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Linear listing order and hierarchical classification: history, conflict, and use

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Abstract. Taxonomic criteria alone are not sufficient to determine a linear sequence for the arrangement of collection specimens according to a preferred classification or the linear sequence according to which taxa are best discussed in articles or books. The choice of methodology to obtain a linear sequence of taxa in agreement with a hierarchical classification has been little studied and remains controversial. In this article, I offer an historical background, before examining properties, use and limits of possible listing criteria. The result of a linearization effort depends on arbitrary choices with respect to two aspects of the hierarchical classification we intend to linearize. One is the order to be followed in listing the immediately subordinate members of a given taxon, the other is the choice of the sets of taxa to be linearized according to tradition, alphabetic order or other criterion. The example presented here, related to the "orders" of Hexapoda, demonstrates the need to specify very clearly the extent and composition of the uncollapsed classification backbone retained in the linearization procedure.

Keywords. Alphabetic order of taxa, collapsing nodes, hierarchical classification vs linear listing order, history of taxonomy, linear classification.

> "As the Tree of Life is estimated with increasing confidence, resolution and completeness, linear sequences for many groups of organisms will be sought at all ranks – orders, families, genera within families, species within genera, etc. – both to order collections of specimens (dead or living) and [to organize the contents of] books of all sorts from taxonomic monographs to floras and field identification guides"
>
> Hawthorne & Hughes 2008: 698

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Introduction

Combining the efforts to align zoological and botanical classifications with the continuous progress of systematics as well as with the practical needs of the classifications' users is a difficult task that has been the subject of heated discussion, proposals and criticisms for many years now. In recent times, attention has been increasingly focused on the taxonomic and nomenclatural stability of species lists: a group of six articles published two years ago in *Organisms Diversity and Evolution* (Conix *et al.* 2021; Hobern *et al*. 2021; Lien *et al.* 2021; Pyle *et al.* 2021; Thiele *et al.* 2021; Thomson *et al.* 2021) deserve particular attention for the depth of the analysis.

In addition to the thorny questions concerning taxonomy and nomenclature of species-level taxa, there are other important issues, in this trading area between creators and users of taxonomy, that are much less frequently and less critically discussed. In this article I focus on the criteria to arrange taxa in a linear sequence in satisfactory agreement with a hierarchical (e.g., phylogenetic) classification. There are many circumstances where a linear sequence of taxa is needed, for example, in arranging the specimens of a collections, or in writing textbooks and other kinds of publications. Unfortunately, there is no definitive, unambiguous solution to this problem.

Today, the intractability of linearization can be seen as a consequence of a mismatch between the unidimensional sequence of items in a list and the multimensional structure of the tree of life, but the problem emerged well before the advent of phylogeny-informed classifications, i.e., in a context of Linnaean taxonomy.

To put the problem in adequate context, I will first offer an historical and conceptual background, before examining properties, use and limits of some of the possible listing criteria.

A key issue is the distinction between linear order and hierarchical classification. As recently discussed (Minelli 2022a, 2022b; based on Hjørland 2017), simple ordering e.g., by alphabetic sequence may satisfy some relaxed definitions of classification (e.g., Bliss 1929), but a classification in the sense acceptable to a zoologist or a botanist requires a hierarchical structure with at least two levels. In the following historical account we will find examples of ordering in the absence of a classification, and vice versa. Independence between order and classification was acknowledged long ago, at the time an ascending order of taxa (from those of simplest to those of most complex organization) was suggested as a better alternative to the opposite order: "The inversion of classes, adopted for ease of study, cannot harm the progress of science, so long as these classes are simply transposed without experiencing any decomposition, and the families are preserved in their integrity" (Jussieu 1824: 466; all translations from French, German and Latin are mine). By arranging the main groups of invertebrates from the simplest to the most complex, thus reversing the traditional order, Lamarck (1815–22) in the *Histoire naturelle des animaux sans vertèbres* had also demonstrated that the link between classification and ordering is not indissoluble.

In the following sections, I will clarify, by means of examples from the scientific literature of the XVI to XVIII centuries, the increasingly clear distinction between order and classification, the emerging awareness of the inadequacy of ordering taxa by alphabet, and the eventual realization of the incompatibily between a strictly linear distribution of plant or animal species and their classification according to their affinities, whatever this term may have meant to different authors and in different times.

Order – by alphabet, or otherwise

It is convenient to start with authors preceding the foundational efforts in systematics of John Ray and Joseph Pitton de Tournefort and also, before them, Andrea Cesalpino (Caesalpinus), the Italian botanist often mentioned as the first author to have organized a treatise on plants in the frame of explicit, although quite loose, classificatiory criteria.

In sixteenth-century encyclopaedic works such as the great herbal of Fuchs (1542) and Gessner's volumes on animals (e.g., Gessner 1551), there is hardly evidence of a classification in the ordinary sense of the term. In Gessner's case, the division of the text into volumes dedicated to different kinds of animals (viviparous quadrupeds, oviparous quadrupeds, birds, fishes) does not extend beyond the lowest degree of taxonomy recognizable in ethnoclassifications (Berlin *et al*. 1966, 1973; Berlin 1973, 1992). Within each volume, some sets of animals (or plants, in the case of herbals) very similar to each other are often illustrated in close sequence, as if informally put in the same class, but this effort is by no means uniform (see below, Beyond alphabetic ordering).

Some of these works, e.g., Brunfels's (1530) herbal or Thomas Moffett's (1634) *Insectorum sive minimorum animalium theatrum*, show no clear sign of an ordering effort. In other cases, however, e.g., in Fuchs' herbal *De historia stirpium* (1542), the author adopted the alphabetic order of the Latin names of the illustrated plants. Other authors were critical towards alphabetical ordering. In describing the many kinds of fishes illustrated in his magnum opus *De piscibus*, Rondelet (1554: 113) explained that he intended to "keep the most important order. I pondered for a long time: whether I should begin with the grey mullet (*mugil*), as Galen did, or whether I should begin with something else, the most prominent among its kind, like the parrotfish (*scarus*) among those of rocky bottoms (*saxatiles*), or one of the most delicious like the sole (*solea*) or the sturgeon (*acipenser*). But at last I thought it would be most convenient to begin with a fish well known to everybody, and most famous among the ancients, and one that is to be found at every season of the year, and is distinguished from others by a well-known trait, that is, with the gilt-head bream (*aurata*), to subsequently move to others, similar to it in many respects, yet diverging in their peculiar traits. But I do not want anyone to think that we first describe *auratam* because it begins with the letter A, for we consider this alphabetic order to be defective, no less in the description of fishes than in the descriptions of herbs: and that those who followed this were rightly criticized by Dioscorides because, that way, it is necessary to unite many things that are unlike, and to separate things that are similar." Ironically, this is the same critical remark of Willoughby (1686: 20) on Rondelet's (1554: 7) partitioning into sea, river, lake, and swamp fishes (*marinos*, *fluviatiles*, *lacustres*, and *palustres*) because this criterion "keeps apart fishes of the same genus (*ejusdem generis*), i.e., those that agree in body shape, number and position and other traits characterizing genera, such as salmons and trouts, eels and congers, etc."

