/111>
- Cave, M.S. 1953. Cytology and embryology in the delimitation of genera. *Chronica Botanica*. 14(3/4): 140-153.
- Chamberlin, R.V. 1919. The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology, Harvard*. 48: 1-493. <http://www.biodiversitylibrary.org/bibliography/49195#/summary>
- Chambers, K.L. 1992. Evolution before Darwin: The musings of Constantine Rafinesque. *Kalmiopsis*. 1992: 5-9. <http://www.npsoregon.org/kalmiopsis/kalmiopsis02/chambers1.pdf>
- Cifelli, R.L. & Kielan-Jaworowska, Z. 2005. Diagnosis: Differing interpretations of the ICZN. *Acta Palaeontologica Polonica*. 50: 650-652. <http://www.app.pan.pl/archive/published/app50/app50-650.pdf>
- Clarke, D.J. 2011. Testing the phylogenetic utility of morphological character systems, with a revision of *Creophilus* Leach (Coleoptera: Staphylinidae). *Zoological Journal of the Linnean Society*. 163: 723-812. <http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2011.00725.x/abstract>
- Clayton, W.D. 1972. Some aspects of the genus concept. *Kew Bulletin*. 27: 281-287. http://www.jstor.org/stable/4109454?seq=1#page_scan_tab_contents
- Clayton, W.D. 1983. The genus concept in practice. *Kew Bulletin*. 38: 149-153. http://www.jstor.org/stable/4108098?seq=1#page_scan_tab_contents
- Collins, R.A. & Cruickshank, R.H. 2013. The seven deadly sins of DNA barcoding. *Molecular Ecology Resources*. 13: 969-975. <http://onlinelibrary.wiley.com/doi/10.1111/1755-0998.12046/abstract>
- Cronquist, A. 1978. Once again, what is a species? In: Romberger J.A., Foote R.H., Knutson L. & Lents P.L. (Eds), *Beltsville Symposia in Agricultural Research, 2. Biosystematics in Agriculture*: 3-20. Wiley, Montclair, 340 pp. [this is difficult to find; a pdf can be shared upon request].
- Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London, 502 pp <https://archive.org/details/onoriginofspec00darw>
- de Blainville, H.-M. D. 1828. Vers. *Dictionnaire des Sciences Naturelles*. 57: 365-625. <http://www.biodiversitylibrary.org/item/81595#page/371/mode/1up>
- de Candolle, A.P. 1815. *Théorie Élémentaire de la Botanique, ou Exposition des Principes de la Classification Naturelle et de l'Art de Décrire et d'Etudier les Végétaux*. Déterville, Paris, 500 pp (+ 25 unnumb pages for Index). <http://www.biodiversitylibrary.org/item/193841>
- de Candolle, A.P. 1820. Géographie Botanique. *Dictionnaire des Sciences Naturelles*. 18: 359-422. <http://www.biodiversitylibrary.org/item/74506#page/365/mode/1up>
- de Hoog, G.S. 1981. Methodology of taxonomy. *Taxon*. 30: 779-783. <https://www.jstor.org/stable/pdf/1220079.pdf>
- de Jussieu, A.L. 1789. *Genera Plantarum secundum Ordines Naturales Disposita, juxta Methodum in Horto Regio Parisiensi Exaratam, Anno MDCCCLXXIV*. Herissant, Paris, 594 pp. <http://www.biodiversitylibrary.org/bibliography/284#/summary>
- de Mirbel, C.-F.B. 1828. Théorie Fondamentale de la Botanique. *Dictionnaire des Sciences Naturelles*. 53: 470-508. <http://www.biodiversitylibrary.org/item/81615#page/480/mode/1up>
- de Quatrefages, A. 1864. Note sur la distribution géographique des annélides. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*. 59: 170-174. <http://gallica.bnf.fr/ark:/12148/bpt6k3016q/f172.image.r=>
- de Quatrefages, A. 1865. Mémoire sur la distribution géographique des annélides. *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris*. 1: 1-14. <http://www.biodiversitylibrary.org/item/49413#page/9/mode/1up>
- de Quatrefages, A. 1866(1865). *Histoire Naturelle des Annélés Marins et d'Eau Douce: Annélides et Gephyreans*. Librairie Encyclopédique de Roret, Paris, 2 vols, and atlas.
- de Queiroz, K. & Gauthier, J. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics*. 23: 449-480. <http://www.annualreviews.org/doi/abs/10.1146/annurev.es.23.110192.002313>
- de Saint-Hilaire, A. 1840. *Leçons de Botanique, comprenant Principalement la Morphologie Végétale, la Terminologie, la Botanique Comparée, l'Examen de la Valeur des Caractères dans les divers Familles Naturelles, etc*. Loss, Paris, 2 vols. <http://gallica.bnf.fr/ark:/12148/bpt6k6540140c/f9.image.r=Lecons%20de%20Botanique>

- Des Cilleuls, J. & Girard, V. 1968. L'étrange maladie de M.J.C. Lelorgne de Savigny, Naturaliste, Membre de l'Institut d'Égypte et de l'Académie des Sciences (1777-1851). *Histoire des Sciences Médicales*. 2: 29-40. <http://www.biusante.parisdescartes.fr/sfhm/hsm/HSMx1968x002x001/HSMx1968x002x001x0029.pdf>
- DeSalle, R. 2007. Phenetic and DNA taxonomy; a comment on Waugh. *BioEssays*. 29: 1289-1290. <http://desalle.amnh.org/pdf/DeSalle.2007.BioEssays.pdf>
- Di Carlo, J.J., Zoccolau, D. & Rust, N.C. 2012. How does the brain solve visual object recognition? *Neuron*. 73: 415-434. <http://www.cell.com/neuron/abstract/S0896-6273%2812%2900092-X>
- Di Gregorio, M.A. 1982. In search of the Natural System: Problems of zoological classification in Victorian Britain. *History and Philosophy of the Life Sciences*. 4: 225-254 <http://www.jstor.org/stable/23328374>
- Dubois, A. 1982. Some comments on the genus concept in Zoology. *Monitore Zoologico Italiano, nova serie*. 22: 27-44. <http://www.tandfonline.com/doi/abs/10.1080/00269786.1988.10736539#.VpP1WFKaXKA>
- Dubois, A. 1988. The genus in zoology: a contribution to the theory of evolutionary systematics. *Mémoires du Muséum National d'Histoire Naturelle, série A, Zoologie*. 140: 1-122.
- Dubois, A. 2010. Describing new species. *Taprobanica*. 2: 6-24. <http://tapro.sjoi.info/articles/abstract/10.4038/tapro.v2i1.2703/>
- Dubois, A. 2017. Diagnosis in zoological taxonomy and nomenclature. *Bionomina*. 12: 63-85 <https://doi.org/10.11646/bionomina.12.1.8>
- Duméril, A.M.C. 1805(1806). *Zoologie Analytique, ou Méthode Naturelle de Classification des Animaux rendue plus facile à l'aide de Tableaux Synoptiques*. Allais, Paris, 344 pp. <http://www.biodiversitylibrary.org/item/44011#page/9/mode/1up> (1806 is the date for the second printing and this is the BHL copy; See Gregory S.M.S. 2010. The two 'editions' of Duméril's *Zoologie analytique*, and the potential confusion caused by Froriep's translation *Analytische Zoologie*. *Zoological Bibliography* 1: 6-8 in http://www.iucn-tftsg.org/wp-content/uploads/file/Articles/Gregory_2010.pdf
- Dumont, E.R., Dávalos, L.M., Goldberg, A., Santana, S.E., Rex, K. & Voigt, C.C. 2012. Morphological innovation, diversification and invasion of a new adaptive zone. *Proceedings of the Royal Society, B*. 279: 1797-1805. <http://rspb.royalsocietypublishing.org/content/279/1734/1797>
- Dunn, E.R. 1943. Lower categories in Herpetology. *Annals of the New York Academy of Sciences*. 44: 123-131. <http://onlinelibrary.wiley.com/doi/10.1111/j.1749-6632.1943.tb31298.x/abstract>
- Dupuis, C. 1974. Pierre André Latreille (1762-1833): The foremost entomologist of his time. *Annual Review of Entomology*, 19:1-14. <https://www.annualreviews.org/doi/abs/10.1146/annurev.en.19.010174.000245>
- Eames, A.J. 1953. Floral anatomy as an aid in generic limitation. *Chronica Botanica*. 14(3/4): 126-132.
