PERSPECTIVE ARTICLE

The Linnaean revolution – A history of the Natural System

Magnus Lidén

Uppsala University, Evolutionary Biology Centre (EBC), Systematic Biology, Norbyvägen 18D, 75236 Uppsala, Sweden
Address for correspondence: *Magnus Lidén, magnus.liden@ebc.uu.se*

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Abstract A very brief history of the Natural System (NS) is presented, focusing on angiosperms. The account is divided into four parts. The first, "Setting the stage", gives an outline of my understanding of evolutionary ontology and how this reflects on taxonomy. I emphasise the necessity of an *information flow* approach (in contrast to an organismic approach) to understand the *process* shaping the evolutionary tree, and I defend a *realistic* interpretation of phylogenies. On the other hand, I stress that *pattern* (clades) is the only viable interpretation of *taxa* of all ranks including "species". I also list the several criteria I use to judge attempts at the NS. The second (main) part is a history of the NS from 1730 to today's DNA world. We get acquainted with the pioneering contributions by Linnaeus to our conception of the NS, such that natural taxa are individuals that we aim to *discover* (not define), and the necessity of a *synthetic* approach to discovery as opposed to the scholastic top-down "Logical Division". Various systematists and systems of the past three centuries are highlighted, such as Adanson, Candolle, Darwin and Hennig. Via the cladistic revolution and the implementation of DNA sequence analysis, we end up with a *probabilistic* approach to phylogeny reconstruction. The third part, "Linnaeus revisited", discusses some widespread myths concerning Linnaeus's systematic philosophy; a few examples of late 20th century allegations of dogmatism and "essentialism" in Linnaeus's taxonomic thinking are rebutted. An Epilogue concludes the text.

Keywords evolutionary ontology; history of systematics; Linnaeus; philosophy of systematics

■ SETTING THE STAGE

1. The tree of life and the atoms of phylogeny. — In my student days, 'the biological species concept' (BSC) was somehow understood as explanatory; as an *hypothesis* of what makes preconceived entities exist and persist. Imperceptibly it was transformed into two logically unconnected *definitions*, referring to either process (evolutionary units ['actual interbreeding']) or pattern (crossability ['potential interbreeding']). Many species concept designs (including versions of the BSC) assume a one-to-one correspondence between process and recognisability (pattern), which – except trivially in the "nondimensional" local eco-situation (Mayr, 1949) – lacks substantiation (Bock, 1986). These formulas typically invoke integrating forces or "homeostasis", often confusing *explanandum* and *explanans*. Within a phylogenetic framework, all such tailorings are exposed as *ad hoc*, and are unceremoniously effaced by Ockham's razor (Lidén & Oxelman, 1989; Lidén, 1990; Cellinese & al., 2012; Mishler, 2021; Matzke, 2022).

As the evolving branch tips of phylogeny are discoverable only in retrospect, *pattern* is the only possible framework for *taxonomies*. To conceptualise 'species' as *actors* in an evolutionary drama is misguided; taxonomic *rank*, including the species rank, is necessarily arbitrary and all natural *taxa* are coequal as to ontological status, as visualised in Fig. 1.

Scientific biological taxonomy is a discovery endeavour. It presupposes a *realist* conception of the pattern of biodiversity. Realism about *taxa* is perfectly compatible with nominalism (if that should bother you), as an understanding of biodiversity as momentary manifestations of information-continua has the correlate that clades (taxa) are *historical individuals*. To refer to an individual taxon (tiger, Rhodophyta, *Tussilago*) as 'a natural kind' is a common category mistake that has caused mystification of both taxa and 'natural kinds'. An individual taxon is an individual; a natural kind, like 'gold', is not. One can perhaps argue that all clades taken together is a kind of natural kind.

Individual organisms (interactors, 'gene vehicles') are ephemeral manifestations in the information flow; it is a grave category mistake to treat 'the organism' as a level in the tree-of-life hierarchy. The fate of individual replicators[1] is of course mediated by differential fecundity of interactors, but phylogenetic analysis and taxonomy are concerned with interactors only as 'semaphoronts' (sign bearers).

I thus advance an information flow picture of evolution and phylogeny. This may at first seem harder to visualise than beings of flesh-and-blood (or marrow-and-bark), but actually makes it far simpler to comprehend the process/pattern distinction. The irreducible branch tips of phylogenies, the

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evolutionary units, these atoms of phylogeny that correspond to the 'process' interpretation of the BSC (I avoid the static and misleading metaphor 'gene pools') – each is a system of integrated replicator continua, a system that changes through time (anagenesis), occasionally branches (cladogenesis), and is manifested at a certain time slice as a metapopulation of ephemeral interactors. This information flow perspective is all but forced onto us botanists, as our study objects are haplo-diplonts and usually modular, but it has application to all of life.

Anagenesis and cladogenesis are independent processes, but it takes anagenesis (i.e., time) to eventually make a cladogenetic event apparent to us; hence the inevitability of a pattern approach in *taxonomy*. The atoms of phylogeny are unavailable to us and certainly vastly outnumber what we can ever recognise as 'species'.

Thus, the task of taxonomy is to discover and describe the *incorporative*[2] *hierarchy of historical individuals*, each originating from a once cohesive ancestral entity (epiphenomena, like alloploidy, introduce occasional modifications to the pattern).

The above exposition (based on Lidén, 1990), may be trivial to taxonomists, but is needed to set the stage for my essay – the history of the Natural System. The assessment of the systems and concepts discussed below will thus be guided by the following standards: acceptance of a realistically interpreted incorporative hierarchy and of arbitrary ranks; a rejection of typology, teleology, ideas of taxa forming a continuum, and the *scala naturae* picture (that taxa can be regarded as 'higher' or 'lower'); a synthetic approach to discovery.

Lindley (1830), Gilmour (1937), Stearn (1971) and Heywood (1989) classify classifications simply by whether *many* or *few* 'characters' are considered, and *define* those of the former class as 'natural'. Bather (1927) provides a classic formulation of this view: "A natural classification is a summarising of knowledge by classing together the things that possess in common the greatest number of attributes, reflecting the totality of characters." A similar operationalist (but hardly operational) definition was given by Adanson 164 years earlier (see endnote 25). To the Lindley of 1830 (1830: xvi) it makes good sense: "This is the only intelligible meaning that can be attached to the term Natural System, of which Nature herself, who creates species only, knows nothing" (but see section 18 and Fig. 8 for an 1838 Lindley convert). However, the 20th century authors above, who do regard biodiversity as a product of evolution,

> "improperly confound the recognition of the existence of a natural group with the invention of a technical mark or definition of it … characters do not *constitute*, but *indicate* the genus […] [a natural taxon] is without the mind, not within; in nature, not in art" (Whewell, 1840: 474, discussing Adanson).

This passage mirrors a fundamental tenet of an earlier scholar – Linnaeus (1751: §169): ‹Characters do not define the genus […] they make possible its recognition.›[3]

2. Is the term 'natural taxon' irreparably compromised? — It can be argued that the connotations of this term

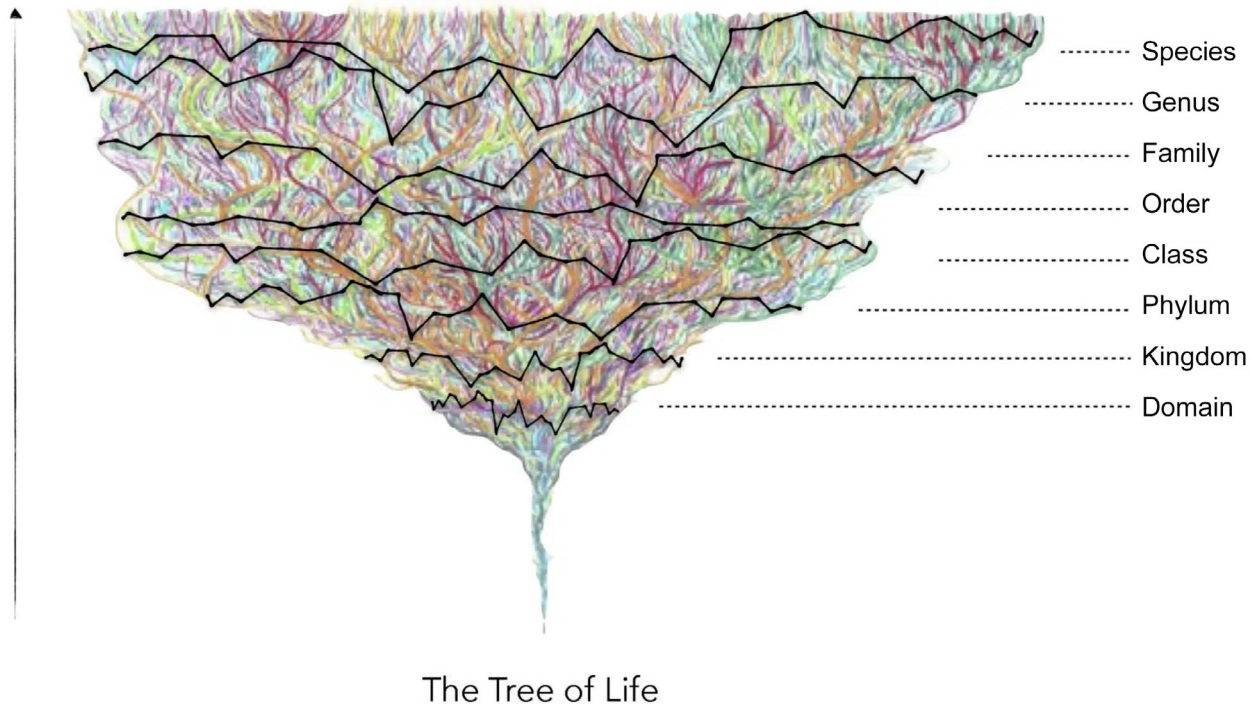


Fig. 1. The arbitrariness of taxonomic ranks (Karen Klitz in Swartz & Mishler, 2022: 10). With kind permission from Klitz and Mishler.

depend on which of the four main taxonomic approaches one subscribes to (key-like schemata not here considered):

Realism: Taxa's existence are independent of anyone's cognition, taxa are explained by natural causes (typically phylogeny) and taxa are hypothesised through synthetic evaluation of empirical data. A statement on a taxon's circumscription (rank disregarded) is true or false, according to the correspondence theory of 'truth'.

Idealism: Nature's pattern, simultaneously static and dynamic, is logical and findable by rational reasoning. Numerology, symmetry and degree of perfection are the keys to Nature's Plan.

Instrumentalism: Taxa are defined by an arbitrarily selected algorithm applied to arbitrarily selected 'characters' with arbitrary 'states'. Statements on taxa's circumscriptions lack truth value, and do not claim to correspond to anything but the means by which these were generated.

Eclecticism (here = 'evolutionary systematics'): Grounded in phylogeny, but invoking absence of 'fundamental' evolutionary innovations as arbiters for circumscription of selected taxa (see section 19, last paragraph).

As proponents of all four schools have on occasions used the term 'natural' to refer to their approach or to their taxa, it may seem advisable to refrain from using the term altogether. It would be a mistake to give in to this temptation. To a vast majority of biologists 'natural' means 'existing in nature', and this is the meaning of 'Natural System' (NS) adopted in this paper; it involves an ontological commitment. Attempts at redefinition, e.g., Bather's stipulative definition mentioned above, have been too restricted and short-lived to force a discontinuation of its usage.

3. Apologia – the whys of this paper. — Much of what has been written lately about taxonomic philosophy and history is written by scholars in fields like science history, philosophy, or even economy, rather than by taxonomists. This is not necessarily unwelcome. As is true of all science sectors, tunnel vision may impede a broader perspective from our ivory towers, and as biologists we are aware that cross-breeding is preferable to inbreeding in several situations.

But taxonomists *have* an understanding of, for example, the nature of taxa, how to interpret phylogenetic trees, and the concepts guiding the nomenclatural codes – things that non-taxonomist writers on taxonomy surprisingly often fail to comprehend. Some papers on the philosophy of systematics show disturbingly little acquaintance with its principles and concepts – in particular 'the nomenclatural type' and 'the individuality thesis' – and do not understand our strict separation of scientific inquiry and naming (see section 22).

Admittedly, an outsider's influence can sometimes contribute to conceptual clarity. A nice example is Kripke's (1980) theory of names, which helps us explain to non-taxonomists the 'nomenclatural type' as a prolongation of our index finger. When we name a taxon, we do not point at the type; we point *with* the type at a clade.

Linnaeus's crucial contribution to the understanding of the Natural System has not always been appreciated. He was particularly poorly treated during the second half of the last century, a period that saw considerable theoretical and methodological progress – as well as considerable confusion – in taxonomy. The situation has certainly improved since then. Härlin (1999), Skvortsov (2007), Winsor (2006), Müller-Wille (2013), Lidén (2020) and others have (almost) managed to lay to rest for example the myth about Linnaeus's taxonomy being *essentialist* or *typological*, herein agreeing with several earlier scholars (Candolle, 1819; Sachs, 1875; Lindman, 1907).

So why this paper, if our man has already been rehabilitated and I have nothing new to add? First, I feel that his rehabilitation is not well enough known, not even among taxonomists. Second, I think that there is a need for a very short educational chronicle of the search for the Natural System, where the pros and cons of the attempts along the way are filtered through cladistic glasses (shamelessly 'presentist' a historian would say).

My account is written from the perspective of an angiosperm taxonomist. Flowering plants is also the taxon in which Linnaeus's revolution is particularly articulated. I do not attempt to give a catalogue of all efforts on the subject. I am most generous with Linnaeus and his contemporaries (even allowing some anecdotes). After Candolle, I only give a few examples to illustrate progress (or lack thereof), and several great botanists are left out. I should add that there are commendable analyses of Linnaeus and of the history of systematics (e.g., Larsson, 1971; Stevens & Cullen, 1990) that treat some aspects in much greater detail.

Italics is used for all non-English text, for titles of books and journals and for emphasis, ‹…› for translations, and '…' for distinction.

The term 'hierarchy' is used strictly in the sense of *nested* hierarchy (i.e., completely unrelated to *graded* hierarchy, as in a classic *scala naturae*).