Nevertheless, for a long time species were still listed according to the alphabet, including in *Catalogus plantarum circa Cantabrigiam nascentium* (Ray 1660) and *Catalogus plantarum Angliae* (Ray 1677), early works of an author who will later offer a very important contribution to the development of systematics.

Beyond alphabetic ordering

In these Renaissance encyclopedic works, alphabetical ordering is not strict, due to the frequent disregard for the letters in positions other than the first. For example, the first ten entries in the nearly alphabetic sequence of the plants illustrated in Fuchs (1542) are *Absinthium*, *Abrotonum*, *Asarum*, *Acorum*, *Althaea*, *Anagallis*, *Alsine*, *Anthemis*, *Anethum* and *Arnoglossum*. More important, the different initial letter does not prevent the author from describing, after one of the 'focal' species whose name occupies a place dictated by the alphabetic order, other animals or other plants comparable to the first in terms of shape and/or for other properties. For example, Fuchs inserts *Seriphium absinthium* after *Absinthium vulgare* and illustrates three species of *Chamaemelon* (or *Chamaemelum*) after *Anthemis* and several species of *Sedum* and *Plantago* next to (or, in a sense, under) *Anethum*.

Andrea Cesalpino (Caesalpinus) (*De Plantis*, 1583) looked for an ordering criterion other than the alphabet: "As in all scientific texts order makes science more accessible and also helps memory, in explaining trees I regarded advisable to begin with the simplest one. Namely, the trees that under each flower bear only one seed or one seed-containing vessel (*conceptaculum*) are simpler than those that bear more than one. I call here *conceptaculum* a vessel that may contain a number of seeds with their own barks, such as the chestnut" (Caesalpinus 1583: 31).

Table 1. Brisson's (1756) classes of mammals based on the number of teeth and digits.

	upper teeth			lower teeth			digits		
Class	**I**	**C**	**M**	**I**	**C**	**M**	**Anter.**	**Poster.**	
I	–	–	–	–	–	–			*Myrmecophaga*, *Pholidotus*[1]
II	–	–	+	–	–	+			*Tardigradus*,[2] *Cataphractus*[3]
III	–	+	+	–	+	+			*Elephas*, *Odobenus*
IV	–	+	+	3	+	+			*Camelus*
V	–	+	+	4	+	+			*Giraffa*, *Hircus*[4], *Aries*[5], *Bos*, *Cervus*, *Tragulus*
VI	+	+	+	+	+	+	1	1	*Equus*
VII	+	+	+	+	+	+	2	2	*Sus*
VIII	+	+	+	+	+	+	3	3	*Rhinoceros*
IX	1	+	+	1	+	+	4	3	*Hydrochærus*
X	5	+	+	5	+	+	4	3	*Tapirus*
XI	+	+	+	+	+	+	4	4	*Hippopotamus*
XII	1	+	+	1	+	+	4	4	*Hystrix*, *Castor*, *Lepus*, *Cuniculus*, *Sciurus*, *Giis.*, *Mus*, *Musaraneus*[6], *Erinaceus*
XIII	2	+	+	2	+	+	4	4	*Simia*, *Pteropus*
XIV	2	+	+	3	+	+	4	4	*Prosimia*, *Vespertilio*
XV	3	+	+	2	+	+	4	4	*Phoca*
XVI	3	+	+	3	+	+	4	4	*Hyæna*, *Canis*, *Mustela*, *Meles*, *Ursus*, *Felis*, *Lutra*
XVII	3	+	+	4	+	+	4 *ungula*	4 *ungula*	*Talpa*
XVIII	5	+	+	4	+	+	4 *unguiculæ*	4 *unguiculæ*	*Philander*[7]

Abbreviations: I = incisors; C = canines; M = molars. Linnaean names for some less familiarly named animals: [1]*Manis*; [2]*Bradypus*; [3]*Dasypus*; [4]*Capra*; [5]*Ovis*; [6]*Sorex*; [7]*Didelphis.*

In this early example of order based on the degree of complexity in a key feature, Cesalpino's criterion is just a matter of numbers: plants with one piece are simpler than plants with many. Taking increasing numerosity as a proxy of increasing complexity is disputable in principle and eventually wrong in Cesalpino's case, as in many others; the number of parts will turn instead into a diagnostic criterion for one or more levels of a true hierarchical classification, as with *Quadrupèdes*, *Bipèdes*, *Multipèdes* and *Apodes* as the four main groups in Klein's (1734) classification of animals, or in Brisson's (1756) arrangement of mammals according to the number of teeth and digits (Table 1), and in the sequence of plant classes characterized by the different number of stamens in Linnaeus' *systema sexuale* (Linnaeus 1735) (Table 2).

Order for what?

Despite the development of hierarchical classifications that apparently replaced the simple linear order of earlier works, this order was still important and useful, and arguably it is still so today, for example, when distributing the topics to be treated in a textbook on systematic zoology or botany. Let us examine the contexts in which it is imperative to adopt a linear ordering criterion and what constraints this criterion must satisfy.

Table 2. Linnaeus' (1735) *systema sexuale* of plant classes mainly based on the number of stamens and listed according to the increasing number of the same.

1	Monandria	stamen unicum in flore hermaphrodito
2	Diandria	stamina duo in flore hermaphrodito
3	Triandria	stamina tria in flore hermaphrodito
4	Tetrandria	stamina quatuor in eodem flore cum fructu
5	Pentandria	stamina quinque in flore hermaphrodito
6	Hexandria	stamina sex in flore hermaphrodito
7	Heptandria	stamina septem in flore eodem cum pistillo
8	Octandria	stamina octo in eodem flore cum pistillo
9	Enneandria	stamina novem in flore hermaphrodito
10	Decandria	stamina decem in eodem flore cum pistillo
11	Dodecandria	stamina duodecim in flore hermaphrodito
12	Icosandria	stamina [viginti communiter, sæpe plures, raro pauciores] (non receptaculo) calycis lateri interno adnata
13	Polyandria	stamina à 15 ad 1000 in eodem, cum pistillo, flore
14	Didynamia	stamina quatuor, quarum 2 proxima longiora sunt
15	Tetradynamia	stamina sex, quarum 4 longiora, 2 autem opposita sunt
16	Monadelphia	stamina filamentis in unum corpus coalita sunt
17	Diadelphia	stamina filamentis in duo corpora connata sunt
18	Polyadelphia	stamina filamentis in tria vel plura corpora coalita
19	Syngenesia	stamina antheris (rarum filamentis) in cylindrum coalita
20	Gynandria	stamina pistillis (non receptaculo) insident
21	Monoecia	flores masculini & feminini in eadem planta sunt
22	Dioecia	flores masculini in diversa planta, à femininis nascuntur
23	Polygamia	flores hermaphrodit. & masculini s. femin. in eadem specie
24	Cryptogamia	florent intra fructum, vel parvitate oculos nostros subterfugiunt

It is no coincidence that the oldest among the works mentioned in the previous section belong to the first season of the great printed naturalistic works, where the reader (and the author before him) needed a criterion according to which to orient himself in navigating the vast treatment. By its physical nature, a book is primarily made to be read from the first to the last page and this is a linear succession traced by page numbers. Therefore, a linear order is needed in which to arrange the objects to be treated and the alphabetic order presents itself as an easy choice. However, this order is extrinsic to the nature of the objects treated.

