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HIERARCHICAL ROOTS AND SHOOTS OR *OPERA JEHOVAE MAGNA!* (PSALMS 111:2)

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ABSTRACT

The philosophy of Linnaeus's classification, *Systema Naturae*, is briefly reviewed, as well as those of post-Linnaean systems of plant classification. Texts of current codes of nomenclature pertaining to hierarchy, including associated rank terminations, are compared.

Key words: biological classification, classification, hierarchy, Linnaeus, nomenclature.

INTRODUCTION

The Symposium title speaks of the hierarchy of Linnaeus, especially misnamed for plants since Linnaeus's (1759) artificial system of 24 sexual classes was replaced by Jussieu's (1789) natural families. The Natural System has survived, although its underlying assumptions have drifted. Jussieu's (1789) and Cuvier's (1798) assumption was that God's Creation is continuous (a solid map with artificial lines drawn on it). Later pre-Darwinian thought was discontinuity, islands and archipelagos with peninsulas indicating affinities. Taxa can be located on the map by definitions functioning as coordinates. Current thought is three-dimensional, time, i.e., evolution, being the 3rd dimension.

For me, reality lies in the specimens. What we say about the specimens are hypotheses, i.e., the taxa that we construct, the hierarchies that we design, the systematics that we debate, and the evolutionary steps that we wring from our data. The problem is that we don't like ambiguity and have accorded some value to particular hypotheses for practical purposes, such as identification of unknowns. It is fascinating to see proposals aiming to create hierarchies with same names at different ranks.

What do our Codes, including the Draft Biological Code (Greuter et al. 1996), say about hierarchy (see Appendices)?

LINNAEAN PLANT HIERARCHY

My title expresses two things: The first part came when I agreed to say something about the past. At the time I had no idea what a difficult subject hierarchies would be. The second part is generally translated as "How great are the works of the Lord." It appears opposite the title page of at least two editions of Linnaeus' *Systema Vegetabilium* (10th ed. of 1759 and Murray's 14th ed. of 1784). It expresses a philosophical rooting of early workers who not only knew their

Bible, but knew it in Latin. They were exposing the richness that God created, perhaps in six days before he rested on the seventh.

As outlined by Stearn (1957: 26–34), the Linnaean hierarchy involved 24 named classes based on sexual characters termed by Siegesbeck (1737) as "loathsome harlotry" (scortationes quasi destestabiles) Linnaeus named *Sigesbeckia* for him, an unpleasant, small-flowered weed. Croizat (1945: 55) commented that Linnaeus, "By a bold stroke of the pen the nebulous world of plants was made to act like husbands and wives in unconcerned freedom, and everybody prepared to grasp the meaning of *Monoecia* [husbands and wives live in the same house but have different beds], *Dioecia* [husbands and wives live in different houses], *Syngenesia* [husbands joined together at the top] and *Polygamia* [Husbands live with wives and concubines in the same house] without effort."

These classes were fundamentally based on study of the stamens (husbands) which could be unrelated to each other, i.e., free, as in *Monandria*, *Diandria* [two husbands in the same marriage], etc., or related to each other, i.e., united, as in *Monadelpchia* [husbands arise from one base, like brothers], *Diadelphchia* [husbands arise from two bases, as if from two mothers], etc. Each class could be broken into orders based on the wives, *Monogynia*, *Digynia*, calculated by counting the number of styles or stigmas. The orders [i.e., wives] of *Polygamia* are especially lascivious.

The point is that the Linnaean hierarchy was absolutely artificial and that's why we botanists are a little surprised to have the Linnaean hierarchy taken so seriously. Linnaeus (1753) gave plants the binomial naming system, i.e., the foundations of the generic and species names that we use today in biology. But is this the part of the hierarchy that we are discussing today? I think not.

EARLY POST-LINNAEAN (NATURAL) HIERARCHIES

On the other hand, Linnaeus and the Linnaeans were the last to comprehend the Natural World with works like *Systema Naturae* (A System of Nature) with the vision of Kingdoms (*Regnum*) of Animals (*Animalium*) and Vegetables (*Vegetabilium*). It was really the Post-Linnaeans, Jussieu (1789), for plants, and Cuvier (1798), for animals, who laid the cornerstones of higher ranked taxa, especially families (then called orders). Peter Stevens's (1994) book on Antoine-Laurent de Jussieu discussed what was known as the Natural Method (as opposed to Linnaeus' Artificial Method). I have relied on his work and apologize for any misunderstandings.