■ A HISTORY OF THE NATURAL SYSTEM

> ‹No one can deny Linnaeus the honour of being the first to explicitly lay out the conceptual basis for a natural system, argue for its necessity and project its possible realisation›[4] (Lindman, 1907: 53).

4. Introduction. — In a manuscript from summer 1730, titled "Fundamenta botanica" (Fig. 2), a young Linnaeus announces an ambitious programme, promising to lay out rules and recommendations for how systematic biology is to be carried out. His open mind as well as his unlimited self-confidence are both abundantly clear:

> ‹When I explored Nature on her own terms, and found her to disagree with the dictates of authorities, I cast off all

prejudices, became a *scepticus*, doubted everything, and my eyes opened.›[5]

In this manuscript he heralds new systems and encyclopedias to come, not – as the title suggests – restricted to botany; he also boasts about a "Nova Methodus Avium" as well as one for "Insecta". He acknowledges that minerals and fish will be covered by other people; fish by his close friend Peter Artedi (p. x) ‹a devoted naturalist to whom I owe a lot, not least the [Apiaceae].›[6] Artedi's *metod* for this family (based on bracts and bracteoles) is first applied in Linnaeus's second version of "Hortus Uplandicus" 1730 (1730–31) and appears in print in *Systema naturae* (1735a). The same as Artedi was responsible for fish and Apiaceae and Linnaeus for the rest in the early 1730s, a few decades earlier in Cambridge John Ray took on plants while Francis Willughby dealt with animals, and preceding *them* by 2000 years Aristoteles and Theophrastos similarly shared natural history between them. The same as it was bequeathed to Linnaeus to publish Artedi's *Ichthyologia* after the latter's premature death, it fell to Ray to adapt Willughby's *Pisces* for print.

The preamble ends with a long hexameter poem titled "Na[tur]ae qverela ad Jovem",[7] dedicated to earlier botanists. Today the item (Fig. 2) has 16 additional pages (appended after Ähring's London visit) which contain diverse ruminations and notes, presumably jotted down earlier than the preamble. They are paginated 29 to 44 by Linnaeus (at least 28 pages thus seem to be missing or elsewhere).

Unlike most grand plans, Linnaeus's project did materialise. Already in late 1731, Linnaeus was confident enough to communicate some manuscripts to Johann Kohl, editor of the newsletter *Hamburgische Berichte von gelehrten Sachen*. In a first letter, Kohl was presented with "Hortus Uplandicus", a version dated Dec. 1731, which he announced on 19 January 1732 (p. 45). This is the first time the *Systema sexuale* (henceforth = SS) is mentioned in print. Shortly after, on 9 February, Kohl (pp. 94–95) published an outline of Linnaeus's "Fundamenta" project, planned to cover all of botany in 12 parts; we are told that part II will cover a number of artificial systems (e.g., the SS), part V will contain guidelines, such that all characters must be considered (particularly "*alle Theile der Fructification*" but also "*die äusserliche Gestalt*"),

Fig. 2. Three pages from Linnaeus's (1730) "Fundamenta" manuscript; Linnean Society of London LM/LP/BOT/3/1/1.

and that the final part will be dedicated to the Natural System (henceforth = NS).

Two years later, a *prodromus* of *Fundamenta Botanica* arrived in the hands of Christian Nettelbladt, who had promised to help Linnaeus find a publisher, and Kohl (1734: 494) pushes for it in his '*Kohlblätter*'. Kohl's appeal was to no avail and Nettelbladt failed to find anyone willing to take on the printing.

Kohl's bulletins show an interesting evolution. In the first, he announces "Hortus Uplandicus" in a subtly patronising style, his summary of the "Fundamenta" synopsis is neutral, and in 1734 (p. 494) we are informed that ‹Mr Linnaeus is a young but very talented botanist, who gives promise of many important contributions to plant science.›[8]

Linnaeus persisted with his project; *Systema naturae* (1735a), *Fundamenta botanica* (1735b), *Genera plantarum* (1737a), *Critica botanica* (1737b), and *Classes plantarum* (1738b) consolidated him as a rising star in botany. *Musa Cliffortiana* (1736a) established a model for species description. With *Systema naturae* and *Genera plantarum* Linnaeus publicly launched his grand three-part encyclopedia. A sketch of a *Species plantarum* was initiated very early (1731–33), though it took some years to mature (1753).

Linnaeus writes in an autobiography (in third person): ‹He had it all clear in his mind before his 23rd birthday; everything worked out abroad before his return home›[9] (Malmeström & Uggla, 1957: 84). This is not quite true. Among subjects (which we will revisit) that he brooded over later in life are microevolution, hybridity, names, and ranking.

In *Genera plantarum* ed. 6 (1764), he proposes an explanation for the existence of plant families and genera, namely common ancestry. His hypothesis – based on Cesalpino's cortex-medulla idea (originally from Aristoteles) combined with successive cycles of hybridisation between some five dozen (or even much fewer; *fide* Eriksson, 1962: 12) originally created plants – is ingenious and completely bonkers, but certainly 'bold and falsifiable'. That hybridisation cycles create a nested hierarchy rather than chaos, is explained by the female medulla keeping the integrity of the lineages and the male contribution via pollen being more superficial (Linnaeus's cortex-medulla theory is discussed in Stevens & Cullen, 1990).

In a travelogue (1745b) he introduces *nomina trivialia*, and defines them by the *Flora Svecica* (1745a) numbers of the species. This experiment is only briefly mentioned in *Philosophia botanica* (1751: §257), but is fully implemented in *Species plantarum* (1753).

5. 1730 to 1735. — How far had Linnaeus's thoughts on the NS advanced at the time of the 1730 "Fundamenta" manuscript? Several families (here, as in *Systema naturae* 1735a, called *classes naturales*) appear in the appended 16 pages. On the first one (XXIX; Fig. 2), 20 examples are listed. The names of 12 of these he attributes to earlier botanists: Stellatae, Asperifoliae and Pomiferae to Ray ("Raj."), Personatae, Labiati, Cruciformes, Umbellati, Liliacei, Amentacei, Compositi and Caryophyllacei to Tournefort ("Tourn."), Graminae to Scheuchzer ("Scheuch."), but 8 (Cucumerini, Solanacei, Malvacei, Apocyniformes, Decaphidae, Calyciferi, Haemisphaerici and Tripetali) he claims for himself. This list was not meant to be exhaustive. For example the legume family, recognised since antiquity, is lacking. However, it turns up on the last page (XLIV; Fig. 2) where Linnaeus notes the constancy of stamen arrangement in Stellatae, Asperifoliae, Cruciformes, Umbellati and Papillionaceae, but also notes that some families include genera differing in stamen number (e.g., Liliacei 3 and 6; Labiati 2 and 4).

Those correlations, though very far from perfect, nevertheless inspired his invention of the SS, which he briefly mentions in the 1730 "Fundamenta" preamble as a work in progress.[10] But he worked fast. In his first two versions of "Hortus Uplandicus" the system of Tournefort is used (with several improvements in details; Lindman, 1907), but already in the third version (29 July 1730) the SS is applied for the first time. Linnaeus also uses the SS in "Flora Kofsöensis" (1731) and in "Florula Lapponica", a list of plants from his 1732 Lapland journey, presented to his sponsor, the Royal Scientific Society of Uppsala, already in the fall of the same year. As the printing of the society's proceedings was much delayed (1738c, 1742), and as "Hortus Uplandicus" never made it to the presses despite attempts (Ährling, 1878), the first public presentation of the SS is in *Systema naturae* (1735a).

Even an artificial system has to have, in order to make any kind of sense, natural basic building blocks (Whewell, 1840). In the SS, *genus* fulfils this role.

6. Towards the Natural System. — In spite of all the effort he put into the SS, Linnaeus saw an understanding of the NS, the 12th and final part of his "Fundamenta" project, as the prime objective of botany.[11] His "Fragmenta methodi naturalis", hinted at in 1730 and in *Systema naturae* (1735a), first appear in print in *Classes plantarum* (1738b), where 65 unnamed *ordines naturales* (natural families; not to be confused with the rank *ordo* in the SS) are tabulated with their included genera. They reappear in *Philosophia botanica* (1751), *Systema naturae* ed. 10 (1758b) and *Genera plantarum* ed. 6 (1764; now with 58 families), but – despite 25 years of refinement – Linnaeus considered them too preliminary to be used in Floras. In his advanced teaching, however, the NS was his main subject (Giseke, 1792), and Linnaeus himself saw his efforts in this field as among his most important contributions to science.

His goal, to eventually unmask the NS, is announced in the introduction to the plant kingdom in *Systema naturae* (1735a). He points out that chemical properties distinguish, for example, Ranunculaceae, Brassicaceae, Papilionaceae Poaceae, Boraginaceae, Lamiaceae, Rubiaceae, Apiaceae, Solanaceae and Rosaceae. He also notes (as he did in the 1730 "Fundamenta" addendum) that several families are remarkably constant in stamen number and stamen arrangements. With the help of a supplementary rank labelled by Greek letters, inserted between *genus* and *ordo* in the SS, he explains how to pick out some families, e.g., Rubiaceae (*Tetrandria Monogynia β*), Boraginaceae (*Pentandria Monogynia β*),

Apiaceae (*Pentandria Digynia γ δ ε ζ*) and Brassicaceae (*Tetradynamia*).

7. A natural nested hierarchy – taxa and ranking. — Linnaeus has only two expressed levels in his NS tables (genus and family or *ordo*), but he admits of more (1738b, 1751: §162), such as between species and genus, genus and family, and above family, such as Monocotyledons and Dicotyledons. He eventually suggests, in agreement with modern DNA data, that the water lilies may not fit into either, but is a third taxon, and that fungi are not plants (Giseke, 1792 *fide* Smith, 1824).

Mostly unnamed levels intercalated between the formal ranks are common. In *Species plantarum* they are often mere artificial keys, but in other works they designate what he perceives as natural taxa. The genera tabulated in his various versions of the *ordines naturales* are ordered into subgroups, often corresponding to taxa ranked as tribes or families today, and subgenera are not uncommon in *Genera plantarum*.

In *Systema naturae* (1735a: obs. regn. veg. #14) Linnaeus writes: ‹Every genus is natural, originally created as such.›[12] In 1764, however, he explains plant genera and families by common ancestry (see section 4), and he realises that *ranking* is indeed arbitrary. In *Genera plantarum* (1764: 256), Linnaeus writes that ‹*Tormentilla* and *Potentilla* differ only by number, and could be united›.[13] With his very broad concept of the genus *Simia* (apes + monkeys) he finds nothing that could defend generic status for *Homo* (1747), but recognises it as a genus in order not to provoke the theologicians, but he adds that ‹perhaps I should have [combined them], to honour scientific principles›[14] (in modern parlance: without *Homo*, his *Simia* is ‘paraphyletic’).

In *Philosophia botanica* §246 (1751) he devises a pragmatic nomenclatural strategy for generic splits (for the not unlikely scenario that such will be contemplated by future taxonomists), even vaguely hinting at a nomenclatural type concept (Lidén, 2020).

In *Genera plantarum*, we find five subgenera in *Fumaria*. They had all been treated as genera by earlier authors, and were again raised to generic rank after Linnaeus. This is, by the way, a common fate of Linnaeus’s broadly circumscribed genera (and species, for that matter); they were split up by later authors – for better or for worse. Linnaeus’s *Fumaria* is evidently natural. Its current status as a subfamily with 18 genera is arguably more informative, but the number of species recognised by Linnaeus was only 15; today’s count is 40 times higher (close to the increase in the total number of angiosperms).

When it comes to the species rank, there are many examples. In his general deliberations, Linnaeus is following Ray (1686), emphasising reproductive continuity (Müller-Wille, 2007), but in practice he is more advanced. In *Species plantarum*, he uses expressions like *filia praecedentis* (daughter of the previous) or *temporis filia* (daughter of time) for some species, hinting at common origin, a time dimension, and arbitrary ranking. Some examples from *Flora Suecica* (1755) are illustrative: 1°, on *Juncus* [*Luzula*] *pilosus* (p. 115): ‹This has so much in common with the two next, that it seems probable that they have a common mother›;[15] 2°, on *Chenopodium hybridum* (p. 80): ‹Has much in common with the previous [*C. viride*], and may have originated from this›;[16] 3°, on *Hypericum montanum* and *hirsutum* (p. 266): ‹Their close similarity indicates that one is born from the other, and it is all the same to me if they are recognised as the same or different species›.[17] The idea is evidently close at hand. His contemporary Buffon also invokes descent with modification (in his case chiefly *dégénération*) to explain very close similarity (see section 15), and both of them suggest that climate and soil may be involved.

In the same spirit, Linnaeus suggests (1751, 1756) that the distinction between constant varieties and species is arbitrary (like Darwin, 1859). In *Flora Suecica* (1755: 245–247), *Fumaria bulbosa* is composed of α *solida*, β *intermedia* and γ *cava*. He observes that they remain distinct when cultivated ‹but what causes two different [*solida* and *cava*] to be produced from one is unknown›.[18] I am not sure that his notation and naming of varieties is fully consistent throughout his works, but in, for example, *Species plantarum* a full α-β-series designates constant varieties. Cultivars, atavisms and colour forms are always indicated by β, γ, δ, …, with a ‘normal’ form implied, but not explicitly spelled out. However, when the varieties/subspecies together constitute ‘the species’ – without, *nota bene*, any one given primacy – he uses the complete series (α, β, γ, …), and usually provides them with formal epithets (Fig. 3).

8. A paradigm shift. — An understanding of biodiversity as a nested hierarchy is as old as mankind. For plants, the intuitive ordering by Cordus (1561) and L’Obel (1576) took this understanding to a new level. However, their lack of method did not satisfy Cesalpino (1583), who tried to pinpoint *the essential* properties that could divide the whole in a way that would recover these intuitively evident but elusive taxa.

