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Reformulation of the Foundations of Taxonomy Using Evolutionary Mechanics

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Abstract

Macroevolutionary analysis evaluating structural monophyly as descent with modification allows recasting of taxa in terms of physics as evolutionary mechanics. There are four natural ranks, as generalized taxa: the species, genus, lineage, and metalineage, each with distinctive evolutionary processes. The species is the smallest group of organisms whose traits exclude two-sigma of uncertainty and otherwise are active in processes at the genus level. The genus is a complex engine using the Rule of Four and the Pareto Fractal Dimension to fashion and control changes over time in minimally monophyletic groups. Immediate descendant species are limited to four per genus. The lineage is modeled as a caulogram, a stem-taxon tree of present-day species and genera arranged in a timelike sequence. The metalineage is an informationally structured n-tuple set of caulograms for one lineage as calculated at successive times in the past following a morphological clock. Metalineages reveal sustained similar numbers of species across ca. 100 million years, or four or five ticks of a Nemesis extinction clock. Force values associated with evolutionary processes are calculated and compared for two bryophyte lineages at species, genus, and lineage levels. These comparisons include Efficiency Ratio and Evolutionary Force, as well as analogues of classical mechanics: evolutionary distance, velocity, acceleration, force, work, and kinetic energy. A geometric explanation is offered for the Rule of Four constraining the size of minimally monophyletic groups.

Keywords: biophysics; evolutionary energy; evolutionary force; fractal evolution; macroevolution; Pareto fractal dimension; Rule of Four; structural monophyly; taxology; taxonomy

1. Introduction

This paper on the biophysics of macroevolution presents new definitions of taxa as fundamental, measurable structures in spacetime, a reformulation of the foundations of systematics. It is written in response to a general attitude on the part of cladists that all extant taxa have equally long lineages because there are no extant ancestral taxa [1,2], and to recent calls for abandoning the concepts of species [3,4] and genera (e.g., [5,6]) as notional and lacking scientific substance. In addition, there are philosophical and logical rejections of taxa as merely convenient artificial categories for transmission and naming of cladistic concepts [7], valuable only for their nomenclatural persistence. In the present work, a taxon is a group of organisms evolving through time as controlled by unifying principles based on measurable forces. The foundation of taxonomy is imbued in the various formal rules of nomenclature. Taxonomy is from the Greek taxis (τάξις), meaning rank or order, and nomos (νόμος), and means classification or ordering by rules. In nomenclature, a taxon

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is a taxonomic group at any rank, while a rank is a position in a taxonomic hierarchy. A rank is, in practice, a generalized taxon. The fact that groups at all hierarchical taxonomic ranks are ruled alike in nomenclature (there are exceptions) is due to the self-similarity of groups at all taxonomic ranks, such groups being controlled in substance by the same fundamental processes.

Inasmuch as the present paper encourages a mathematically described physical extension to the aims of the central Linnaean endeavor (discovery, description, classification, identification), perhaps "taxology" paralleling the mathematical extension of astronomy into cosmology might represent this expansion of our field. Taxology uses taxonomic data (descriptions at various ranks) to reveal and measure physical processes in nature and create a dynamic evolutionary framework for each group of organisms.

Degrees of freedom in statistics are calculated as sample size (n) minus the number of parameters (p) or units of measure, that is, d.f. = $n - p$. In taxonomy, n stands for numbers of character states (or of specimens or of species), while p stands for characters (the kind of thing measured). For example, "3 cm" is a character state and "leaf length" is a character. Parameter-wise, a species is the smallest group for which one can write an unambiguous distinguishing description. Descriptions of species can be large (many parameters), but descriptions of genera are smaller (fewer parameters, more facts explained), and family descriptions are smaller still, and so on until a description is a universal or set of universals explaining major groups of organisms. This technique of increasing degrees of freedom by generalizing parameters and their explanations through increasing ranks is the practical, physical basis for hierarchical systems of naming.

The fewer the parameters, the more complex are the patterns than can be captured in a greater sample size. In physical terms, taxonomy "eats the multi-parameter multi-state elephant" a bite at a time by confining sets of individual organisms to taxa and ranks to decrease parameters and increase degrees of freedom. Eventually, broadly shared features and in some cases universals are revealed. Analysis of smaller groups reduces parameters vastly, and the task is to maximize n while reducing to an optimum p description.

Taxology provides comparative measures of shared features and universals as the results of evolutionary processes. An example of a universal is the evolutionary interpretation of morphological variation p in Darwin's finches n extensible to greater n as a universal. Central universals presented here are measurements such as calculable evolutionary mass, velocity and acceleration, and processes such as two-sigma exclusion of uncertainty, the Rule of Four, and the Pareto Fractal Dimension. In this paper, the minimally monophyletic group is that key smaller group allowing process-based models that apply to taxa and more universally to ranks. Structural monophyly analysis provides an optimization of the parameter-to-data ratio, allowing the querying of biological collections. Taxology measures and predicts changes in biodiversity controlled by evolutionary processes.

The empiric content and context of the present paper's apprehension of taxa as functional informational structures [8] generative of order in groups of physical organisms is continued from previous papers that presented macroevolutionary systematics in terms of classical mechanics [9]. New inferences and hypotheses support the value of morphologically based analysis by descent with modification versus the shared ancestry concept of cladistics, that is, for taxa versus clades [9]. Van Valen [10] long ago pointed out that species clearly ancestral to extant species are also extant and common. It has been pointed out [11] that laws of evolutionary dynamics may be constructed, but such underlying structures as speed of evolution are difficult to translate into laws of physics when the dynamical component structure is unknown. This is directly addressed here. On the other hand, Torday [12] has reviewed a robust selection of the literature, arguing that the laws of physics determine the natural sciences, including evolutionary biology.

2. Materials and Methods

2.1. Recent Advances

A list of new information on processes associated with descent with modification-based macroevolution [8], on most of which this paper is based, is given below.

Classification: (1) Genera may be sorted into microgenera (demonstrably minimally monophyletic), mesogenera (most genera not yet studied), and macrogenera (massive genera of hundreds of species often inflated by cladistic synonymies); (2) microgenera or minimally monophyletic groups are nomenclaturally treated as genera.

Traits: (3) Effective use of morphology in evolutionary analysis, (4) molecular paraphyly–apophyly pairs implying ancestor-descendant relationships, and (5) integration of morphological and molecular results without recourse to mapping the former to the latter.

Macroevolution: (6) Distinction of morphological trait sets as ancestron and novon, (7) examples of minimally monophyletic groups as genera, (8) genera—as microgenera, these are proposed as having fundamental control over macroevolution—(9) informational redundancy measures, which are indicative of flexibility in survival at genus level, (10) measurement of rate of extinction versus rate of speciation, (11) establishment of punctuated equilibrium of extant genera with speciation in bursts while extinction is gradual, (12) well-supported caulograms (stem-taxon trees) of major bryophyte lineages, which show evolutionary series to 100 and to 88 mya, (13) plateaus in graphs of species per genus, which show ancient quadratic patterns of speciation, (14) demonstration of a strict morphological evolutionary clock, (15) postulation of a two-sigma conduit exclusion of uncertainty for timewise taxa, (16) the most-recently acquired traits of the single ancestral species (the immediate ancestron), which are apparently selectively inviolate and passed on without change to each immediate descendant species, (17) ancient morphological traits, which are preserved over millions of years by the Rule of Four redundancy, such that a lineage maintains maximum biodiversity at minimum expense to resilience, and (18) hollow curves of species per genus and genera per family are explained.

Analysis and statistics: (19) Stopping rules for sampling design in evolutionary analysis, (20) the Rule of Four, involving apparent optimization of four traits per species and four descendant species per ancestral species, commonly self-similar across taxonomic scales, (21) the Pareto Fractal Dimension of ln5/ln4, where a descendant species of one genus gives rise to about four species in another genus then becomes its ancestor, resulting in five species all sharing the new traits of the ancestor (the Pareto ratio being involved in fractal generation of four that results in five), (22) efficacy of Shannon–Turing sequential Bayesian analysis for statistical support, (23) second-order Markov chains, which are used such that the ancestral species of a minimally monophyletic group is both most similar to an outgroup and most generalist to its more specialized descendants, and (24) an extinct taxon, which can be inferred when the number of traits at a caulogram node are double or more the average number of traits changed.

Physics: (25) Evolutionary equivalence of classical mechanics, in which control of evolution follows first and second differentials of the fitted curve, and (26) serial evolution, which has a parallel in mirror parity.

2.2. Support for Major Concepts

The present paper asserts that, as part of an ongoing search for scientific organizing principles [13], biological systematics, commonly considered intuitive pattern detection prior to the advent of cladistics, can now be explained as operations of structured information in spacetime that provide forceful templates constraining, individuating, and empowering groups of organisms at species, genus, and lineage levels. The physical expressions of these structural templates are effective at the ecosystem level as conduits through

time maximizing changing Gibbs free energy into entropic dispersed energy in an orderly manner that eliminates catastrophic flushes [14] (p. 209).

Species, genera, and lineages (both present-day and reconstituted across time of existence) have distinctive physically measurable features that justify recognition as taxonomic ranks with different actions and effects in macroevolutionary events that follow clear-cut physical processes. The physicist Cockell [15] (p. 277) asserted that inferring which traits are important to an organism and what their optimized properties are is extraordinarily difficult, yet this is the exact proficiency of the taxonomist. This paper builds on an introduction to evolutionary mechanics using taxonomic data [16], refining the data in that paper and providing clear-cut physical definitions for ranks of taxa based on how they operate in macroevolution.

The number of species per genus [17,18], and genera per family [19] have similar hollow-curve graphs (Figure 1A,B). An additional graph (Figure 1C) of families per order is here calculated from Web data [20]; it shows much the same curve but with a thickening of the curve beyond five families, probably reflecting the increase in number of family synonyms due to recent molecular phylogenetic studies. Given quadrate speciation (generally four immediate descendants from one ancestral species, yielding five total initial species per genus), we can identify the area from five to one on the x-axis as gradual extinction from a burst of five. That punctuational burst [21] has been described and justified [21] (p. 41). Given that secondary speciation from descendant species occasionally produced genera of six or seven species, this explains the continued curve, while macrogenera that have not yet been separated into minimally monophyletic groups comprise the low number of genera and families with high numbers of species or genera, respectively. This similarity of the graphs is fractal, as the graphs follow a curve with a fractal dimension of about ln5/ln4, or 1.161.

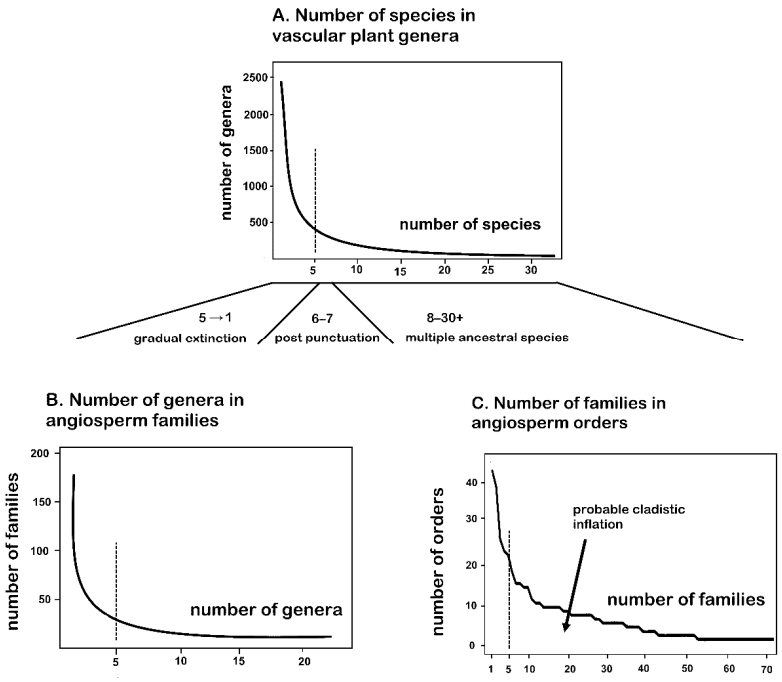

Figure 1. Number of species per genus, genera per family, and families per order have self-similar graphs, implying similar causative processes across scale. Number of species in a genus is 5 at dashed line. Explanations of portions of the curves are given with 1A. These inverse power curves reflect the universal and unifying self-similarity of processes at all taxonomic ranks.

Figure 2 presents an exemplary case for the Rule of Four, where recently evolved microgenera commonly have four immediate descendant species, with up to two secondary

descendants possible later. The Pottiaceae tribe Trichostomeae was analyzed for the West Indies [22], an area recently exposed (45 mya) and available for new taxa. Recent land masses are good laboratories for evolution. One branch of Trichostomeae, with *Neotricvhostomum crisplum* as the ancestor, has four descendant genera in that area and contiguous Gulf of Mexico lands. *Tainoa* is endemic, with three immediate descendants and one secondary speciation. *Chiololoma* has four descendants, three being endemic and more broadly distributed, and there were two other species in the East Indies that may have originated when these dry island habitats were more or less contiguous during habitat propinquity associated with climate extremes. The other two genera, *Weissia* and *Hymenostomum*, are nearly worldwide in distribution, originating from populations of *N. crispulum* elsewhere in the world. The study used the Principle of Mediocrity (aka the Copernican Principle [23]) to establish an age of origination of the local taxa at ca. 22 mya. At least regionally, the Rule of Four operated in this group at both the genus and species level, while numbers of traits (in Figure 2) are also mostly four or fewer, not exceeding six. Self-similarity is evident at trait, species, genus, and tribe levels. Taxonomy, the classification by hierarchical ranks, is based on this self-similarity. Information from taxonomic descriptions may be used to reveal the complexity-based processes governing biodiversity.

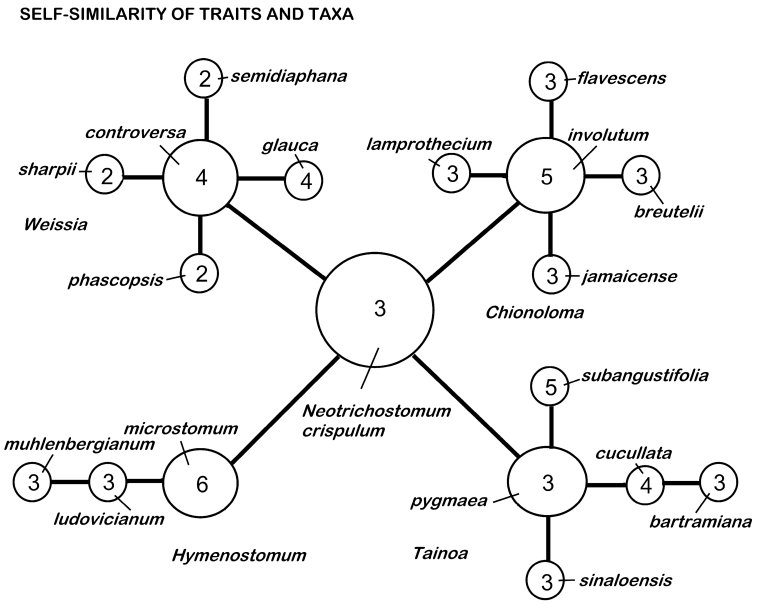

Figure 2. The Rule of Four illustrated for recently evolved bryophyte taxa in West Indies, a recently (45 mya) exposed land mass. Numbers are of new character states (evolutionary velocity).