The philosophical underpinnings of the hierarchies are important but were rarely commented upon by the workers themselves. In essence these early post-Linnaeans saw nature as a map of a single land-mass, on which they were drawing lines to separate taxa. One could, by giving latitude and longitude, locate taxa on the map. Perceived gaps between taxa were thought to be an artifact of incomplete knowledge. Thus, Cuvier could be quoted as saying "classes, orders and genera are abstractions by man and do not exist in nature."

Corollaries to this perception of nature as continuous meant that criteria for drawing lines could include considerations such as (1) taxa should not be too big, i.e., genera should not have more than 100 species, or families more than 100 genera, (2) taxa should not be too small, i.e., genera should not comprise only a single species and no unigeneric families. Indeed, Jussieu (1789) only recognized 100 families, leaving a pile of miscellaneous genera (l.c. 416-446) at the end that he would not place.

The taxa created within this philosophy of continuous variation, meant that the centers of taxa were quite different from the centers of other taxa but taxa adjoining the centers would grade toward other centers. This philosophy of the continuous chains of nature (*scalae naturae*) had a corollary that any perceived gaps between taxa represented lack of knowledge—another expedition would return with previously unknown material that would neatly fill in the gaps.

LATE POST-LINNAEAN OR PRE-DARWINIAN HIERARCHIES

The new materials from the great expeditions were being worked up and work on the great British colonial floras was initiated, a veritable taxonomic flood. It was becoming increasingly evident that nature wasn't woven of continuous chains—there really are gaps between taxa. The view was changing from a map of a continuous land-mass with arbitrary lines on it (like a map of the U.S.A. with states, counties, etc.) to a map covered by continents/islands of various sizes sometimes with peninsulas and archipelagos suggest-

ing closer relationships between some areas than with others.

Although the underlying philosophy was changing, it did not result in much change, differences between classifications of De Candolle (1813), Bentham and Hooker (1862-1883), etc., are clearly rooted in those of Jussieu. In the 20-year period from 1825 to 1845, 24 systems of plant classifications were proposed, characterized by Lawrence (1951: 31) as "only minor improvements or elaborations of the system of de Jussieu and, aside from the major contributions of de Candolle and of [Robert] Brown, gave little indication of deep analysis of basic considerations."

If this period is said to have ended with Darwin (1859), its last flowering was the system laid out in Bentham and Hooker's *Genera Plantarum* (1862-1883) in three massive volumes. The publication of Darwin's theories of evolution and the origin of species, coincided with the preparation of the first volume and Hooker wanted to start all over, completely reorganizing. Bentham opposed this, since he didn't accept the essentials, although he did a decade later. One of the great strengths of this work is that its descriptions were based on actual study of specimens in the Kew Herbarium, which was and is phenomenally rich, not on the descriptions compiled from literature.

POST-DARWINIAN HIERARCHIES

Eichler (1875-1878), who did accept evolution, proposed a system that involved rudiments of genetic relationships. It was important because he elaborated it into a unified system accounting for all major groups of the plant kingdom. Engler (1886) introduced modifications in detail and nomenclature and his system was applied to all plants of the world in a 20-volume work with Prantl, *Die natürlichen Pflanzenfamilien* (1897-1915).

One could go on with the various systems of Hallier (1905), Bessey (1915), Hutchinson (1926-1934), Cronquist (1968, 1988), Takhtajan (1980), Dahlgren (1989), Thorne (1976, 1983, 1992) and the latest contributors. By and large, especially when viewed from a distance, most of these do not appear radically different from the pre-Darwinian systems. There are reasons for this, perhaps more of a practical nature than theoretical. In essence, most of these workers had/have a lot of experience with the study of specimens. This results in a practical focus by workers who are thinking, how can I organize all this knowledge so that others can more quickly identify unknowns? Can I fit my thoughts within the framework of my predecessors?