- Ebach, M.C., Williams, D.M. & Vanderlaan, T.A. 2013. Implementation as theory, hierarchy as transformation, homology as synapomorphy. *Zootaxa*. 364: 587-594. <http://dx.doi.org/10.11646/zootaxa.3641.5.7>
- Ehlers, E. 1864. *Die Borstenwürmer (Annelida: Chaetopoda) nach Systematischen und Anatomischen Untersuchungen, Erste Abtheilung*. Wilhelm Engelmann, Leipzig, 191 pp. <http://www.biodiversitylibrary.org/item/18348#page/5/mode/1up>
- Envall, M. 2008. On the difference between mono-, holo-, and paraphyletic groups: a consistent distinction of process and pattern. *Biological Journal of the Linnean Society*. 94: 217-220. <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.2008.00984.x/abstract>
- Eronen, J.T., Polly, P.D., Fred, M., Damuth, J., Frank, D.C., Mosbrugger, V., Scheidegger, C., Stenseth, N.C. & Fortelius, M. 2010. Ecometrics: the traits that bind the past and present together. *Integrative Zoology*. 5: 88-101. <http://onlinelibrary.wiley.com/doi/10.1111/j.1749-4877.2010.00192.x/epdf>
- Ezard, T.H.G., Quental, T.B. & Benton, M.J. 2016. The challenges of inferring the regulators of biodiversity in deep time. *Philosophical Transactions Royal Society B*. 371: 20150216, 11 pp, <http://dc.doi.org/10.1098/rstb.2015.0216>
- Fabricius, J.C. 1775. *Systema Entomologiae, sistens Insectorum Classes, Ordines, Genera, Species, adiectis Synonymis, Locis, Descriptionibus, Observationibus*. Kortii, Flensburgi et Lipsiae, 832 pp. <http://www.biodiversitylibrary.org/item/82400#page/3/mode/1up>
- Fabricius, J.C. 1776. *Genera Insectorum eorumque Characteres Naturales Secundum Numerum, Figuram, Situm et Proportionem omnium Partium Oris Adiecta Mantissa Specieum Nuper Detectarum*. M.F. Bartschii, Chilonii, 310 pp. <http://www.biodiversitylibrary.org/item/82410#page/5/mode/1up>
- Fauchald, K. 1963. Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia*. 13: 1-32. <http://www.tandfonline.com/doi/abs/10.1080/00364827.1963.10409514#.VpQQwIKaXKA>
- Fauchald, K. 1968. Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand 1959-1961, Naga Report*. 4: 5-22, 5 Pls.
- Fauchald, K. 1977. The polychaete worms: Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series*. 28: 1-188. <https://repository.si.edu/handle/10088/3435>
- Fauvel, P. 1897. Observations sur l'*Eupolyodontes cornishii* Buchanan (annélide polychète errante). *Bulletin de la Société Linnéenne de Normandie, 5e série*. 1: 88-112. <http://www.biodiversitylibrary.org/item/17688#page/188/mode/1up>
- Fauvel, P. 1925. Bionomie et distribution géographique des annélides polychètes. In: *Livre du Cinquantenaire de l'Université Catholique d'Angers*: 307-317. Société Anonyme des Editions de l'Ouest, Angers.
- Filatov, M.V., Frade, P.R., Bak, R.P.M., Vermeij, M.J.A. & Kaandorp, J.A. 2013. Comparison between colony morphology and molecular phylogeny in the Caribbean scleractinian coral genus *Madracis*. *PLoS ONE*. 8(8), e71287, 6 pp. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0071287>
- Fitzhugh, K. 2006. DNA barcoding: An instance of technology-driven Science? *BioScience*. 56: 462-463. <http://bioscience.oxfordjournals.org/content/56/6/462.full.pdf+html>
- Fitzhugh, K. 2012. The limits of understanding in biological systematics. *Zootaxa*. 3435: 40-67. <http://www.mapress.com/zootaxa/2012/f/zt03435p067.pdf>
- Fitzhugh, K., Nogueira, J.M.M., Carrerette, O. & Hutchings, P. 2015. An assessment of the status of Polycirridae genera (Annelida: Terebelliformia) and evolutionary transformation series of characters within the family. *Zoological Journal of the Linnean Society*. 174: 666-701. <http://onlinelibrary.wiley.com/doi/10.1111/zoj.12259/abstract>
- Folta, K.M. 2015. Molecular-genetic extensions of Vavilov's predictions. *HortScience*. 50: 777-779. <https://hort.purdue.edu/newcrop/pdfs/777.full.pdf>
- Foote, M. 2012. Evolutionary dynamics of taxonomic structure. *Biology Letters*. 8: 135-138. <http://rsbl.royalsocietypublishing.org/content/early/2011/08/16/rsbl.2011.0521>

- Fransen, C.H.J.M. 2002. Taxonomy, phylogeny, historical biogeography, and historical ecology of the genus *Pontonia* (Crustacea: Decapoda: Caridea: Palaemonidae). *Zoologische Verhandelingen*. 336: 1-433. www.vliz.be/imisdocs/publications/213124.pdf
- Garbino, G.S.T. 2015. How many marmoset (Primates: Cebidae: Callitrichinae) genera are there? A phylogenetic analysis based on multiple morphological systems. *Cladistics*. 31: 652-678. <http://onlinelibrary.wiley.com/doi/10.1111/cla.12106/abstract>
- Gillis, W.T. 1971. The systematics and ecology of Poison-Ivy and Poison-Oaks (Toxicodendron, Anacardiaceae). *Rhodora*. 73: 72-159, 161-237, 370-443, 465-540. <http://www.biodiversitylibrary.org/part/124398>
- Gould, S.J. 2000. *The Lying Stones of Marrakech: Penultimate Reflections in Natural History*. Harmony, New York, 368 pp.
- Grasshoff, J.L. 1975. *Metastevia* (Compositae: Eupatorieae): A new genus from Mexico. *Brittonia*. 27: 69-73. <http://link.springer.com/article/10.2307%2F2805648>
- Grassle, J.P., Gelfman, C.E. & Mills, S.W. 1987. Karyotypes of *Capitella* sibling species, and of several species in the related genera *Capitellides* and *Capitomastus* (Polychaeta). *Bulletin of the Biological Society Washington*. 7: 77-88.