"Self-similarity" is a refrain in this paper. A familiar parallel may better explain it: Consider a standard deck of 52 cards. You obtained this deck from a box of 52 decks, each deck in its own package illustrated with a unique card of the 52 cards. That box is one of 52 boxes, each labeled with one of the 52 cards, and so on as nested boxes of boxes. You can play gin-rummy with any set of 52 decks or boxes because the nested sets are self-similar. The game is evolution, and it is played at any rank by ecosystems, communities, realized niches, and other ecological and floristic/faunistic groups, following the statistical and physical rules suggested in the present paper. They are the equivalent of laws in physics because they are possibly universal and apparently are effective for at least 100 million years. The result is an ecosphere with taxa that together promote and control a maximum generation of entropy diversly, persistently, and resiliently.

Figure 3 shows steps in the inferred timeline of a standard microgenus, a minimally monophyletic group. The caption is fully informative. All the red, blue and green dots are species presently extant. A caulogram is a set of concatenated microgenera connected

through their ancestral species by lines indicating timewise origination. Because there are about four traits in all speciation events, and there are no reversals among immediate descendants, all microgenera are statistically well supported through Shannon–Turing sequential Bayesian analysis [24]. Because 20 percent of one ancestral genus generating 80 percent of another descendant genus matches the Pareto ratio, and inasmuch as this process may be found at different taxonomic levels, it is fractal [25] and self-similar (cf. Figure 1). The Pareto ratio states that approximately 80% of the effects in any given process results from 20% of the causes; it is an optimizing principle devised from observation in the past, considered rather loosely effectuated and not a physical rule. This may change.

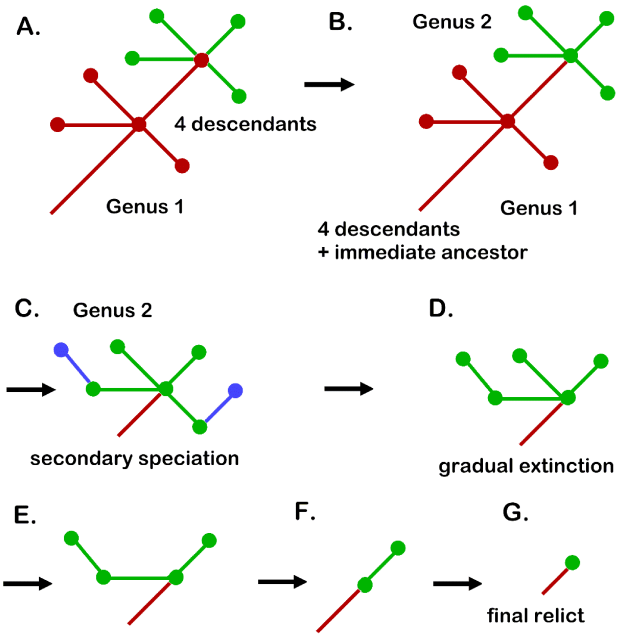

Figure 3. Generalized fate of microgenera. (**A**). A descendant of Genus 1 (red) generates about four descendants (green). (**B**). Because all descendants have the novel traits of their ancestor, all are recognized as Genus 2 (green). (**C**). Genus 2 may generate additional species from the immediate descendants (blue). (**D**–**G**). Genus 2 gradually goes extinct.

2.3. Data on Trait Changes in Species

The results of the evolutionary mechanics analysis are based on the spreadsheet variant of caulograms given below (Tables 1 and 2), which show the ancestor–descendant relationships in genera together with the numbers of new traits established for each speciation event (refined from [16]).

The Rule of Four limits the number of immediate descendant species, i.e., the number of immediate descendant branches, including those ending in the ancestor of a descendant genus. This is well-illustrated in Figure 2, which shows recently evolved taxa in the West Indies. The two lineages here studied are older and more dissected by extinction but exhibit reasonable adherence to the constraint on numbers of descendant species. Streptotrichaceae (STR) has 13 ancestors (including 2 unknowns) with 22 immediate branches, and thus 1.7 branches per ancestor. There are no more than 3 immediate branches for any one ancestor, and no more than 3 secondary ancestry branches occurring as one per secondary ancestor. Range of immediate branches is 2 zero branches, 4 one, 3 two, 4 three. Pleuroweisieae (PLE) has 11 ancestors (including 1 unknown) with 25 immediate branches, thus 2.3 immediate branches per ancestor. No more than 3 immediate branches for any one ancestor, and no more than 3 secondary ancestry branches as one per secondary ancestor. The range of immediate branches is 1 zero, 4 one, 4 two, and 1 three.

Table 1. Spreadsheet caulogram of the bryophyte family Streptotrichaeceae. Numbers in header show sequential species events. Color coding distinguishes genera. Each column represents a speciation event. IEG is inferred extinct genus. Numbers in squares are morphological trait (character-state) changes for one species at its speciation event. Double-line arrows show ancestor-descendant relationships.

Streptotrichaeceae Genus	Species	1	2	3	4	5	6	7
IEG 1	unknown	4						
IEG 2	unknown	⟹	4					
Trachyodontium	unknown	‖	⟹	3				
	zanderi	‖	‖	⟹	4			
Crassileptodontium	*pungens*	‖	⟹	6				
	wallisii	‖		⟹	3			
	erythroneuron	‖			⟹	4		
	subintegrifolium	‖			⟹	3		
Streptotrichum	*ramicola*	⟹	4					
Austroleptodontium	*interruptum*		⟹	8				
Leptodontiella	*apiculara*		⟹	3				
Microleptodontium	*unknown*		‖	⟹	7			
	flexifolium		‖		⟹	3		
	gemmascens		‖		‖	⟹	4	
	umbrosum		‖		‖	⟹	4	
	stellaticuspis		‖		‖	⟹	3	
Rubroleptodontium	*stellatifolium*		‖		⟹	5		
IEG 3	*unknown*		⟹	5				
Williamsiella	*araucarieti*			⟹	6			
	tricolor				⟹	4		
	aggregata				⟹	6		
	lutea				‖	⟹	2	
Leptodontium	*unknown*				‖	⟹	5	
	excelsum				‖		⟹	3
	viticulosoides				‖		⟹	3
	scaberrimum				‖		⟹	5
Stephanoleptodontium	*longicaule*				⟹	4		
	syntrichioides					⟹	4	
	bryachyphyllum					⟹	3	
	filicola					‖	⟹	5
	capituligerum					⟹	3	
	latifolium						⟹	3
	stoloniferum						⟹	4

Table 2. Spreadsheet caulogram of the rated moss Pottiaceae tribe Pleuroweisieae. Caption is the same as that for Table 1.

Pleuroweisieae Genus	**Species**	**1**	**2**	**3**	**4**	**5**
IEG	unknown	**8**				
Tuerckheimia	*guatemalensis*	⊫	**4**			
	svihlae	‖	⊫	**2**		
	valeriana	‖	⊾	**2**		
Eobryum	*anoectangioides*	⊾	**5**			
	hildebrantii		⊫	**3**		
	xeerophilum		⊫	**2**		
Anoectangium	*aestivum*		⊫	**5**		
	euchloron		‖	⊫	**5**	
	radulans		‖	‖	⊾	**3**
	clarum		‖	⊫	**4**	
	incrassatum		‖	‖	⊾	**4**
	stracheyanum		‖	⊾	**3**	
	sikkimense		‖		⊾	**3**
Ardeuma	*gracillimum*		⊫	**4**		
	recurvirostum		‖	⊾	**2**	
	crassinervium		‖		⊫	**3**
	annotinum		‖		⊫	**3**
	aurantiacum		‖		⊾	**3**
Gymnostomum	*aeruginosum*		⊫	**5**		
	viridulum		‖	⊫	**2**	
	calcareum		‖	⊾	**3**	
	mosis		‖		⊾	**2**
Hymenostyliella	*llanosii*		⊫	**5**		
	alata		‖	⊾	**2**	
Hymenostylium	*xanthocarpum*		⊫	**4**		
	townsendii		‖	⊾	**4**	
Molendoa	*sendtneriana*		⊫	**5**		
	hornschuchiana		‖	⊫	**5**	
	peruviana		‖	⊾	**3**	
	handelii		‖		⊾	**3**
Ozobryum	*warburgii*		⊫	**5**		
	missing link		‖	⊾	**5**	
	ogalalense		‖		⊫	**3**
	mexicanum		‖		⊾	**3**
Reimersia	*inconspicua*		⊾	**4**		

Table 3 summarizes the terms and concepts from physics used here to describe analogous processes in evolution. The processes in evolutionary systematics underlying the

formulae are more than just likenesses of physical processes; their results are proportional to those of simple mechanics as a kind of Mass Action. Darwinian evolution obeys physical laws [11]. Bryophytes are used as models because they commonly show clear reduction and elaboration series, useful in polarizing lineages morphologically.

Table 3. Physics analogues for evolutionary mechanics.

Term and Abbreviation	Physics Analogue	Evolutionary Definition
Evolutionary mass (m)	Inertia	One species, or resistance to change.
Evolutionary distance (d)	Displacement	Total evolutionary path since taxon origination; total sum of trait changes in a caulon.
Evolutionary time	Steps	Speciation events
Evolutionary velocity (v)	Rate of innovation	Number of traits changed per speciation event; current speed of adaptation.
Evolutionary force (F)	Net force ($F = ma$)	Magnitude of selective pressure accelerating the rate of change; a jump in rate of change.
Kinetic energy (KE)	$\frac{1}{2}mv^2$	Evolutionary momentum, high KE implies rapid change; a scalar; the state of the energy.
Potential energy (PE)	$F \times \Delta d$	Adaptive tension, pressure for future trait changes by an environmental shift; a vector.
Work (W)	$F \times d$	Total environmental effort to reach that state; the transfer of energy.
Total energy (E)	$KE + PE$	Total evolutionary energy of the taxon.
Taxonomic Action Unit (TAU)	Selective force $\times$ d, which is same as traits^2/event^2	Energy required for 1 species ($m = 1$) to undergo 1 trait change ($v = 1$) in 1 speciation event; evolutionary equivalent to joule (newton $\times$ meter); a change in momentum.
Efficiency ratio (η)	Useful energy	Percent of kinetic energy as work output.

Results of a past study listed above and previously described in detail [9] are here presented as interpreted in timelike and spacelike contexts. Timelike simply means that macroevolutionary processes are conceived as relict groups (extant species and genera) arranged on a caulogram (stem-taxon dendrogram) serially by origination through time, with the oldest species at the tree base. The justification for using morphological data in this is as follows: (1) the genera are easily distinguished as *microgenera* with one ancestral species and one to four immediate descendants, all sharing the ancestor's novel traits (about four, optimally); (2) about half the species studied are ancestral to one or more other species in the same group; (3) the progenitors of the microgenera all differ in about the same number of novel traits, ca. 4, allowing reasonable connections (*caulons*, or connecting lines on the caulogram reaching from a species down to the lineage base) between them, such that origination of genera is not a new and distinctive operation although the new genera

are distinctive qualitatively; (4) the microgenera exhibit gradual extinction as expected; and (5) the new groupings match or are well justified dissections of past accepted taxonomic groups that were originally based on standard omnispection, apprehension of a Gestalt, and generally of innate pattern recognition. Most importantly, the use of morphological data in the context of descent with modification (stem-taxon trees) allows detailed and effective analysis with evolutionary mechanics.

Data from Tables 1 and 2 are analyzed for analogous processes in classical mechanics. The analogues are first defined for taxa and data (Table 3), then used to infer macroevolutionary relationships that reveal processes affecting the relationships of taxa (see Results). Possible constants or universals (e.g., Figure 1) that may also operate as predictive or retrodictive with taxa other than those studied are identified.

The caulograms of the lineages used in this study are then processed to infer what they would look like if viewed at various times in the past. The object is to create a time-ordered set of caulograms as a *synchronogram*, which would be an image modeling the actual appearance of the caulogram changing over time following its particular evolutionary trajectory. As information, the ordered set of caulograms exists in the present, yet reflects a timewise evolutionary process.

The time scales of the lineages used, the moss family Streptotrichaceae [14] and the Pottiaceae tribe Pleuroweisieae [16], have been estimated—using an anchoring fossil and strict morphological clock at 22 my intervals based on origination of certain taxa in the West Indies [22] to span 100 my and 88 my, respectively, yielding five and four "slices" evenly spaced through past time—as an informational variant of the Block Universe concept [26,27]. These slices approximate in time the evenly spaced extinction events associated with theories of periodic cometary impacts, caused by, for instance, the visits of a Nemesis sun [28,29] with periodicity of 26 my, the Shiva hypothesis [30], associated with galactic plane oscillation of 30–35 my, or the dark matter trigger hypothesis [31], of about 36 my periodicity. There has been no detection of a Nemesis sun, but the data for 26 my periodic extinctions remain valid and match well the clock used in this paper. I attest that the 22 and 26 my correlation was a surprise.

The synchronogram is a spacelike calculation; that is, each past version of the relict-based caulogram is as presented as though viewed in a Common Now. The method of constructing a synchronogram of an ordered set of past caulograms is to reverse the evolution of the present-day caulogram along the lines given by known processes in a single caulogram as illustrated in Figure 3, which also reflects the time scales of the order of speciation of the present-day relict genera. As best as possible, the actual caulogram at each time level of the present-day caulogram is estimated. The tuples align with a principle of conservation of information such that distinctive objects do not evolve into the same object.

2.4. Physics Analogues

This paper is intended primarily for taxonomists, who are famously innumerate (meaning duffers at mathematics). The calculations are at spreadsheet level and not difficult, but they do reflect complex processes in nature. The infinitesimal calculus is, for this exercise, unnecessary, but the data are amenable to further analysis.

3. Results

3.1. Redefinition of Taxa

The point of doing this is that analysis using descent with modification and morphological data has demonstrably higher resolving power than cladistics. This is supported by 250 years of successful independent taxonomic study and the above-listed recent advances in systematic methodology. Also, the macroevolutionary diagrams (Tables 1 and 2) are

directly based on actual taxa, not nodal intermediates representing sets of species calculated through various methods and data in cluster analysis. Minimally monophyletic groups are maximally paraphyletic and are powerful tools for ancestor–descendant analysis. Because there is evidence of ancestral–descendant relationships using molecular data (paraphyly–apophyly pairs) that is congruent with morphologically based results [32], morphology is justly freed from being mapped to (constrained to duplicate) molecular cladograms. We start with a redefinition of critical taxonomic ranks or groups, some of which are exemplified in past taxonomic study [9]. We can identify four *natural taxonomic ranks*. The natural taxonomic ranks are hierarchical sets of species associated with distinctive macroevolutionary processes and different analytical data fields. These natural ranks are the species, genus, lineage, and metalineage. Because the last two are not recognized nomenclaturally, standard rank names and concepts are used in practice.