These practical, as opposed to theoretical, concerns are very much in the minds of all of us, especially when we are rooted in the realization that the speci-

mens are the facts—the things we make of the specimens, including hierarchies for organizing them, are our hypotheses.

Wallace Ernst's (1972) posthumous work on *Lamourouxia* showed that the genus almost certainly had evolved long tubular flowers (pollinated by hummingbirds) twice, presumably from shorter, more open (bee-pollinated) flowers. It was clear that the relationships of some bird-pollinated species were with bee-pollinated species, not with other bird-pollinated species, although they, superficially, looked rather similar.

At a dinner meeting in Washington in 1965, another colleague, Phil Humphries, said something that stuck with me. Another worker, who was into programming on the latest computer 30 years ago, begged him for data to crunch. He gave it to him and it came back in the form of a mobile with the comment that all his data could be expressed in this form. Phil hung the mobile over his desk and began contemplating the relationships as the various parts rotated. Suddenly he realized that now he was studying relationships two steps removed from reality, his data were one step removed and the mobile was a second step removed.

My final image of the evolutionary system is no longer a two-dimensional map but a transparent globe with a single point at the center from which everything evolved through the third dimension, time, to the surface which is covered with the living species more or less arranged by their genealogies. I think Kevin de Queiroz' (Queiroz and Gauthier 1994) idea is that we need to abandon the current taxonomic and nomenclatural system of the surface and replace it with a system based on the branches reaching from the core.

Perhaps Alphonse de Candolle (1867) expected something like this when he said in his introduction to his *Lois*: "There will come a time when all the plant forms will have been described; when herbaria will contain indubitable material of them; when botanists will have made, unmade, often remade, raised or lowered, and above all modified several hundred thousand taxa ranging from classes to simple varieties, and when synonyms will have become much more numerous than accepted taxa. Then science will have need of some great renovation of its formulae. This nomenclature which we now strive to improve will then appear like an old scaffolding, laboriously patched together and surrounded and encumbered by the debris of rejected parts. The edifice of science will have been built, but the rubbish incident to its construction not cleared away. Then perhaps there will arise something wholly different from Linnaean nomenclature, something so designed as to give certain and definite names to certain and definite taxa."

This is my first visit (outside of an airport) to California since my two years at Stanford ended in 1957. Even then, I was aware of a problem with the red-

woods: does the giant redwood, the Big Tree, belong to the same genus as the coast redwood (*Sequoia*)? In other words, is there one genus with two species or two genera with one species each? This problem was known to me when I first visited the Big Trees in the Sierra foothills and met the General Sherman Tree. This is one BIG tree. The first branch was 100 ft. up and was 6 ft in diameter, the size of the mighty elms arching over our streets back at home in Iowa. That's just the first branch! It is difficult to express how insignificant I felt looking at such a giant that had been standing there for about 2000 years. I felt like a flea contemplating an elephant. Then came a moment of truth—that tree really didn't care what I, or anyone else, called it.

How great are the works of the Lord! (*Opera Jehovahae magna!*).

EPILOGUE

After listening to the other speakers and the discussions I now believe that my image of that globe is not too bad. The surface of this globe is the currently living biological world which is hierarchically subdivided geographically by the so-called Linnaean hierarchy—continents, such as the Animal Kingdom is here and the Plant Kingdom is over there. This image lends itself to the idea that we can more or less agree over how many geographic ranks to recognize—regions (phyla), countries (subphyla), states (classes), counties (orders), townships (families), etc. Such a system has value and I, for one, am not ready to say that it must be abandoned.

But the relationships of this biological world are not the product of what is on the surface and what seems sufficient for organizing the taxa on this "surface" may be insufficient for organizing by the roots. The relationships are, ultimately genealogical and to be revealed by their roots through time. I would be dumbfounded if I were told that I must fit my wife's known genealogy into a fixed number of generations with only a certain number of relationships allowed. If you have parents, you may have other relationships, siblings. If you have grandparents you have more relationships, first cousins, nephews, nieces, maybe a first cousin, once removed. Then there are the second marriages and their products.