- Greenman, J.M. 1940. The concept of the genus, 3. Genera from the standpoint of Morphology. *Bulletin of the Torrey Botanical Club*. 67: 371-374. http://www.jstor.org/stable/2481070?seq=1#page_scan_tab_contents
- Griffing, L.R. 2011. Who invented the dichotomous key? Richard Waller's watercolors of the herbs of Britain. *American Journal of Botany*. 98: 1911-1923. <http://www.amjbot.org/content/98/12/1911.full>
- Grube, E.A. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte*. 16: 249-364. <http://www.biodiversitylibrary.org/item/51061#page/257/mode/1up>
- Grube, E.A. 1851. *Die Familien der Anneliden mit Angabe ihrer Gattungen und Arten. Ein systematischer Versuch* (The new section is entitled as Uebersicht der Annelidengattungen und Arten zu ihrer vorläufigen Unterscheidung; pp 117-164). Nicolai'schen Buchhandlung, Berlin, 164 pp. <http://www.biodiversitylibrary.org/item/101174#page/5/mode/1up>
- Hagen, J. 2003. The statistical frame of mind in Systematic Biology from Quantitative Zoology to Biometry. *Journal of the History of Biology*. 36: 353-384. <http://link.springer.com/article/10.1023/A:1024479322226>
- Hall, E.R. 1943. Criteria for vertebrate subspecies, species and genera: the mammals. *Annals of the New York Academy of Sciences*. 44: 141-144. <http://onlinelibrary.wiley.com/doi/10.1111/j.1749-6632.1943.tb31300.x/pdf>
- Hamilton, A. & Wheeler, Q.D. 2008. Taxonomy and why History of Science matters for Science: A case study. *Isis*. 99: 331-340. <http://www.journals.uchicago.edu/doi/pdfplus/10.1086/588691>
- Hamy, E.-T. 1892. *Hommage a la Mémoire de M.A. de Quatrefages de Bréau*. Discours prononcé a l'Ouverture du Cours d'Anthropologie du Muséum d'Histoire Naturelle, le 31 Mai 1892. Ernest Leroux, Paris, 24 pp. <http://gallica.bnf.fr/ark:/12148/bpt6k6571729j.r=>
- Hartman, O. 1938. The types of the polychaete worms of the families Polynoidae and Polyodontidae in the United States National Museum and the description of a new genus. *Proceedings of the United States National Museum*. 86: 107-134. <http://library.si.edu/digital-library/book/proceedingsofuni861940unit>
- Hartman, O. 1955. Endemism in the North Pacific Ocean, with emphasis on the distribution of marine annelids, and descriptions of new or little known species. In: *Essays in the Natural Sciences in Honor of Captain Allan Hancock on the Occasion of his Birthday*: 39-60. University of Southern California, Los Angeles. <http://www.biodiversitylibrary.org/item/27606#page/55/mode/1up>
- Hartman, O. 1968. *Atlas of the Errantiate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles, 828 pp.
- Hartman, O. 1969. *Atlas of the Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.
- Hebert, P.D.N., Stoeckle, M.Y., Zemlak, T.S. & Francis, C.M. 2004. Identification of birds through DNA barcodes. *PLoS Biology*. 2(10), e 312, 7 pp. <http://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.0020312>
- Hennig, W. 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana, 263 pp.
- Hitchcock, A.S. 1921. The type concept in systematic Botany. *American Journal of Botany*. 8: 251-255. <https://archive.org/details/jstor-2434993>
- Holt, B.G. + 14 coauthors. 2013. An update of Wallace's zoogeographic regions of the world. *Science*. 339: 74-78. <https://www.sciencemag.org/content/339/6115/74.full>
- Hołyński, R.B. 2005. Philosophy of science from a taxonomist's perspective. *Genus*. 16: 469-502. <http://www.biol.uni.wroc.pl/cassidae/Philosophy%20taxonomy.pdf>
- Hoquet, T. 2005. *Les Fondaments de la Botanique: Linné et la Classification des Plantes*. Vuibert, Paris, 290 pp.
- Hörandl, E. & Stuessy, T.F. 2010. Paraphyletic groups as natural units of biological classification. *Taxon*. 59: 1641-1653. http://www.explorelifeonearth.org/cursos/Hoerandl_Stuessy_2010.PDF
- Hubbs, C.L. 1943. Criteria for subspecies, species and genera, as determined by researches on fishes. *Annals of the New York Academy of Sciences*. 44: 109-121. <http://deepblue.lib.umich.edu/bitstream/handle/2027.42/74997/j.1749-6632.1943.tb31297.x.pdf?sequence=1&isAllowed=y>
- Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*. 22: 414-427. <http://www2.unil.ch/biomapper/Download/Hutchinson-CSHSymQunBio-1957.pdf>
- Inger, R.F. 1958. Comments on the definition of genera. *Evolution*. 12: 370-384. http://www.jstor.org/stable/2405859?seq=1#page_scan_tab_contents
- International Commission on Zoological Nomenclature (ICZN). 1987. Opinion 1461: A ruling on the authorship and dates of the text volumes of the *Histoire naturelle* section of Savigny's *Description de l'Égypte*. *Bulletin of Zoological Nomenclature*, 44, 219-220. <http://www.biodiversitylibrary.org/part/388>
- Ipucha, M.C., Santos, C.G., Lana, P.C. & Sbalqueiro, I.J. 2007. Cytogenetic characterization of seven South American species of Nereididae (Annelida: Polychaeta): Implications for the karyotypic evolution. *Journal of Basic & Applied Genetics*. 18: 27-38. www.scielo.org.ar/pdf/bag/v18n2/v18n2a03.pdf
- Jaafar, T.N.A.M., Taylor, M.I., Nor, S.A.M., de Bruyn, M. & Carvalho, G.R. 2012. DNA barcoding reveals cryptic diversity within commercially exploited Indo-Malay Carangidae (Teleostei: Perciformes). *PLoS ONE*. 7(11), e49623, 16 pp. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0049623>
- Jablonski, D. & Finarelli, J.A. 2009. Congruence of morphologically defined genera with molecular phylogenies. *Proceedings of the National Academy of Sciences*. 106: 8262-8266. <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2688841/>
- Janssen, A., Kaiser, S., Meißner, K., Brenke, N., Menot, L. & Martínez Arbizu, P. 2015. A reverse taxonomic

- approach to assess macrofaunal distribution patterns in abyssal polymetallic nodule fields. *PLoS ONE*. 10(2), e0117790, 26 pp. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0117790>
- Jenyns, L. 1833. Some remarks on genera and subgenera, and on the principles on which they should be established. *Magazine of Natural History*, 6: 385-390. <https://www.biodiversitylibrary.org/item/19636#page/399/model/1up>
- Johns, G.C. & Avise, J.C. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. *Molecular Biology and Evolution*. 15: 1481-1490. <http://faculty.sites.uci.edu/johncavise/files/2011/03/192-cyt-b-summary.pdf>
- Just, T. 1953. Generic synopses and modern taxonomy. *Chronica Botanica*. 14(3/4): 103-114.
- Kahneman, D. 2011. *Thinking Fast and Slow*. Macmillan, New York, 512 pp.
- Kawano, K. 2000. Genera and allometry in the stag beetle family Lucanidae, Coleoptera. *Annals of the Entomological Society of America*. 93: 198-207. <http://aesa.oxfordjournals.org/content/aesa/93/2/198.full.pdf>
- Kellog, V.L. 1902. The development and homologies of the mouth parts of insects. *American Naturalist*. 36: 683-706. http://www.jstor.org/stable/2453776?seq=1#page_scan_tab_contents
- Kemp, T.S. 2016. *The Origin of Higher Taxa: Palaeobiological, Developmental and Ecological Perspectives*. Oxford University Press, Oxford, 201 pp.
- Kinberg, J.G.H. 1857-1910. Annulater (with a postscript by H. Théel). *Kongliga Svenska Fregatten Eugenies resa Omkring under bafäl af C.A. Virgin, Ånnen 1851-1853, Zoologi*. 3: 1-77, Pls 1-29.