3.1.1. The Species

A *species* is a group that may include any species concept that works well with the minimally monophyletic genus concept. It is the fundamental unit of macroevolution and classification, and of course is distinctive in all the processes of microevolution. The number of new traits established during speciation is about four, which generates by an odds table a two-sigma conduit eliminating uncertainty through space-time, which also individuates the taxon [24]. In information theory, having four bits of information is powerful—it allows one to distinguish between $2^4 = 16$ equally likely possibilities. Two bits reduce uncertainty by 75% (four options), which can be acceptable in distinguishing many species. The species is the natural embodiment of the Hamiltonian concept of momentum as a unit, an observable, in classical mechanics. Speciation is, as a taxonomic measure of macroevolution (i.e., "computational taxonomy"), a change in a species description, commonly requiring at least two-traits difference to avoid recognizing simple mutations (as one new trait) as evidence of a valid evolutionary group in the context of descent with modification. Taxonomically, four new traits at speciation means being able to identify a species at least 19 times out of 20. This concept is entirely valid for evolutionary mechanics. Physically, a species is a unitary operator stitched together through time by serial isomorphisms applied at the genus level.

3.1.2. The Genus

The *genus* has the basic *control* of evolution, and through self-similarity such control may be effective to some extent at all taxonomic ranks (Figures 1 and 2). The genus, specifically the *microgenus* of minimal monophyly, is identifiable and defined by two criteria: (1) it includes one demonstrable extant or otherwise strongly inferable immediate ancestral species, and (2) the novel traits of the ancestral species are all shared with immediate descendants. The number of important expressed character states changed during speciation is commonly about four traits (Tables 1 and 2). The number of descendant species is, significantly, commonly about four, quadratic perhaps due to initial sympatric crowding or later crowding via the squeezing of geographic range during glaciations. Extinction reduces over time the number of species in the genus (Figure 1A) and the ancestral species is most resistant to loss. When molecular paraphyly–apophyly pairs are available in molecular cladistic studies [32] the implied ancestor–descendant relationships support this definition.

Operationally, the microgenus, before onset of extinction, is initially mostly of about five species: one ancestral species and about four descendant species [33]. The ancestral species of a genus is determined by a second-order Markov chain [34], the ancestor identifiable as most similar to an outgroup species and most generalist to the more specialized ingroup species. The microgenus is a complex of long-lasting information mediating

macroevolution. In a fashion self-similar to that of the species, the 5-species microgenus establishes a two-sigma path through spacetime excluding uncertainty. It uses or is composed of two critical processes embodied in the Pareto Fractal Dimension: (1) The Rule of Four, which consists of optimally four new traits per speciation event and four immediate descendant species; there is evidence that taxa at higher ranks also are quadratic in nature, and in physics it is a meta-law of nature [35,36], while, of course, there are four primary nitrogenous bases in DNA, optimally so through information theory and pairing constraints [15,37] (p. 128); (2) The Evolutionary Fractal Dimension, which operates such that a descendant of one genus generates four of its own descendants sharing the same novel traits of itself. In such a manner the new genus then has five species sharing the same traits. Thus, we have the Pareto ratio, where 20% of the first genus generates 80% of the second genus, involving a fractal dimension of ln5/ln4, or 1.161 [34]. The hollow curves of Figure 1 are of a form equivalent to the Pareto Fractal Dimension:

$$f(x) = 16/x^{\frac{ln5}{ln4}} = \frac{16}{x^{1.161}} \quad (1)$$

This expression is a power-law decay and is modeled by Figure 3, in which one species of one genus gives rise to four species of a second genus, where that second genus has all new traits of its immediate ancestor. Genera larger than five species may originate after the initial punctuational event by secondary speciation of descendant species. Unstudied larger groups are called mesogenera and may include more than ancestral species. The equation for the Pareto Fractal Dimension (Equation (1)) is doubtless a result of underlying variables [38] associated with fundamental constraints on speciation; this paper follows the distinction between underlying laws and equations and the theory of the mechanisms applying these laws [39].

The denominator ln5/ln4 in Equation (1) is the shape of the curve reflecting Pareto evolutionary change, while the numerator in power laws [40,41] sets the height of the curve relative to the y-axis, which reflects the number of items (species richness) involved. The numerator of 16 moves the curve up and to the right so that the number on the x-axis (number of species) tells you the number on the y-axis as the actual counted number of genera. That numerator is a scaling factor [42,43] that best fits the actual curve and represents the resistance (possibly by crowding) to adding new species (species per genus) as the genus grows (where work or $F \times d$ is four times four traits per immediate descendant species). The number is sufficiently large that even a small environmental shift results in a large evolutionary pressure. The numerator is the proportionality constant λ in the inverse power function $f(x) = \lambda x^{-\alpha}$, and α is the fractal dimension ln5/ln4. That dimension is a taxonomic crowding factor related to the Pareto ratio. The numerator 16 represents a fractal square of the Rule of Four for immediate descendants and is apparently universal (Figure 1).

3.1.3. The Lineage

All taxa of rank larger than the genus may be modeled as descent with modification on a stem-taxon tree, a *caulogram*. Ancestral taxa of microgenera are connected along lines leading to the base of the caulogram; each line is a *caulon* consisting of a timewise ordered series of ancestors. Numbers of trait changes between ancestors of microgenera on speciation are much the same as internally in a genus, about four. When double or more traits separate microgenera (ancestor to ancestor), an extinct genus may be inferred. All taxa above genus may be arranged as a caulogram and subsumed under the natural taxon "lineage", although for historical reasons lineage has no formal nomenclatural standing. A lineage is a natural taxon because, like species, genus, and metalineage, it is associated with distinctive evolutionary processes and is not simply a hierarchically nested self-similar set

of the species, as are tribe, family, and order. Lineages of Streptotrichaceae, Pleuroweisieae, and other bryophyte taxa are diagramed and discussed in previous papers [9]. The former two have been somewhat refined and are arranged as spreadsheets in Tables 1 and 2.

3.1.4. The Metalineage

Aside from species and genera, higher taxonomic ranks are here all addressed by the taxon-like constructs of a *timelike lineage* or a *spacelike metalineage*. Timelike means a process sequential in time. Spacelike means simultaneous or coetaneous, with all information immediately functional [8], controlling the physical expression. The timelike lineage is modeled as a caulogram (e.g., Table 1), which is a branching evolutionary connection between the progenitors of microgenera as ordered by inference through time. This is the unitary lineage of branching lines of sequential descent on a stem-taxon tree and is featured in recent major publications [9]. A morphological clock for the timelike series has been employed with caulograms [33], although the clock is not conceived as ticking by neutral mutation accumulation. The morphological clock used here matches the breadth of time of the "modern flora" reaching back to the Upper Cretaceous, matches a fossil anchor, and fits the 26 my large extinction periodicities, and the relevant caulograms show only even, gradual change in accumulated numbers of novel traits. Evolution does not jump.

The spacelike metalineage is a new concept that acts as a taxonomic rank. It summarizes the substance and history of timelike data. A metalineage is modeled as a synchronogram, being an *n*-tuple or ordered set of caulograms, a superset of data about the present-day lineage. (A tuple is like a row in a spreadsheet.) The subject of this paper is the distinction of species, genera, lineages, and metalineages as measurable, scientifically real structured information lasting millions of years in the genetics of groups of organisms and influencing the course of evolution.

The synchronogram of a metalineage consists of series of caulograms of the same lineage, each in a form inferred to have existed at some particular time in the past. Four caulograms in the set are sufficient to ensure a two-sigma exclusion of uncertainty because they are the equivalent of the number of species in the genus. The future of the present-day lineage, given that no information is available except that of the past, may be predicted only to the extent of extinction of present-day taxa, while prediction of potential new taxa must be calculated with other techniques, if possible.

The calculations for generating a metalineage are made from present-day relicts (extant species and genera) modified by expectations of past change taking into account the common evolutionary processes (Figures 2 and 3) established by the Rule of Four and Pareto Fractal Dimension.

The two metalineages (Figure 4) extend 88–100 my. The five caulogram slices for the Streptotrichaceae image are calculated caulograms that were extant in the earlier and the later Upper Cretaceous, the Paleocene-Eocene boundary, the late Eocene and Oligocene, and the Miocene up through the Pleistocene. The synchronogram for the Pleuroweisieae is ordered similarly, but this lineage is apparently (by clock calculation of only four "ticks") absent in the earlier Upper Cretaceous. This tribal lineage is apparently somewhat less ancient than the Streptotrichaceae. The synchronograms are similar to the evolutionary time-form lattice of Gingerich [44], except that the time-form lattice is scaled by generation time, while the synchronogram is scaled by a 22 my morphological clock. Gingerich, also, found for Cenozoic mammals rapid, punctuational filling of available niches followed by long-term stabilizing selection.

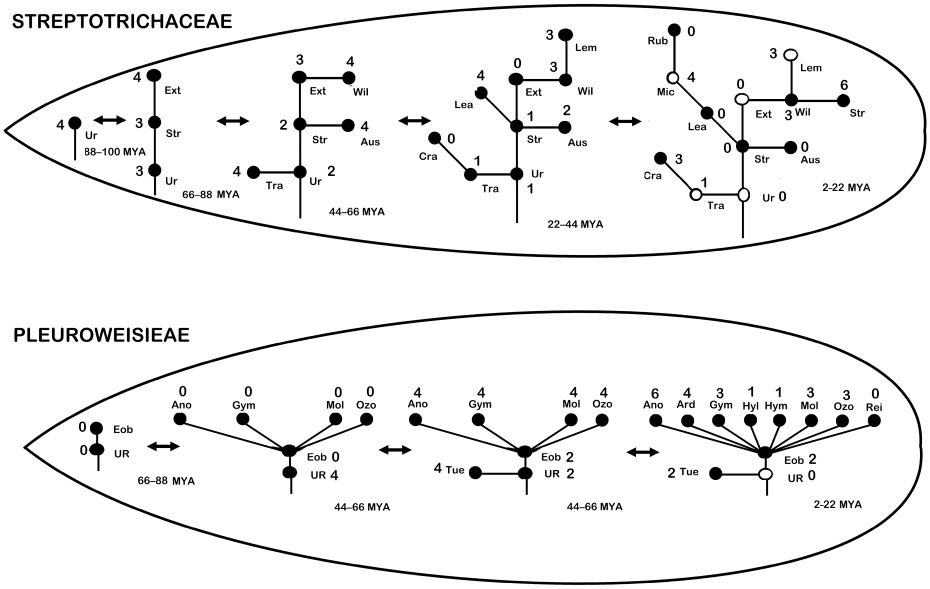

Figure 4. Two metalineages are shown, the related moss taxa Streptotrichaceae and Pottiaceae tribe Pleuroweisieae. These are imaged as synchronograms ordering calculated past caulograms as tuples. There is no timelike vector as all caulograms, as inferred samples, are considered to operate as information at once. The caulogram farthest to the right in each metalineage is that of the present-day composition of the lineage, essentially the past 22 my. Dots are genera: solid dots are extant genera and hollow ones are extinct but with inferable traits. Numbers are of numbers of descendants estimated as extant at the time slice; the branch leading to next genus should be considered as an additional descendant. Double-headed arrows indicate that these are calculations free of the arrow of time, i.e., the information is extant, here treated as a unitary living structure.

Twenty-two million years have been proposed as the time interval for the morphological clock for these groups [22]. The numbers of species and genera in the four or five time slices used (Figure 4) indicate no great change across time in numbers of taxa for both groups since inception in the Late Cretaceous. The numbers of species for each slice of time in the caulograms are an indication of the impetus (momentum or mass times velocity). The numbers of species for Streptotrichaceae time slices, from origin through the present, are 5, 13, 25, 24, and 27. Those for Pleuroweisieae are 2, 20, 31, and 35. Apparently, after lineage origination, the numbers of species in each of the two lineages at any one time are not much different across time. The increase in numbers of species is at most linear. This may be attributable to saturation of the available habitats given phyletic constraint on the available adaptations of that taxonomic lineage. Formulae for modeling numbers of taxa generated in time from fossil evidence have been suggested [45].

In ecological terms, if the species is equivalent to its niche, then the numbers measure the niche availability where evolutionary change deals with changing environment. If the spacetime path of each species is a branching "fiber", then the "rope" of the metalineage is remarkably even in thickness. Its long-lasting individuation is due to a massive adaptive exclusion of uncertainty on a broad front.

The changes in the species composition given origination and extinction are rather balanced, possibly reflecting the gradual diminution of global temperature and other environmental changes through the Miocene and Pliocene since the Paleocene-Eocene Thermal Maximum about 56 mya. In addition, the Rule of Four implies constraint on the generation of descendant species. One may assume, given that each species has long persisted under the same habitat conditions, that the average numbers of traits per species (4.3 for Streptotrichaceae (STR) and 4.54 for Pleuroweisieae (PLE) [16]) are much the same in the timewise slices as in the present. The present evolutionary force values (ToTrCa) for

each lineage are also similar: 710 for STR and 753 for PLE. Given that the habitats of the two lineages are rather different [14], there may be an optimal or maximal size in numbers of species globally, reinforced through competition associated with periodic crowding during glaciation and other climate-related habitat consolidations.

3.2. Formulae for Taxon-Based Evolutionary Processes

Analysis of taxonomic data is predicated on successful use of physics and statistical methods in other fields and with other taxa [46–54]. These prior studies, on the other hand, are usually focused on microevolution—e.g., evolution in and between populations—and not macroevolution, and are commonly statistical rather than deterministic (as is mostly the case in the present paper).

Classical mechanics uses position and momentum for many basic calculations, the standard six metric dimensions being three for position and three for momentum. Position, in the context of taxonomy, is where an individual or group is placed somewhere in taxonomic space, in particular on an evolutionary tree. Knowing a species' immediate ancestor establishes position immediately.

Velocity and momentum are first and second differentials of position, easily applicable when acceleration (change in velocity) is constant, but this is not the case in evolution. If an arithmetic progression grows by a constant rate, the total grows according to the square of the number of steps, but trait changes along a caulon are not constant in number. The workaround is to consider instantaneous acceleration as the plus or minus change in velocity of a species in respect to its immediate ancestor, with the historical acceleration being the sum of all current positive and negative accelerations on the caulon for any one species.

The formulae for evolutionary mechanics are based on those of classical mechanics and prove informative. Evolutionary mass is simply a species, e.g., 1 sp., and analytic focus changes from the motion (displacement) of an object to the motion of a species. Mass is the resistance of any particle interacting with its own field (inertia), and such resistance analogically in evolution is the environmental friction against which lineages of species adapt by generating new species. Taxonomically, an evolutionary species is a species description, which changes somewhat during each speciation event; that description travels, changing with speciation events, from the beginning of a lineage to its present-day terminus. The species' description is equivalent to its position on a caulogram, clamped by its novel traits.

Evolutionary time t_{evol} is a speciation event, e.g., 1 sp.ev., which involves ca. four species originating about the same time (i.e., among 22 my) from one joint ancestor. Time may also be measured in larger units for purposes of comparison, such as evolutionary distance per lineage when comparing lineages.