This tension – between analytic logic and recognition of natural taxa – fell to Linnaeus to dispel. His realisation (1737a) that Logical Division gives arbitrary classes and that natural taxa can only be discovered by building synthetically from the basic atoms upwards (“*à singularibus ad generalia*”; see section 23: A, B, C), was a fundamental breakthrough, turning the scholastic tenet ‹A natural method always proceeds from the whole to the parts›[19] (Burgersdijk, 1626: 380) on its head. Linnaeus’s famous canon that genera are not defined by characters (see endnote 3), which he impressed on his advanced students, points forward to a conception of taxa as individuals. Illuminating are the teacher-disciple dialogues (Giseke, 1792) on some families (Apiaceae, Rosaceae, Ranunculaceae). Linnaeus demonstrates that they cannot be identified by any single ‘character’, yet they are obviously natural. In this he echoes Magnol (1689: praefatio p. [7]), who writes that we perceive an affinity ‹which is not possible to put into words; take *Agrimonia* and *Potentilla* that all botanists consider to be relatives›.[20]

9. *Philosophia botanica*. — *Philosophia botanica* (1751) is based on his earlier publications and lecture notes. The skeleton from *Fundamenta botanica* (1735b) is considerably amended. *Philosophia* is aimed at students, but is often

regarded as Linnaeus's botanical testament. It is a collection of guidelines and tables of the most varying kind, some a few sentences only, some really witty, some going to several pages with long tedious impenetrable lists of examples. The distinction between paragraphs is of an arbitrary nature in places, to make them sum up to 365.

It had a formidable normative impact. Linnaeus organises botanical descriptive vocabulary as we know it. Several of his terms had earlier been used in wider, ambiguous or different meanings, but Linnaeus's stipulative definitions triumphed (with some exceptions – his *calyx* includes several subterms, of which *perianthium* equals today's [and Tournefort's] calyx).

However, some abstract general terms are also used in unorthodox senses. Unlike his hijacked morphological terms, they have caused considerable confusion: *essence*, *differentia* and *nomen* are particularly prone to misinterpretation.

In *biology*, the terms 'genus' and 'species' had acquired their current meaning – divorced from their relative sense in antique and scholastic analytic logic – long before Linnaeus's time. Still, expressions like *differentia specifica* and *character essentialis* automatically signal 'Aristoteles' or 'scholasticism' to some authors (Cain, 1958; Mayr, 1982; Jonsell, 1978; Ereschefsky, 2001), although Linnaeus's use of these terms are unrelated to logical division.

The term *character essentialis* has in Linnaeus's works a pragmatic meaning: an omnipresent feature of, for example, a genus. *Character naturalis* stands for the whole set of attributes that is common to a genus (i.e., its *description*; a subtractive algorithm for working out the *character naturalis* is given in §193; see Lidén, 2020). *Nomen specificum legitimum* (phrase name, diagnosis) is the minimum description needed to distinguish a species from its congeners, thus not a 'name' in the normal sense (see section 14 below).

In §154 and §155, we are again warned that a *synopsis* creates arbitrary divisions, and therefore is not permissible for distinguishing *genera*; yet a *Clavis* ***Classis*** *Synoptica* [like the SS] is a methodological necessity to avoid chaos. §160 tells us that ‹artificial classes will have to stand in for the natural ones, until all the latter have been discovered›.[21]

An often quoted sentence from §162 states that species and genera are products of nature, whereas orders and classes are products of *naturae & artis* [craft]. To interpret the conjunction here as 'or' rather than 'and' makes sense. The

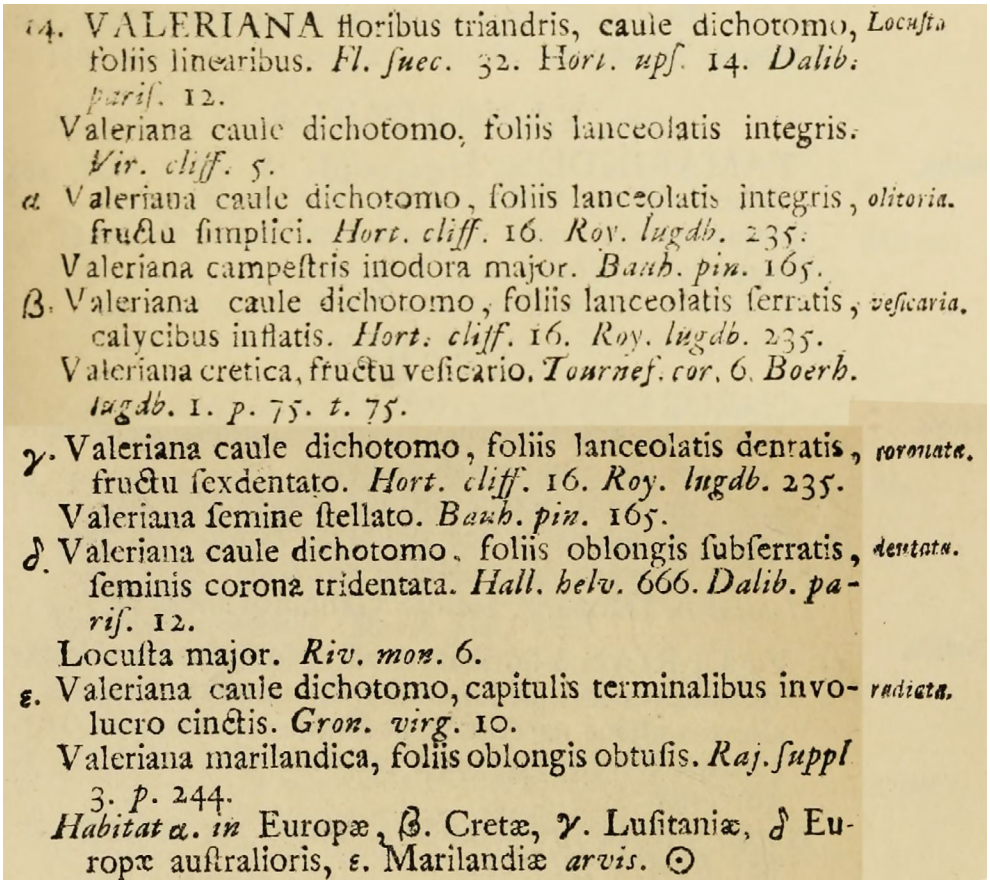

14. VALERIANA floribus triandris, caule dichotomo, foliis linearibus. *Fl. ſuec.* 32. *Hort. upſ.* 14. *Dalib. pariſ.* 12. *Locuſta*
Valeriana caule dichotomo, foliis lanceolatis integris. *Vir. cliff.* 5.
α Valeriana caule dichotomo, foliis lanceolatis integris, fructu ſimplici. *Hort. cliff.* 16. *Roy. lugdb.* 235. *olitoria.*
Valeriana campeſtris inodora major. *Bauh. pin.* 165.
β. Valeriana caule dichotomo, foliis lanceolatis ſerratis, calycibus inflatis. *Hort. cliff.* 16. *Roy. lugdb.* 235. *veſicaria.*
Valeriana cretica, fructu veſicario. *Tournef. cor.* 6. *Boerh. lugdb.* 1. *p.* 75. *t.* 75.
γ. Valeriana caule dichotomo, foliis lanceolatis denratis, fructu ſexdentato. *Hort. cliff.* 16. *Roy. lugdb.* 235. *coronata.*
Valeriana ſemine ſtellato. *Bauh. pin.* 165.
δ. Valeriana caule dichotomo, foliis oblongis ſubſerratis, ſeminis corona tridentata. *Hall. helv.* 666. *Dalib. pariſ.* 12. *dentata.*
Locuſta major. *Riv. mon.* 6.
ε. Valeriana caule dichotomo, capitulis terminalibus involucro cinctis. *Gron. virg.* 10. *radiata.*
Valeriana marilandica, foliis oblongis obtuſis. *Raj. ſuppl* 3. *p.* 244.
Habitat α. *in* Europæ, β. Cretæ, γ. Luſitaniæ, δ Europæ auſtralioris, ε. Marilandiæ *arvis.* ☉

Fig. 3. *Valeriana [Valerianella] locusta* in *Species plantarum* (Linnaeus, 1753: 33–34) has five stable varieties (or subspecies). Note that "α" is accidentally put one line to low. The discrepancy between *foliis linearibus* for the species and the description of the subspecies is due to his system of quoting 'synonyms'. The picture has been put together from two pages.

paragraph is of an umbrella nature, and the option posed is whether the natural system or an artificial system is the referent. A similar case is found in §246 (Lidén, 2020).

A few aphorisms in *Philosophia botanica* are leftovers from *Fundamenta botanica* (1735b), retained to appease the clergy, but already misdoubted by Linnaeus. Here belongs §1, which states that all species were created as such in the beginning, a phrase absent from later works.

10. Cognitive dissonance. — True to §154 in *Philosophia* – that Logical Division is not permitted for demarcation of genera – Linnaeus does not hesitate to include species with 1, 2, 3 or 4 stamens in *Valeriana*, confident that they all belong in the same genus (arbitrarily put in Triandria in the SS). But with *Bidens cernua* he struggles. In 1745, he simply says that the radiate form has not yet been found in Sweden. From 1751 (*Philosophia* §209) and onwards, however, he places the discoid and radiate forms in separate genera (*Bidens*, *Coreopsis*), though still realising that they are possibly conspecific. In this instance of Nature competing with Art ("*facies & natura certat cum lege & arte*"), *Nature* has to yield to his key-like technical treatment of Asteraceae, violating his basic tenet that *characterem non constituere genus*.

A second example concerns how the generic delimitations in the Silenoideae develop over time. In the first edition of *Genera plantarum* (1737a) Linnaeus describes both *Cucubalus* and *Silene* as having 3 or 5 styles. In the 1754 edition, however, he describes them both as having 3 styles, and 5-styled species are now in *Lychnis* or *Agrostemma*. One cannot help suspecting that these rearrangements are influenced by the SS.

An epigenetic mutant of *Linaria vulgaris* with radially symmetric flowers is apparently recognised as a 'genus' named "*Peloria*" (monstrosity) in a student dissertation under his praesidium in 1744, and may at first sight seem to be a similar case. However, in *Flora Svecica* (1745a: 182) Linnaeus adds under *Antirrhinum* 501 (*Linaria vulgaris*) simply that ‹a stunning metamorphosis of this plant is described in the Uppsala dissertation *de* Peloria›.[22]

11. To picture biodiversity – nested hierarchy versus continuum and *scala naturae*. — Regarding how the pattern of biodiversity is best understood, Linnaeus is ambiguous. In *Philosophia botanica*, §77 deals with his *ordines naturales*: now 67 families and several *incertae sedis* genera. Some higher and lower groupings are implied. His basic idea is a nested hierarchy (Gustafsson, 1985: 126), but this picture is contradicted by his initial and concluding remark "*Natura non facit saltus*" (Nature makes no leaps), as well as by an often cited metaphor: taxa as countries on a map with relations in various directions,[23] differing from another contemporary metaphor, a [branched] chain (Fig. 4).

In §153, he contrasts *plantas imperfectas* with *perfectissimas* (as did Ray, 1682), and he assumes a link between the most *im*perfect animals and the most *im*perfect plants. He did not work in a vacuum. The *scala naturae* was firmly entrenched ever since Aristoteles, and has influenced biology up to the present day, usually correlated with the idea of continuous transitions between taxa.

Linnaeus seems to be aware of the tension between nested hierarchy and continuum ideas (Gustafsson, 1985: 126). In his private copy of *Philosophia*, "*Natura non facit saltus*" is crossed out. In Giseke's "Tabula" (1792) (Fig. 5) the map picture is considerably modified, and the families are shown as islands in an archipelago. The "Tabula" is flat; no categories above family are indicated explicitly, though some – such as monocotyledons – are suggested by proximity of islands.

But the picture continues to be mixed (as it has into our day). In several cases – in particular among 'cryptogams' and monocots – supposedly linking genera are set in the margins where islands touch. Linnaeus considered these genera significant (Giseke, 1792), like *Lycopodium*, a *Musci* that has aspects of *Filices* (Fig. 5).

12. Adanson. — Michel Adanson's *Familles des plantes* (1763; 1186 pages!) parallels Linnaeus's "Fundamenta" project and includes botanical history, morphology, nomenclature, and not least descriptive treatments of families with included genera. Adanson and Linnaeus recognise roughly the same number of families, and agree about their content to a large extent (though this is not the impression you get from Adanson's acrimonious text).

To forestall eyebrows raising, I should alert you to Adanson's eccentric spelling. He set out (but rather half-heartedly) on a quixotic mission to simplify French orthography (even introducing 'francophone' spelling of some scientific names). In his text he mixes the standard variants with his own. It is possible that this unorthodoxy contributed to the lack of response from his countrymen. Also his inflating the number of genera was less popular at the time, although several have been later adopted.

Adanson tabulates, in 65 *Systêmes* (Fig. 6), the proportion of each family that possesses a certain state (*Classe*) of 65 different traits, such as root structure, corolla colour or leaf position. The number of *Classes* varies from 3 to 41 in different *Systêmes*. A summary table illustrates to which degree the *Classes* are compatible with *les sections*[24] *natureles*; number of cotyledons scores highest at 85%, whereas plant height is a lousy predictor at 0% (but if plant height had had 3 rather than 11 *Classes*, it had scored differently).

The tables show that arbitrary subdivisions of a single organ or parameter is a poor guide to the NS; they do not constitute a data matrix from which circumscriptions of families are derived. The families are already fixed here and are largely intuitively delimited, save for difficult-to-place genera, where Adanson may have resorted to counting 'characters'.

Adanson also purports to rank the naturalness of earlier botanist's systems based on how well they agree with his own, but his actual rankings reflect his personal likings rather than his declared method.

Scholars differ in their appreciation of Adanson. Candolle (1819) and Whewell (1840) both assert that Adanson fails to grasp the concept of naturalness. Candolle debunks Adanson's approach with arguments similar to those used against 'numerical taxonomy', adding that those of Adanson's families that seem best to approach natural groups are those where he

side-steps his declared method and trusts his intuition. Whewell takes issue with Adanson's families being defined as, rather than hypothesised to be, natural.