- Kitcher, P. 1984. Species. *Philosophy of Science*. 51: 308-333. http://155.97.32.9/~mhaber/Documents/Course%20Readings/Kitcher_Species_PhiSci_1984.pdf
- Kocielek, J.P. & Williams, D.M. 2015. How to define a diatom genus? Notes on the creation and recognition of taxa, and a call for revisionary studies of diatoms. *Acta Botanica Croatiana*. 74: 195-210. <http://www.degruyter.com/view/j/botcro.2015.74.issue-2/botcro-2015-0018/botcro-2015-0018.xml>
- Kodric-Brown, A., Sibly, R.M. & Brown, J.H. 2006. The allometry of ornaments and weapons. *Proceedings of the National Academy of Sciences*. 103: 8733-8738. <http://www.pnas.org/content/103/23/8733.full>
- Kreft, H. & Jetz, W. 2013. Comment on "An update of Wallace's zoogeographic regions of the world. *Science*. 341: 343-344. <http://www.sciencemag.org/content/341/6144/343.3.full>
- Krug, A.Z., Jablonski, D. & Valentine, J.W. 2008. Species-genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proceedings of the Royal Society, B*. 275: 1117-1123. <http://rspb.royalsocietypublishing.org/content/275/1639/1117>
- Kurzweil, R. 2012. *How to Create a Mind: The Secret of Human Thought Revealed*. Viking, New York, 352 pp.
- Kvist, S. 2016. Does a global DNA barcoding gap exist in Annelida? *Mitochondria DNA A, DNA Mapping, Sequencing and Analysing*. 27: 2241-2252. <http://www.ncbi.nlm.nih.gov/pubmed/25431824>
- Kvist, S. & Siddall, M.E. 2013. Phylogenomics of Annelida revisited: A cladistic approach using genome-wide expressed sequence tag data mining and examining the effects of missing data. *Cladistics*. 29: 435-448. <http://onlinelibrary.wiley.com/doi/10.1111/cla.12015/abstract>
- Lamarck, J.B. 1786a. Espece (Species). *Encyclopédie Méthodique, Botanique*. 2: 395-396. <http://www.biodiversitylibrary.org/item/15260#page/397/model/1up>
- Lamarck, J.B. 1786b. Genres (des plantes), *Genera Plantarum. Encyclopédie Méthodique, Botanique*. 2: 630-634. <http://www.biodiversitylibrary.org/item/15260#page/632/model/1up>
- Lamarck, J.B. 1809. *Philosophie Zoologique*. Dentu, Paris, 2 vols. http://www.lamarck.cnrs.fr/ice/ice_book_detail-fr-text-lamarck-ouvrages_lamarck-29-1.html
- Lamarck, J.B. 1818. Classe Neuvième: Les Annelides. *Histoire Naturelle des Animaux sans Vertèbres*. 5: 274-374. <http://gallica.bnf.fr/ark:/12148/bpt6k64280058>
- Latreille, P.A. 1796. *Précis des Caracteres Génériques des Insectes, disposés dans un Ordre Naturel*. Bordeaux, Paris, 201 (+ 7 unnumb. pp). <http://www.biodiversitylibrary.org/bibliography/58411#/summary>
- Latreille, P.A. 1806. *Genera Crustaceorum et Insectorum Secundum Ordinem Naturalem in Familias Disposita, Iconibus Exemplisque*. Amand Koenig, Paris, 3 vols. <http://www.biodiversitylibrary.org/bibliography/34916#/summary>
- Latreille, P.A. 1808. Notice biographique sur Jean Chrétien Fabricius, conseiller d'état du roi de Dannemarck, professeur d'histoire naturelle et d'économie rurale à Kiell, et membre d'un grand nombre d'académies. *Annales du Muséum d'Histoire Naturelle*. 11: 393-404.
- Lawrence, G.H.M. 1953. Plant genera: Their nature and definition. The need for an expanded outlook. *Chronica Botanica*. 14(3/4): 117-120.
- Lawrence, G.H.M., Bailey, I.W., Eames, A.J., Rollins, R.C., Cave, M.S. & Mason, H.L. 1953. Plant Genera: Their Nature and Definition. A symposium. *Chronica Botanica*. 14(3/4): 89-160.
- Lee, M.S.Y & Palci, A. 2015. Morphological phylogenetics in the genomic age. *Current Biology*. 25: R922-R929. <http://dx.doi.org/10.1016/j.cub.2015.07.009>
- Legendre, P. 1971. Circumscribing the concept of the genus. *Taxon*. 20: 137-139. http://www.jstor.org/stable/1218542?seq=1#page_scan_tab_contents
- Legendre, P. 1972. The definition of systematic categories in Biology. *Taxon*. 21: 381-406. http://www.jstor.org/stable/1219102?seq=1#page_scan_tab_contents
- Legendre, P. & Vaillancourt, P. 1969. A mathematical model for the entities species and genus. *Taxon*. 18: 245-252. http://www.jstor.org/stable/1218824?seq=1#page_scan_tab_contents
- Leitão, A., Carvalho, S., Ben-Hamadou, R. & Gaspar, M.B. 2010. Cytogenetics of *Hediste diversicolor* (Annelida: Polychaeta) and comparative karyological analysis within Nereididae. *Aquatic Biology*. 10: 193-200. <http://www.int-res.com/articles/ab2010/10/b010p193.pdf>
- Lemen, C.A. & Freeman, P.W. 1984. The genus: A macroevolutionary problem. *Evolution*. 38: 1219-1237. <http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1022&context=natrespapers>
- Leroy, J.-F. 1956. Tournefort (1656-1708). *Revue d'Histoire des Sciences et de leurs Applications*. 9: 350-354. http://www.persee.fr/doc/rhs_0048-7996_1956_num_9_4_4372
- Linnaeus, C. 1737. *Genera Plantarum, Eorumque Characteres Naturales secundum Numerum, Figuram, Situm, & Proportionem omni fructificationis Partium*. Conrad Wishoff, Lugduni Batavorum (Leiden), 384 pp (+ Index in 20 unnumb. pp) <http://linnean-online.org/120003/>
- Linnaeus, C. 1751. *Philosophia Botanica in qua explicantur Fundamenta Botanica cum Definitionibus Partium, Exemplis Terminorum, Observationibus Rariorum*. Kiesewetter, Stockholm, 362 pp. <http://www.biodiversitylibrary.org/bibliography/37652#/summary>
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Laurentii

- Salvii, Holmiae, 824 pp. <http://www.biodiversitylibrary.org/item/80764#page/3/mode/1up>
- Linnaeus, C. 1767. *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Laurentii Salvii, Holmiae, 3 volumes. <http://www.biodiversitylibrary.org/item/137337#page/5/mode/1up>
- Linnaeus, C. 1790. *Disquisitio de Sexu Plantarum cum Annotationibus D. Jacobi Eduardi Smith et P.M. Aug. Broussonet*. *Amoenitates Academicae* 10(9):100-131. <http://sammlungen.ub.uni-frankfurt.de/botanik/periodical/pageview/4611455>
- Lubischew, A. 1969. Philosophical aspects of Taxonomy. *Annual Review of Entomology*. 14: 19-38. www.annualreviews.org/doi/pdf/.../annurev.en.14.010169.00031
- Macleay, W.S. 1819. *Horae Entomologicae: Essays on the Annulose Animals*. Bagster, London (part 2 publ. 1821), 524 pp. <https://archive.org/details/horaeentomologic112macl>
- Maggenti, A.R. 1989. Genus and family: concepts and natural groupings. *Revue de Nématologie*. 12: 3-6. http://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_5/pt5/nemato/27743.pdf
- Malik, V. 2017. The genus: a natural or arbitrary entity. *Plant Archives*, 17: 251-257.