Evolutionary distance d_{evol} is simply the number of traits changed in each speciation event added up from the position of a species on a caulogram down to the base of the caulogram.

$$d_{\text{evol}} = \sum \Delta\text{traits} \tag{2}$$

Distance is an important measure by itself and is a justifiable measure of comparative resilience through time as historical sustainability. In evolutionary terms, it is equivalent to a measure of fixed mutations of adaptive value.

Velocity is a measure of motion, and momentum, as mass times velocity, is a measure of persistence. Current or instantaneous evolutionary velocity v_{evol} is the single number of changed traits (Δtraits) divided by the time as one speciation event sp.ev.

$$v_{\text{evol}} = \frac{\Delta\text{traits}}{\text{sp.ev.}} \tag{3}$$

Current velocity measures the present speed of change for one species as a single increase of traits in one speciation event, and it also establishes a two-sigma conduit excluding uncertainty through spacetime for that one new species, individuating it. Velocity of lineages has also been modeled for cladograms [48].

Cumulative velocity v_{cumevol} is the summed numbers of trait changes along a caulon divided by the number N of speciation events sp.ev., here $N_{\text{sp.ev.}}$:

$$v_{\text{cumevol}} = \frac{\sum \Delta\text{traits}}{N_{\text{sp.ev.}}} = \frac{d_{\text{evol}}}{N_{\text{ sp.ev.}}} \tag{4}$$

Cumulative velocity is a scalar measure of the almost steady pace of change of position (an average) of that species since the origin of the lineage.

Momentum p classically is $p = mv$, or mass times velocity, a vector. Current momentum is the directional force of the lineage at one speciation event. If mass is 1 species, then

$$p_{\text{evol}} = v_{\text{evol}} \tag{5}$$

This is the same as velocity given that $m = 1$ (that is, one species). The difference is that the velocity is the rate of change, while momentum is the force of inertia as an impact. Momentum increases linearly with speed (v). The current momentum is a measure of the amount of force needed to stop that one species in the lineage from any evolutionary change (turn it to stasis). Also, the average of all current momenta is a measure of the average force needed to stop into stasis any one species in the lineage, while the sum of all current momenta is the force needed to stop a lineage by stopping all species at once.

Cumulative momentum is a vector measure given the average directional strength of the lineage over its time of existence (a bar or arrow above the variable means it is a vector):

$$\overline{p} = \overline{v} \tag{6}$$

where $\overline{v}$ is total distance (trait changes) divided by total speciation events leading to the species on the caulogram; this may be termed historical inertia for that one species. This is the historical legacy or weight of evolution for that series of ancestral species ending in that one species. Summing cumulative momentum gives the directional weight of evolution for the lineage. A high cumulative momentum implies a deep macroevolutionary trend.

Force is mass times acceleration ($F = ma$) or deceleration if a is negative. It may be interpretable as increasing or decreasing resistance to environmental change, and is a measure of natural selection. Given the formula $F = ma$, evolutionary force is the amount of natural selection changing the description of an ancestral species into that of a descendant species via new traits (as mutations fixed through adaptive value). Acceleration implies more traits needed to successfully survive greater resistance in the environment, while deceleration implies fewer traits needed to survive, perhaps in a newly discovered narrow niche.

Acceleration is the difference, positive or negative, between the number of novel traits of one species (its rate) from that of its immediate ancestor. Cumulative acceleration is the sum of rate changes for one species (one mass) in a caulon divided by the number of speciation events. If the acceleration is not constant, as in evolutionary series, then the average rate (velocity at end minus velocity at beginning) is used such that a = average velocity/number of speciation events. Total force for a mass of two or more species is then the total mass times their average acceleration. For example, if the ancestor's initial rate (v_i) is two traits per event, and the current species rate (v_c) is five traits per event, the acceleration would be $5 - 2 = 3$. The force for that current species would be +3.

Force may be measured in other units of time, not just speciation events. Force using acceleration per speciation event is used for comparing internal processes of a lineage, but one may use time as per lineage for comparing lineages. For instance, force was

measured [16] in time units of lineage events, where acceleration is the difference between final velocity (∑ trait changes) and initial velocity (zero) divided by time (1 lineage). Of course, a species only exists since its origination in the lineage, not back to the origin of the lineage, but what is accelerated as mass during each speciation event is a species description, of about 45 characters in the present study, borne along by a succession of trait changes. This is like the final speed of the final stage of a multistage rocket. As the description lasts fairly intact with each speciation event (shared description is why it is a lineage), acceleration of any one species per lineage (as time) is the sum of all trait changes in the caulon down to the lineage base (accelerating from zero trait changes at lineage origin), divided by time (1 lineage).

Total work is the force needed to displace an object by a given distance. In this case, the sum of one species' average acceleration times current velocity (distance/time). Work is equal to the change in kinetic energy, except when there is a push-back against work from environmental resistance. Work energy is expended by transference to kinetic energy with various efficiencies.

The *TAU* is a new measure defined here as the work ($F \times d$) done by one unit of selective force over a distance of one trait change for one unit of time (a speciation event). This is equivalent in units to *KE* or ($\frac{1}{2}mv^2$) of one species ($m = 1$) changing at a rate of one trait per speciation event ($v = 1$), given the shared fundamental dimension of traits^2/events^2. The *TAU* is the evolutionary analogue of the joule (J) and is used as a unit for both work and potential energy.

Kinetic energy (*KE*) increases exponentially with speed (v^2), and is given by the formula (sp. means number of species)

$$KE = \frac{1}{2} \times \text{sp.} \times \text{V}_{\text{evol}}{}^2 \quad (7)$$

Work and kinetic energy are both measures of energy with the same units (joules in physics) but arrived at in different ways. Kinetic energy is the realized energy of evolution, exclusive of that wasted by resistance from environmental pressures.

Potential energy (PE) is tension to diversify, or force of selection times the unrealized change in traits. It differs from work by being stored energy, while work is a transference of energy.

$$PE = \text{Selection Force } (F) \times \text{Unrealized Change } (\Delta d) \quad (8)$$

(Think of Unrealized Change as how high above the ground a weight is or potential trait changes.) It is the as yet unrealized portion (*PE*) of the initial adaptive potential of 16 (numerator of Equation (1)), representing a potential of one species accelerating by four traits over a distance of four units (work = $ma \times d$), having total energy (*KE* + *PE*). It is the initial evolutionary capital, or stored work. Total energy (*KE* + *PE*) is when the genus is young (when *KE* is zero) and not yet undergoing resistance. The difference between total energy and *KE* is the draining of energy, where *PE* is dissipated by being converted to *KE.* The force decays by the power law function as genus grows in number of species.

3.3. Analysis of Spreadsheet Data

Tables 4 and 5 summarize numbers and rates of change in two lineages, Streptotrichaceae (STR) and Pottiaceae tribe Pleuroweisieae (PLE). These are here interpreted as to their evolutionary significance given processes similar to those of classical mechanics.

Table 4. Spreadsheet data on Streptotrichaceae caulogram. TotrCa is summed new traits or evolutionary distance in the caulon. ToEvSp is total number of speciation events leading to that species. InVel is instantaneous velocity (changed traits) of species at last species event. CuVel is cumulative velocity or total velocity divided by number of species events. AccIns is instantaneous acceleration (plus or minus change in distance (changed traits) of last species at that speciation event. ToAccGe is total acceleration of all species in the genus. Work is force times distance or total acceleration times total distance. *KE* is kinetic energy or 0.5 times one species times velocity squared.

Streptorichaeceae Genus	**Species**	**ToTr Ca**	**ToEvSp**	**InVel**	**CuVel**	**Acc Ins**	**ToAcc Ge**	**Work**	***KE***
IEG 1	unknown	4	1	4	4.00	4	4	16.0	8.0
IEG 2	unknown	8	2	4	4.00	0	0	0.0	8.0
Trachyodontium	unknown	11	3	3	3.67	−1	0	−11.0	4.5
	zanderi	11	4	4	2.75	1		11.0	8.0
Crassileptodontium	*pungens*	14	3	6	4.67	2	2	28.0	18.0
	wallisii	17	4	3	4.25	−1		−17.0	4.5
	erythroneuron	20	5	4	4.00	1		20.0	8.0
	subintegrifolium	20	5	3	4.00	0		0.0	4.5
Streptotrichum	*ramicola*	8	2	4	4.00	4	0	32.0	8.0
Austroleptodontium	*interruptum*	16	3	8	5.33	4	4	64.0	32.0
Leptodontiella	*apiculara*	11	3	3	3.67	−1	−1	−11.0	4.5
Microleptodontium	unknown	18	4	7	4.50	4	2	72.0	24.5
	flexifolium	18	5	3	3.60	−4		−72.0	4.5
	gemmascens	18	6	4	3.00	1		18.0	8.0
	umbrosum	18	6	4	3.00	1		18.0	8.0
	stellaticuspis	18	6	3	3.00	0		0.0	4.5
Rubroleptodontium	*stellatifolium*	24	5	5	4.80	−2	−2	−48.0	12.5
IEG 3	unknown	13	3	5	4.33	1	1	13.0	12.5
Williamsiella	*araucarieti*	24	4	6	6.00	1	−1	24.0	18.0
	tricolor	23	5	4	4.60	−2		−46.0	8.0
	aggregata	25	5	6	5.00	0		0.0	18.0
	lutea	27	6	2	4.50	−4		−108.0	2.0
Leptodontium	unknown	30	6	5	5.00	−1	−7	−30.0	12.5
	excelsum	37	7	3	5.29	−2		−74.0	4.5
	viticulosoides	37	7	3	5.29	−2		−74.0	4.5
	scaberrimum	39	7	5	5.57	−2		−78.0	12.5
Stephanoleptodontium	*longicaule*	17	5	4	3.40	−1	−3	−17.0	8.0
	syntrichioides	27	6	4	4.50	−2		−54.0	8.0
	brachyphyllum	26	6	3	4.33	0		0.0	4.5
	filicola	31	7	5	4.43	2		62.0	12.5
	capituligerum	31	6	3	5.17	−1		−31.0	4.5
	latifolium	34	7	3	4.86	−2		−68.0	4.5
	stoloniferum	35	7	4	5.00	1		35.0	8.0
Total		710	161	137	143.50	−1	−1	−326.0	312.5
Average		21.52	4.88	4.15	4.35	−0.03	0	−9.9	9.5

Distance (ToTrCa): STR and PLE have about the same number of traits: in total, 710 and 753, respectively, averaging about the same number of total caulon trait changes per species, 21.5 and 20.9. This is their evolutionary distance in total numbers of trait changes.

Time (ToEvSp) is here measured by successive speciation events, with STR having 161 sp.ev. averaging 4.88 per caulon, and PLE with 135 sp.ev. averaging 3.75 per caulon. STR has a longer time of evolutionary existence than PLE, as shown by the number of numbered columns in Tables 1 and 2.

Current or instantaneous velocity (InVel) is restricted to the number of traits changed in the last speciation event for one species, that is, $v = d/t$ for just one speciation event. STR has 137, averaging 4.15, and PLE has 131, averaging 3.64. Thus, comparing averages, STR has a more robust adaptive response than PLE, corresponding to a more robust environmental resistance or challenge.

Table 5. Spreadsheet data on Plueroweisieae caulogram. Table headings are the same as for Table 4.

Pleuroweisieae Genus	**Species**	**ToTr Ca**	**ToEvSp**	**InVel**	**CuVel**	**Acc Ins**	**ToAcc Ge**	**Work**	***KE***
IEG	unknown	8	1	8	8.00	8	8	64.0	32.0
Tuerckheimia	*guatemalensis*	12	2	4	6.00	−4	−8	−48.0	8.0
	svihlae	14	3	2	4.67	−2		−28.0	2.0
	valeriana	14	3	2	4.67	−2		−28.0	2.0
Eobryum	*anoectangioides*	13	2	5	6.50	−3	0	−39.0	12.5
	hildebrantii	16	3	3	5.33	−2		−32.0	4.5
	xeerophilum	15	3	2	5.00	−3		−45.0	2.0
Anoectangium	*aestivum*	18	3	5	6.00	0	−5	0.0	12.5
	euchloron	23	4	5	5.75	0		0.0	12.5
	radulans	26	5	3	5.20	−2		−52.0	4.5
	clarum	22	4	4	5.50	−1		−22.0	8.0
	incrassatum	26	5	4	5.20	0		0.0	8.0
	stracheyanum	21	4	3	5.25	−2		−42.0	4.5
	sikkimense	24	5	3	4.80	0		0.0	4.5
Ardeuma	*gracillimum*	17	3	4	5.67	−1	0	−17.0	8.0
	recurvirostum	19	4	2	4.75	−2		−38.0	2.0
	crassinervium	32	5	3	6.40	1		32.0	4.5
	annotinum	32	5	3	6.40	1		32.0	4.5
	aurantiacum	32	5	3	6.40	1		32.0	4.5
Gymnostomum	*aeruginosum*	20	3	5	6.67	0	−6	0.0	12.5
	viridulum	22	4	2	5.50	−3		−66.0	2.0
	calcareum	23	4	3	5.75	−2		−46.0	4.5
	mosis	22	5	2	4.40	−1		−22.0	2.0
Hymenostyliella	*llanosii*	18	3	5	6.00	0	−3	0.0	12.5
	alata	20	4	2	5.00	−3		−60.0	2.0
Hymenostylium	*xanthocarpum*	22	3	4	7.33	−1	−1	−22.0	8.0
	townsendii	26	4	4	6.50	0		0.0	8.0
Molendoa	*sendtneriana*	18	3	5	6.00	0	−2	0.0	12.5
	hornschuchiana	23	4	5	5.75	0		0.0	12.5
	peruviana	21	4	3	5.25	−2		−42.0	4.5
	handelii	24	5	3	4.80	0		0.0	4.5
Ozobryum	*warburgii*	18	3	5	6.00	0	−4	0.0	12.5
	missing link	23	4	5	5.75	0		0.0	12.5
	ogalalense	26	5	3	5.20	−2		−52.0	4.5
	mexicanum	26	5	3	5.20	−2		−52.0	4.5
Reimersia	*inconspicua*	17	3	4	5.67	−1	−1	−17.0	8.0
Total		753	135	131	204.25	−30	−22	−610.0	268.5
Average		20.92	3.75	3.64	5.67	−0.83	−2	−16.9	7.5

Cumulative velocity (CuVel) is the total velocity divided by total speciation events. It is the average speed of the lineage's change, or historical legacy or evolutionary weight. Comparing current velocity with overall velocity shows whether there is a slowing or increase in evolutionary velocity for that species. All the species travel at somewhat different rates yet the lineage moves as a unit, being adaptively coherent on account of their shared traits. For STR, this measure is 143.5, averaging 4.35; for PLE, it is 204.3, averaging 5.67. Comparing cumulative and current velocities indicates that STR (137:143.5) is slowing its rate of adaptation, while PLE (123:204.3) is slowing even more so. A common cumulative velocity is the result of processes holding a lineage together.