> Adanson: ‹The true natural arrangement of plants is that which takes into account the correlation of all parts and qualities, not excluding a single one; it brings together all plants into natural and invariable Families, based on all possible correlations […] no other *Métode* can be called natural.›[25]

Arguably, Candolle – as well as the 'neo-Adansonians' of late 20th century – take Adanson's rhetoric too literally; his general message is not that everything should be given equal weight, but rather (Stafleu, 1963) that nothing should be dismissed *a priori*. Notably, Adanson's absolute favourite among botanists, Tournefort (1694), is of the opinion that *only* those organs that best reflect relationship should be considered, which according to him are flowers and fruits (Linnaeus [1736b: 184] classified Tournefort as *corollista*).

13. The Jussieus. — Antoine Laurent de Jussieu published his *Genera plantarum secundum ordines naturales disposita* in 1789, 11 years after Linnaeus's death. His system is an insightful development of that of his uncle Bernard, prepared 30 years earlier and included in Antoine's book. Bernard de Jussieu, regarded by Linnaeus as a truly great botanist, was well acquainted with Linnaeus's NS, ever since their warm and inspiring encounter in Paris in 1738, the same year that saw Linnaeus's *ordines* in print for the first time. It is not surprising that the three systems are fairly similar.

Where the SS has *genus* as the basic natural sortal, *ordo* (family) fulfils this role in the system of Antoine Laurent de Jussieu. He appears to apply a largely synthetic or intuitive

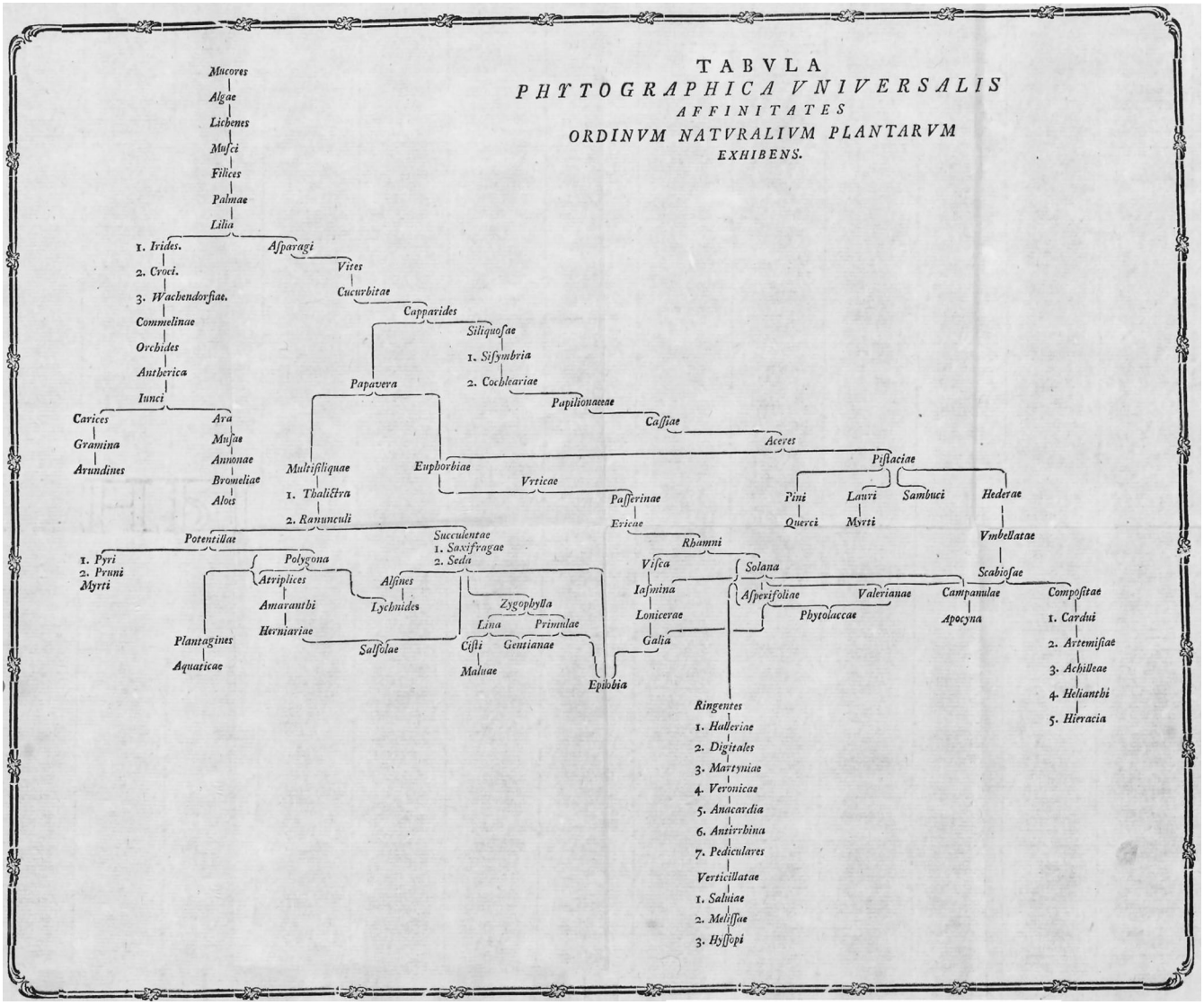


Fig. 4. *Tabula phytographica universalis* (Rüling, 1774: 36v).

approach for forming families and genera, but for higher categories and for subdivisions of families his classification is analytic and key-like. Like Candolle (see below), he often relies on rationalist *a priori* reasoning for selection of characters (Stafleu, 1963). The Jussieus are also more consistent than Linnaeus in their belief in a continuum and a *scala*; they regard taxon boundaries as ± arbitrary and admit of degrees of naturalness.

14. Linnaeus, Adanson, the Jussieus – how do they compare? — Like Adanson, Linnaeus (1738b) emphasises that *symmetria* among all parts, in particular – but not restricted to – those of the *fructificatio* (inflorescence, flower,

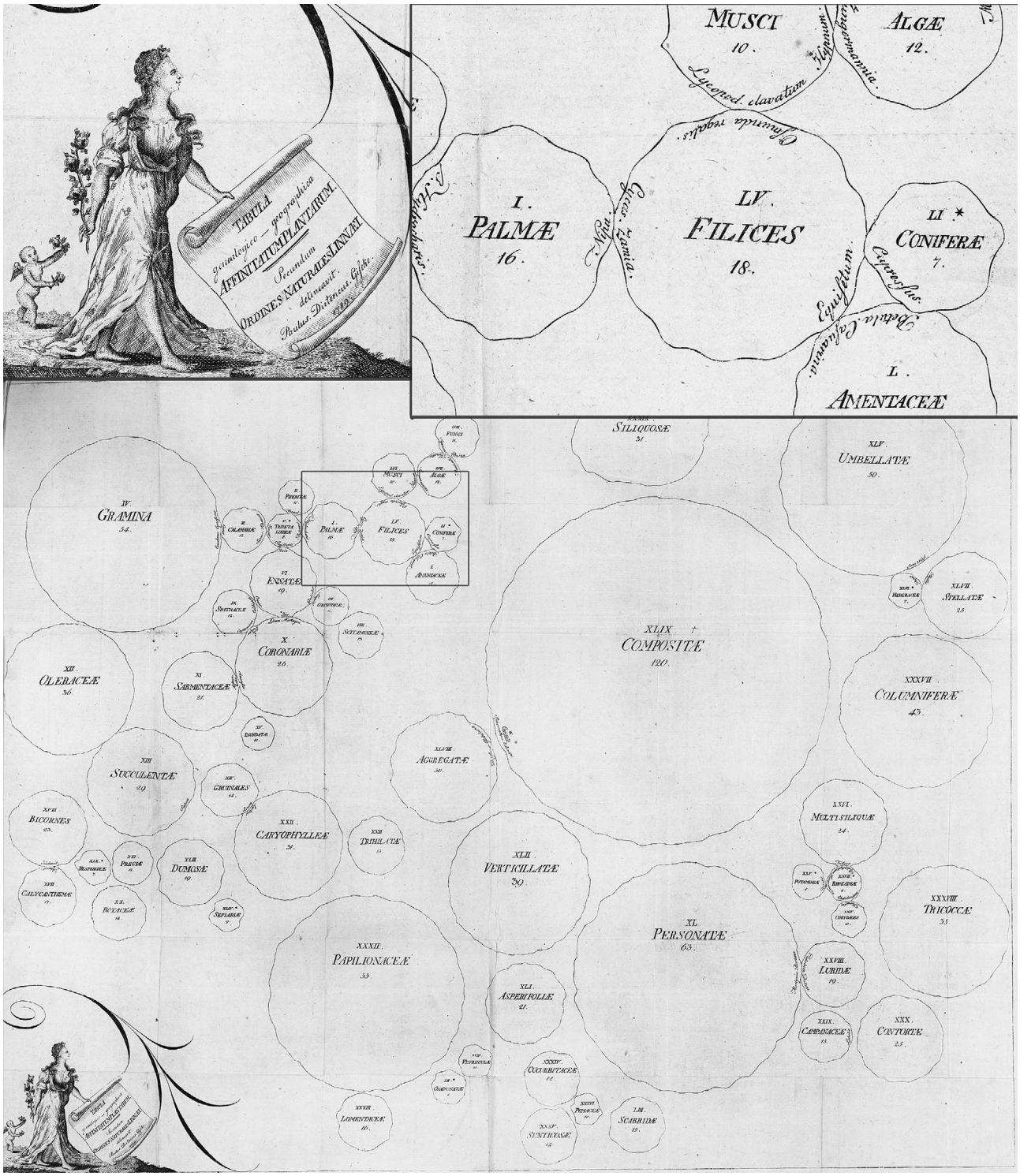


Fig. 5. *Tabula genealogico-geographica affinitatum plantarum secundum ordines naturales Linnaei* (Giseke, 1792: 662v).

fruit, seed), is key to recognising natural taxa, but that there are no *a priori* rules.[26] *Symmetria* could possibly translate as 'correlation' (Adanson: *raport*), but to Skvortsov (2007) it prefigures the concept of *homology* (sameness). Candolle (1819) emphasises that correlation often suggests homology.

Fundamental in the NS is that taxon-names are 'proper', i.e., simple tags and nothing more (Adanson: *propres*, *simples*, *primitifs*, *sans signification*), and Adanson and Linnaeus agree also here. Indeed, in his first "Fragmenta methodi naturalis" (1738b: columns 489–514), Linnaeus labels the families with numbers only (in 1751 they are named).

For *species names*, however, Linnaeus's insight appears long in waiting. Following Tournefort, he continues to use the term *nomen specificum legitimum* for the descriptive phrase that gives *differentiae* to congeneric species. These phrases, data-dependent and subject to change with new knowledge, thus function as determination guides and are not 'names' in the normal sense. When Linnaeus eventually introduces binomials (1745b) it is – according to Jonsell (1978) – for pragmatic reasons. With *Species plantarum* (1753) he has, however, realised their fundamental role, and came to regard them as his most important innovation, ‹like putting a clapper in the bell; giving botany a new and natural substance›[27] (1769: 75). In *Species plantarum* (1762: [x]) he declares that ‹changes of names, even for more fitting ones, do more harm than good›,[28] emphasising their status of *nomina propria*.

Adanson dismisses Linnaean binomials for not being *simples*, only to reinvent them in uninomial guise, i.e., hyphenated but still recombinable. However, the 'first' species of a genus is not considered to need an epithet but simply equals the genus name, which might have been confusing had Adanson ever come around to implement his species nomenclature.

In *Philosophia* (1751 §253, 254) Linnaeus recommends that names of suprageneric taxa should reflect a characteristic feature, as names are *onera artis inevitabilia* (inescapable burdens of our craft), but that for *natural* taxa, which is what concerns us here, nondescriptive names are equally admissible. Later, he explained to his advanced students that what matters is that the *referent* is clear (Giseke, 1792); whether names are descriptive or non-descriptive in *form* is immaterial. Adanson is much more concerned about this, even accusing Linnaeus of forging *significatif* the name *Bauhinia*, because Linnaeus (1737a) makes a humorous analogy between the two Bauhin brothers and the bifid leaves in this genus. Still Adanson himself feels compelled to conserve, for the sake of nomenclatural stability and a lack of synonyms,[29] several names of both genera and families that are *comparatifs* or otherwise *significatifs*, such as Polugonifolia or Umbellatae.

Though names that are descriptive in form may have mnemonic advantages, they certainly risk being misinterpreted as defining. The biologist Theodor Klein (1743) opines that it is absurd to put humans in Quadrupedia Antropomorpha (four-footed and human-like). Linnaeus had the backbone to keep these well-established names still in 1756, but eventually had to give in,[30] changing to Mammalia and Primates (1758a). Klein, by the way, also suggests changing *Homo* to *Knodalomorphon* (Greek: like a brute), honouring Linnaeus's laconic 'diagnosis' (1735a) ‹know thyself›.[31]

The Jussieus should be credited for more consistently using derivations of genus names for names of plant families, thus removing any risk of *signification* – as well as of nomenclatural issues should a family be divided.

The differences between the three authors' actual systems are of little significance. Whose family circumscriptions perform best, judged by DNA, varies with family. Adanson is more explicit than Linnaeus in his recognition of subgroups (*sections*) within families, but is also slightly more prone to

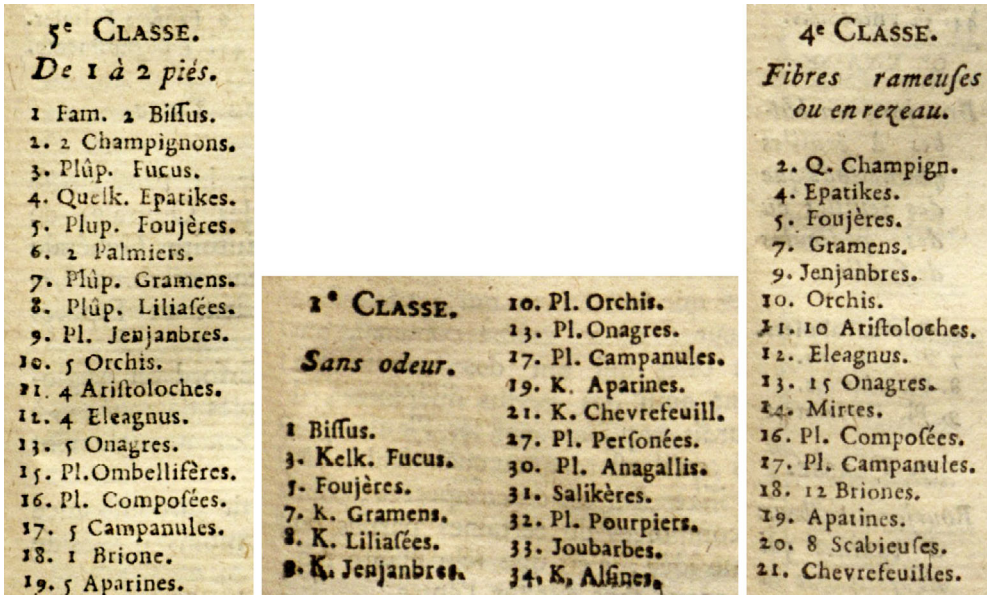


Fig. 6. The first part of random examples of a *Classe* from *Systême* 2 (height), 11 (smell) and 13 (root system) of Adanson (1763). Plûp. = most; Pl. = many or most; Quelk., Q., Kelk., K. = some, a few.

what we would today regard as major misplacements. Linnaeus partly avoids this by leaving several problematic genera *incertae sedis*. Antoine de Jussieu gains precision by recognising almost twice as many families. His circumscription of the Papaveraceae is spot on, whereas Linnaeus and Adanson both include extraneous elements.