- Maruvka, Y.E., Shnerb, N.M., Kessler, D.A. & Ricklefs, R.E. 2013. Model for macroevolutionary dynamics. *Proceedings of the National Academy of Sciences*, 110: E2460-E2469. <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3703965/>
- Mason, H.L. 1953. Plant geography in the delimitation of genera: The role of plant geography in taxonomy. *Chronica Botanica*. 14(3/4): 154-159.
- Maurer, B.A., Brown, J.H. & Rusler, R.D. 1992. The micro and macro in body size evolution. *Evolution*. 46: 939-953. <http://biology.unm.edu/jhbrown/Documents/Publications/MaurerBrown%26Rusler1992E.pdf>
- Mayr, E. 1943. Criteria of subspecies, species, and genera in Ornithology. *Annals of the New York Academy of Sciences*. 44: 133-139. <http://onlinelibrary.wiley.com/doi/10.1111/j.1749-6632.1943.tb31299.x/pdf>
- Mayr, E. & Ashlock, P.D. 1991. *Principles of Systematic Zoology*, 2nd ed., McGraw-Hill, New York, 475 pp.
- Mayr, E., Linsley, E.G. & Usinger, R.L. 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill, New York, 336 pp.
- McGregor, R.C. 1921- Genera and species. *Condor*. 23: 127-129. <https://sora.unm.edu/sites/default/files/journals/condor/v023n04/p0127-p0129.pdf>
- McNeill, J. 1972. The hierarchical ordering of characters as a solution to the dependent character problem in numerical taxonomy. *Taxon*. 21: 71-82. http://www.jstor.org/stable/1219225?seq=1#page_scan_tab_contents
- McVaugh, R. 1945. The genus *Triodanis* Rafinesque, and its relationships to *Specularia* and *Campanula*. *Wrightia*. 1: 13-52. <http://www.biodiversitylibrary.org/item/15463#page/31/mode/1up>
- Merz, R.A. & Woodin, S.A. 2006. Polychaete chaetae: Function, fossils, and phylogeny. *Integrative and Comparative Biology*. 46: 481-496. <http://icb.oxfordjournals.org/content/46/4/481.full>
- Milne-Edwards, H. 1838. Classe Neuvième: Les Annelides. *Histoire Naturelle des Animaux sans Vertèbres, deuxième édition*. 5: 499-639.
- Minelli, A. 2014. Book Review: The Nature of Classifications: Relationships and Kinds in the Natural Sciences. *Systematic Biology*. 63: 844-846. <https://academic.oup.com/sysbio/article/63/5/844/2847793/The-Nature-of-Classification-Relationships-and>
- Minelli, A., Fusco, G. & Sartori, S. 1991. Self-similarity in biological classifications. *BioSystems*. 26: 89-97. [http://dx.doi.org/10.1016/0303-2647\(91\)90040-R](http://dx.doi.org/10.1016/0303-2647(91)90040-R)
- Monro, C.C.A. 1928. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-16, 45. On the Polychaeta collected by Dr. Th. Mortensen off the coast of Panama. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*. 85: 75-103.
- Mosquin, D. 2012. Constantine Rafinesque, a flawed genius. *Arnoldia*. 70: 2-10. <http://arnoldia.arboretum.harvard.edu/pdf/articles/2012-70-1-constantine-rafinisque-a-flawed-genius.pdf>
- Müller-Wille, S. 2005. La science baconienne en action: La place de Linné dans l'histoire de la taxonomie; pp 57-102 In Hoquet T. (Ed.), *Les Fondaments de la Botanique: Linné et la Classification des Plantes*. Vuibert, Paris, 290 pp.
- Müller-Wille, S. 2007. Collection and collation: Theory and practice in Linnaean Botany. *Studies in History and Philosophy of Biological and Biomedical Sciences*. 38: 541-562. <http://www.sciencedirect.com/science/article/pii/S1369848607000428>
- Müller-Wille, S. 2013. Systems and how Linnaeus looked at them in retrospect. *Annals of Science*. 70: 305-317. <http://www.tandfonline.com/doi/abs/10.1080/00033790.2013.783109>
- Müller-Wille, S. & Charmantier, I. 2012. Natural history and information overload: The case of Linnaeus. *Studies in History and Philosophy of Biological and Biomedical Sciences*. 43: 4-15. <http://www.sciencedirect.com/science/article/pii/S1369848611001130>
- Müller-Wille, S. & Reeds, K. 2007. A translation of Carl Linnaeus's introduction to *Genera Plantarum* (1737). *Studies in History of Philosophy and Biomedical Sciences*. 38: 563-572. <http://www.sciencedirect.com/science/article/pii/S1369848607000349>
- Nelson, G. 1978. From Candolle to Croizat: Comments on the History of Biogeography. *Journal of the History of Biology*. 11: 269-305. <http://link.springer.com/article/10.1007%2FBF00389302>
- Newman, M.E.J. 2005. Power laws, Pareto distributions and Zipf's law. *Contemporary Physics*. 46: 323-351. http://arxiv.org/PS_cache/cond-mat/pdf/0412/0412004v3.pdf
- Nicholson, D.J. & Gawne, R. 2015. Neither logical empiricism nor vitalism, but organicism: what the philosophy of biology was. *History and Philosophy of the Life Sciences*. 37: 345-381. <http://link.springer.com/article/10.1007/s40656-015-0085-7>
- Ohler, A. & Dubois, A. 1999. The identity of *Elachyglossa gyldenstolpei* Andersson, 1916 (Amphibia, Ranidae), with comments on some aspects of statistical support to taxonomy. *Zoologica Scripta*. 28: 269-279. <http://onlinelibrary.wiley.com/doi/10.1046/j.1463-6409.1999.00002.x/pdf>
- Olson, E. 1991. *George Gaylord Simpson, 1902-1984*. National Academy of Sciences, Biographical Memoir, 25 pp. <http://www.nasonline.org/publications/biographical-memoirs/memoir-pdfs/simpson-george.pdf>
- Padial, J.M. & de la Riva, I. 2007. Integrative taxonomists should use and produce DNA barcodes. *Zootaxa*. 1586: 67-68. <http://digital.csic.es/bitstream/10261/120859/1/Zootaxa%201586%2067-68%20%282007%29.pdf>
- Paláu y Verdèra, A. 1778. *Explicación de la Filosofía y Fundamentos Botánicos de Linneo, con la que se Aclaran y Entienden Fácilmente las Instituciones Botánicas de Tournefort*. Antonio de Sancha, Madrid, 306 pp, 9 Pls. https://books.google.es/books/about/Explicacion_de_la_filosofia_y_fundamento.html?id=wo1QAzpe5JoC&hl=es
- Páll-Gergely, B. 2017. Should we describe genera without molecular phylogenies? *Zootaxa*. 4232: 593-596. <http://mapress.com/j/zt/article/view/zootaxa.4232.4.11>

- Pallary, P. 1931. Les manuscrits et les vélins de Savigny. *Bulletin du Muséum National d'Histoire Naturelle, Paris, 2ème série*. 3: 711-720. <http://gallica.bnf.fr/ark:/12148/bpt6k55294762/f9.image.r=Pallary%20P>
- Panchen, A.L. 1992. *Classification, Evolution, and the Nature of Biology*. Cambridge University Press, Cambridge, 403 pp.
- Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D. & Vinther, J. 2016. The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proceedings of the Royal Society, B*. 283: 20161378, 9 pp. <http://rspb.royalsocietypublishing.org/content/royprsb/283/1837/20161378.full.pdf>
- Pavlinov, I.Y. 2011. Concepts of rational Taxonomy in Biology. *Biology Bulletin Reviews*. 1: 225-244. http://zmmu.msu.ru/personal/pavlinov/doc/rat_tax_e.pdf
- Pesch, C.G. & Mueller, C. 1988. Chromosome complements from two populations of the marine worm *Neanthes arenaceodentata* (Annelida: Polychaeta). *Ophelia*. 28: 163-167. <http://www.tandfonline.com/doi/abs/10.1080/00785326.1988.10430810>
- Pleijel, F., Jondelius, U., Norlinder, E., Nygren, A., Oxelman, B., Schander, C., Sundberg, P. & Thollesson, M. 2008. Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. *Molecular Phylogenetics and Evolution*. 48: 369-371. <http://www.sciencedirect.com/science/article/pii/S105579030800136X>
- Portères, R. 1950. La variation parallèle. *Revue Internationale de Botanique Appliquée et d'Agriculture Tropicale*. 30: 468-481. <https://hort.purdue.edu/newcrop/pdfs/777.full.pdf>
- Proches, S. & Ramdhani, S. 2012. The world's zoogeographical regions confirmed by cross-taxon analyses. *BioScience*. 62: 260-270. <http://bioscience.oxfordjournals.org/content/62/3/260.abstract>
- Purschke, G., Bleidorn, C. & Struck, T. 2014. Systematics, evolution and phylogeny of Annelida - a morphological perspective. *Memoirs of Museum Victoria*. 71: 247-269. http://museumvictoria.com.au/pages/58031/247-270_mmv71_purschke_2bpz_web.pdf
- Radulovici A.E., Arcchambault, P. & Dufresne, F. 2010. DNA barcodes for marine biodiversity: Moving fast forward? *Diversity*. 2: 450-472. <http://www.mdpi.com/1424-2818/2/4/450>
- Rafinesque, C.S. 1836. *Flora Telluriana, First Part*. Probasco, Philadelphia, 103 pp. <https://archive.org/details/floratelluriana00rafi>
- Ramsbottom, J. 1938. Linnaeus and the species concept. *Proceedings of the Linnean Society, London*. 1938: 192-219. <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.1938.tb00181.x/pdf>
- Raven, P.H., Berlin, B. & Breedlove, D.E. 1971. The origins of Taxonomy. *Science*. 174: 1210-1213. <http://science.sciencemag.org/content/174/4015/1210.long>
- Regan, C.T. 1926. Organic evolution. *British Association for the Advancement of Science, Report of the 93rd Meeting, Southampton 1925, Aug. 26-Sep. 2*. 75-86. London, 494 pp. <http://www.biodiversitylibrary.org/part/117948>
- Reindl, A., Strobach, T., Becker, C., Scholtz, G. & Schubert, T. 2015. Crab or lobster? Mental principles underlying the categorization of crustaceans by biology experts and non-experts. *Zoologischer Anzeiger*. 256: 28-35. <http://dx.doi.org/10.1016/j.jcz.2015.03.001>
- Reish, D.J., Anderson, F.E., Horn, K.M. & Hardege, J. 2014. Molecular phylogenetics of the *Neanthes acuminata* (Annelida: Nereididae) species complex. *Memoirs of Museum Victoria*. 71: 271-278. http://museumvictoria.com.au/pages/58033/271-278_mmv71_reish_4pz_web.pdf
- Ridgway, R. 1923. Generic subdivision: The genus debased. *Auk*. 40: 371-375. <https://sora.unm.edu/sites/default/files/journals/auk/v040n02/p0371-p0375.pdf>
- Roemer, F. 1880. Adolph Eduard Grube. *Leopoldina, Kaiserlichen Leopoldina-Carolinischen Deutschen Akademie der Naturforscher*. 16: 114-117.
- Rogers, D.P. 1958. The Philosophy of Taxonomy. *Mycologia*. 50: 326-332. <http://www.jstor.org/stable/3756070>.
- Rogers, D.J. & Appan, S.G. 1969. Taximetric methods for delimiting biological species. *Taxon*. 18: 609-624. http://www.jstor.org/stable/1218915?seq=1#page_scan_tab_contents
- Rollins, R.C. 1953. Cytogenetical approaches to the study of genera. *Chronica Botanica*. 14(3/4): 133-139.
- Rose, H. (1775) *The Elements of Botany: Containing the History of the Science (with Accurate Definitions of all the Terms of Art, exemplified in Eleven Copper-Plates; The Theory of Vegetables; The Scientific Arrangement of Plants, and Names used in Botany; Rules concerning the general History, Virtues, and Uses of Plants, Being a Translation of the Philosophia Botanica, and other Treatises of the celebrated Linnaeus)*. Cadell & Hingeston, London, 471 pp, 11 Pls. <https://archive.org/details/elementsofbotany00rose>
- Round, F.E. 1997. Genera, species and varieties - are problems real or imagined? *Diatom*. 13: 25-29. https://www.jstage.jst.go.jp/article/diatom1985/13/0/13_25/_article
- Rubinoff, D., Cameron, S. & Will, K. 2006. A genomic perspective on the shortcomings of mitochondrial DNA for 'barcoding' identification. *Journal of Heredity*. 97: 581-594. <http://jhered.oxfordjournals.org/content/97/6/581.full>
- Saint-Hilaire, I.G. 1832. Considérations sur les caractères employés en Ornithologie pour la distinction des genres, des familles et des orders, et Détermination de plusieurs genres nouveaux. *Nouvelles Annales du Muséum d'Histoire Naturelle, Paris*. 1: 357-397. <http://www.biodiversitylibrary.org/item/103417#page/403/mode/1up>
- Salazar-Vallejo, S.I. 2019. Reflexiones sobre cómo llegar a ser un buen taxónomo. *Biología Sociedad*. 2: 4-18.
- Salazar-Vallejo, S.I. 2020. Revision of *Leocrates* Kinberg, 1866 and *Leocratides* Ehlers, 1908 (Annelida, Errantia, Hesionidae). *Zootaxa*. 4739: 1-114. <https://doi.org/10.11646/zootaxa.4739.1.1>
- Salazar-Vallejo, S.I., Carrera-Parra, L.F., González, N.E. & Salazar-González, S.A. 2014. Biota portuaria y taxonomía; pp 33-54 In: Low-Pfeng, A.M., Quijón, P.A. & Peters-Recagno, E.M. (Ed.), *Especies Invasoras Acuáticas: Casos de Estudio en Ecosistemas de México*. SEMARNAT, INECC & Univ. Prince Edward Island, México, 643 pp. Available: http://www2.inecc.gob.mx/publicaciones/consultaPublicacion.html?id_pub=713
- Salazar-Vallejo, S.I. & González, N.E. 2016. Crisis múltiples en taxonomía, implicaciones para la biodiversidad y recomendaciones para mejorar la situación. *Códice, Boletín Científico y Cultural del Museo Universitario, Universidad de Antioquia*. 17: 42-56. https://issuu.com/muua/docs/c_dice_29_web
- Salazar-Vallejo, S.I. & Hutchings, P. 2012. A review of characters useful in delineating ampharetid genera (Polychaeta). *Zootaxa*. 3402: 45-53. <http://www.mapress.com/zootaxa/2012/fz03402p053f.pdf>
- Savigny, J.-C. 1822. Système des Annelides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les caractères tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Espèces. *Description de l'Égypte, Histoire Naturelle*, 1(3), 1-128, Pls 1-5 (first edition 1820, as indicated in page 128; second edition 1826). <http://www.biodiversitylibrary.org/item/193034#page/8/mode/1up>
- Sbordoni, V. 2010. Strength and limitations of DNA barcode

- under the multidimensional species perspective. In: Nimis, P.L. & Lebbe, R.V. (Ed.), *Tools for Identifying Biodiversity: Progress and Problems*: 275-280. Edizioni Università Trieste, Trieste, 455 pp. <http://www.openstarts.units.it/dspace/handle/10077/3790>
- Sclater, P.L. 1858. On the general geographical distribution of the members of the Class Aves. *Journal of the Proceedings of the Linnean Society, London, Zoology*. 2: 130-136. <http://biodiversitylibrary.org/item/35033#page/140/mode/1up>
- Seifert, B. 2014. A pragmatic species concept applicable to all eukaryotic organisms independent from their mode of reproduction or evolutionary history. *Soil Organisms*. 86: 85-93 <https://zenodo.org/record/218030>
- Sherborn, C.D. 1897. On the dates of the Natural History portion of Savigny's 'Description de l'Égypte.' *Proceedings of the Zoological Society, London*. 1897: 285-288. <http://www.biodiversitylibrary.org/item/97165#page/349/mode/1up>
- Sherff, E.E. 1940. The concept of the genus, 4. The delimitations of genera from the conservative point of view. *Bulletin of the Torrey Botanical Club*. 67: 375-380. http://www.jstor.org/stable/2481071?seq=1#page_scan_tab_contents
- Sigwart, J.D., Sutton, M.D. & Bennett, K.D. 2018. How big is a genus? Towards a nomothetic systematics. *Zoological Journal of the Linnean Society*, 183: 237-252. <https://academic.oup.com/zoolinnear/article-abstract/183/2/237/4554320?redirectedFrom=fulltext>
- Simpson, G.G. 1943. Criteria for genera, species, and subspecies in Zoology and Paleozoology. *Annals of the New York Academy of Sciences*. 44: 145-178. <http://onlinelibrary.wiley.com/doi/10.1111/j.1749-6632.1943.tb31301.x/abstract>
- Simpson, G.G. 1944. *Tempo and Mode in Evolution*. Columbia University Press, New York, 237 pp.
- Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*. 85: 1-350. <http://digitallibrary.amnh.org/handle/2246/1104>
- Sinha, P. 2002. Recognizing complex patterns. *Nature Neuroscience, Supplement*. 5: 1093-1097. <http://www.nature.com/neuro/journal/v5/n11s/full/nn949.html>
- Sivarajan, V.V. & Robson, N.K.B. 1991. *Introduction to the Principles of Plant Taxonomy*. 2nd ed., Univ. Cambridge Press, Cambridge, 295 pp.
- Stadler, T., Rabosky, D.L., Ricklefs, R.E. & Bokma, F. 2014. On age and species richness of higher taxa. *American Naturalist*. 184: 447-455. http://www.jstor.org/stable/10.1086/677676?seq=1#page_scan_tab_contents
- Stafleu, F.A. 1971. Lamarck: The birth of Biology. *Taxon*. 20: 397-442. <http://www.blc.arizona.edu/courses/schaffer/449/Lamarck/Stafleu%20-%20Birth%20of%20Biol.pdf>
- Stearn, W.T. 1959. The background of Linnaeus's contributions to the nomenclature and methods of Systematic Biology. *Systematic Zoology*. 8: 4-22. <http://www.jstor.org/stable/2411603>
- Stevens, P.F. 1985. The genus concept in practice: But for what practice? *Kew Bulletin*. 40: 457-465. http://www.jstor.org/stable/4109605?seq=1#page_scan_tab_contents
- Stevens, P.F. 1994. *The Development of Biological Systematics: Antoine-Laurent de Jussieu, Nature, and the Natural System*. Columbia University Press, New York, 627 pp.
- Stevens, P.F. 1997. Mind, memory and history: How classifications are shaped by and through time, and some consequences. *Zoologica Scripta*. 26: 293-301. <http://onlinelibrary.wiley.com/doi/10.1111/j.1463-6409.1997.tb00419.x/abstract>
- Stevens, P.F. 2002. Why do we name organisms? Some reminders from the past. *Taxon*. 51: 11-26. <http://www.jstor.org/stable/pdf/1554959.pdf>
- Stevens, P.F. 2009. Characters, taxonomic groups, and relationships in Botany 1770-1850 as exemplified by the work of Henri Cassini. *Taxon*. 58: 32-42 <http://www.jstor.org/stable/27756821>
- Stoeckle, M. 2003. Taxonomy, DNA, and the barcode of life. *BioScience*. 53: 796-797. http://barcoding.si.edu/BackgroundPublications/BioScience03_Sept_View_Stoeckle.pdf
- Strand, M. & Panova, M. 2015. Size of genera - biology or taxonomy? *Zoologica Scripta*. 44: 106-116. <http://onlinelibrary.wiley.com/doi/10.1111/zsc.12087/abstract>
- Strickland, H.E. 1841. On the true Method of discovering the Natural System in Zoology and Botany. *Annals and Magazine of Natural History*. 6: 184-194. <http://www.biodiversitylibrary.org/item/139444#page/214/mode/1up>
- Strickland, H.E., Phillips, J., Richardson, J., Owen, R., Jenyns, L., Broderip, W.J., Henslow, J.S., Shuckard, W.E., Waterhouse, G.R., Yarrell, W., Darwin, C. & Westwood, J.O. 1843. Series of propositions for rendering the Nomenclature of Zoology uniform and permanent, being the report of a Committee for the consideration of the subject appointed by the British Association for the Advancement of Science. *Annals and Magazine of Natural History*. 11: 259-275. <http://www.biodiversitylibrary.org/item/19570#page/283/mode/1up>
- Struck, T.H. 2011. Direction of evolution within Annelida and the definition of Pleistoannelida. *Journal of Zoological Systematics and Evolutionary Research*. 49: 340-345. <http://onlinelibrary.wiley.com/doi/10.1111/j.1439-0469.2011.00640.x/abstract>
- Struck, T.H. 2013. The impact of paralogy on phylogenomic studies - A case study on annelid relationships. *PLoS ONE*. 8(5): e62892, 22 pp. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0062892>
- Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G. & Bleidorn, C. 2011. Phylogenomic analyses unravel annelid evolution. *Nature*. 471: 95-98. <http://www.nature.com/nature/journal/v471/n7336/full/nature09864.html>
- Stuessy, T.F. 2009a. *Plant Taxonomy: The Systematic Evaluation of Comparative Data*. 2nd ed., Columbia Univ. Press, New York, 538 pp.
- Stuessy, T.F. 2009b. Paradigms in biological classification (1707-2007): Has anything really changed? *Taxon*. 58: 68-76. <http://www.ktriop.bio.ug.edu.pl/upload/preview/7b100a2d1e90c9587c9f9532778914c7.pdf>
- Svenson, H.K. 1945. On the descriptive method of Linnaeus. *Rhodora, Journal of the New England Botanical Club*. 47: 273-302, 363-388. <http://www.biodiversitylibrary.org/item/14517#page/420/mode/1up>
- Tollit, M.E. 1986. Dates and authorship of the text volumes of the Histoire Naturelle section of Savigny's Description de l'Égypte. *Bulletin of Zoological Nomenclature*. 43: 107-110. <http://www.biodiversitylibrary.org/part/388>
- Tournefort, P. 1694. *Elemens de Botanique, ou Methode pour Connoître les Plantes*. Imprimerie Royale, Paris, 2 vols. <http://gallica.bnf.fr/ark:/12148/btv1b8454361d/f9.item>
- Turrill, W.B. 1942a. Taxonomy and phylogeny, 1. Introduction and historical development of plant classification. *Botanical Review*. 8: 247-270. <http://www.jstor.org/stable/4353269>
- Turrill, W.B. 1942b. Taxonomy and phylogeny, 2. Taxonomic and phylogenetic concepts and criteria, and data used in classification and phylogenetic studies. *Botanical Review*. 8: 473-532 <http://www.jstor.org/stable/4353275>
- Turrill, W.B. 1942c. Taxonomy and phylogeny, 3. Classification and phylogeny in the major groups, Logical as opposed to phylogenetic classifications, Phylogenetic diagrams, Conclusions, and Epilogue. *Botanical Review*. 8: 655-707

- <http://www.jstor.org/stable/4353279>
- Tuxen, S.L. 1967 The entomologist, J.C. Fabricius. *Annual Review of Entomology*. 12: 1-15. <http://www.annualreviews.org/doi/pdf/10.1146/annurev.en.12.010167.000245>
- Tyrl, R.J. 2010. "Being a method proposed for the ready finding... to what sort any plant belongeth". *Oklahoma Native Plants Record*. 10: 77-84. <http://ojs.library.okstate.edu/osu/index.php/ONPR/article/viewFile/422/402>
- Varma, C.S. 2013. *Beyond Set Theory: The Relationships between Logic and Taxonomy from the early 1930 to 1960*. Ph D. Diss., Univ. Toronto, 329 pp. <https://tspace.library.utoronto.ca/handle/1807/68972>
- Vasilyeva, L.N. 1999. Systematics in Mycology. *Bibliotheca Mycologica*. 178: 1-253.