Current or instantaneous acceleration (AccIns) is simply the increase or decrease in numbers of new traits from the one immediate ancestor. Adding current acceleration for all species (negative and positive rate changes in the spreadsheet column) for STR yields −1, averaging −0.03, and for PLE gives −30, averaging −0.83. Here PLE shows a major lineage-wide (and long) decrease in adaptive power.

Force, when used to compare internal lineage processes, is mass (species) times current acceleration for one species, which is essentially the same as current acceleration (AccIns) for any one species. The average current acceleration is used for force of multiple species. Force is equivalent to selection pressure. When comparing lineages, force is calculated with acceleration as change in velocity from the beginning of a lineage (zero) to each species (∑trait changes). The total force for lineages is simply the sum of all trait changes leading to each species (ToTrCa), which provides comparative force values of 710, averaging 21.52, for STR, and 753, averaging 20.92, for PLE. Evolutionary force is similar for the two lineages but distributed differently through the lineage and through time; see comparative values of velocity, acceleration, and work.

Total acceleration of genera (ToAcGe) summarizes the change in rate of trait changes for all species in a genus. For STR, the total is −2, averaging 0, while for PLE the total is −22, averaging −2. Again, STR demonstrates higher rate or at least force of adaptation. Particular genera in these lineages may be signaled out as well adapted in STR (*Crassileptodontium* and *Austroleptodontium*), while some in PLE are apparently very weakly adapted to current conditions (*Anoectangium*, *Gymnostomum*, *Ozobryum*), although some species in each genus are much better adapted than others.

Work is force times total distance as a measure of evolutionary power overcoming entropy and ensuring homeostasis, as measured in Taxonomic Action Units (*TAU*) (see Table 3). Work for STR is −326.0, averaging −9.9, while for PLE it is −610.0, averaging −16.9. The negative values are the energy cost of the environment and indicate that work is energy dissipated by environmental friction (resistance). Clearly, STR is more efficient in operating against environmental resistance. This may be why PLE has a shorter time frame than STR.

Kinetic energy is viewed as an acting force of evolution. For STR, the values are 312.5, averaging 9.5, and for PLE the values are 268.5, averaging 7.5. Comparing total work and kinetic energy values (Tables 3 and 4) gives an idea of the resistance of the environment to the evolutionary force of the lineage. For Streptotrichaeceae, work value is −9.9 and *KE* is 9.5; there is a net (between absolute values) energy of 0.4. In Pleuroweisieae, work value is −16.9 and *KE* is 7.5; there is a net energy of 9.4. There is an energy deficit for both lineages, but the amounts differ greatly. See discussion of the Efficiency Ratio below.

Potential energy is the difference between *KE* actually realized and total possible energy (*E*), as measured in Taxonomic Action Units (*TAU*). For example, if a species is currently changing at six traits per event ($v = 6$) and pressure is steady with force = 1, it is almost at its adaptive peak and thus the adaptive gap (Δd) = 1. According to Equation (7), $KE = 18$ and $PE = 1 \times 1$, or 1. Total energy ($PE + KE = E$) = 19. If the force is higher, *PE* is higher, and so is *E*. If an ancestral species has two changed traits and its immediate descendant changed six traits, then acceleration is $6 - 2 = 4$; mass = 1; and force is then $1 \times 4 = 4$. In this latter case, the environment provided a force of 4 to the descendant to make it evolve three times faster than its ancestor. Evaluations of the *PE* of individual species are easily made from Tables 1 and 2, where high *PE* implies high adaptive tension with environmental force restricted by high resistance or drag (*k*). The *PE* provides the initial impulse for speciation by the environment, and immediately becomes KE, which decays at the rate of $16/x^{1.161}$, the inverse function for the Pareto Fractal Dimension. This is the evolutionary mechanics of the origination of species.

The Efficiency Ratio

Efficiency Ratio (η) is a measure of the percent of total energy input (work) converted to useful output (*KE*). It is possibly the best measure for comparing the evolutionary

mechanics of lineages. The formula uses the absolute value of energetic work |W| because the value simply reflects environmental resistance or friction:

$$\eta = (\frac{KE}{|W|}) \times 100\% \quad (9)$$

The efficiency ratio for STR is, 96%, while that for Pleuroweisieae is 44%, this latter being a figure characteristic of high evolutionary impedance. The Streptotrichaeceae is highly efficient in using its evolutionary power to generate *KE*, but the Pleuroweisieae apparently has much of its energy dissipated by genetic load (deleterious mutations), environmental buffering (cost of retaining stasis in face of hostile environment), or adaptive constraints (difficulty adapting given form and function); thus, in all, it is dissipated as "evolutionary entropy," that is, wasting work while trying to generate *KE*. On the other hand, the Pleuroweisieae caulogram (Table 2 and Figure 4) shows eight branches from one ancestral species near the caulogram base. There is room for at least two extinct genera each of four or five species to be inserted between the terminal genera and their extant ancestor *Eobryum anoectangioides*. The "lost" *KE* may well have been used to generate now-extinct intermediate genera not presently inferable from morphological data and which conform to the expected smaller size of microgenera. Forces theoretically involved in balancing speciation rate versus extinction rate have been detailed for cladograms [18] but without the present interpretation via evolutionary mechanics.

Other metrics for evolutionary distance use phenotypic units like centimeters, e.g., haldanes, using standard deviation per generation (e.g., [44]), or darwins, this being *e*-fold change in a trait per million years. The present equivalence of species, speciation events, and character-state change with physical units of mass, time, and distance provides a new, rich perspective on macroevolution.

3.4. Geometric Modeling of the Rule of Four

3.4.1. Ecology

The caulograms, represented as Tables 1 and 2, depict genera as having up to four immediate descendant species (including all branches), each of which shares the ancestor's novel traits as imbued monothetic isomorphism, plus some secondary ancestry, descendants of descendants, these often not with full isomorphism. Theoretically the immediate descendant species are buffered by this partial isomorphism for a shared sympatric niche, while the secondary descendants are somewhat more prepared for survival in any discovered peripatric and allopatric niche. The secondary descendant species are freed by diminution of ancestral isomorphism to explore for niches occupiable by heterophyletic groups, all with shared adaptive novel traits [22] (p. 121). This sympatric clustering of immediate descendants by isomorphism and peripatric and allopatric fanning of secondary descendants with apparent out-clustering by novel traits is clearly expressed in the caulograms. Inasmuch as all taxa (Figure 1) are apparently controlled by the formula of Equation (1), success through resilience, as moderated by processes of evolutionary mechanics, extends to the ecosphere. The Pareto ratio of 20:80 may be active in ecosystem processes involving primary productivity and dominance, resource use and niche occupancy, and spatial and abundance scaling, but fractions in Pareto ratios are of fractions of one group (20%) controlling fractions of a different group (80%), not simple proportions, and this difference is not emphasized in the literature. There are, however, some intriguing observations of an apparent Pareto ratio functioning in nature [55]. Some ecological studies e.g., [56–58], cite Pareto-like fractions.

3.4.2. Environmental Limitation on Size of Microgenera

A geometric model of radiative evolution has been advanced [59] to provide an explanation for the Rule of Four constraining the number of immediate descendant branches to a maximum of four. The model for Pareto Fractal speciation shown in Figure 2 requires the one species to be at the same time the descendant of one microgenus and the ancestor of the next. An analogy [59] for this double-duty is "soap," a surfactant molecule that is soluble in water at one, ionic, end, and in oil at the other, non-ionic end. Thus, an ancestral species may be modeled as two entities distinguishable as two sets of isomorphic traits. A descendant species includes about four traits contributed from the newest traits of the ancestral species plus about four traits newly evolved from old less important traits of the ancestor. The "action" is with the eight newest traits, four shared by the immediate ancestor and immediate descendants, and four shared by each descendant with other species in other groups, each eventually ending up in a novel phyletically heterogeneous niche [22] (p. 121). Shared ancestral traits comprise the isomorphic buffering for descendant species sympatrically, while the new traits of the descendant species explore survival opportunities peri- and allopatrically and, if particularly successful, generate a new genus of four new species buffered by those new traits. If not so successful, survival is enhanced by sharing their newest traits with other species of other groups adapted to the same habitat and together protecting that habitat. For this reason, the double-duty of surfactant genus-ancestors may be duplicated in models of crowding as generative of the curves in Figure 1, the model of genusation in Figure 3, and the numerator of 16 as the square of 4 in Equation (1). Double-duty species acting as both descendant and ancestor also resist extinction longer than other species, perhaps due to double-buffering.

3.4.3. Individuation

To place these metaphors in a complexity-related perspective, these sections of taxa through time reveal a two-sigma exclusion field effective at multiple scales. Each species, through an odds table associated with sequential Bayes [16,22], excludes about 95% of uncertainty, which promotes individuation, that is, by two sigma (two standard deviations). A species with fewer than four traits is to some degree selected against by established taxa, while more than four traits do not increase exclusion of uncertainty by any great extent. It is apparent, given the Rule of Four (optimally four traits per species, four species per genus, four genera per family), that this exclusion of uncertainty operates self-similarly at many biological levels.

More exactly, in information theory, having four bits of information allows one to distinguish between $2^4 = 16$ equally likely possibilities. For a pool of, say, 20 potential species, you need 4.32 bits of information or $\log_2(20)$ to identify one species with certainty. Actual data indicate that Streptotrichaceae (STR) averages 4.3 traits per species, and has 22 immediate branches requiring distinction, and Pleuroweisieae (PLE) averages 4.54 traits per species, and has 25 immediate branches needing individuation. Given $\log_2(22) = 4.46$, and $\log_2(25) = 4.64$, it is clear that both lineages have just enough average informational bits per speciation event to individuate all species by exclusion of at least 95% of uncertainty. Because traits do change and, in quantity, are not affected by extinction, numbers of traits per species is a better measure for two-sigma analysis than numbers of taxa per higher rank. In any case, individuation is apparently similar across scales, given the 16 estimated as the numerator of three graphs of taxa per higher rank (Figure 1).

The above suggestions are about the "how" of individuation. The "why" is speculative. The strong differentiation of species replaces at the lineage level the combinational variation in species associated with genetic exchange, while shared ancestral traits anchor the general adaptive character of the lineage. Rampant or even moderate genetic exchange between

species would tend to homogenize groups (actual horizontal genetic exchange not being massive). Exposure to strong selection on homogenized lineages that are as vulnerable to extinction as are species would have a negative impact on whole ecosystems. A fan of species, each with new, divergent traits (Tables 1 and 2), is of positive value to the survival of lineages. Darwinian selection acting at the lineage level may eliminate homogeneous sets of species in toto or in part. Individuation through 2-sigma exclusion of uncertainty for taxa at all ranks may be a very early adaptation for the survival of ecosystems. Natural selection against genetic exchange above the species level may be the reason why species differ in the first place.

3.4.4. The Rope Model

Square-section microgenera as evolutionary ropes model the speciation results shown in Figure 3. The figures for square-section microgenera (Figures 5–8) show that increasing the diameter of the lineage modeled as rope-through-time by adding four duplicates creates a self-similar reconstruction of the rope at a larger scale, with the same exclusion of two sigma of uncertainty at the new scale. Those who appreciate a visual explanation might view the outside of a single circle (species) as the improbability preserved by natural section, and the larger inner portion as the excluded more probable, higher entropic, and less adaptive possible expressions of the species. The outside of the circle represents the shared novel traits, or immediate ancestron, of the shared ancestral species. The larger the number of filaments in an evolutionary rope, the more inclusive are the shared traits, acting as an immediate ancestron for the nested taxonomic group. The distinguishing descriptions of these nested taxonomic entities are emergent properties associated with individuation through two-sigma exclusion of uncertainty.

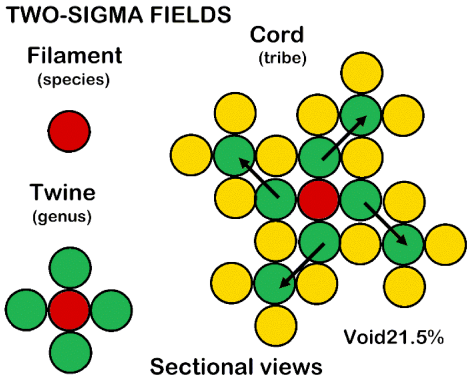

Figure 5. Two-sigma fields for taxonomic species, genus, and tribe. FILAMENT: Section through time of a four-dimensional species, excluding uncertainty in center of circle. TWINE: The same for a four-dimensional genus (progenitor in red) of five species (descendant species in green). CORD: The twine of the genus is wound about by four other, different genera (progenitors in green, each generated by ultimate ancestor in red) to make a fractal taxonomic tribe. This is a hypothetical projection of the results of Rule of Four coupled with self-similar fractal dimension of ln5/ln4. Arrows connect descendant species with their double-duty action as progenitors of the next microgenus (the two connected circles are the same species). Although circles with arrows in them are the same species, the base of the arrow marks the immediate ancestron traits all shared by species of the ancestral microgenus, and the arrowhead marks the shared novon traits of that descendant-turned-ancestor of the new microgenus. Thus, evolutionarily speaking, the two arrowed circles, though of the same species name, participate in distinct adaptive processes associated with their two distinct but causally connected microgenera.

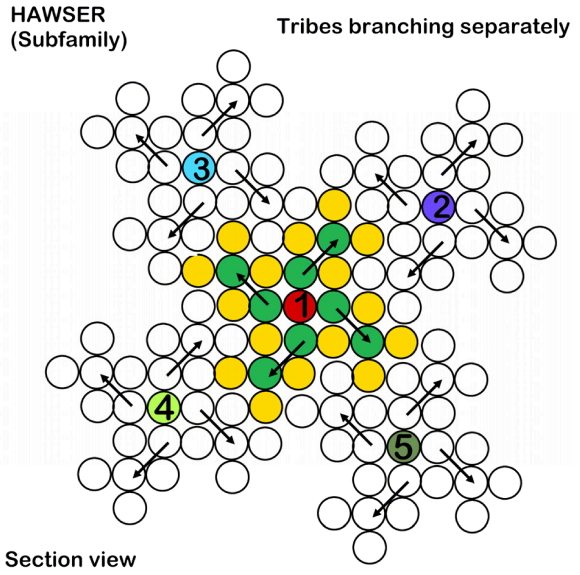

Figure 6. Two-sigma fields, continued. HAWSER: Section through time of a fractally wound lineage hawser composed of a central genus of five species (central progenitor 1 is deep red). The central genus (deep red progenitor and green descendants) of an ancestor plus 4 species is wound about by four other genera (green circles with yellow descendants), to make a tribe of 20 (16 plus 4) immediate descendant species. This central-colored complex is, again hypothetically, wound again by four other tribes (generated by progenitors numbered 2, 3, 4, and 5) to make a subfamily of 100 (20 times 4 plus 20) immediate descendant species. This is a thicker rope of another, higher taxonomic rank, an evolutionary hawser. Again, the arrows connect species that are both descendants of an ancestral genus and are themselves ancestors of a new genus. Tribes generated on separate branches maintain the fractal dimension of ln5/ln4. Ancestors 1–5 on separate branches ultimately generate separate tribes that tile well.