Linear (in a temporal rather than spatial sense) is also the succession of topics covered in a speech or, on a larger scale, in the lectures of a course. Here too, the problem arises of arranging the topics according to an explicit order.

In his lectures on invertebrate animals, preparatory to the monumental *Histoire naturelle des animaux sans vertèbres*, Lamarck arranged the animal classes from the simplest to the most complex: "I demonstrate in my lessons, and I will establish positively in the work that I am preparing, the progressive order I have just mentioned. We will see that, based on the observed zoological facts, it entails consequences very different from those which have been hitherto drawn from them, consequences very proper to enlighten us more and more on animal physics" (Lamarck 1812: 6). However, the problem had already emerged in botany, a discipline taught to medical students both through formal lectures and with the help of practical exercises. As early as the 16th century, in the first universities equipped with a botanical garden, the latter was the natural site for these demonstrations. Consequently, the problem of the order to give to the plants described in the lectures can suggest the criterion for arranging herbaceous plants and shrubs in a corresponding sequence of flower beds. In de Jussieu's words, "The embarrassment that exists in the editing of a book must be the same in the arrangement of a botanical garden" (Jussieu 1824: 458).

Living plants in a botanical garden are not the only kind of specimens that require a sensible spatial arrangement. No less important are the dried plants in the herbaria and animals in zoological museum collections. Examples of the tight links between zoological or botanical catalogues and classifications and ordering of (first private, later also institutional) collections are numerous, since the early eighteenth century (Daudin 1926). Schmitt (2022) has recently analyzed the hitherto overlooked contribution of Klein, who published a number of little works primarily intended as systematic descriptions of his own collection, but eventually expanded their scope up to obtaining a "table générale de méthode zoologique" (Klein 1734) very different from the arrangement Linnaeus was about to publish in the first edition of *Systema Naturae* (Linnaeus 1735).

But also in the case of Linnaeus, arranging and describing collections was tightly joined with the development of his systematization of nature's kingdoms. This is demonstrated by a comparison between his museum catalogues (*Museum Adolpho-Fridericianum*, Linnaeus 1749, 1754, 1764b; *Museum Tessinianum*, Linnaeus 1753; *Museum Ludovicæ Ulricæ Reginæ*, 1764a) and his *Systema Naturæ*. I give here some detail about the last mentioned work (acronym: MLUR), in which linear ordering, classification and nomenclature all closely match those of the tenth edition of *Systema Naturæ* (Linnaeus 1758) (acronym: SN).

The orders (Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Hymenoptera, Diptera, Aptera) among which is distributed the small sample of exotic insects described in MLUR are those recognized and treated, in the same sequence, in SN; the main difference between the two works is the position of two genera (*Blatta* and *Gryllus*), listed among the Hemiptera in MLUR, but in Coleoptera in SN. The other insect genera are treated within each order in similar but not identical sequence. But in the case of Pisces and Testacea, the linear order of the genera treated in both works is literally the same. This is most obvious in the Testacea, because all 33 genera recognized by Linnaeus in SN are also present in MLUR; in both works, these are treated in this order: *Chiton*, *Lepas*, *Pholas*, *Mya*, *Solen*, *Tellina*, *Cardium*, *Donax*, *Venus*, *Spondylus*, *Chama*, *Arca*, *Ostrea*, *Anomia*, *Mytilus*, *Pinna*, *Argonauta*, *Nautilus*, *Conus*, *Cypræa*, *Bulla*, *Voluta*, *Buccinum*, *Strombus*, *Murex*, *Trochus*, *Turbo*, *Helix*, *Nerita*, *Haliotis*, *Patella*, *Dentalium*, *Serpula*.

Less obvious is, prima facie, the correspondence between MLUR and SN in the case of fishes, because only 25 of the 51 genera in SN are also in MLUR, but their names appear in exactly the same sequence (those mentioned in both works are listed here in **bold**): ***Murœna***, *Gymnotus*, *Trichiurus*, *Anarhichas*, *Ammodytes*, *Stromateus*, *Xiphias*, *Callionymus*, ***Uranoscopus***, *Trachinus*, ***Gadus***, ***Blennius***, *Ophidion*, *Cyclopterus*, *Echeneis*, *Coryphæna*, ***Gobius***, ***Cottus***, *Scorpæna*, ***Zeus***, ***Pleuronectes***, ***Chætodon***, ***Sparus***, ***Labrus***, ***Sciæna***, ***Perca***, ***Gasterosteus***, *Scomber*, ***Mullus***, ***Trigla***, ***Cobitis***, ***Silurus***, *Loricaria*, ***Salmo***, *Fistularia*, ***Esox***, *Argentina*, ***Atherina***, ***Mugil***, *Exocoetus*, *Polynemus*, ***Clupea***, ***Cyprinus***, ***Mormyrus***, *Balistes*, *Ostracion*, *Tetrodon*, *Diodon*, *Centriscus*, *Syngnathus*, *Pegasus*.

One series only?

Eventually, a number of authors acknowledged the fundamental difference and potential conflict between linear ordering and hierarchical classification, a conflict that raised a number of new questions ranging from metaphysics to taxonomy and the origin of biological diversity.

The metaphor of the scala naturae was often accepted as suggestive of the real path of nature by steps of increasing complexity, a sequence that taxonomic works should aim to imitate. However, in principle, if an order exists in nature, this is not necessarily a linear one. Between the end of the eighteenth century and the first decades of the following century, different patterns of interrelationships were suggested, including the two-dimensional 'geographic map' model of Donati (1750) and others (cf. Barsanti 1992) and the quinarian system of Macleay (1819/1821) (cf. Novick 2016). A tree-like pattern of relationships among the living beings would be later suggested in the light of evolution.

The impossibility to arrange all living species in a linear sequence was soon understood at least by the most perceptive naturalists. Interestingly, the mismatch between the linearity of the hypothesized path of nature and the hierarchical topology of the classification was equally clear to scientists open to an evolutionary perspective, as Lamarck, and those far from this view, as Antoine-Laurent de Jussieu. The latter remarked: "Although one is forced to recognize that such must be the plan of nature, one will conceive at the same time that this plan cannot be rigorously followed in a book in which the typographical form requires the arrangement of objects, not in bundles, but in series, to pass them all successively in review. […] The difficulty must be the same to arrange in a series the genera of the same family which offer the same multiplicity of relationships; and if we go back further, it will increase for the distribution of families in a class" (Jussieu 1824: 458).

One hundred years later, Wettstein (1924: 939–940, abdridged here in Table 3) included in his *Handbuch der systematischen Botanik* (*Handbook of Systematic Botany*) an *Overview of the series of angiosperms and their putative evolutionary relationships*, with "The purpose […] to present the presumed genetic connection between the groups of angiosperms, since this connection does not emerge directly from the sequence of groups in the book caused by the need for a linear arrangement." Wettstein's table demonstrates that a linear arrangement of groups broadly corresponding to the orders of other plant classifications has anyway to be adopted, despite the failure of the 'natural' distribution of dejussieuian tradition.