All in all, Linnaeus can comfortably lay claim to the NS by priority (25 years), conceptual clarity, and degree of agreement with the standards set out in section 1. On the other hand, Adanson and Jussieu integrate the systematic, encyclopedic and descriptive aspects into a single presentation (down to genus), and they place every genus into a family. Compared to these, Linnaeus's NS-lists indeed look paltry – if seen in isolation.

15. Buffon. — The Comte de Buffon's reputation as an adversary of everything Linnaean calls forth some examples of his take on taxonomy. The differences between the two have not only been exaggerated, but also confused.

In 1749, Buffon claims that the pattern of biodiversity forms a continuum (except for the Kingdoms), and that petty details of mammalian teeth (a rebuke at Linnaeus's *Systema naturae*) do not justify a belief in a natural nested hierarchy.

By 1766, his ideas have changed. He now explains genera/families[32] of mammals by common descent, based on correlation of characters. The 200 species stem from 38 creations. These creations 'indisputably' took place in the Old World; the dispersal by some offspring into America happened in a very distant past when the continents were united. Side branches of the original species evolve mainly by *dégénération*: reindeer and deer, for example, are explained as secondary degenerate branches of the moose. Only a few of the primary creations (elephant, rhinoceros …) remain unique and without side-branches[33] (1766: 335). The idea turns up already in 1753 (when he even rhetorically alludes to a single origin for all animals), but is at this time dismissed as incompatible with Scripture as well as with his understanding of 'species'.

Buffon (1766) is adamant that a common-origin explanation can only be contemplated for closely similar species; he believes that the original creations, like the moose, are still extant and – though individually variable – eternally true to their archetypes.

We see a parallel to Linnaeus's suggestions of 'microevolution' in plants (endnotes 15–18). Note also that, like Linnaeus, Buffon concludes that the female fiber is more dominant in procreation, and he even provides empirical evidence (the mule and the hinny).

16. Lamarck. — Jean-Baptiste Lamarck (1809), a student of Bernard de Jussieu, takes the animal *scala naturae* literally, from primordial infusoria (*Monas*) to *Homo*, its obvious summit. He believes in perpetual spontaneous creation, with lineages smoothly progressing towards complexity and perfection. He modifies the picture by adding a few branches. Gaps in the continuum he ascribes mainly to lack of knowledge, though extinction may be a factor for animals hunted by man. By 1815, the picture has become slightly more complicated with two separate sparsely branched chains of *animaux sans vertèbres* (p. 457).

Lamarck's *scala* is obscured (*or* enhanced) by a complementary force: adaptive evolution caused by use or disuse coupled with inheritance of acquired characters. This dimension can also explain anomalies in the progressive *scala*, such as lack of legs in snakes.

Lamarck denies the existence of a natural nested hierarchy, and states in the introduction to *Flore Françoise* (1778: xviii; repeated in Lamarck & Candolle, 1805a: 9) – long before his transformation theory – that taxon borders are arbitrary partitions in a continuum:

> ‹Nature rejects our classes and families […] when we study her in greater detail, when observations accumulate or we discover new plants with mixed characters that disobey all our rules, we will be forced to make new genera, splitting those we have already distinguished. Without doubt we will end up having in each genus only one species, often with as many varieties as there are individuals.›[34]

Though both Lamarck and Buffon are firm believers in the *scala naturae*, their views are widely different. Where Buffon believes in separate and single creations for the primary species, with some secondary species explained by *dégénération*, Lamarck pictures a permanent progress from ever newly formed protists. Hull (1988: 29–30) states that "Lamarck's world of entities cycling endlessly through time-less categories was nearly as eternal, immutable, and cyclical as that of the early Greeks."

17. Candolle. — In some regards, A.P. de Candolle is a link between Linnaeus and today (Lindman, 1907). He compares (1819) the pattern of biodiversity to the subordination of continents, countries, provinces, etc., and his bubble-gram of Leguminosae (1825: pl. XXVIII) (Fig. 7), with four hierarchical levels, is topologically equivalent to a cladogram. Candolle holds that a nested hierarchy gives a (mostly) correct picture of biodiversity, and that taxa are (mostly) discrete and real, and not mere conventions. He emphasises the distinction between *analogie* and *affinité*, and introduces the term *homologie*.

But Candolle also maintains archaic views. *Scala* and continuum components are still there. In Leguminosae (Fig. 7), he aims to arrange the subgroups in the 'true' sequence *from* Terebinthaceae *to* Rosaceae (the neighbours in his family sequence), and he suggests that the *Detariae* is transitional to Rosaceae-Amygdalae.

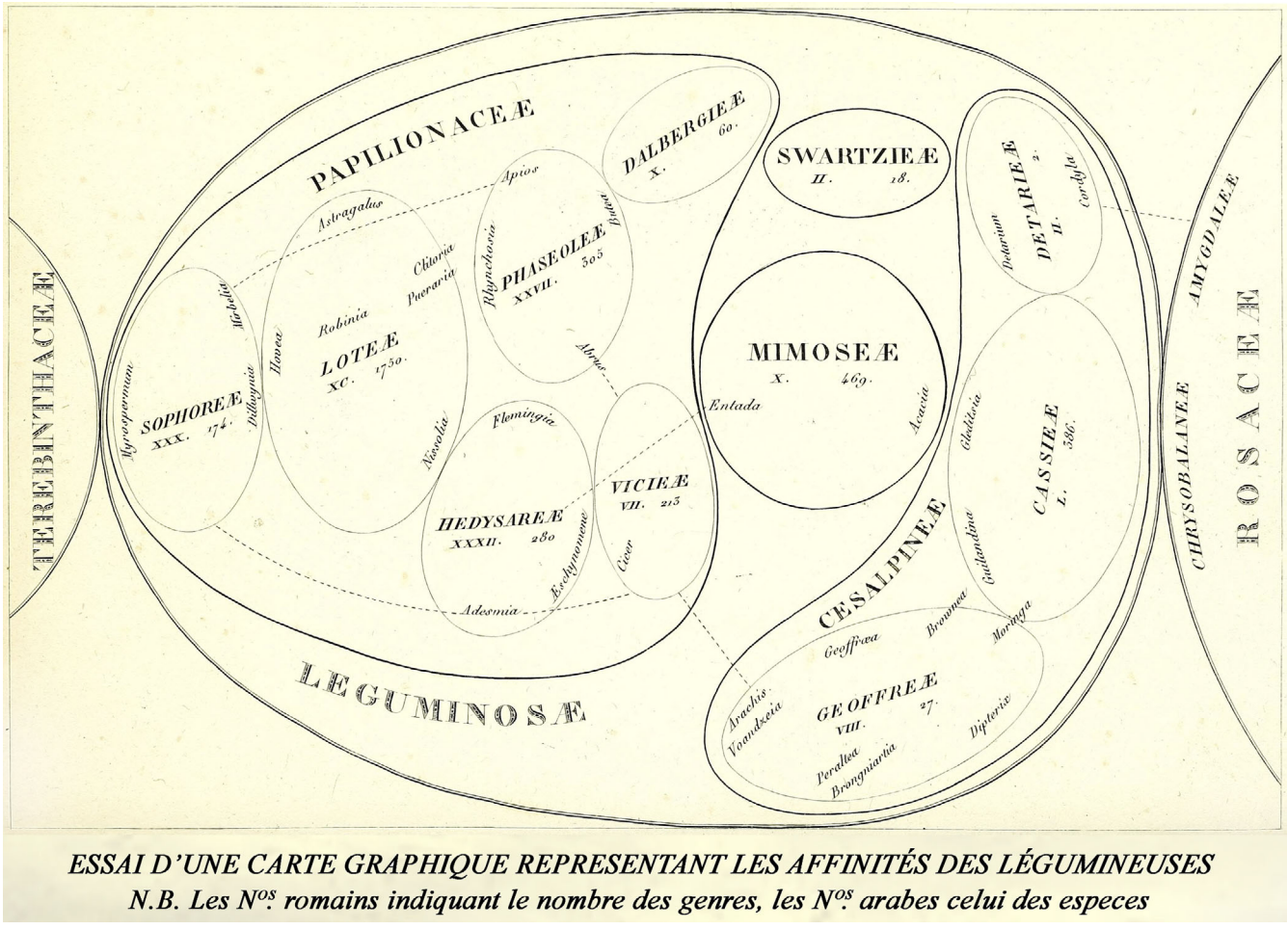
Second, Candolle uses – like Cesalpino – a *rationalist* top-down approach to recognition of some taxa (e.g., taxa above family or between family and genus), aiming to determine *the* decisive character to be used for division at each level. As the embryo (he claims) is the most primary and essential aspect of the plant it should *for this very reason* be used for the primary division. Still he quotes Linnaeus's famous dictum "*characterem non constituere genus*" with approval, but seems oblivious of Linnaeus's auxiliary principle: that there are no *a priori* rules to discovery of natural taxa – one step forwards, one step backwards.

18. Naturphilosophie – a blind alley. — Augustin Augier's (1801: 1) stated aim is to ‹combine the advantages of artificial *systêmes* and natural *méthodes*›[35] (note that for French botanists *systême naturel* would have been a contradiction in terms; cf. Adanson, 1763), but his *arbre botanique* is simply a synoptic key. Augier asserts, however, that it reflects divine reason and is really 3-dimensional and symmetric (if a branch is missing, it has not yet been discovered). He strongly emphasises continuity[36] and degree of perfection; more petals and stamens, for example, makes more perfect.

Whereas a 'tree' can reflect any nested hierarchy, other *naturphilosophische* visualisations we today perceive as more bizarre. They are numerological (based on 2, 3, 4, 5, 6 or 7), assume a centre or platonic idea for each taxon, emphasise degrees of perfection, and often have a spherical or kabbalistic geometry.

The *Systema orbis vegetabilis* by Elias Fries (1825), is a multidimensional sphere with a hierarchy of radially connected subspheres, where all higher taxa include 4 (or 2 + 2) subordinate taxa. He eventually modifies this strict approach (even contemplating the idea that only genera were originally created), but he keeps his vision of Nature as a "harmonious unity, governed by a divine reason" (Eriksson, 1962: 462).

In many of these constructs, analogy[37] (parallel similarities or parallel levels of complexity or perfection in different taxa) is considered a part of Nature's plan as important as affinity (like rows and columns in a table). In Lindley's (1838: 129–130) system for Exogens (dicotyledons) this is particularly evident (Fig. 8). Influenced by *Naturphilosophen* like Fries, he has made a volte-face from his earlier 'species only' stance (1830; see section 1) and is now positive that "Truth is surely to be found". His system has 5 leaves, that can be folded to make a polyhedron. Families within each leaf show "real affinities". "Possibly each group will comprehend within itself a maximum, a medium, and a minimum type of structure, the second being typical of the group, the first an exaggerated form of it, and the last a degraded form." Analogous taxa are shown by lateral proximity (indicated by dotted lines in



ESSAI D'UNE CARTE GRAPHIQUE REPRESENTANT LES AFFINITÉS DES LÉGUMINEUSES
N.B. Les N^os. romains indiquant le nombre des genres, les N^os. arabes celui des especes

Fig. 7. The relationships within the Leguminosae (Candolle, 1825: pl. XXVIII). Surprisingly, his primary division into *Curvembriées* (Papilionaceae + Swartzieae) and *Rectembriées* (Cesalpineae + Mimoseae) is not depicted. The *Curvembriées* is placed closer to the Terebinthaceae, the *Rectembriées* to the Rosaceae, in agreement with the embryo characters of these two families. Some genera are inscribed at the margin of the bubbles, just as in Giseke's "Tabula" (Fig. 5). The enigmatic *Moringa* (now in Moringaceae, Brassicales) is even crossing two bubbles. Roman numerals indicate number of genera, arabic of species; dotted lines show *analogies*.

Fig. 8). A sixth main group, the Apocarposae (Rosaceae, Ranunculaceae, Fabaceae, etc.), is hidden in the "centre". A yet undiscovered taxon ("??") he finds necessary to postulate in order to make the Dicarposae leaf complete.

The last botanical design in this tradition is (to my knowledge) four charts by Fries's student Matts Lindblad (1857), where even different slope gradients convey information (Fig. 9). Lindblad emphasises that every natural taxon has a *centrum*, which is discoverable by its general morphology and by being intermediate between 'the highest' and 'the lowest' in its taxon (intuitively obvious, according to Lindblad).

For more on *Naturphilosophie*, see Rieppel (2016). In taxonomy it was a cul-de-sac, but it enforced the homology concept and inspired other branches of biology.