- Vasilyeva, L.N. & Stephenson, S.L. 2010. The problems of traditional and phylogenetic taxonomy of fungi. *Mycosphere*. 1: 45-51. http://www.mycosphere.org/pdfs/MC1_5.pdf
- Vasilyeva, L.N. & Stephenson, S.L. 2012. The hierarchy and combinatorial space of characters in evolutionary systematics. *Botanica Pacifica*. 1: 21-30. https://www.researchgate.net/publication/273492790_The_Hierarchy_and_Combinatorial_Space_of_Characters_in_Evolutionary_Systematics
- Vasilyeva, L. & Stephenson, S.L. 2013. "I have come to some conclusions that shock me ...". *Mycosystema*. 32: 321-329. <http://manu40.magtech.com.cn/Jwx/EN/Y2013/V32/I3/321>
- Vavilov, N.I. 1922. The law of homologous series in variation. *Journal of Genetics*. 12: 47-89. <http://link.springer.com/article/10.1007%2FBF02983073>
- Vinarski, M.V. 2013. One, two, or several? How many lymnaeid genera are there? *Rutenica*. 23: 41-58. <http://www.biotaxa.org/Ruthenica/article/viewFile/1020/1669>
- Voss, E.G. 1952. The history of keys and phylogenetic trees in systematic biology. *Journal of Science Laboratory, Denison University*, 43, 1-25 (difficult to find; a pdf is available upon request).
- Wadhawan, V. 2014. Kurzweil's pattern-recognition theory of mind, 1 & 2. <http://vinodwadhawan.blogspot.in/2014/03/125-kurzweils-pattern-recognition.html>, <http://vinodwadhawan.blogspot.mx/2014/04/126-kurzweils-pattern-recognition.html>
- Wallace, A.R. 1876. *The Geographical Distribution of Animals, with a Study of the Relations of Living and Extinct Faunas as elucidating the past Changes of the Earth Surface*. Harper & Brothers, New York, 2 vols.
- Wallace, A.R. 1895. The method of organic evolution. *Fortnightly Review, new series*. 57: 211-224, 435-445. <http://people.wku.edu/charles.smith/wallace/S510.htm>
- Ward, L. 2005. The publications of Kristian Fauchald and the polychaete taxa named in those works. *Marine Ecology*. 26: 145-154. <http://onlinelibrary.wiley.com/doi/10.1111/j.1439-0485.2005.00068.x/abstract>
- Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. & Hebert, P.D.N. 2005. DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society B*. 360: 1847-1857. <http://rstb.royalsocietypublishing.org/content/360/1462/1847.long>
- Warren, L. 2004. *Constantine Samuel Rafinesque: A Voice in the American Wilderness*. University Press of Kentucky, Lexington, 252 pp.
- Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanynch, K.M., Purschke, G., Bleidorn, C. & Struck, T.H. 2014. Illuminating the base of the annelid tree using transcriptomics. *Molecular Biology and Evolution*. 31: 1391-1401. <http://mbe.oxfordjournals.org/content/early/2014/02/23/molbev.msu080>
- Wheeler, Q.D. 2008. Undisciplined thinking: Morphology and Hennig's unfinished revolution. *Systematic Entomology*. 33: 2-7. <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-3113.2007.00411.x/full>
- Wilkins, J.S. & Ebach, M.C. 2014. *The Nature of Classification: Relationships and Kinds in the Natural Sciences*. Palgrave Macmillan, New York, 197 pp.
- Williams, C.B. 1951. A note on the relative sizes of genera in the classification of animals and plants. *Proceedings of the Linnean Society, London*. 162: 171-175. <http://onlinelibrary.wiley.com/doi/10.1111/j.1095-8312.1951.tb00610.x/abstract>
- Williams, R.L. 2001. Botanophilia in Eighteenth-Century France: The Spirit of Enlightenment. *Archives Internationales d'Histoire des Idées*. 179: 1-206. <http://www.springer.com/la/book/9780792368861>
- Winsor, M.P. 2001. Cain on Linnaeus: The scientist-historian as unanalysed entity. *Studies on the History of Philosophy, Biology and Biomedical Sciences*. 32: 239-254. <http://www.marypwinsor.com/wp-content/uploads/2014/01/Winsor2001a-Cain-Linn.pdf>
- Winsor, M.P. 2003. Non-essentialist methods in pre-Darwinian taxonomy. *Biology and Philosophy*. 18: 387-400. <http://www.marypwinsor.com/wp-content/uploads/2014/01/Winsor-2003-NonEssentialist-Methods.pdf>
- Winsor, M.P. 2006. Linnaeus Biology was not essentialist. *Annals of the Missouri Botanical Garden*. 93: 2-7. http://www.jstor.org/stable/40035041?seq=1#page_scan_tab_contents
- Winsor, M.P. 2009. Taxonomy was the foundation of Darwin's evolution. *Taxon*. 58: 43-49. <https://www.jstor.org/stable/pdf/27756822.pdf>
- Winston, J.E. 1999. *Describing Species: Practical Taxonomic Procedure for Biologists*. Columbia Univ. Press, New York, 518 pp.
- Zaddach, G. 1880. *Adolph Eduard Grube. Gedächtnissrede gehalten in der Physikalisch-ökonomischen Gessellschaft zu Königsberg*. Königsberg, 17 pp.
- Zakharov, E.V., Lobo, N.F., Nowak, C. & Hellmann, J.J. 2009. Introgression as a likely cause of mtDNA paraphyly in two allopatric skippers (Lepidoptera: Hesperidae). *Heredity*. 102: 590-599. <http://www.nature.com/hdy/journal/v102/n6/full/hdy200926a.html>
- Zander, R.H. 2013. *A Framework for Post-Phylogenetic Systematics*. Zetetic Publications, Saint Louis, 209 pp.
- Zapata, F. & Jiménez, I. 2012. Species delimitation: Inferring gaps in morphology across geography. *Systematic Biology*. 61: 179-194. <http://sysbio.oxfordjournals.org/content/61/2/179.long>
- Zrzavý, J., Říha, P., Piálek, L. & Janouškovec, J. 2009. Phylogeny of Annelida (Lophotrochozoa): Total evidence analysis of morphology and six genes. *BMC Evolutionary Biology*. 9: 189, 14 pp. <http://bmcevolbiol.biomedcentral.com/articles/10.1186/1471-2148-9-189>