Nature: ascending or descending order of complexity?

In zoology, increasing or decreasing resemblance to our species was often suggested as the best ordering criterion. This does not necessarily mean that humans are the most perfect of animals; rather, it can simply mean that the species best known to both the author and his reader is used as a convenient term of reference: "To begin with, we must take into consideration the parts of Man. For […] is the animal with which we are all of us the most familiar" (Aristotle, *Historia Animalium* 491 a 19 sgg). Essentially the same was Pierre Belon's approach in the *Histoire de la nature des oyseaux* (1555), where he proposed an extraordinary comparison between a human skeleton and the skeleton of a bird, labelling with same letter(s), on the two illustrations printed on facing pages, the individual bones that today we describe as homologous. In this exercise ante litteram in comparative anatomy, humans only serve as a convenient reference, as his anatomy can be taken for granted, at least for those who practice medicine, like Belon himself.

Later, however, the distance that separates the different animal forms from humans was generally taken as a global measure of 'perfection' or, at least, as a measure of complexity. On the subject, the significant texts are many and well known, but some of these deserve to be cited here.

When mentioning perfect and imperfect animals, Lamarck feels the need to clarify that "These expressions of perfect animals and imperfect animals are rhetoric abbreviations, convenient to designate those whose organization approaches most that of man or moves away from it more; the organization of man can be regarded as the most perfect, as that which gives the most faculties, and above all the most eminent combination of faculties" (Lamarck 1812: 44).

Table 3. Excerpt from the overview of the series of angiosperms and their putative evolutionary relationships in Wettstein's (1924) *Handbuch der systematischen Botanik*, showing the deep mismatch between the linear order of angiosperm series as treated in the text and their putative patterns of affinities.

Class Dicotyledones

Subclass **Choripetalae**

Evolutionary level **Monochlamydeae**

Seventeen series, among which

14	**Polygonales**. Like series 15., 16. and 17. mediating the transition from the typical Monochlamydeae to the Dialypetaleae. Possible relationships to series 10. on the one hand and to series 15. on the other
15	**Centrospermae**. Relationships to typical Monochlamydeae on the one hand, clear relationships to the Caryophyllaceae of the Dialypetalae and to series 1. and 2. of the Sympetalae on the other
16	**Tricoccae**. Relationship to series 10. on the one hand and to series 24.–28. on the other
17	**Hamamelidales**. On the one hand, close to the Monochlamydeae, on the other hand, relationships to series 10. and 22.

Evolutionary level **Dialypetaleae**

Twelve series, among which

18	**Polycarpicae**. Probable relationship to series 17., clear relationship to series 19.–23. and to the Monocotyledones
29	**Umbelliflorae**. Origin uncertain. Possible relationships to the type of series 26. and 27. on the one hand, to series 22. and 23. on the other

Subclass **Sympetalae**

Ten series, among which

7	**Ligustrales**. Probable relationship to series 5. of the Sympetalae, but also a resemblance to series 27. of the Choripetalae
8	**Rubiales**. Relations on the one hand to series 29. of the Choripetalae, on the other hand perhaps to series 7. of the Sympetalae
9	**Cucurbitales**. Relations to series 20. of the Choripetalae hardly doubtful
10	**Synandrae**. Probable genetic relationships to series 9. of the Sympetalae

Class Monocotyledones

Nine series, among which

1	**Helobiae**. Relations to series 18. of the Choripetalae hardly doubtful
2	**Liliiflorae**. Clear relationships on the one hand to the Helobiae, on the other hand to series 18. of the Choripetalae

At the time, it was still a matter of dispute whether the most convenient distribution would be one from imperfect to perfect, or the other way around (Minelli 2021). Vicq-d'Azyr (1792) acknowledged that "There are two ways of arranging living bodies […]. The first, which is the most used, consists in placing man at the head, and in describing successively after him, those of the living bodies with which he has the most analogy; so that in this series the number of organs always decreases, as follows: man, viviparous quadrupeds, cetaceans, birds, oviparous quadrupeds, snakes, fishes, insects, worms, plants. I followed this method, believing that the anatomy of man should be found in the first volume of this work, and fearing that I would be accused of oddity, if, in this treatise, the anatomy of plants was offered first. The second method would be absolutely the opposite of this one. In proceeding from the simple to the compound, we would arrive from plants to quadrupeds to man. This way of proceeding is perhaps preferable to the first […]. [However, s]ubjugated by a tradition from which I was perhaps too afraid to deviate, I have not adopted, in my anatomical system, this path, which I believe will offer great advantages to the reader. [Nevertheless,] If only to keep track of it or to try it out, I will follow it in this first part of my text" (Vicq-d'Azyr 1792: vii).

But does a linear order actually exist in nature?

Vicq d'Azyr was not convinced: "Let us not be deceived as certain species are regarded as a passage from one class to another. The flying squirrel, for example, is said to link quadrupeds with birds; but if we except the membranous expansions which resemble wings, the flying squirrel is, in all respects, a quadruped properly so called; there is no organ in it that really resembles those of birds. Likewise the ostrich is a bird whose wings are very short; but its alleged hairs are real feathers; its larynx, its throat, its intestines, its eggs, are absolutely, and in every point, shaped like those of birds. […] It is therefore not demonstrated that the great families of living beings end in insensible shades and that they merge with each other as some Naturalists have thought; and as, according to them, Philosophers have written it" (Vicq d'Azyr 1792: xxi).

At the time, Lamarck still favored an arrangement according to that criterion of decreasing complexity he had already adopted, before being recruited as zoologist at the Muséum, in his main botanical work, *Flore Françoise* (Lamarck 1778). Still in the *Système des animaux sans vertèbres* he draws attention to "this astonishing degradation in the composition of the organization, and this progressive reduction of the animal faculties which must interest the Naturalist philosopher so much; finally they lead us imperceptibly to the inconceivable end of animalization, that is to say to the one where the most imperfect, the most simply organized animals are placed, those in a word that we hardly suspect gifted of animality, those perhaps with which nature began, when with the aid of much time and favorable circumstances she formed all the others" (Lamarck 1801: 11–12) and specifies that "invertebrate animals […] present a series that seems to be deteriorating in relation to the increasingly growing simplification of the organization of these beings; so that those who end the series really offer only the outline of animality" (Lamarck 1801: 49).

Order by increasing complexity

Before the end of the eighteenth century, there are very few catalogues of local flora or enumerations of plants cultivated in a botanical garden, in which the plants traditionally described as inferior, i.e., those without flowers, are listed first, followed by flowering plants. Among these few examples are a list of plants in cultivation in the botanical garden of Leyde (Hermann 1689) and Charles Plumier's book on American plants (Plumier 1693). In both, enumeration begins with ferns.

At the time, botany was dominated by the systematic approach of Tournefort (1694), who divided plants into 21 classes; those without flowers were placed in a couple of classes among the last in the sequence. But in 1718, the Italian botanist Giulio Pontedera, who the following year would become praefectus of the botanical garden of Padua, opted for the opposite order: "It may be permitted for us to deviate a little from the Tournefortian system, perhaps only in reversing his order. He proceeds from perfect plants to imperfect plants; [instead,] it has always seemed best to us to ascend from the Imperfect through the Perfect to the More Perfect" (Pontedera 1718: xi). Thus, the first groups recognized by Pontedera (*Plantae Incertae*; *Plantae gemmas non ferentes extra terram*, *minus perfectae*; *Plantae Flore Imperfecto apetalo*) correspond to Tournefort's classes XVII–XV (Minelli in press).