I don't want to go into the practice and theory of human genealogy. However, one has two choices in looking at genealogy. A descent chart rotates the data so that you see only the direct descendants of a given person—the relationships to those marrying descendants are rotated away. An ancestor chart rotates the data so that you see only the direct ancestors of a given person—all sibling relationships are rotated away. Nei-

ther two-dimensional chart can give a picture of all relationships.

My point is that there is a problem in applying the two-dimensional Linnaean hierarchy to a three-(or more) dimensional system that is far more complex. Alternatively, there is a problem in applying a three-dimensional hierarchy to a two-dimensional system. Maybe we can devise parallel systems.

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Table 1. Hierarchy and rank endings cited in current Codes.

Domain	Kingdom	Subkingdom	Phylum/Division	Subphylum	Class	Sub class	Order	Sub order	Super family	Family	Sub family	Tribe	Sub tribe
Botany			- <i>phyta</i>	- <i>phytina</i>	- <i>opsida</i>	- <i>idae</i>	- <i>ales</i>	- <i>ineae</i>		- <i>aceae</i>	- <i>oideae</i>	- <i>eae</i>	- <i>inae</i>
Fungi			- <i>mycota</i>	- <i>mycotina</i>	- <i>mycetes</i>	- <i>mycetidae</i>							
Algae					- <i>phyceae</i>	- <i>phycidae</i>							
Zoology									- <i>oidae</i>	- <i>idae</i>	- <i>inae</i>	- <i>ini</i>	- <i>ina</i>

Notes:

1. Existing conflicts:

1a. Zoological families and botanical subclasses currently have the same ending: *-idae*.1b. Zoological subfamilies and botanical subtribes currently have the same ending: *-inae*.

2. Potential conflicts:

2a. To avoid conflict with upcoming Virological Code, no other names above family should end with *-virinae*, *-virales* or *-viridae*.2b. To avoid conflict with mycological usage (Fungi), no other names above family should end with *-mycota*, *-mycotina*, *-mycetes* or *-mycetidae*.2c. To avoid conflict with phycological usage (Algae), no other names above family should end with *-phyceae* or *-phycidae*.3. Some earlier botanical classifications treated "Phylum" as a subdivision of "Division" but the 1994 *Tokyo Code* made it an alternative to "Division".

APPENDIX 1. Botanical Code (Greuter et al. 1994) on Hierarchy

Art. 2.1. Every individual plant is treated as belonging to an indefinite number of taxa of consecutively subordinate rank, among which the rank of species (*species*) is basic.

Art. 3.1. The principal ranks of taxa in descending sequence are: kingdom (*regnum*), division or phylum (*divisio*, *phylum*), class (*classis*), order (*ordo*), family (*familia*), genus (*genus*), and species (*species*). Thus, except for some fossil plants (see Art. 3.3), each species is assignable to a genus, each genus to a family, etc.

Art. 4.1. The secondary ranks of taxa in descending sequence are tribe (*tribes*) between family and genus, section (*sectio*) and series (*series*) between genus and species, and variety (*varietas*) and form (*forma*) below species.

Art. 4.2. If a greater number of ranks of taxa is desired, the terms for these are made by adding the prefix *sub-* to the terms denoting the principal or secondary ranks. A plant may thus be assigned to taxa of the following ranks (in descending sequence): *regnum*, *subregnum*, *divisio* or *phylum*, *subdivisio* or *subphylum*, *classis*, *subclassis*, *ordo*, *subordo*, *familia*, *subfamilia*, *tribus*, *subtribus*, *genus*, *subgenus*, *sectio*, *subsectio*, *series*, *subseries*, *species*, *subspecies*, *varietas*, *subvarietas*, *forma*, *subforma*.

Art. 4.3. Further ranks may also be intercalated or added, provided that confusion or error is not thereby introduced.

Art. 5.1. The relative order of the ranks specified in Art. 3 and 4 must not be altered (see Art. 33.5 and 33.6).

Art. 10.7. The principle of typification does not apply to names of taxa above the rank of family, except for names that are automatically typified by being based on generic names (see Art. 16). The type of such a name is the same as that of the generic name on which it is based.