19. Phylogeny enters – but halts at the doorstep. — The tension between nested hierarchy and continuum has been part of systematic biology throughout its history. This tension is promptly resolved by adding the time dimension. In a phylogenetic context, gaps between taxa are natural outcomes of divergence, and require as such neither extinctions nor leaps. Discontinuity in *now* and continuity in *time* are best friends. Genetic drift and selection are both unavoidable, given

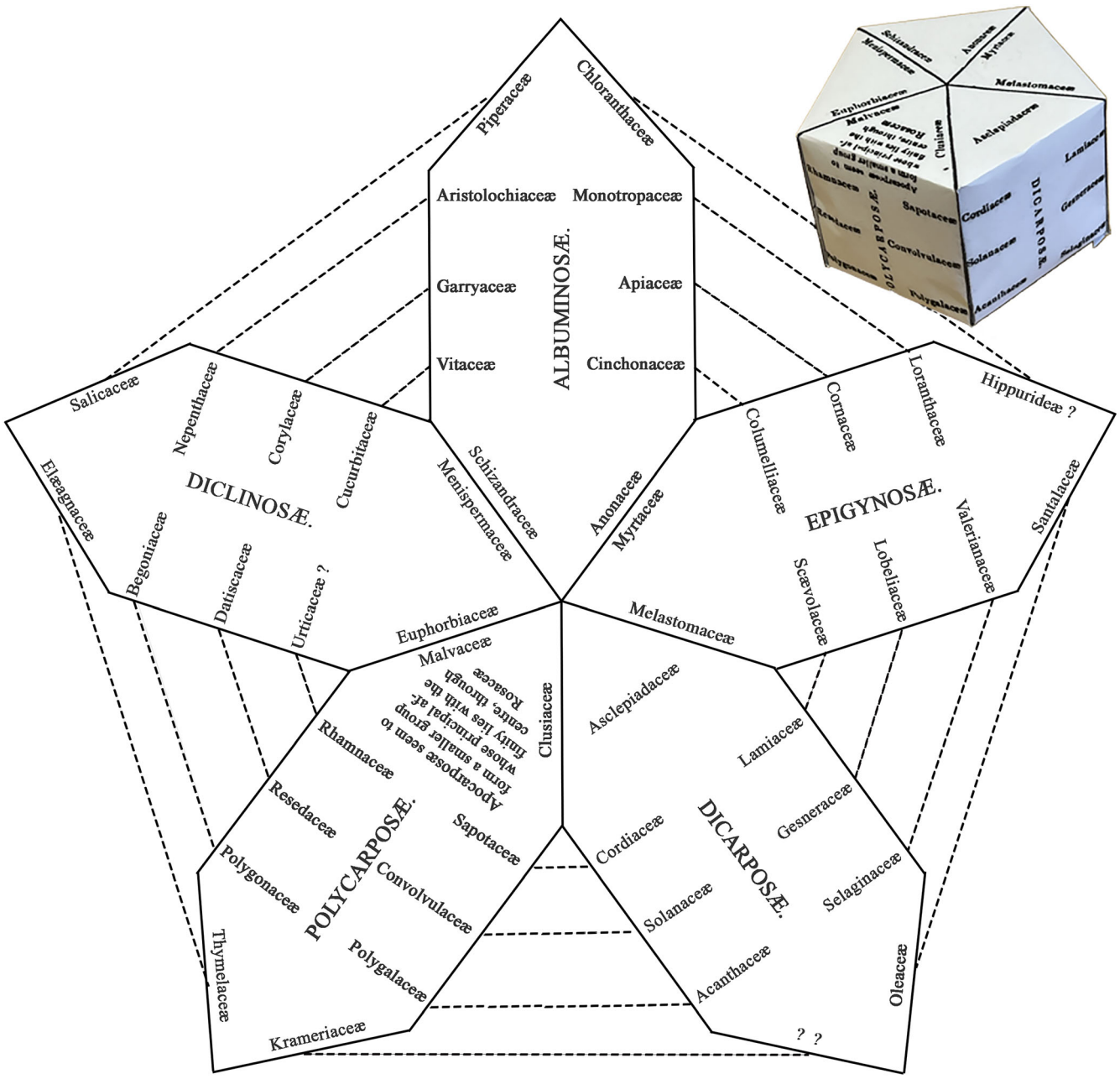


Fig. 8. Lindley's (1838: 130) system for Exogens (dicots), redrawn for clarity. See text (section 18) for details.

necessarily imperfect replication. In other words, evolution is thermodynamically inevitable. These insights, today self-evident, were surprisingly slow in coming.

One would have thought that one correlate to the tree-of-life – that all parts of current biodiversity are equally old – should have spelled the death sentence for the *scala naturae*, but the opposite happened. Even Charles Darwin (1859) refers to organisms as higher or lower on the evolutionary ladder (cf. section 21), and 56 years later, Charles Bessey's (1915) *Phylogenetic taxonomy* (Fig. 10) cannot be told from Lamarck's one hundred years older picture:

> "In both classes we begin with apocarpous plants and proceed toward those that are syncarpous. So the Ranales on the one hand, and the Alismatales on the other, are near the point of beginning. In [Monocots] syncarpy is attained after the passing of a few hundred species (*Alismatales*, 409 species), while in [Dicots] it is not reached until much beyond the limits of the order Ranales […]. All told, fully 10,000 species of this class are passed before complete syncarpy is attained." (Bessey, 1915: 115)

Also later macrosystematic representations of angiosperms (for example Hutchinson, 1959) have similar elements of a *scala naturae*.[38] They describe some extant orders as 'ancestral' to more 'derived' orders, like simply adding a time arrow to Rüling's branched sequence from 1774 (Fig. 4). As late as 1992, when cladograms were commonplace (Fig. 11), Robert Thorne gives the following surreally anachronistic explanation to his sequence of families (Lamarck would have been pleased indeed):

> "As each superorder, order, or suborder terminates, the classification drops back down the evolutionary ladder to the beginning of the next major line of ascent." – and he continues in the same vein – "extinctions have broken up the near phyletic continuum [sic] and made it possible to develop our classification, largely based upon phyletic gaps." (Thorne, 1992: 371 and 373)

However, it was only *after* Willi Hennig's (1950) concrete demonstration (see next section) of how to discover natural groups, that a taxonomic doctrine was contrived – in opposition to Hennig – in order to post-rationalise 'eclectic' classifications like those above. It became known as 'evolutionary systematics' and applies Logical Division (*have* vs *have not*) for defining selected taxa, the same scholastic approach that had been debunked by Linnaeus. This results in 'paraphyly', a term designating arbitrary classes that are defined negatively; by *absences* or by what they are *not* (e.g., 'cryptogams'). Formal recognition of the *not-haves* is defended by the corresponding *haves* being based on *significant* innovations, like the seed. In contrast, the Hennigian method is synthetic (thus more 'Linnaean'), with taxon-recognition positively defended: by *presences* (apomorphies; i.e., 'characters' in a strict sense).

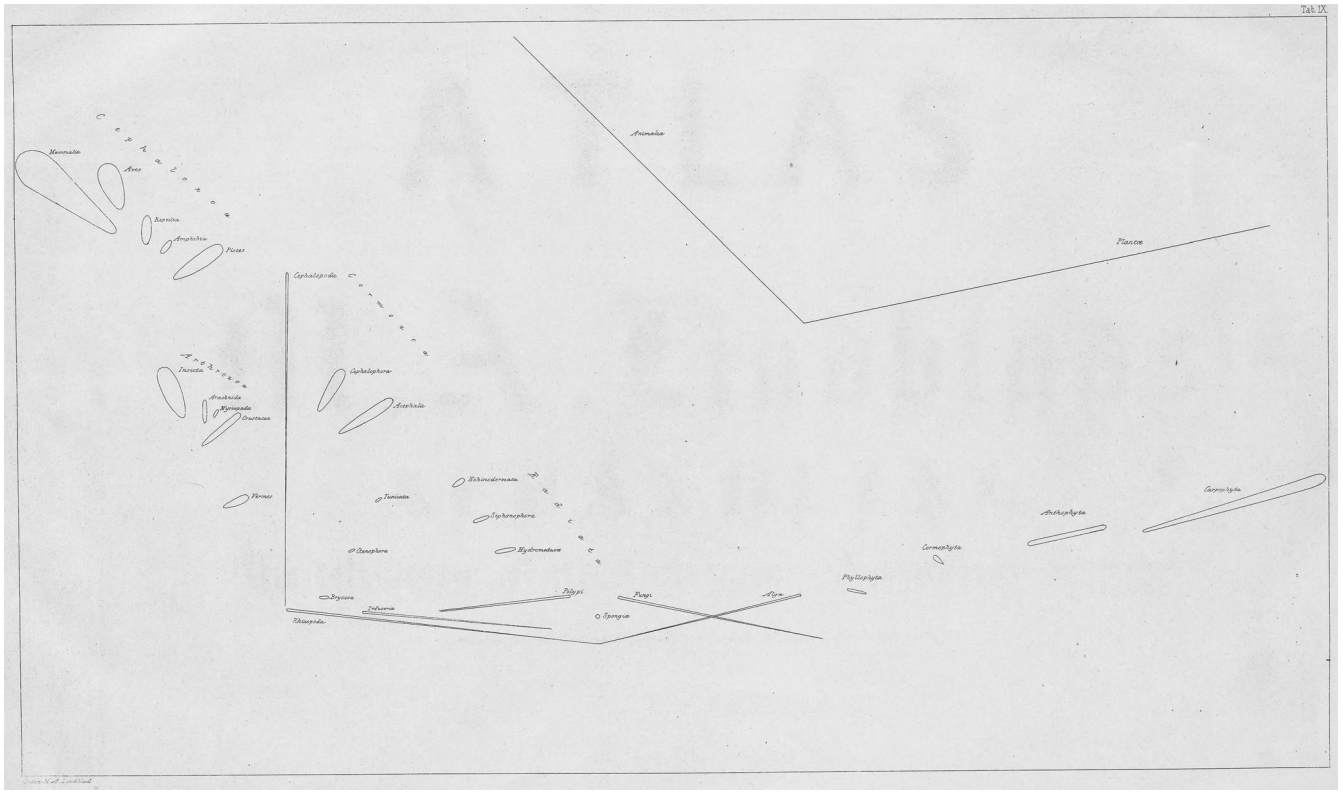


Fig. 9. The pattern of total biodiversity according to Lindblad (1857: t. IX).

20. The Natural System – at last? — The tree-of-life soon became the standard frame – as it straightforwardly explains a perceived nested hierarchy – but it did not affect taxonomic practice. This is not surprising as it was the nested taxonomic hierarchy that inspired the idea of common ancestry in the first place (for Darwin, Linnaeus, even Buffon), and the concepts of affinity, analogy and homology were already established. Taxonomists simply continued taxonomising as they already did, whereas the 'system builders' rather retrogressed conceptually. But – almost a century after *On the origin of species* – a German zoologist is on to something.

Hennig's (1950) insight that only apomorphies can logically indicate relation (affinity; monophyly) was a great leap forward. The idea had been hovering in the background long before Hennig – we have an embryo already in Linnaeus's (1738b) rejection of logical division – but practised piecemeal and intuitively. For example Fritz 'Mimicry' Müller, a correspondent and avid supporter of Darwin, applies the synapomorphy concept as well as outgroup comparison in his study of the crab genus *Melita* (Müller, 1864; see Rieppel, 2016), but Hennig takes this insight to the next level and provides a vocabulary.

Of equal importance has been the implementation of DNA sequence data analysis. Finally we have arrived (at least in theory) at a *probabilistic* approach to phylogenetics, based on assumptions about quantifiable processes. It is a common observation (at least in botany) that last century's numerical cladistic analyses based on morphology gave results inferior to intuitive trees (as later judged by DNA). The blame is on the naïve 'character *state*' concept, coupled to the need to squeeze arbitrary measures into a matrix. We should be happy that we are past that era, which also saw a spurious discourse about alleged differences between 'cladograms', 'trees' and 'scenarios'. In the words of Härlin (1999: 497), "the logical priority of the tree over characters" entails mapping morphological synapomorphies *onto* realistically interpreted phylogenetic hypotheses.

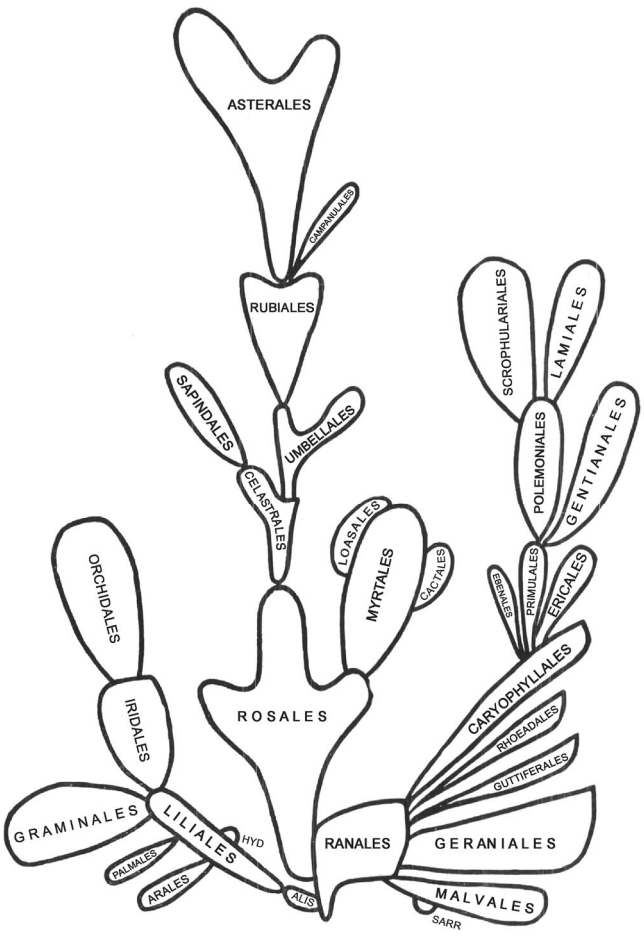


Fig. 10. Bessey's 'cactus' (Bessey, 1915: 118), names rewritten.

Concomitantly, we have cast off the phantom of the idealistic 'species', that had long haunted the conceptualisation of evolutionary trees. In the original Hennigian vocabulary, phylogeny is a succession of ancestral and descendent temporally extended 'biological species'. This view forced Hennig to the strained, yet logically unavoidable, declaration that 'a species' goes extinct when it gives rise to [two] daughter 'species', without anything material going extinct (Bock, 1986). One would have expected that Hennig, master of neologisms (of which most have made it into our terminological toolbox), had devised a non-occupied shorthand for these systems of integrated replicator continua (see section 1) that produce phylogenies. In his absence, I take the liberty to suggest *bion*(*s*).