Pontedera followed his reversed order of plant classes also in his lectures, as explained in the third of the eleven dissertations that follow his major work (*Anthologia*, 1720) based on the lectures of his first course of *Ostensio Simplicium*. On this occasion, after briefly recalling the structure of Tournefort's system, he presents his new order with solid certainty: "we reverse the order of the classes; since it seemed to us best to begin with imperfect plants, […] and soon ascend through the perfect, which are grasses and suffruticums, to the more perfect, that is, to trees and shrubs. Therefore we have divided all plants into two parts: in the first are placed the *uncertain*, which, of course, produce neither flowers, nor seed, nor buds (as is the common opinion of botanists); in the second, the *certain*, which grow from seed" (Pontedera 1720: dissertatio tertia, p. 44).

This message received virtually no response, perhaps because Pontedera did not offer a comprehensive systematic account of his new arrangement of plant classes. According to current historiography (e.g., Stevens 1984), the arrangement of plant classes starting from the 'imperfect plants' would be the result of an innovation developed in Paris starting from the mid-eighteenth century, in which the most representative figures would be Bernard de Jussieu and his nephew Antoine-Laurent de Jussieu. It was the latter who illustrated in a publication (Jussieu 1774) the new order adopted by Bernard since 1759 in his demonstrations at the royal garden of the Trianon near Paris; Antoine-Laurent himself would follow this disposition in *Genera Plantarum* (Jussieu 1789; see Stevens 1994).

Twenty years later, this arrangement was eventually accepted in zoology by Lamarck: "the order of distribution I have proposed with regard to the animals, which I have just explained, the same I have been using for several years in my lessons at the Museum, and the exposition of which is found in my *Philosophie zoologique* (vol. I: 269), becomes indispensable, and cannot be replaced by any other. It also establishes this conformity between zoology and botany: that, on both sides, the method employed as natural will present a distribution in which one must proceed from the simplest to the most complex" (Lamarck 1815: 374–5).

In a section of the *Philosophie zoologique* entitled *De l'Ordre naturel des Animaux et de la disposition qu'il faut donner à leur distribution générale pour la rendre conforme à l'ordre même de la nature*, (*On the natural order of animals and the way their general distribution must be represented in order to render it in accordance with the natural order*), Lamarck had indeed declared his debt to botany: "Botanists were the first to offer an example to zoologists of the true disposition to give to a general distribution to represent the very order of nature; for it is with acotyledonous or agamic plants that they form the first class among plants, that is to say, with the plants simplest in organization, the most imperfect in all respects" (Lamarck 1809: 271).

Lamarck's philosophical speculations were tempered by his wide-ranging familiarity with animals and plants: "By this nuanced gradation in the complication of the organization, I do not mean to speak of the existence of a linear series, regular in the intervals of species and genera: such a series does not exist; but I speak of a series almost regularly graduated in the main masses, such as the great families; a series certainly existing, either among the animals, or among the plants; but which, in the consideration of genera and especially of species, forms in many places lateral ramifications, the extremities of which offer truly isolated points" (Lamarck 1801: 16–17). Similarly, with respect to invertebrates, he wrote a few years later that "In the distribution of their races, and even of their genera, it is impossible, as I have said, to establish a gradual and regular scale, in respect to the characters and forms of these animals" (Lamarck 1812: 7).

Linearization rules

"The choice of methodology to obtain a linear sequence of taxa in agreement with a hierarchical classification (with or without absolute ranks) is controversial, and the linear sequence can be misleading if not understood in the context of a tree" (Haston *et al*. 2009).

The need to operate an arbitrary choice to get a compromise between hierarchical classification and linear ordering was early noticed by perceptive authors like de Jussieu and Lamarck, but explicit discussion about the criteria to be adopted, and the pro and cons of different methods, have been very limited up to now. The most extensive treatment is Hawthorne & Hughes' (2008) critical analysis of the linear classification of angiosperm orders and families proposed by the Angiosperm Phylogeny Group. This group of botanists has been formulating and steadily revising angiosperm classification for a quarter of a century (APG 1998, 2003, 2009, 2016). Based on APG II (2003), Haston *et al*. (2007: 7) first presented a "linear classification of the angiosperm orders", stressing that "Linear sequences of families are required for herbarium curators who wish to arrange collections systematically rather than alphabetically, and there are currently a wide range of systems in use." Two subsequent editions of the APG classifications (APG III 2009; APG IV 2016) have offered the opportunity to progressively update the linear classification, too (Haston *et al*. 2009; APG IV 2016). The main criterion according to which the taxa issued from the same node are listed is such that "clades with fewer families were placed before clades with greater number of families. For sister clades that have an equal number of families, the clade with fewer species was placed first" (Haston *et al*. 2007: 7–8; see also Stevens 2007).

To the best of my knowledge, no previous author has clearly shown that the result of a linearization effort depends on arbitrary choices in respect to *two* different aspects of the hierarchical classification we intend to linearize. Of these two aspects, one is quite obvious and has been indeed discussed many times, although from different perspectives and with different results. This aspect is the order to be followed in listing the immediately subordinate members of a given taxon, for example the families of an order, as in the APG case, where Linnean ranks are used. Acknowledged or not, different criteria are available, among which:

- tradition
- alphabetic order
- increasing size (number of further subordinate taxa); this is the primary criterion in APG

The lack of absolute criteria for solving this problem was stressed long ago by Nelson: "One may enquire, […] if there is a suitable sequencing convention that could be used so that the equivalent subgroups of a given group can be listed in only one way. A criterion based simply on consideration of the relationships […] seems impossible. But an alphabetical listing is possible and, indeed, has been used (Nelson 1972), and perhaps alphabetizing is the only convention that in practice is generally applicable" (Nelson 1974).

The lack of a general solution and the difficulty of consciously choosing and uniformly using it is shown by internal inconsistencies often found within one and the same paper, where the linear listing of terminals of a tree (usually, top to bottom on the right side of the figure) is different from the linear sequence in which the same terminals (or a selection of them) are discussed in the text. This divergence is even noticeable in APG IV (2016), see Table 4.

No less important, but essentially ignored, is the other fundamental choice that must be operated before attempting linearization. This is the choice of the sets of taxa to be linearized according to one or another of the available criteria. In fact, many lists are based on mixed criteria, usually a more conservative one for the most comprehensive taxa and a different one for lower ones. Let's present a couple of examples (Table 5).

Ruggiero *et al*. (2015) have produced a Linnaean classification of all living organisms including ranks from superkingdom down to order, specifying that "Names below rank of infrakingdom are arranged alphabetically within each parent rank." This means that all taxa of ranks from superkingdom to infrakingdom are arranged according to a criterion other that alphabetic sequence. This part of their

Table 4 (continued on next page). Mismatch between the linear order of terminal taxa ("orders") in the tree (fig. 1) and the sequence of the same taxa in the linear classification suggested in the same paper (APG IV 2016).