Art. 11.9. Priority is not mandatory for names of taxa above the rank of family (but see Rec. 16B).

Art. 16.1. Names of taxa above the rank of family are automatically typified if they are based on generic names (see Art. 10.7).

Rec. 16A.1. The name of a division or phylum is taken either from distinctive characters of the division or phylum (in descriptive names) or from the name of an included genus; it should end in *-phyta* unless it is a division or phylum of fungi, in which case it should end in *-mycota*.

Rec. 16A.2. The name of a subdivision or a subphylum is formed in a similar manner; it is distinguished from a divisional name by an appropriate prefix or suffix or by the termination *-phytina*, unless it is subdivision or phylum of fungi, in which case it should end in *-mycotina*.

Rec. 16A.3. The name of a class or of a subclass is formed in a similar manner and should end as follows:

- (a) In the algae *-phyceae* (class) and *-phycidae* (subclass).
- (b) In the fungi: *-mycetes* (class) and *-mycetidae* (subclass).
- (c) In other groups of plants: *-opsida* (class) and *-idae* (subclass).

Rec. 16B.1. In choosing among typified names for a taxon above the rank of family, authors should generally follow the principle of priority.

Art. 17.1. The name of an order or suborder is taken either from distinctive characters of the taxon (descriptive name) or from a legitimate name of an included family based on a generic name (automatically typified name). An ordinal name of the second category is formed by replacing the [family] termination *-aceae* by *-ales*. A subordinal name of the second category is similarly formed, with the termination *-ineae*.

Art. 18.1. The name of a family is a plural adjective used as a substantive; it is formed from the genitive singular of a legitimate name of an included genus by replacing the genitive singular inflection (Latin *-ae*, *-i*, *-us*, *-is*; transliterated Greek *-ou*, *-os*, *-es*, *-as*, or *-ous*, including the latter's equivalent *-eos*), with the termination *-aceae*.

Art. 19.1. The name of subfamily is a plural adjective used as a substantive; it is formed in the same manner as the name of family (Art. 18.1) but by using the termination *-oideae* instead of *-aceae*.

Art. 19.3. A tribe is designated in a similar manner, with the termination *-eae*, and a subtribe similarly with the termination *-inae*.

[For specified botanical ranks and their specified terminations, see Table 1]

APPENDIX 2. Zoological Code (Ride et al. 1985) on Hierarchy

Pre. [2nd paragraph]. The object of the Code is to promote stability and universality in the scientific names of animals and to ensure that the name of each taxon is unique and distinct.

Art. 29(a). Formation of family group names. A family or a subfamily name is formed by adding to the stem of the name of the type genus the latinized suffix *-idae* for a family name and *-inae* for the subfamily.

Rec. 29A. It is recommended that the suffix *-oidea* be added to the stem for the name of a superfamily and *-ini* for the name of a tribe.

Art. 35(a). Taxa. The family group includes all taxa at the ranks of

superfamily, family, subfamily, tribe and any other rank below superfamily and above genus that may be desired, such as subtribe.

[For specified zoological ranks and their specified terminations, see Table 1.]

APPENDIX 3. Biological Code (Greuter et al. 1996) on Hierarchy

Abbreviations used for references to parallel texts:

BC = Bacteriological Code.

ICBN = International Code of Botanical Nomenclature.

ICZN = International Code of Zoological Nomenclature.

Art. = Article; Pre. = Preamble; Prin. = Principle; Rec. = Recommendation; Rule = Rule.

Principle 5. Each taxon in the family-group, genus-group or species-group with a particular circumscription, position and rank has only one accepted name, except as may be specified in earlier Codes [BC: Prin. 8; ICBN: Prin. 4; ICZN: Pre. 2nd paragraph].

CHAPTER I. TAXA AND RANKS

Art. 2.1. Every individual organism is treated as belonging to an indefinite number of consecutively subordinate rank, among which genus and species are essential [ICBN: Art. 2.1].

Art. 3.1. The principal ranks of taxa in descending sequence are kingdom, phylum, class, order, family, genus and species [BC: Rule 5b; ICBN: Art. 3.1].