21. Why linguists were first. — Nested hierarchies can be interchangeably illustrated by tables, Euler diagrams, branch diagrams (trees), or with nested brackets. For the more inclusive levels, the influence of the *scala naturae* tended to obstruct a translation of such hierarchies into hypotheses of nested genealogies. In Lamarck's time there was even a negative correlation between transmutation ideas and use of the tree metaphor (Hellström, 2019).

Scala-free nested genealogies were therefore first imagined for more restricted groups, like angiosperms, Galapagos finches or languages. That, for example, Latin had given rise to a number of descendants was early recognised, and the more inclusive Indo-European language family was hypothesised in the mid 18th century. In 1764, Linnaeus presented his hybrid-cycle explanation for the nested hierarchy of angiosperms, and both he and Buffon early recognised microscale phylogenies of sister species, but it took until 1837, when Darwin drew his famous "I think" tree (Fig. 12), for biology to catch up with linguistics and the picture of divergent gradual evolution from a common origin.

But the *scala* continued to haunt biology for quite some time. When Darwin (1859), zooms out from the species/genus level to the bigger picture, even he backslides into the *scala naturae* trap (see section 19).

22. Remarks on types and 'types'. — The *nomenclatural type* – our tool to rid taxonomy of typology by a strict separation of science and nomenclature – is a recurring source of misunderstanding among non-taxonomists, who all too often believe that *species* have types and that types are *typical* of, or even *define*, taxa. In a recent popular book, the absurd idea

is put forward that Linnaeus used to designate 'types' to define taxa, and that this is still the approach of taxonomists. Such thinking was as alien to Linnaeus as it is to us today. Taxa do not have types; *names* of taxa do. A nomenclatural type in the sense of the *Code* (Turland & al., 2018) fixes the reference of a name. It is decoupled from all taxonomic considerations, and has nothing whatsoever to do with being typical.

That the term 'type' is confusing is understandable. Its current use in biology is of fairly recent date; during the 19th century it was used in a sense antithetical to that of today's nomenclatural codes. This is best understood with a quote from Whewell (1840: 476–477), for whom a genus is

> "steadily fixed […] though not circumscribed; it is determined, not by a boundary line without, but by a central point within […] by an example, not by precept; in short, instead of a Definition, we have a Type for our director […] which possesses all the characters and properties of the genus in a marked and prominent manner […] near the centre of the crowd, and not one of the stragglers."

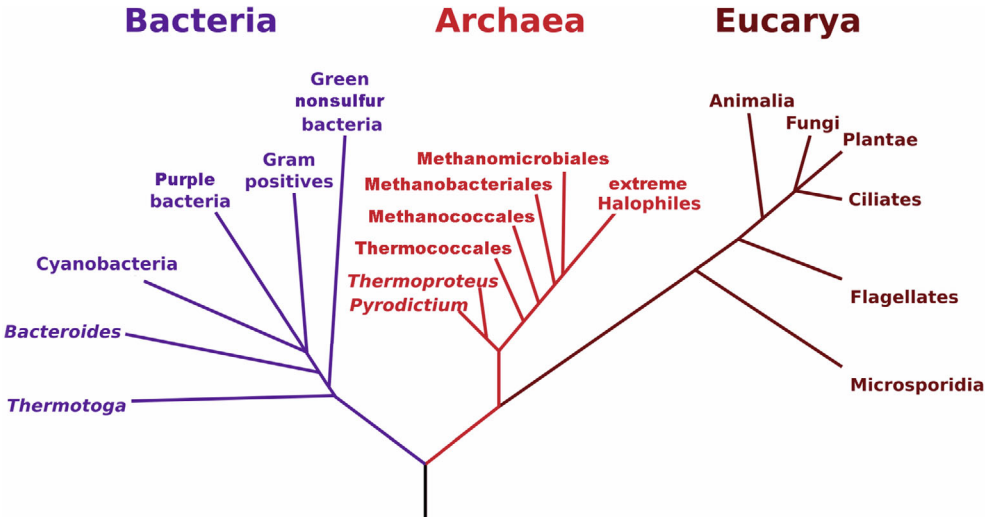


Fig. 11. The Tree of Life (Woese & al., 1990: 4578, curated by Boundless under CC BY-SA 4.0 license, from https://bio.libretexts.org). An example of a classic cladistic hypothesis – no taxon is 'ancestral'.

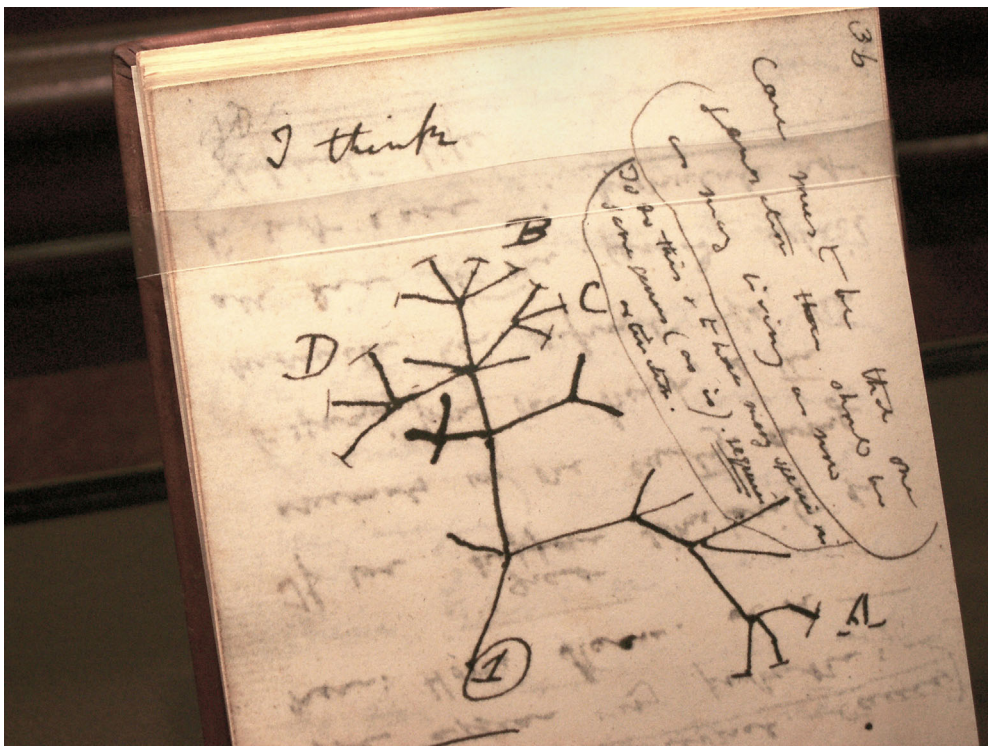


Fig. 12. The groundbreaking phylogeny sketch from Darwins notebook B (Darwin, 1837).

Whewell's typological approach aims to avoid 'essentialism' in the down-to-earth sense of necessary characters. Fortunately for us, the 'individuality thesis' voids all quests for *quidditas* (whatness) or essence of individual taxa.

To Linnaeus a genus is an individual (see further below, section 23 on Mayr). To say that a part of a genus (for a example a certain species) is more typical of that genus than any other part is like saying that the chimney is the most typical part of that house over there, that a certain brick in a wall is more wally than the others, or that Whewell's left foot is near the centre of the crowd that makes up Whewell.

■ LINNAEUS REVISITED

Linnaeus's taxonomic philosophy is sometimes grossly misconstrued, both today and by early 'Linnéans' who had ‹misunderstood this great master, and attributed to him opinions contrary to those he held. It is remarkable, that those who today call themselves Linnéans, are in direct opposition to all that Linné stood for›[39] (Candolle, 1819: 52–53).

Linnaeus regarded his SS, from its inception, as a *key*, or as a *methodus artificialis* (Kohl, 1732). In *Systema naturae* (1735a), *Linum* 'keys out' both in Pentandria and Tetrandria, and there are in total 27 such double entries with cross-references (in the 1748 edition they count in the hundreds). It is a mystery why Stearn (1971: 244), who otherwise reveals detailed knowledge of Linnaeus's works, claims that Linnaeus never thought of providing double entries and cross-references. In *Genera plantarum*, where there is no feasible mechanism for double entries, infrageneric variations that do not fit the class to which a genus is assigned (more or less by majority rule), like deviating stamen number or reproductive system, are added in a note under the individual genus (in early editions in general terms; in later editions deviating species are sometimes mentioned).

Linnaeus's botanical encyclopedias thus constitute one integrated whole. There is no redundancy. You need them all three together, and sometimes additional sources. There is not a single species mentioned in *Genera plantarum*. In *Species plantarum*, if there is a satisfactory description of a species in an earlier publication (like his *Hortus Cliffortianus* or *Flora Svecica*), he only gives the diagnosis and a list of 'synonyms', where an asterisk indicates a reference with a particularly good description.

23. Common misconceptions. — There are lacunae and errors in Linnaeus's voluminous production. Though he breaks with old dogma in systematics, in some other branches of biology he is less up to date and/or freely speculating (but so is, e.g., Buffon). His limited command of modern languages may have been a barrier to part of the non-taxonomic literature.

However, theoretical critique levelled at his approach to *taxonomy* is often based on ignorance or parroting other scholars, in particular the early Cain (1958). Here belong accusations against Linnaeus of dogmatism, essentialism, scholasticism, or typology (Jonsell, 1978; Mayr, 1982; Isely, 1994; Ereschefsky, 2001; Witteveen, 2016), which have all been shown to be false (Skvortsov, 2007 [2002]; Winsor, 2006; Lidén & Kårehed, 2018; Lidén, 2020; this paper).

I give below a couple of examples of authors casting their arguments to fit their prejudices. But first four pronouncements by Linnaeus that are central to my rebuttals:

A. ‹A teacher takes you from the whole to the parts, for pedagogical reasons. To *discover*, on the other hand, we must start with the particulars and proceed to the whole›[40] (1737a: Ratio Operis [p. 2] no 8, referencing Boerhaave, 1720: 4).

B. ‹Using Logical Division, with hypothetical and arbitrary key-characters, they [unnamed systematists] divided [the plant kingdom] into classes and orders all the way down to species, thereby splitting natural genera›[41] (1737a: Ratio Operis [p 2] no. 8).

C. ‹Genera are not defined by characters› (1751: §169; see endnote 3).

D. ‹Scientific theories must be confirmed by observations›[42] (the finale of *Philosophia botanica*, 1751: 287).

Jonsell (1978: 524). – Uncritically accepting Cain's (1958: 162) pronouncement – "the method [Linnaeus] adopted was to classify by the rules of Logical Division, which involve the determination of the essence of each entity" – as verity, Jonsell feels obliged to squeeze Linnaeus's taxonomic ideas into a "dogmatic" and "scholastic" model: "In the spirit of Aristotelian[43] Logic the essence of the plant is to be revealed."

"That the Linnaean Genera, in spite of the dogmatic way in which they were defined, have so well stood the test of time [is because] his intuition […] superseded the dogmatic logic." – However, for Linnaeus, genera are not "defined", neither by "logic" nor otherwise (see A–C above).

"The number of categories [ranks] is dogmatically set as five." – In *Philosophia* (1751: §155) Linnaeus (referencing Tournefort) says that it is ‹appropriate/suitable to have five ranks in a classification›,[44] and he also provides an argument from information science for the introduction of a level between genus and class (§161): ‹it is easier to distinguish between 10 genera than 100›.[45] Further, he is no stranger to intercalated ranks.

Mayr (1982). – "The first author who had the intellectual courage to question openly the validity of the method of logical division was Michel Adanson" (p. 194). – Not true; Linnaeus explicitly rejects logical division already in *Genera plantarum* (1737a; see section 8).

"The terms used by Linnaeus, like 'genus', 'species', 'name', 'to know', and 'natural system', have the very special meanings which these terms have in the system of scholastic logic" (p. 173). – In scholastic logic, however, 'genus' and 'species' are relative terms. Their current biological meanings were established already in the 17th century – which Mayr is well aware of – and further cemented by Linnaeus and his contemporaries. Regarding 'name', see section 14; for 'to know',

I have not been able to figure out what Mayr refers to; for 'natural system', see this paper.

Mayr correctly describes Linnaeus's view on genera as "monolithic", and concludes that this is "a backward step from the genus of Tournefort, which was an aggregate of species, hence a collective category […]. The modern genus concept thus traces back to Tournefort rather than to Linnaeus" (p. 177). – As is obvious from section 1 of this paper, I would switch his labels "backward" and "modern" (or avoid them – they easily backfire).

24. Religion. — Linnaeus keeps science and religion separate (Takman, 1957; Frängsmyr, 1969). He explains Eden's snake and forbidden fruit allegorically, and came to regard the Bible's young earth and Flood as fairy tales. He argued for large cuts in religious teaching, in favour of more economic subjects. No wonder he had a difficult relation with parts of the clergy. Linnaeus wittily observes that ‹the stupider the priest, the more heretics he will recognise›[46] (1750: 40).

The theologicians wielded a lot of power at Uppsala university, however. Linnaeus survived accusations of pantheism and worse, because of his international fame and good contacts with royalty and nobility, but he still had to tread carefully. Had he put the following passage in print, his career might have suffered: ‹Where you are allowed to think and write what you like, science prospers. Where religion is free, the country prospers. Where theology rules nothing prospers, there lousy›[47] (1733[–1742]: 199).

His disdain for dogma and censorship, as well as for beliefs in gnomes and miracles, was passed on to his students; some of his 'apostles' were outspoken freethinkers.

Stearn (1971) argues that Linnaeus's realistic interpretation of the natural hierarchy (that higher taxa exist independently of a sentient observer) has a creationist underpinning. However, in 1764, Linnaeus explains families and genera of angiosperms by common ancestry, precisely because separate creation does *not* explain a nested hierarchy.