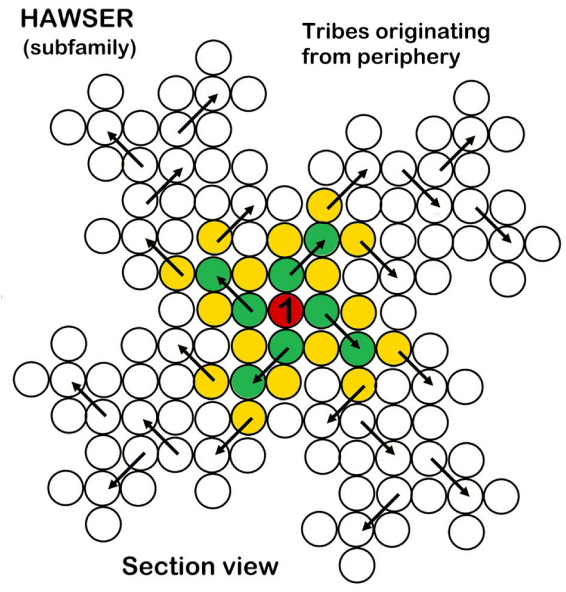

Figure 7. Two-sigma fields, continued. HAWSER: All genera originate from one central ancestor (red). The quadrate section of the evolutionary rope is maintained by optimizing mutualism, but new crowding in outer layers of tribes lowers exposure to environmental resistance and constrains descendants of descendants to origination of only one or two new genera each, as reflected in Tables 1 and 2. Most outer genera are incapable of generating more than two secondary descendants capable of becoming new genera, while the central genus originates four. Every generation, however, continues to allow four immediate descendants per genus, maintaining the ln5/ln4 fractal dimension at that level.

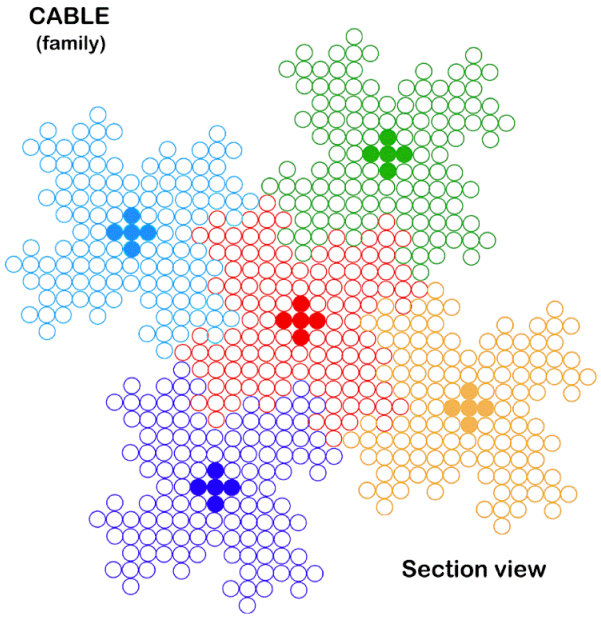

Figure 8. Two-sigma fields, continued. CABLE: Section through time of a massively fractal lineage of a central genus of five species, or evolutionary twine (solid red dots), wound about by four other genera (all in red), to make a tribe, or evolutionary cord. This complex is, again hypothetically, wound by four other tribes to make a subfamily, or evolutionary hawser (all red). Four hawsers are wound about this to make a five-hawser family, or evolutionary cable. Different colors distinguish the five subfamilies.

The arrows in Figures 5–7 connect circles of the same species name; the arrow base is isomorphic to the ancestral genus and the head is isomorphic to the descendant genus. Because of this overlap, each set of five circles in a cruciform arrangement represents one isomorphism. To the extent that these different newest traits (ancestral for arrow base and novel for arrowhead) operate in the macroevolutionary process, the same ancestral species can do double duty in modeling environmental crowding. The central deep red circle represents ancestor as the arrowhead of a more ancient descendant species of an unknown or unmodeled ancestral genus. The geometric crowding model of the control of speciation is remarkably reminiscent of the Bohr atom electron shells being controlled by the Pauli Exclusion Principle. Doubtless the actual forces involved are different.

The identity of a descendant species with an ancestral species (diagrammatically two circles connected by an arrow) requires modeling of two minimally monophyletic groups with the same species in both ancestral and descendant positions. To understand this, a familiar parallel may be made: Consider a cook who takes meals in one restaurant and makes meals in a second, different restaurant. The second restaurant has only cooks for customers, and they dine there but likewise make meals in other restaurants that also serve only cooks. The question is how many cooks are there in one restaurant at mealtime (which parallels the problem of how many species there are in a microgenus when a burst of speciation generates the microgenus)? Inference from data says about five, this being one ancestor and four descendants. A genus is also distinguished as monothetic (all five species share at least some traits) by a characteristic isomorphism of about four identical traits. This is paralleled by assigning each restaurant a different specialty (French, Thai, Tex-Mex fusion).

An image of a present-day section of various thicknesses of evolutionary rope is given in Figures 5–7. There is evidence that the empirically based optimally sized genera of five species (one ancestor plus four immediate descendants) (Figures 5–8) are largely generated most recently, while genera with five or six immediate descendants (Figures 9–12) are

lacking. Thus, for the five-species microgenus, the rope section at a recent moment in time shows a central filament of an ancestral species (red) surrounded by four immediate descendant species' filaments (green) (the "twine" in Figure 5). That hypothetical optimal microgenus ("twine") is, self-similarly, surrounded by four similar genera ("cord") (green and yellow). Gradually increasing wrapping of rope from twine to cable models the hierarchical nature of ranks in taxonomic nomenclature.

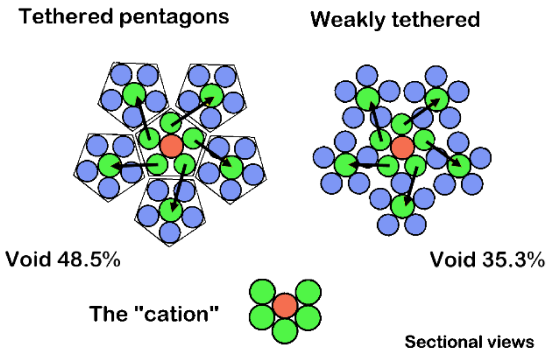

Figure 9. Pentagonal arrangement of ropes of one central ancestor (red) surrounded by five descendants (green) with their own descendants (Blue). Arrows indicate ancestor-descendant identifies. Tethered arrangement has parallel sides. Weakly tethered microgenera are more strongly pressed together. The "cation" is hypothetical critical arrangement easily collapsing to (1 + 4) microgenus by extinction or ratcheting up to (1 + 6) microgenus.

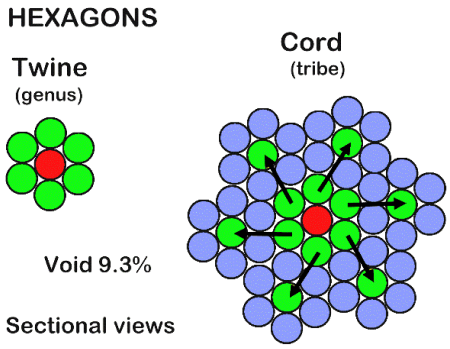

Figure 10. Two-sigma fields for a hexagonal genus section. The microgenus or twine shows the ancestor or central filament as red, and six immediate descendant species in green. The tribe or cord shows the central genus wound about with six other, related genera (blue with central double-duty ancestor in green). As in all figures, arrows show critical ancestor-descendant identities leading to overlap.

An image of a section in the Now of a hypothetical larger evolutionary rope or hawser is given in Figure 6, where the cord of Figure 5 is further wound about with four other cords (uncolored), making the entire "hawser" of branching filaments a cylinder through time composed of species, genera, tribes, families, etc. Note the deep indentations that accurately accept additional evolutionary quadrate taxa. Arrows connect descendant species with their double-duty status of progenitors of the next 5-species genus. The original genus has all descendants capable of originating a new genus, and this obtains if each additional genus is originated separately by a more basal branch.

A variant of hawser evolution is modeled in Figure 7, in which the central tribe generates directly the four surrounding other tribes in the evolutionary rope section. The arrows show generation of the quadrate genera from peripheral genera of the central cylinder resulting in 16 descendant species. Four species generate four species each the source of the numerator in the inverse power function (Equation (2)). Although the five-

species genus is maintained, only one or two new genera are possible peripherally because of crowding (limiting the speciation to 16). This matches the Figure 3 model of speciation showing only two descendants of descendants; such secondary descendants are common in Tables 1 and 2.

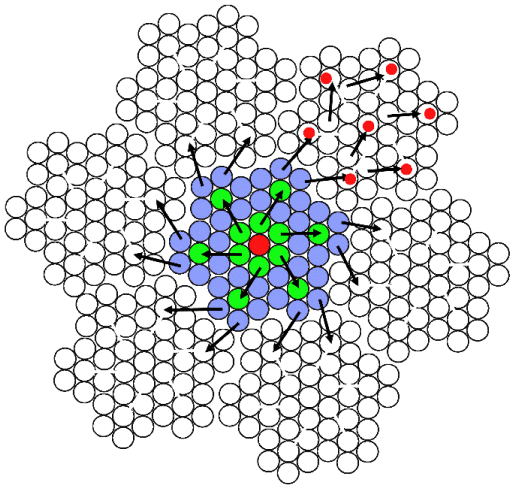

Figure 11. Hexagons fused closely, showing potential gradual accumulation of additional hexagons from one ancestral species (in red). Void is 9.3%. Generation of hexagons by outer species (in uncolored circles) is limited to one or two per genus by crowding although the potential for six immediate descendants remains an option. Arrows are ancestor-descendant identities where one descendant acts as the next genus' ancestor.

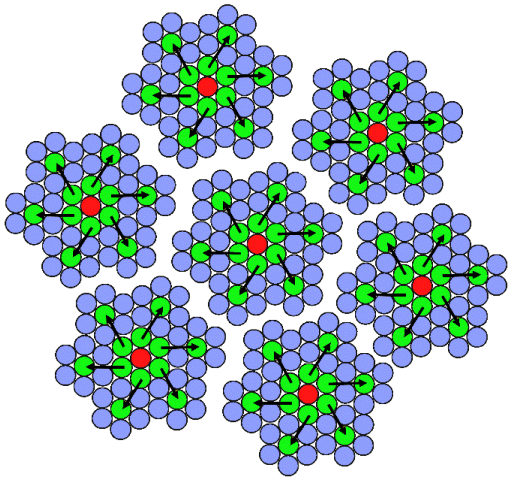

Figure 12. Hexagons separated to imply separate origin in past from a shared common ancestor. There is presently no evidence of this.

The evolutionary hawser may be compounded into a "cable" (Figure 8) by additional winding with four hawsers. The circles of the diagram fit together precisely because the five-species central element is essentially a square in section, and squares fit perfectly. Because the graphs in Figure 1 are generated by the numerator 16 for Equation (1), and the hawser (subfamily) model in Figure 7 requires two not four genera originated peripherally, evidence maintaining the numerator 16 (Equation (1)) favors windings of an evolutionary rope by separate "cords" of about five genera branching from the main line (caulon) and not peripheral generation of new genera from only one ancestor (Figure 7).

Circles generating singletons, pairs, triads, and 1 + 6 hexagons also fit perfectly, but evolution is apparently, at least initially, quadratic and followed by gradual extinction. The point of this exercise in geometric modeling of crowding is to encourage the apprehension

of taxa as complex and self-sustaining systems in time that exhibit coordinated trends towards both regularity and change.

3.4.5. Analysis

The nested sets of species in Figures 5–12 are intellectually neat, but do they represent real emergent processes? What are the underlying causes? Using the somewhat fraught principle of the excluded middle, one might say that taxa must be supported by this process because no other postulated process generates the observed individuation of taxa. (The excluded middle principle can be dubious, e.g., "the Earth is either hollow or flat, so proving that it is not flat proves it is hollow.") The challenge of having a theory is at least better than no theory at all, but there is also a geometric explanation.

The little quadratures of five-species microgenera (Figures 5–8) each have a fractal dimension of ln5/ln4, or 1.161. The four sides fit perfectly and represent interaction with other species through competition and mutualism in a crowded habitat (niche or community). This maximizes the necessity of individuation. If there is too small a number of immediate descendants, then the genus erodes through competition, and if there is too high a number of immediate descendants then the genus has wasted some of its kinetic energy or power of sustainability.

If species are energetically equivalent to their niche, then the fact of secondary descendants (Figure 3) implies heterogeneity to the genus' habitat. It may well be that genera like *Stephanoleptodontium* with many secondary descendants integrate over tens of millions of years the changes in their environment and reveal this in their sequential adaptations. This is a potential tool for ecologists, paleontologists, and biodiversity researchers.

A model of a genus with one ancestral species and five immediate descendants clearly makes a loosely wound rope (Figure 9), whether arranged by pentagons or tightly fused. If the descendants are not equally spaced (the "cation") the genus is readily modified into a potentially more stable 4- or 6-descendant genus.

A hexagonal arrangement of one central ancestor and six immediate descendant species also can be tightly packed into a well-fitted, fractal model (Figures 10–12). The number of species in a genus is only critical, apparently, at the onset of speciation, where four not six new isomorphic species are immediately (within 22 my [22]) generated. During a series of extinction events for a genus, the observed continued survival of the established immediate ancestron—with its set of four generalist traits—is apparently sufficient to sustain even one species of the genus for as long as 100 my.

The quadrate model of one ancestor and optimally four descendant species in four dimensions may also be represented more compactly by a Boerdijk–Coxeter helix, a linear stacking of regular tetrahedra [41], also known as a tetrahelix [42]. This does make an evolutionary rope, assuming an ancestor in the center of each tetrahedron, but how these tetrahedral series might branch and fit laterally timewise to form a larger group is a complex and as yet unexplored subject [43]. It is possible that time may be modeled as distance in three dimensions from a central ancestor, with quadrate speciation as expanding tetrahedra or caltrops.

3.4.6. Calculations and Packing Ratio

The geometrical support for this analysis may be had in the special relationships of an analogous 4-dimensional evolutionary rope, each fiber a microgenus of one ancestral species surrounded at least initially by several descendant species. The question is, how are numbers of descendant species limited under this model? Here a minimally monophyletic genus of one ancestor and four descendant species is coded as (1 + 4); for one ancestor and five descendant species, use (1 + 5), etc.

In one microgenus (minimally monophyletic group) the maximum number of immediate descendant species is empirically [9] four, while a maximum of two more secondary descendants may occur, occasionally, as descendants of descendants, possibly reflecting in part generation at the periphery (Figure 7), where crowding limits speciation. Two species, *Stephanoleptodontium* in STR and *Anoectangium* in PLE, have three secondary descendants, which may be explained by extinction of related species that relieves crowding. (An isomorphism of shared novel traits of the ancestral species unites all immediate descendants as monothetic, and no secondary descendants show the burst of speciation characteristic of generation of another minimally monophyletic group, again because of possible crowding.) The tentative suggestion is that maximizing numbers of immediate descendant species is evolutionarily positive, but there is an ultimate cap to this. Although some few microgenera in the studied lineages are of up to seven total species (1 + 3 + 3), most genera max out at five total species (see Tables 1 and 2).