Sequence of terminals in the tree	Sequence of orders in the linear classification	**Superordinal groups**
Amborellales	**Amborellales**	
Nymphaeales	**Nymphaeales**	
Austrobaileyales	**Austrobaileyales**	
Magnoliales	Canellales	**Magnoliids**
Laurales	Piperales	
Piperales	Magnoliales	
Canellales	Laurales	
Chloranthales	**Chloranthales**	
Arecales	Acorales	**Monocots**
Poales	Alismatales	
Commelinales	Petrosaviales	
Zingiberales	Dioscoreales	
Asparagales	Pandanales	
Liliales	Liliales	
Dioscoreales	Asparagales	
Pandanales	Arecales	
Petrosaviales	Commelinales	
Alismatales	Zingiberales	
Acorales	Poales	
Ceratophyllales	**Ceratophyllales**	
Ranunculales	**Ranunculales**	
Proteales	**Proteales**	
Trochodendrales	**Trochodendrales**	
Buxales	**Buxales**	
Gunnerales	**Gunnerales**	
Fabales	Dilleniales	**Superrosids + Dilleniales**
Rosales	Saxifragales	
Fagales	Vitales	
Cucurbitales	Zygophyllales	
Oxalidales	Fabales	
Malpighiales	Rosales	
Celastrales	Fagales	

Table 4 (continued). Mismatch between the linear order of terminal taxa ("orders") in the tree (fig. 1) and the sequence of the same taxa in the linear classification suggested in the same paper (APG IV 2016).

Sequence of terminals in the tree	Sequence of orders in the linear classification	**Superordinal groups**
Zygophyllales	Cucurbitales	
Geraniales	Celastrales	
Myrtales	Oxalidales	
Crossosomatales	Malpighiales	
Picramniales	Geraniales	
Malvales	Myrtales	**Superrosids + Dilleniales**
Brassicales	Crossosomatales	
Huerteales	Picramniales	
Sapindales	Huerteales	
Vitales	Sapindales	
Saxifragales	Malvales	
Dilleniales	Brassicales	
Berberidopsidales	**Berberidopsidales**	
Santalales	**Santalales**	
Caryophyllales	**Caryophyllales**	
Cornales	**Cornales**	
Ericales	**Ericales**	
Aquifoliales	Icacinales	
Asterales	Metteniusales	
Escalloniales	Garryales	
Bruniales	Gentianales	
Apiales	Boraginales	
Dipsacales	Vahliales	
Paracryphiales	Solanales	
Solanales	Lamiales	**Campanulids + Lamiids**
Lamiales	Aquifoliales	
Vahliales	Asterales	
Gentianales	Escalloniales	
Boraginales	Bruniales	
Garryales	Paracryphiales	
Metteniusales	Dipsacales	
Icacinales	Apiales	

Table 5. Ranks on which the linear sequence is built in Fauna Europaea (https://fauna-eu.org/) and in Ruggiero *et al.*'s (2015) classification of living beings. For all ranks listed here in italics, the taxa belonging to the immediately higher taxon are given in alphabetic order.

Fauna europaea	Ruggiero
	Superkingdom
Kingdom	Kingdom
Subkingdom	Subkingdom
	Infrakingdom
	Superphylum
Phylum	*Phylum*
Subphylum	*Subphylum*
Infraphylum	*Infraphylum*
	Superclass
Class	*Class*
Subclass	*Subclass*
	Infraclass
Superorder	*Superorder*
Order	*Order*
Suborder	
Infraorder	
Superfamily	
Family	
Subfamily	
Tribe	
Subtribe	
Genus	
Subgenus	
Species	
Subspecies	

classification is reproduced here in Table 6. We may ask if there is a common criterion ruling the order preference in the following choices:

Prokaryota vs Eukaryota
Archaea vs Bacteria
Negibacteria vs Posibacteria
Protozoa vs Chromista vs Plantae vs Animalia
Eozoa vs Sarcomastigota
Euglenozoa vs Excavata
Hacrobia vs Harosa vs Dikarya vs Eomycota
Halvaria vs Rhizaria
Biliphyta vs Viridiplantae

Chlorophyta vs Streptophyta
N.N. [Cnidaria + Ctenophora + Placozoa + Porifera] vs Bilateria
Protostomia vs Deuterostomia

The main (implicit) criterion is probably tradition, backed in turn, when this may apply, by a rough estimate of overall complexity, e.g., in the case of taxon N.N. vs Bilateria. But mere tradition is an obviously poor, easily overturned criterion. For example, in their recent textbook on invertebrate zoology, Giribet and Edgecombe (2020) put deuterostomes before protostomes, but not for alphabetic reasons. Another example: while Giribet & Edgecombe (2020) treat the panarthropodan taxa Tardigrada, Onychophora and Arthropoda in this order, other zoologists who similarly do not list taxa in alphabetic order prefer different sequences: Arthropoda Onychophora Tardigrada (Nielsen 2012) or Onychophora Euarthropoda Tardigrada (Ax 2000). Examples could be easily multiplied, but let's limit further ones to the APG linear classification(s), as the most extensive, deliberate effort in this domain.

In their critical remarks on APG linear II (Haston *et al*. 2007), Hawthorne & Hughes (2008) remarked that "in this and some other recent Angiosperm linear sequences, monocots are sandwiched between the eudicots and more basal clades, although it would be equally correct, in terms of the APGII tree topology, to list the monocots at one end of the sequence, in a position which would be more in harmony with earlier, familiar systems such as those of Thorne (1992) and Cronquist (1981), and the sequence in many books and herbaria." The mixed criteria for linearization adopted by the authors were explained to some extent in the paper (Haston *et al*. 2007: 7–8), where the first edition of the linear classification, based on APGII, was presented: "following APG II, we decided to keep as close as possible to the order presented in that paper, and we therefore maintained the order of the major clades in APG II such as magnoliids, monocots, commelinids, etc., as long as this did not conflict with more recent results. Although the sequence of the major groups of APG II (2003) was retained, within each of these groups nodes were rotated such that clades with fewer families were placed before clades with greater number of families."

This is fairly clear. However, the (potentially very strong) destabilizing effect of the entity and specific position of nodes or classification levels that are collapsed before adopting a specific criterion (e.g., alphabetic order, or number of included taxa) for the subordinate taxa has never been explored. I give here an example, to demonstrate the need to specify very clearly the extent and composition of the uncollapsed classification backbone retained in the linearization procedure, and as a basis for future studies.

A linearization exercise

This example is performed on the hexapod "order"-level taxa currently accepted (e.g., Beutel *et al*. 2017) except for minor differences, e.g., uniting or not Blattodea and Mantodea into a single "order" Dictyoptera (Table 7).

The hierarchical arrangement from which different linear classifications will be extracted here, according to different node collapsing and name listing criteria, is given in **A**.

A list of the "order"-level taxa that may be accepted as traditional is given in **B**, to be compared with the purely alphabetic list obtained in **C** by collapsing all nodes up to the basal one. Note, for example, that Archaeognatha and Zygentoma occupy the fourth and the fifth positions, respectively, in **B**, but the first and the last positions in **C**. Another conspicuous difference is the fate of the two palaeopteran "orders" (Ephemeroptera and Odonata), alphabetically dispersed in **C** with many neopteran taxa in between.