Art. 4.1. Secondary ranks of taxa, when required, include, in descending sequence: domain above kingdom, superfamily above family, subfamily, and tribe between family and genus, subgenus, section and series between genus and species, and subspecies, variety and form below species [BC: Rule 5b; ICBN: Art. 4.1-2].

Art. 4.2. If an even greater number of ranks of taxa is desired, the terms for these are made by adding either of the prefixes super- or sub- to non-prefixed terms denoting the principal or secondary ranks [ICBN: Art. 4.2-3].

Art. 4.4. Further ranks may be intercalated or added, but designations of taxa in such ranks are not governed by this Code [ICBN: Art. 4.3].

CHAPTER IV. NAMES BY RANK

SECTION 1. TAXA ABOVE RANK OF SUBFAMILY

Art. 25.1. Names of taxa above the rank of superfamily are treated as substantives in the plural and are written with a capital initial letter. They may be either (a) typified names (see Art. 14.1) that are formed by adding a termination denoting their rank to the genitive singular stem of a generic name or exceptionally to the whole name, or (b) typeless names ("descriptive names") that are formed differently, apply to taxa with a recognized circumscription, and may be used unchanged at different ranks [ICBN: Art. 18.1].

Art. 25.2. For typified names, the name of a subphylum which includes the type of the adopted name of a phylum, the name of a subclass which includes the type of the adopted name of a class, or the name of a suborder which includes the type of the adopted name of an order, are to be based on the same type.

Art. 25.3. The typified name of a phylum or subphylum is formed from the same generic name as an acceptable name of an included class. The phylum name termination is *-mycota* for fungi, *-phyta* for other botanical taxa. The subphylum name termination is *-mycotina* for fungi, *-phytina* for other botanical taxa [ICBN: Rec. 16A.1-2].

Art. 25.4. The typified name of a class or subclass is formed from the same generic name as an acceptable name of an included order. The class name termination is *-mycetes* for fungi, *-phyceae* for algae, *-opsida* for other botanical taxa. The subclass name termination is *-mycetidae* for fungi, *-phycidae* for algae, *-idae* for other botanical taxa [ICBN: Rec. 16A.3].

Art. 25.5. The typified name of an order or suborder is formed from the same generic name as an acceptable name of an included family. The order name termination is *-ales* for all botanical and bacteriological taxa. The suborder name termination is *-ineae* for all botanical and bacteriological taxa [BC: Rule 9; ICBN: Art. 17.1].

Art. 25.6. The name of a taxon above the rank of family may not have the termination *-virinae*, *-virales*, or *-viridae* [reserved for virus names].

Art. 25.7. When a name is published with a Latin termination not agreeing with the provisions of this Article, the termination is changed to accord with it, but the name retains its authorship and date [ICBN: Rec. 16A.4; Art. 17.3].

SECTION 2. FAMILY-GROUP TAXA

Art. 26.1. Family-group names are treated as substantives in the plural and are written with a capital initial letter. They are formed by adding to the genitive singular stem of a generic name, or to the whole name if necessary to avoid homonymy, a termination denoting their rank [BC: Rule 9; ICBN: Art. 18.1; ICZN: Art. 11f]. The superfamily name termination is *-oidea* for zoological taxa [ICZN: Rec. 29A]. The family name termination is *-aceae* for all botanical and bacteriological taxa, *-idae* for zoological taxa [ICZN, Art. 29a]. The subfamily name termination is *-oideae* for all botanical and bacteriological taxa, *-inae* for zoological taxa [ICZN, Art. 29a]. The tribe name termination is *-eae* for all botanical and bacteriological taxa, *-ini* for zoological taxa [ICZN, Rec. 29A]. The subtribe name termination is *-inae* for all botanical and bacteriological taxa, *-ina* for zoological taxa.

Art. 26.2. The name of a family may not have the termination *-viridae*; the name of a subfamily or subtribe may not have the termination *-virinae*.

Art. 26.3. When a name is published with a Latin termination not agreeing with the provisions of this Article, the termination is changed to accord with it, but the name retains its authorship and date. Normally any required change will be made during the registration process [ICBN: Art. 18.4; ICZN: Art. 35(d)].