Assuming all species have the same radius of the analogous evolutionary filament running through time, the packing ratios may gauge the level of competition and mutualism of the species in the genus. Given that the ancestor and four immediate descendant species have the same set of the ancestor's new traits, mutualism as tolerance to crowding seems supremely important at least to the taxa studied, which mostly have a patchy, marginal synecology.

For a genus of 1 + 4 species, the section of filaments is quadratic and cross-shaped in section, called "twine" or genus in Figure 5. Four other microgenera of the cross-shaped morphotype fit into the original twine microgenus to make a "cord" or tribe of the fractal dimension of ln5/ln4 or 1.161, the same as for a (1 + 4) microgenus (Figure 5). The cord of the tribe can be entwined about with four similar (1 + 4) tribes to make a "hawser" or subfamily (Figures 6 and 7) and then again, self-similarly, to make a "cable" or family further entwining four more hawsers (Figure 8). Clearly, a hierarchical system of nomenclature nesting similar groups is implied here, with increasingly nested taxa of five elements each. The four indentations in cords, hawsers, and cables make this model evolutionarily open.

The five-species cross in Figures 5–8 is loosely packed but more coherent than that of the six-species pentagon (Figure 9). The somewhat loose packing then allows for easy tiling with other five-species genera, that is, the fractal group is topologically open. In a checkerboard grid of many quadrate (1 + 4) microgenera, each circle with area = πr^2 can be inscribed in a square of side $2r$, or area $4r^2$. Thus, the packing ratio of a single (1 + 4) fiber is about 78.5%, leaving a total void of 21.5%:

$$\text{Packing ratio} = \frac{\pi r^2}{4r^2} = \frac{\pi}{4} = 0.7854 \quad (10)$$

Pentagonal packing is problematic because there is no geometric stability. The outer species (circles) do not touch each other, do not provide mutual support, and are less coherent monophyletically. Viewed as separate ropes, pentagonal cords have either 48.5% voids ("tethered" in Figure 9) or 35.3% voids ("weakly tethered") when closely fused.

Hexagonal packing, one ancestral species surrounded by six descendant species, is optimal as the densest way to pack circles in two dimensions. The packing ratio is $\pi/\sqrt{12}$, or 90.6%. It is the Hexagonal Close Packing Limit. Considered as nucleation, the energy needed to add new species is superseded by ease of starting a new cluster. The geometrically hexagonal (1 + 6) microgenus is, in terms of 2-sigma individuation, over-defined, with many redundant species as a buffer to extinction. The crowding inhibits origination of new microgenera, leading to a dead end in novelty, which is perhaps why no clear-cut microgenera with five or six immediate descendant species are extant.

Square packing (1 + 4 genera) leaves about 21.5% as empty gaps, but hexagonal packing (1 + 6 genera) leaves only 9.3% as empty space. The voids model environmental resistance that powers, through adaptation, the generation of new species, but hexagonal packing isolates evolvability.

Implied then is that during the initial burst of speciation, the maximization of descendants is interrupted by the instability of pentagonal packing of the (1 + 5) microgenus with variable, large voids of 48.5 to 37.3%, while the cross-shaped section of the (1 + 4) microgenus has immediate fitness through a balanced mutualism, and makes quadrate groups most likely to initiate new adaptable microgenera without over-crowding. Thus, the evolvability of the five-species quadrate mutualism, plus the geometric barrier of the six-species pentagonal configuration, limits immediate descendants to four. In addition, the hexagonal section of seven-species microgenera (1 + 6) is evolutionarily closed because the bundle is saturated and there are no "hard points" or buds to attract tiling. In seven-species microgenera, evolution has shut down. Minimally monophyletic groups of four immediate descendants are thus of survival value to the ecosystem.

3.4.7. The Rule of Four

The actual curves of numbers of real taxa per next higher rank as given (Figure 1) show the fixed point, where x = y and slope is -1, as 3.6 for the inferred five-species microgenus. The curves of possible six- and seven-species microgenera (one ancestor plus five or six immediate descendants) are rather different (Figure 13). The shapes of the curves are very similar, as controlled by the denominators in Equations (3)–(5), but the positions of the curves on the y-axis are distinctly different because the numerators of the generative formulae are no longer 16, but instead 25 and 36. The fixed points are about 4.6 for the six-species pentagonal curve, and 5.6 for the seven-species hexagonal curve, easily detected if curves of taxa per next higher rank were truly universal as implied by Figure 1. The y intercept is at 16, 25, and 36 for the curves in Figure 13 as squares of the numbers of immediately generated descendant species in one microgenus.

$$\text{Cruciform section } f(x) = \frac{16}{x^{\frac{ln5}{ln4}}} \tag{11}$$

$$\text{Pentagonal section } f(x) = \frac{25}{x^{\frac{ln6}{ln5}}} \tag{12}$$

$$\text{Hexagonal section } f(x) = \frac{36}{x^{\frac{ln7}{ln6}}} \tag{13}$$

Square packing then suggests that 21.5% of potential environmental resistance generates 78.5% of potential evolutionary novelties, so also 21.5% of potential Gibbs free energy generates 78.5% of evolutionary entropy. This is evidence for a further imposition of the Pareto ratio of 20:80 as a force in nature.

The actual curves in Figure 1 have the denominator 16, demonstrating that taxonomic ranks are ordered by powers of 4, where every generation of a set of genera involves four species each generating four new species, totaling 16. Because of the limitation to origination of only two genera peripherally (Figure 7), 16 is the maximum number of species for quadrate origination of genera. A taxonomic magnitude, comparable to decimal magnitudes of powers of 10, is a power of 4. In terms of the optimal four immediate results of the origin of taxa, a twine-genus is 4^1, a cord-tribe is 4^2, a hawser-subfamily is 4^3, and a cable-family is 4^4. Apparently, nature is hexadecimal in the generation of multiples of 16 of new, different taxa in sequential waves.

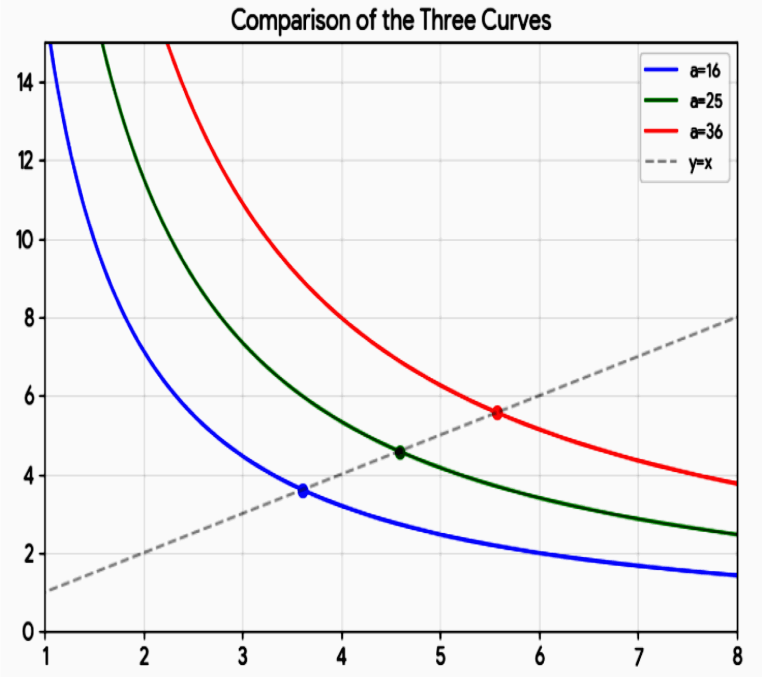

Figure 13. Graph of five-, six-, and seven-species curves. Fixed points (where x = y) are about 3.6, 4.6, and 5.6 for cross (numerator 16), pentagon (25), and hexagon rope (36) sections, respectively, and can be used to easily distinguish curves when axes are poorly numbered.

3.4.8. Extinction

Upon extinction of one or more species of a five-species cruciform microgenus, the resulting microgenus of only one to four species is transitional with lower buffering geometrical support, but the individual surviving species each have about four novel and characteristic traits, which act to exclude two sigma of uncertainty for each species. Thus, tribes and families may only gradually go extinct, with a trail of more ancient species retaining their initial individualization. Speciation is initially rapid, originating new species buffered from competition by mutual isomorphism of novel ancestral traits, while extinction is gradual because the species remain individuated by their ca. four newly fixed traits, and are also buffered by shared novel non-ancestral traits in a phyletically heterogeneous ecological niche.

The strong mutualistic protection offered in long-term survival of genetically heterogeneous niches [22] (p. 121) may explain why origination of new genera is rare from near the base of the caulogram. Figure 14 models the extinction of a five-species microgenus hawser occurring first in the central and older portions of the lineage, leaving four different lineages with extinct ultimate ancestors. If the tribes were separately branched (Figure 6), then extinction would begin at the center of each tribe. The difference between one-ancestor hawsers (Figure 14) and multiple ancestor hawsers (Figure 6) is the isolation of the apparent ancestor (green in Figure 14). Thus, Streptotrichaceae may have been ultimately derived from a single entirely extinct hawser, while Pleuroweisieae was derived from 1 of 4 or 16 centrally extinct hawsers. Then it is probable that Pleuroweisieae consists of reduced forms of an early extinct ancestral set of Trichostomoideae, given the shared lanceolate leaves with plane leaf margins and occasional pleurocarpy, just as Rhabdoweisiaceae is a reduced set with roots in extinct ancestors of Dicranaceae. Failing fossil evidence, geometric and morphological evidence provide the only window onto the evolution of these lineages in the early and middle Cretaceous.

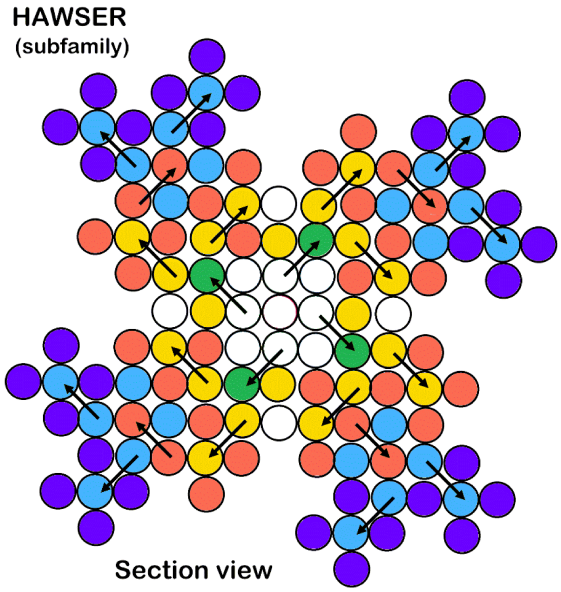

Figure 14. Rope of quadrate five-species microgenera is similar to that in Figure 6, but many of oldest species are extinct (empty circles). The remaining four branches of this lineage become isolated as separate lineages with unknown ultimate ancestral species. The arrows indicate ancestor-descendant identities.

Any isolated remnant units of one, two, and three species naturally fall into the hexagonal packing clustering, with characteristic minimum 9.3% void, effectively cutting off generation of new species by limiting exposure to environmental resistance. The rarity of new branches from relict species near the base of the caulogram is borne out by Tables 1 and 2. In addition, such smaller portions of a microgenus have had time and opportunity to establish in multi-taxon ecological niches that mutually protect from competition.

3.4.9. Extinction Pressure

Given that any descendant species can potentially become an ancestor of a descendant genus, why are there so few genera? Extinction pressure may be calculated as a ratio of the number of taxa theoretically possible given no extinction divided by the actual number of extant taxa. As to number of species possible, we can estimate very generally four descendant species in each genus, assuming each genus is a separate branch and not affected by other branches. We here define a genus by its maximum of four immediate descendant specie. Table 6 provides the calculated potential number of species for the lineages of STR and PLE, including inferred extinct genera and species. Extinction pressure is given as how many times greater the potential taxon origination might be than the actual for numbers of genera and species. Potential is simply a power of four species at each ancestral level leading to the farthest terminal genus.

In STR, the terminal genus *Stephanoleptodontium* is established at five nodes on the caulogram (Table 1), while for PLE, there are only three genus level nodes as farthest distance along the caulon. Potentially then, STR might have 128 genera and 512 species without extinction, compared to PLE (Table 2) with 16 genera and 64 species. Actual genera and species for the two lineages (Table 6), excluding inferred extinct taxa, are as follows: STR 10 genera and 27 species, and PLE 10 genera and 34 species. Extinction pressures for STR are 12.8 for genera and 19.0 for species, and for PLE 1.6 for genera and 1.9 for species.

Table 6. Numbers of potential genera and species and of actual genera and species, excluding inferred extinct genera for Streptotrichaceae (STR) and Pleuroweisieae (PLE). Level is distance from caulogram base along longest caulon (largest number of sequential ancestors and terminal taxa). PLE+ is number of genera and species enhanced by eight extinct genera increasing the potential to level 4. PLE++ provides measures for the lineages if originated at the same time (level 5).

Level	Potential Genera	Actual Genera, Excluding IEG		Potential Species	Actual Species		Extinction Pressure for Genera; Species. PLE at Three Origination Levels, PLE+ at Four, PLE++ at Five (Same as STR)			
	All	STR	PLE	All	STR	PLE	STR	PLE	PLE+	PLE++
1	1			4						
2	4			16						
3	16		10	64		34		1.6; 1.9		
4	64		10	128		34			6.4; 3.8	
5	128	10	10	512	27	34	12.8; 19.0			12.8; 15.1

The pressures are quite disparate. Because even the genera now extinct have that same fundamental strongly adaptive set, i.e., the coherence of the lineage due to the shared ancestron, it may be that extra time exposed to environmental resistance has increased STR extinction pressure. If we add another level of genus and species generation to account for an implied two extinct genera included the eight-branched node, PLE extinction pressures increase to 6.4 for genera and 48 for species (Table 6, PLE+). We then might assume that PLE may be truncated by ancient extinction, reflected in the reduced nature of the morphology, but that it is now strongly resistant to extinction. On the other hand, if both lineages originated at the same time (Table 6, PLE++), at level 5, as is more probable, they would have much the same extinction pressures, implying considerable extinction in PLE in the ancestry of the many extant species. So, the apparent larger extinction pressure of STR is an artifact of inappropriate estimation of time of PLE lineage existence.

3.4.10. A Possible Toggle Switch

The groups of mosses studied for microgenus analysis all support a 1 + 4 rope section. These groups, however, are all characterized by *r*-selection—rapid colonization, great fluctuations in population sizes, unpredictable habitat, and high mortality. If 1 + 6 rope section were found to be characteristic of *K*-selection species—complete and persistent population establishment, stable environment, low mortality—then the 1 + 5 pentagonal rope section may act as a toggle switch for different selection strategies. The unstable 1 + 5 pentagonal section may be viewed as an analogue of a cation, with one outer-shell electron missing, making it possible for this type of microgenus to easily lose a species to revert to the more stable 1 + 4 section or gain one to form a 1 + 6 hexagonal section (Figure 5), which is, however, evolutionarily closed. In the context of the Digital Universe [60], a toggle switch is an error-correcting algorithm.