Table 6. The non-alphabetically arranged higher taxa in the linear classification of Ruggiero *et al*. (2015).

Superkingdom Prokaryota			
	Kingdom Archaea		
	Kingdom Bacteria		
		Subkingdom Negibacteria	
		Subkingdom Posibacteria	
Superkingdom Eukaryota			
	Kingdom Protozoa		
		Subkingdom Eozoa	
			Infrakingdom Euglenozoa
			Infrakingdom Excavata
		Subkingdom Sarcomastigota	
	Kingdom Chromista		
		Subkingdom Hacrobia	
		Subkingdom Harosa	
			Infrakingdom Halvaria
			Infrakingdom Rhizaria
		Subkingdom Dikarya	
		Subkingdom Eomycota	
	Kingdom Plantae		
		Subkingdom Biliphyta	
		Subkingdom Viridiplantae	
			Infrakingdom Chlorophyta
			Infrakingdom Streptophyta
	Kingdom Animalia		
		Subkingdom N.N. [Cnidaria + Ctenophora + Placozoa + Porifera]	
		Subkingdom Bilateria	
			Infrakingdom Protostomia
			Infrakingdom Deuterostomia

In **D**, the names of the taxa that are non-terminal in the tree on which this exercise is performed are given in bold. Linear classifications **E** and **F** are both derived from **D**, but following different criteria.

In **E**, alphabetic precedence has been adopted at each node, from the highest to the lowest, as in the following examples:

under Hexapoda: Collembola, Diplura, Insecta, Protura
under Dicondylia: Pterygota, Zygentoma
under Neoptera: Eumetabola, Polyneoptera

In **F**, the traditional backbone formed by the taxa printed in bold in **D** is retained, but all terminals subordinated to each of them have been alphabetized, e.g.,

Table 7 (continued on next two pages). A selection of linear sequences of hexapod ‘orders’ obtained by different combinations of two criteria: (1) selective collapsing of intermediate named nodes, and (2) traditional vs alphabetic listing. Explanations and comments in the text.

A

- Hexapoda
  - Protura
  - Collembola
  - Diplura
  - Insecta
    - Archaeognatha
    - Dicondylia
      - Zygentoma
      - Pterygota
        - Palaeoptera
          - Ephemeroptera
          - Odonata
        - Neoptera
          - Polyneoptera
            - Dermaptera
            - Zoraptera
            - Plecoptera
            - Orthoptera
            - Blattodea
            - Mantodea
            - Grylloblattodea
            - Mantophasmatodea
            - Embioptera
            - Phasmatodea
          - Eumetabola
            - Condylognatha
              - Hemiptera
              - Thysanoptera
            - Psocodea
            - Holometabola
              - Hymenoptera
              - Aparaglossata
                - Neuropteroidea
                  - Neuropterida
                    - Rhaphidioptera
                    - Megaloptera
                    - Neuroptera
                  - Coleopterida
                    - Coleoptera
                    - Strepsiptera
                - Mecopterida
                  - Amphiesmenoptera
                    - Trichoptera
                    - Lepidoptera
                  - Antliophora
                    - Diptera
                    - Mecoptera

B

- Protura
- Collembola
- Diplura
- Archaeognatha
- Zygentoma
- Ephemeroptera
- Odonata
- Dermaptera
- Zoraptera
- Plecoptera
- Orthoptera
- Blattodea
- Mantodea
- Grylloblattodea
- Mantophasmatodea
- Embioptera
- Phasmatodea
- Hemiptera
- Thysanoptera
- Psocodea
- Hymenoptera
- Rhaphidioptera
- Megaloptera
- Neuroptera
- Coleoptera
- Strepsiptera
- Trichoptera
- Lepidoptera
- Diptera
- Mecoptera

C

- Archaeognatha
- Blattodea
- Coleoptera
- Collembola
- Dermaptera
- Diplura
- Diptera
- Embioptera
- Ephemeroptera
- Grylloblattodea
- Hemiptera
- Hymenoptera
- Lepidoptera
- Mantodea
- Mantophasmatodea
- Mecoptera
- Megaloptera
- Neuroptera
- Odonata
- Orthoptera
- Phasmatodea
- Plecoptera
- Protura
- Psocodea
- Rhaphidioptera
- Strepsiptera
- Thysanoptera
- Trichoptera
- Zoraptera
- Zygentoma

D

- **Hexapoda**
- Protura
- Collembola
- Diplura
- **Insecta**
  - Archaeognatha
  - **Dicondylia**
    - Zygentoma
    - **Pterygota**
      - **Palaeoptera**
        - Ephemeroptera
        - Odonata
      - **Neoptera**
        - **Polyneoptera**
          - Dermaptera
          - Zoraptera
          - Plecoptera
          - Orthoptera
          - Blattodea
          - Mantodea
          - Grylloblattodea
          - Mantophasmatodea
          - Embioptera
          - Phasmatodea
        - **Eumetabola**
          - **Condylognatha**
            - Hemiptera
            - Thysanoptera
          - Psocodea
          - **Holometabola**
            - Hymenoptera
            - **Aparaglossata**
              - **Neuropteroidea**
                - **Neuropterida**

Table 7 (continued). A selection of linear sequences of hexapod 'orders' obtained by different combinations of two criteria: (1) selective collapsing of intermediate named nodes, and (2) traditional vs alphabetic listing. Explanations and comments in the text.

- Rhaphidioptera
- Megaloptera
- Neuroptera
- **Coleopterida**
  - Coleoptera
  - Strepsiptera
- **Mecopterida**
  - **Amphiesmenoptera**
    - Trichoptera
    - Lepidoptera
  - **Antliophora**
    - Diptera
    - Mecoptera

E

Collembola
Diplura
Archaeognatha
Hemiptera
Thysanoptera
Lepidoptera
Trichoptera
Diptera
Mecoptera
Coleoptera
Strepsiptera
Megaloptera
Neuroptera
Rhaphidioptera
Hymenoptera
Psocodea
Blattodea
Dermaptera
Embioptera
Grylloblattodea
Mantodea
Mantophasmatodea
Orthoptera
Phasmatodea
Plecoptera
Zoraptera
Ephemeroptera
Odonata
Zygentoma
Protura

F

Collembola
Diplura
Archaeognatha
Zygentoma
Ephemeroptera
Odonata
Blattodea
Dermaptera
Embioptera
Grylloblattodea
Mantodea
Mantophasmatodea
Orthoptera
Phasmatodea
Plecoptera
Zoraptera
Hemiptera
Thysanoptera
Psocodea
Hymenoptera
Megaloptera
Neuroptera
Rhaphidioptera
Coleoptera
Strepsiptera
Lepidoptera
Trichoptera
Diptera
Mecoptera
Protura