Still Linnaeus was deeply religious. Teleology was not really fashionable in other sciences during the enlightenment, but biologists found it hard to dispense with until Darwin rendered it obsolete. Linnaeus's religious world view is thus most clearly manifested in his belief in a purpose with all God's creatures. Man is a species of ape, yes, but we alone have a mind that can understand and describe the magic of creation; indeed, that is our duty.

■ EPILOGUE

According to Julius von Sachs (1875), Linnaeus did not make a single scientific discovery, but his legacy in taxonomy is nevertheless outstanding:

• His dismissal of Logical Division, providing a fresh comprehension of the NS that matured via Candolle, Darwin and Hennig into today's cladistic paradigm.

• Binomial species names, critical for the advancement of biology. Occasional species binomials that can be regarded as 'proper names' occur in the 16th century (Cordus, 1561, cf. Greene, 1909: 270–314) or possibly earlier. Caspar Bauhin (1623) is often credited as the inventor of binomials. Those of his names that consist of two words can, however, mostly be interpreted as short diagnoses or keys, and they often have a vague correlation to rank.

• His global inventories of vascular plants and many animal groups, from which our nomenclatural priorities count.

• A much upgraded descriptive method and vocabulary. Rousseau (1802: xvii) notes that ‹it has been complained that [Linnaeus's terms] are not all in Cicero. This complaint would have made some sense if Cicero had written a complete botanical treatise›.[48]

Linnaeus is also the first (?) biologist to explain a nested hierarchy by shared ancestry. The speculative theory he propounded for the plant kingdom – hybridisation cycles with female bias; a kind of phylogeny without anagenesis – was not taken seriously by his peers and fell dead on arrival. However, he (and Buffon) also suggests that descent with modification can explain sister-species; he thus comes closer than Lamarck to being a "true evolutionist" in the sense of Ghiselin (1997), albeit at a micro-scale.

Anything more? It is frequently claimed that the SS revolutionised botany and/or made it more accessible and/or made possible the classification and naming of the myriad of plants brought to Europe by explorers and colonialists. A problem with these pronouncements is that we cannot replicate history. The SS is neither as straightforward nor as undemanding as is often claimed. The grass family, that immediately fathomable taxon, is split among several classes by obscure characters. One-fourth of the genera of the British flora include species disagreeing – in stamen number or reproductive system – with their SS-position (Lindley, 1830). Regardless of cross-references, such facts severely compromise its utility as a key, and being a key is its sole justification according to Linnaeus himself (1764; see endnote 35).

In the critique against the SS, its artificiality and inconsistency are two low-hanging apples (on opposite sides), but Georg Siegesbeck (1737: 49) takes issue with its obscenity: ‹eight, nine, ten, twelve husbands, even twenty and more, in one woman's bed chamber›.[49] Their feud is listed in *Philosophia botanica* §21 as one of three cases of "BELLA SYSTEMATICA" (‹systematic botany wars›), but Linnaeus adds that ‹KINGS' WARS over plants [seven examples follow] were bloodier; fought not with pen, but with cannons and swords›.[50] One could wish with Linnaeus that kings would follow the example of botanists.

Once the train had left the station, Linnaeus found it comfortable to stick to the rail. He persisted with his SS, and not without pride. Candolle (1819) suggests that this stubbornly continued routine delayed scientific progress, but though the SS was widely used it was never a scientific paradigm like the *scala naturae*. The latter has been an obstacle to advancements in taxonomy (as well as other biological fields) well into the 20th century. Its complete absence from the SS is one of the latter's few plusses.

At 30, with youthly arrogance, Linnaeus (1738b: 485) seems fairly optimistic regarding the NS, and writes ‹let me present what I have gathered so far; the one who manages to elucidate what little still remains, will be a great Apollo to all›.[51] Incidentally, the Apollon character who brings a torch and unveils Mother Nature in Vandelaar's fabulous frontispicium to *Hortus Cliffortianus* (1738a) (Fig. 13), is alleged to have the features of Linnaeus.

In 1754 (Ratio Operis p. v; repeated in 1764: vi), however, we are told that ‹it is probably too much to hope for, that our generation, or even that of our great grandchildren, will live to see the Natural System completed›.[52] In one of his 'autobiographies' he remarks that ‹my sketch of a Natural System I here leave out, as few have understood it›[53] (Malmeström & Uggla, 1957: 182).

Linnaeus left his final *Fundamenta*-chapter for posterity to polish. No doubt he would have been very pleased with our recent APG system,[54] and equally pleased that his great great […] grandchildren live to see it.

Fig. 13. Frontispicium to *Hortus Cliffortianus* (Vandelaar in Linnaeus, 1738a).

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1 An information-bearing structure showing sufficient integrity during replication as to be comprehended as a 'selfish gene' in the sense of Dawkins (1976).
2 Ghiselin (1997) makes a very apt distinction between *inclusive* (as in set theory) and *incorporative* hierarchies; the latter designate *historical individuals* with subordinate individuals as *parts*, not members.
3 "*Characterem non constituere genus* […]. *Characterem non esse ut genus fiat, sed ut genus noscatur.*"
4 "*Det är Linnés ovanskliga ära att han klart och bestämdt uttalat de första idéerna om ett naturligt system, dess art och väsen, dess nödvändighet och möjligheterna af dess förverkligande.*"
5 "*Ty när jag först ransakade naturen själf och såg henne sträfwa mot Autorers mening, ty aflade jag alla praejudicier, blev en scepticus och tvivlade om allt, då öpnades först ögonen*" (LM/LP/BOT/3/1/1: image 5, small leaf). This and other manuscripts by Linnaeus's hand, were copied out by Ewald Ährling (1888) during a visit to the Linnean Society in 1881.
6 "*vir ad historiam na[tur]alem maxime inclinatus, cui multa debeo, praeprimis divisionem Artaedianarum*" (LM/LP/BOT/3/1/1: image 9)
7 Nature's lament before Jupiter, here much abridged: ‹Nature: nobody appreciates my precious herbs anymore! Jupiter: do not despair, my daughter; soon scholars will again come to know Flora, first in Greece, and then, after a dark period, your glory will be sung by a second generation of botanic luminaries: Caesalpinus, Rajus, Turnefortius, Rivinus›; for once, I leave out the original; see Ährling (1888: 95–96).
8 "*Der Hr. Linnaeus ist übrigens ein zwar junger, aber sehr geschikter Botanicus in Schweden, welcher mit der Zeit sehr vieles in der Kräuter-Wissenschaft leisten wird* […]."
9 "*Alt detta hade Linnaeus conciperat för sig, inan han var 23 åhr; alt utarbetat utomlands för än han kom hem* […]." (*Vita* II: 42)
10 There is a widespread misconception that "Praeludia sponsaliorum plantarum" – Linnaeus's 1729 new-year gift to professor Celsius – introduces the SS, but "Praeludia" deals only with the sex-life of plants, not with classification. Another misconception is that the SS is based on the sexual system of the plants, but this is true only for class 21, 22 and 23. Class 1 to 20 are defined simply by number and configuration of stamens, and orders within classes usually by number of styles.
11 "*Primum & ultimum in parte Systematica Botanices quaesitum est Methodus Naturalis.*" (1738b: 485)
12 "*Genus omne est naturale, in ipso primordio tale creatum.*"
13 "*Tormentilla solo numero differt a Potentilla, hinc possent ambo genera combinari.*"
14 "*Quaero a te et toto orbe differentiam genericam inter Hominem et Simiam. Ego certissime nullam novi* […]. *Si vocassem hominem simiam vel vice versa omnes in me conjecissem theologos* […]. *Debuissem forte ex lege artis.*"
15 "*Tam multa habet hic cum duobus sequentibus communia, ut verosimile videatur eosdem ex una matre olim ortos.*"
16 "*Habet multa communia cum praecedente, ut forte olim ab eodem ortum sit.*"
17 "*Statura & structura totius hujus plantae cum praecedenti conformis indicat unam ex altera natam, quas itaque distinguere vel combinare mihi perinde erit.*"
18 "*Solida & Cava diversae persistunt in eadem specie plantae, sed quae causa ex una produxit duas distinctas etiamnum latet; dantur enim innumerae varietates quae cultura non reducuntur, sed constantes persistunt.*"
19 "*Methodus naturalis semper debet progredi ab universalibus ad particulariora* […]."
20 "*sed verbis exprimi non potest, ut videre est in familiis agrimonioidearum, pentaphyllearium quas omnis botanicus judicabit esse congeneres*"
21 "*Artificiales classes succedanae sunt naturalium, usque dum omnes naturales sint detectae.*"
22 "*Metamorphosin hujus plantae stupendam descriptam legas in diss. acad. de* Peloria *habita Upsaliae 1744.*"
23 "*Plantae omnes utrinque affinitatem monstrant, uti Territorium in Mappa geographica.*"
24 The term *section* is used by Adanson, following Tournefort (1700), for a rank between family and genus. With Candolle (Lamarck & Candolle, 1805b), it is an infrageneric rank.
25 "*La vraie fisique de Plantes est donc celle qui considère les raports de toutes leurs parties & qualités, sans en excepter une seule; elle réunit toutes les Plantes en Familles naturels & invariables, fondées sur tous les raports possibles* […]. *Telle est l'idée qu'on doit se faire de la Métode naturele; il n'i en a & ne peut i en avoir d'autre* […]."
26 "*Nulla hic valet regula a priori* […] *sed solum simplex symmetria omnium partium* […]." (p. 487)
27 "*som att sätta kläpp i klåckan; härigenom fick botaniquen ett helt nytt och naturligt skick*"
28 "*Mutatio horum, licet in melius, plus nocet quam proderit.*"
29 "*pour ne pas trop changer, & faute de synonymes*"
30 "*Mihi perinde erit quo nomine utamur*" ‹it is all the same to me what names are used› (1747).
31 "*Nosce te ipsum*" from the inscription γνῶθι σεαυτόν on Apollon's temple in Delphi.

32 Buffon is not comfortable with fixed ranks, which is confusingly commendable.
33 "*nous n'avons dans tous les animaux terrestres que quelques espèces isolées, qui, comme celle de l'homme, fassent en même temps espèce & genre; l'éléphant, le rhinocéros, l'hippopotame, la giraffe forment des genres ou des espèces simples qui ne se propagent qu'en ligne directe & n'ont aucunes branches collatérales*" (Buffon, 1766: 335)
34 "*la Nature* […] *rejette les classes et les familles* […] *à mesure que l'on examine plus attentivement, on est forcé de former de nouveaux genres aux dépens de ceux que l'on avoit formés d'abord; réduction qui deviendra de jour en jour plus nécessaire, à mesure que les observations se multiplieront, ou que nous découvrirons de nouvelles plantes dont les caractères mi-partis mettront des entraves à toutes nos règles; et nous finirons sans doute par n'avoir dans chaque genre qu'une seule espèce, multipliée souvent en autant de variétés que d'individus (2).*"
35 "*réunît l'avantage des systêmes artificiels & des méthodes naturelles*, *c'est-à-dire qui conduisît en même temps à la connoissance des plantes & des familles naturelles*" – The last sentence alludes to Linnaeus's distinction "*Ordines naturales valent de natura plantarum. Artificiales in diagnosi plantarum*" (1764: unpaginated appendix [ca p. 648]; ‹The NS reflects nature; artificial systems are for determination›), but evidently Augier failed to grasp its meaning, and his contemporaries were not impressed (Hellström, 2019).
36 "*la Nature* […] *passe d'un être à l'autre par des nuances insensibles*" (p. iii)
37 In the 19th century, 'analogous' was used in biology (at times ambiguously) for both characters and taxa.
38 The *scala* (in a broad sense) is still common on popular web pages and in undergraduate textbooks, and has far from been eradicated from science (Omland & al., 2008; Rigato & Minelli, 2013). Even interpretations of cladograms suffer from the malady, like the still occurring practice to regard a seemingly small branch 'primitive', 'ancestral' or 'basal', relative to a seemingly larger sistergroup.
39 "*mal entendu ce grand maître, et lui a attribué des opinions contraires aux siennes. Il est, en effet, très-remarquable que ceux qui se disent aujourdhui Linnéens, soient en opposition directe avec toutes les pages de Linné.*"
40 "*Docenti autem procedendum a generalibus ad singularia quaeque, dum inventa explicat; ut Inventori, contrâ, à singularibus ad generalia eundum fuit.*"
41 "*Assumserunt enim Varii diversas partes fructificationis pro principio Systematico, & cum eo secundum divisionis leges a Classibus per Ordines descenderunt ad Species usque, & hypotheticis ac arbitrariis his principiis fregerunt & dilacerarunt naturalia, nec arbitraria genera* […]."
42 "*In scientia Naturali, Principia veritatis Observationibus confirmari debent.*"
43 Aristoteles actually *rejected* logical division as a way to arrive at the essence of living things (Sloan, 1972).
44 "*Systema Classes per 5 appropriata membra resolvit.*"
45 "*facilius enim distinguuntur genera 10, quam 100.*"
46 "*Ju domare Präst, ju flere kiättare utropar han.*"
47 *"Allestädes hwar man får tänka och skrifwa hwad man will, där florera studier. Hwar frij religion, florerar landet. Hwar theologi regerar, där intet thera, där uselt."*
48 "*On s'est plaint que les mots de cette langue n'étaient pas tous dans Cicéron. Cette plainte aurait un sens raisonnable, si Cicéron eût fait un traité complet de botanique.*"
49 "*Mariti octo, nouem, decem, duodecem, immo viginti et plures in eodem cum una foemina thalamo hic deprehendantur.*"
50 "*BELLA REGUM de Plantis magis cruenta suere, nec Calamo sed Bombard:s & Gladiis scripta.*"
51 "*interim quae novi proponam: qui paucas* [!], *quae restant, bene absolvit plantas, omnibus magnus erit Apollo*"
52 "*Nec sperare fas est, quod nostra aetas Systema quoddam Naturale videre queat & vix seri Nepotes.*"
53 "*Fragmenta methodi naturalis non loquar quia paucis intellecta.*" (Vita V)
54 APG [X] stands for Angiosperm Phylogeny Group [version], an intermittently updated widely accepted classification, admittedly with low information efficiency in one or two places, due to suboptimal choice of ranks, but generally a commendable product of large-scale collaboration.