G

- Hexapoda
  - **Protura**
  - **Collembola**
  - **Diplura**
  - **Insecta**
    - **Archaeognatha**
    - **Dicondylia**
      - Zygentoma
      - **Pterygota**
        - **Palaeoptera**
          - Ephemeroptera
          - Odonata
        - **Neoptera**
          - **Polyneoptera**
            - Dermaptera
            - Zoraptera
            - Plecoptera
            - Orthoptera
            - Blattodea
            - Mantodea
            - Grylloblattodea
            - Mantophasmatodea
            - Embioptera
            - Phasmatodea
          - **Eumetabola**
            - Thysanoptera
            - Psocodea
            - Hymenoptera
            - Rhaphidioptera
            - Megaloptera
            - Neuroptera
            - Coleoptera
            - Strepsiptera
            - Trichoptera
            - Lepidoptera
            - Diptera
            - Mecoptera

H

Collembola
Diplura
Archaeognatha
Coleoptera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Mecoptera
Megaloptera
Neuroptera
Psocodea
Rhaphidioptera
Strepsiptera
Thysanoptera
Trichoptera
Blattodea
Dermaptera
Embioptera
Grylloblattodea
Mantodea
Mantophasmatodea
Orthoptera
Phasmatodea
Plecoptera

Table 7 (continued). A selection of linear sequences of hexapod ‘orders’ obtained by different combinations of two criteria: (1) selective collapsing of intermediate named nodes, and (2) traditional vs alphabetic listing. Explanations and comments in the text.

Zoraptera	Ephemeroptera	Coleoptera
Ephemeroptera	Odonata	Diptera
Odonata	Polyneoptera	Hemiptera
Zygentoma	Blattodea	Hymenoptera
Protura	Dermaptera	Lepidoptera
	Embioptera	Mecoptera
I	Grylloblattodea	Megaloptera
	Mantodea	Neuroptera
Protura	Mantophasmatodea	Psocodea
Collembola	Orthoptera	Rhaphidioptera
Diplura	Phasmatodea	Strepsiptera
Archaeognatha	Plecoptera	Thysanoptera
Zygentoma	Zoraptera	Trichoptera

Ephemeroptera, Odonata, Blattodea, Dermaptera etc. because Palaeoptera (with Ephemeroptera and Odonata) precede Neoptera, Polyneoptera precede Eumetobola, and terminals within Palaeoptera and Polyneoptera are alphabetized.

In **G**, only a few ‘major’ clades are retained as fixed in their traditional sequence (here, in bold) and are thus used for the remaining linearization exercise.

In **H**, similar to **E**, alphabetic precedence has been adopted at each node, from the highest to the lowest, as in the following examples:

within Hexapoda: Collembola, Diplura, Insecta, Protura
within Pterygota: Neoptera, Palaeoptera

In **I**, similar to **F**, the traditional backbone formed by the taxa printed in bold in G is retained, but all terminals subordinated to each of then have been alphabetized, e.g.,

within Eumetabola: all “orders” from Coleoptera to Trichoptera

This linearization example is presented here to show the hidden complexity and arbitrariness of linearization. The wild disparity of results obtained by operating different choices between the subordinate taxa (if any) whose position is arbitrarily fixed e.g., based on tradition, or convenience, and those that are pooled together before being sorted out by alphabet (as in the example) or by any other criterion (e.g., taxon size, as in APG linear classification) is obvious. By throwing light on this less obvious constraint to which any linearization effort is subjected, this example may offer a useful starting point for additional discussion and, perhaps, proposals for standardization.

Conclusions

Today, a growing number of databases dedicated to the names of taxa and the phylogenetic relationships between them have arguably solved some of the problems that until the recent past were addressed through standardized lists. However, the continuously dynamic contents of these databases contrast with the need for a consolidated output that can be used and shared for a reasonably long time, as required, e.g., for arranging a collection. This applies, e.g., to popular important databases such as *Catalogue of*

Table 8. The linear sequence of angiosperm orders in two editions of the Angiosperm Phylogeny Group's classification (APG I 1998; APG IV 2016).

APG I	APG IV
Acorales	**Acorales**
Alismatales	**Alismatales**
Asparagales	
Dioscoreales	**Dioscoreales**
Liliales	Pandanales
Pandanales	Liliales
	Asparagales
Arecales	**Arecales**
Commelinales	**Commelinales**
Poales	Zingiberales
Zingiberales	Poales
Proteales	Ranunculales
Ranunculales	Proteales
Caryophyllales	Buxales
Saxifragales	**Saxifragales**
Geraniales	
Cucurbitales	
Fabales	**Fabales**
	Rosales
Fagales	**Fagales**
Malpighiales	Cucurbitales
Oxalidales	**Oxalidales**
Rosales	
Brassicales	
	Malpighiales
Malvales	Geraniales
Myrtales	**Myrtales**
Sapindales	**Sapindales**
	Malvales
	Brassicales
	Santalales
	Caryophyllales
Cornales	**Cornales**
Ericales	**Ericales**
Garryales	**Garryales**
Gentianales	**Gentianales**
Lamiales	Solanales
Solanales	Lamiales
Apiales	
Aquifoliales	**Aquifoliales**
Asterales	**Asterales**
Dipsacales	**Dipsacales**
	Apiales

Life, *Fauna Europaea*, *World Register of Marine Species* (*WoRMS*), and *Encyclopedia of Life* (*EOL*): in their current version, all these databases essentially offer only an alphabetically ordered output, like example C in Table 7).

As shown above, a satisfactory alternative is not easy to achieve because of the irremediable contrast between the unidimensionality of linear listing and the complexity of hierarchical arrangement, either in the form of a Linnaean classification or of a tree reconstructed according to phylogenetic methods with or without formal ranks.

Difficulties in handling linear taxon listing are shown by the APG linear classification of angiosperms, both in the unavoidable (and arguably desirable) evolution from one edition to the next (Table 8), and in the inconsistency between the linear sequence (top to bottom) of the order of terminals of the tree in APG IV (2016) and the order of the same taxa in the corresponding linear classification adopted in the same paper (Table 4).

With the linearization exercise under alternative criteria of the "orders" of hexapods given above, I have shown the hitherto overlooked importance of identifying the nodes that the author decides not to collapse. More or less consciously, these nodes are highlighted in a number of textbooks where distinct chapters or sections are devoted to some non-terminal taxa, in addition to the chapters or sections devoted to the individual terminal taxa. A recent example is Giribet & Edgecombe (2020), with their chapters on Planulozoa, Bilateria, Xenacoelomorpha, Nephrozoa, Deuterostomia, Ambulacraria, Protostomia, Ecdysozoa, Scalidophora, Nematoida, Panarthropoda, Spiralia, Gnathifera, Platytrochozoa, Rouphozoa, Lophotrochozoa, Lophophorata, Brachiozoa, Phoronida and Brachiopoda that punctuate the usual sequence of chapters dealing with the individual phyla.

Last but not least, naïve users of linear taxon listing may sometimes read the proposed sequence as a proxy for an evolutionary sequence, whatever this expression may actually mean. We are still far from being free from the scala naturae language according to which there are, for example, lower animals and higher animals, lower plants and higher plants (Rigato & Minelli 2013). Still worse, some users may even search among the earliest terms of these sequences for ancestors of taxa further in the list. Jenner's (2022) recent book *Ancestors in Evolutionary Biology. Linear Thinking about Branching Trees* is the best recommended remedy for this faulty reading.

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