3.4.11. Extinction and Effect on Descendant Species

The above treats the ideal case (and the inferred evolutionary process), exemplified in Figures 1 and 2, of four traits per species and four immediate descendant species per ancestral species. For analysis of actual large lineages (Tables 7 and 8), Streptotrichaceae (STR) and Pleuroweisieae (PLE) are compared with respect to number of immediate descendants and number of secondary descendant species per genus, and also comparing number of new traits (the novon set) of the ancestor's ancestor and the total number of new traits in the genus, then assessing the number of new traits in a genus as a percentage of the optimal number of 16 (four traits from each of four descendant species).

Table 7. Streptotrichaceae lineage. Numbers of immediate descendant species in genus (Num Imm Desc); number of secondary descendant species in genus (Num Sec Desc); number of new traits on ancestor's ancestor (Num New Tr An of An); total new traits in genus (Tot New Tr Gen); and, new traits in genus as percent of optimal 16 (Tot New Tr Gen/16). IEG means inferred extinct genus.

STR Genus	Num Imm Desc	Num Sec Desc	Num New Tr An of An	Tot New Tr Gen	Tot New Tr Gen/16
IEG1	0	0	0	4	0.25
IEG2	0	0	4	4	0.25
Trachyodontium	1	0	4	7	0.44
Crassileptodontium	1	2	4	16	1.00
Streptotrichum	0	0	4	4	0.25
Austroleptodontium	0	0	4	8	0.50
Leptodontiella	0	0	4	3	0.19
Microleptodontium	1	3	3	21	1.31
Rubroleptodontium	0	0	7	5	0.31
IEG	0	0	4	5	0.31
Williamsiella	2	1	5	18	1.13
Leptodontium	1	3	6	16	1.00
Stephanoleptodontium	1	6	6	26	1.63
Total	7	15	55	137	
Average	0.54	0.15	4.23	10.54	0.66
Average anan/ total new				2.49	

Table 8. Pleuroweisieae lineage. Same caption as for Table 7.

PLE Genus	Num Imm Desc	Num Sec Desc	Num New Tr An of An	Tot New Tr Gen	Tot New Tr Gen/16
IEG	0	0	0	8	0.50
Tuerckheimia	2	0	8	8	0.50
Eobryum	2	0	8	10	0.63
Anoectangium	3	3	5	27	1.69
Ardeuma	1	3	5	15	0.94
Gymnostomum	2	1	5	12	0.75
Hymenostyliella	1	0	5	7	0.44
Hymenostylium	1	0	5	7	0.44
Molendoa	2	1	5	16	1.00
Ozobryum	1	2	5	16	1.00
Reimersia	0	0	5	4	0.25
Total	15	10	56	130	
Average	1.36	0.91	5	11.82	0.74
Average ann/ total new				2.32	

Tables 7 and 8 directly compare STR and PLE by numbers on immediate descendant and numbers of secondary descendants. The numbers of new traits per species average 4.23 for STR and 5 for PLE, approximately as expected. The average number of new traits in the ancestor's ancestor divided by the total new traits in the genus is a measure of the magnification of the evolutionary energy that propels the genus into its new environment, 2.49 times for STR and 2.32 times for PLE, which is about the same.

STR averages half the number of those of PLE, and has less than 20 percent of the number of secondary descendants as PLE. This is largely due to STR having seven genera with no descendant species at all within the genus, compared to PLE with only two. It is

probable, from their position largely low in the caulogram, that the STR monotypic genera are the results of extinction, not recent genusation.

Assuming a genus has 16 new traits, one can substitute stable traits (immune to extinction) for species. So, in Tables 7 and 8, STR and PLE are evaluated by total actual traits per genus as a percent of the total possible (16): STR has 0.66 while PLE has 0.74. Extinction has removed, then, about 1/3 of STR genera and 1/4 of PLE genera. For STR, the extinct genera need be peripheral, because the genera are on much-branching caulons and are closely knit by small trait differences. Thus, the loss of 33 percent of the peripheral cords in the five-ancestor model (Figure 6) would preserve this tree topology. In PLE, most of the genera are anchored in one ancestral species, and thus the periphery of evolution is preserved instead and the model is removal of a portion (25 percent) of the one-ancestor hawser (Figure 14) in PLE. The table columns of total actual traits per genus as a percent of 16 also identifies genera with abundant resistant to environmental pressures through adaptation. In STR, five genera have percentages of 1.00 or higher, with abundant secondary species in *Stephanoleptodontium*. In PLE, three genera have percentages of 1.00 or higher, while one other is quite near. *Anotectangium* is the genus with the greatest expression of secondary descendancy. Both these genera may be considered to be presently robustly adaptively entering new environments.

4. Discussion

Complex subjects like descriptive taxonomy commonly lack extensive mathematical bases because of the large number of parameters and amount of multitudinous data. Initial sorting into groups is through innate pattern recognition, Gestalt, and omnispection based on overviews of shared traits The present success in using detailed morphological descriptions as primary data on evolution is because the minimally monophyletic group is a simplifying evolutionary construct, easily discernable by second order Markov reasoning and Shannon–Turing sequential Bayes statistics [9]. The processes affecting this construct are few and clear: two-sigma exclusion of uncertainty, the Rule of Four, and the Pareto Fractal Dimension. Interpretation through established principles in physics lends familiarity and confidence to the results.

Physics is a broad subject, but the basics that are applicable to taxonomy are not difficult. An excellent primer for the classical mechanics used in the present paper is the introductory book by S. Carroll [61], and other aids suitable for taxonomists are available. The present study recasts the taxa of evolutionary systematics in terms of physics, particularly position and displacement, which are equivalent to place on a caulogram, and rate and change in rate of character state changes. Macroevolutionary processes and possible universals may be theorized through analysis of expressed traits along the lines of descent with modification. The term "evolutionary mechanics" has been used [62] for phylogenetic analysis of the origination of proteomes, but without direct parallelism with classical mechanics.

This study may be termed "high-resolution phylogenetics" because analyzing minimally monophyletic groups with evolutionary mechanics extracts information not available with molecular systematics. Technically, the reduction of large genera to minimally monophyletic groups (MMGs) vastly reduces parameters while increasing degrees of freedom, allowing mathematically constrained models. Degrees of freedom are calculated by sample size (e.g., number of traits in raw data) minus number of explanatory mathematical rules ($d.f = n - p$). Large numbers of parameters penalize both AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion). Inasmuch as most parameters are global (self-similar) for all MMGs, these MMGs are well-understood, predictable building blocks

for evolutionary trees. Splitting into MMGs does not create numerous localized models because there is no ad hoc set of parameters for each separate MMG.

For instance, evolvability, the capacity for adaptive change, is the second differential of a species' position on a caulogram, i.e., acceleration, or change in rate (velocity or distance divided by time). Taxonomists with little training in mathematics can avoid the infinitesimal calculus with simple calculations by spreadsheet. Evolvability of one species (AccIns) is the instantaneous acceleration as the difference between the number of new traits of one species and the number of new traits of its immediate ancestral species. Evolvability for a genus (ToAccGe) is the cumulative acceleration calculated by adding the plus and minus instantaneous accelerations (differences between each species in the genus and all its immediate ancestral species); stasis at the genus level is indicated by plus and minus acceleration canceling out to around zero, and major change maxima are limited by totaling all pluses or all minuses. Total evolvability for a species (ToTrCa) is simply the difference between the numbers of new traits of the species of interest and that at the base of the caulogram (here set to a rate of zero). Each of these measures from all species can be added to get values for the whole lineage (see values at the bottom of Tables 1 and 2). Such measures should prove important and relevant to predictive analysis as additional lineages are studied.

All taxa have 16 in the numerator of the formula (Equation (1)) for the hollow curves in Figure 1, and *all* taxa follow the basic $1/x^{1.161}$ curve of the denominator that is generated by the Pareto ratio as expressed in the minimally monophyletic group. Thus, the research opportunities in evolutionary mechanics using standard taxonomic data are available to all taxonomists.

There are four hierarchical taxonomic levels here identifiable as well-supported evolutionary groupings (as generalized taxa): the species, the microgenus, the timelike lineage (caulogram), and the spacelike metalineage (synchronogram or tuple of timewise caulograms). These groups are of evolutionary substance initiated and governed by characteristic, clear, effective processes running through time that may be evaluated with the principles of physics. They are useful in predictions of sustainability and evolutionary force that contributes to survival at the ecosystem level, that is, via Darwinian selection among lineages that maximizes an orderly digestion of Gibbs free energy through niche saturation and trait redundancy. The caulograms interpreted with the Rule of Four and the Pareto Fractal Dimension extend the ability to predict and retrodict the evolutionary trajectories of lineages in general, while this helps gauge the extent of a synchronogram, including when and where it may "pinch off" in retrodiction of its origin and the prediction of its possible demise.

Taxonomic information may be used to do rather complex investigations of evolutionary processes. For example, evolution is uniform or stable when velocity, as distance per time, or species per speciation events, is constant, and acceleration is thus zero. If evolution is constant, maintaining its current rate of change (gradual additions and extinctions of traits and species), then the environment is stable or at least matches rates of evolutionary change. Primary speciation may be viewed as bursts of genus-level isomorphism by shared immediate-ancestral traits. Redundancy of expressed traits apparently is a major factor in sustainability.

The complexity principle [63,64] of the conservation of evolutionary processes across scale is suggested here as implied by similar inverse power curves for species per genus and genera per family (Figure 1A,B). This would imply that the two-sigma exclusion of uncertainty, the Rule of Four and the Pareto Fractal Dimension operate as unifying processes at all taxonomic ranks. Further work is needed for confirmation of this replication as part

of the fractal complexity of taxa [65]. Self-similarity would be parsimonious of energy in the development of these powerful controlling mechanisms.

A metalineage is not a causal series, but an ordered series of models of what the caulogram might look like at various times in the past. There is no arrow of time, as all this information exists in the present and is actionable information about at least sections of a single timewise living structure. When a basal species in a caulogram cannot be connected to an earlier species by a few novel traits, then the metalineage is terminated in the past with the expectation that information on earlier taxa is lost due to environmental factors, creating a *process-based* informational gap. Doubtless earlier metalineages are concatenated in series (like gregarines in syzygy), but exact connections are unknown. This may be compared with an attempt by other researchers [47] to characterize mathematically a cladogram as an informationally based living tree of life, this composed of the multi-fractal structure of biological lineages. Results of that study are theoretical, however, without extensive exemplification as in the present paper, but the work has a similar foundation in physics.

The number of possible caulograms comprising a metalineage is limited by the number of relict species available to the observer because information is unitary as bits and is precisely ordered. As an egregore—an influential collective thought-form—a metalineage modifies or educates its observer, but only to the extent that the observer recognizes the information. A metalineage is the largest living structure, with evolution propelled by the central attributes of life: homeostasis, responsiveness, self-corrigibility, entropy-generation, adaptivity, having ecologically integrated parts, and robust sustainability of form and function. One may think that, without the balance of homogenizing and differentiating features associated with microevolution, such a constantly fanning lineage (except for possible horizontal gene transfer) is on initial consideration hardly a functional adaptable unit, but the observed small trait differences between ancestors and descendants plus the multiple million-year survival between speciation events of this long-lived structure indicate otherwise. Perhaps the redundancy of ancestral traits [66] associated with Pareto-ratioed genusation events provides the needed genetic reserve?

The synchronogram, given the extra information it provides, is far more than just an interpretation of that one caulogram. The tuple entries of a metalineage are equivalent to the description of the metalineages as a taxon, with four or five time slices as "traits." The caulograms in the synchronogram tuple are all of the same taxon (tribe or family as a lineage), and thus all have the proper formal nomenclature, with the metalineage as a self-similar superset. If the original present-day caulogram has four or more time levels (series on a caulon line), then it is well individuated with two-sigma exclusion of uncertainty. The number of levels of information depth is equivalent to a set of characters, each of one informational bit. Following an odds table [22] (p. 17), one bit excludes 0.67 of uncertainty (one sigma), four 0.94 (ca. two sigma), and nine 0.998 (three sigma).

This study claims it is high-resolution phylogenetics because analysis by descent with modification on stem-taxon trees independently using morphology and molecular data when available [32] demonstrably yields more and stronger inferences on evolutionary processes than present-day cladistics using any data or analytic method. Given that evolutionary mass is a position on a caulogram (an evolutionary tree of actual species at nodes), the nodes on a cladogram have no directly inferable evolutionary mass and thus have no calculable evolutionary force given $F = ma$. Clades are not taxa.

4.1. New to Science

This essay into the biophysics of macroevolution advances explanations in terms of statistics, classical mechanics, and geometry for what taxa are, how they are generated, why they are hierarchical, how they remain integral over millions of years, how they are

constrained in size and character, and how their comparative evolutionary force and resilience may be compared. Certain results in the physical dynamics of taxonomy should be particularly emphasized as *new to science*: Discerning analogues in evolutionary taxonomy of processes in classical mechanics allows the analysis of heretofore unrecognized physical relationships between taxa. Increasing degrees of freedom by generalizing parameters through reduction through nested ranks allows taxonomic descriptions to be used to generate potential universals. Physical processes involving the Rule of Four, the Pareto Fractal Dimension, and minimally monophyletic groups are all quantifiable and integrate well in complex formulae. Although to date only studied with bryophytes, the hollow curves figured in Willis' Age and Area study [67] unify across taxonomic ranks the inferred processes of evolutionary mechanics. There are four natural taxonomic ranks defined as part of a mathematically coherent grand organizational contribution to ecosystem resilience. The metalineage is introduced as a novelty, described for two lineages with time slices at four and five ticks of a Nemesis extinction clock. Speciation, secondary speciation, stasis, and extinction are common orderly processes that are measurable and predictable as involving energy exchanges. Secondary speciation may prove a tool reflecting in adaptive traits the changes parallel to environment dynamics over millions of years. Evolutionary force is a precise and apparently accurate measure of natural selection. There is a physical exchange rate between the number of species in a genus and the number of traits in that genus. There are almost exactly enough average traits per species in the two lineages (ca. 4.3 to 4.5) to ensure that each species has 95% of uncertainty excluded in establishing individuation. Two lineages have quite different efficiencies in utilizing available energy, with Streptotrichaceae efficient at 96%, but Pleuroweisieae at only 44%. A geometric model of crowding explains the constraint of the Rule of Four in evolution, reflects the Pareto ratio, and may involve a toggle-like control of overcrowding. This paper presents, overall, a strong argument encouraging practicing taxonomists to reject the idea that they are simply sources of data for genome-centric phylogeneticists but may pursue significant new contributions to evolutionary science on their own with morphological data at hand and some faculty with a standard spreadsheet.

Taxa are not notional, arbitrary categories; instead, they are rule-based complex structured sets of information mediating basic processes of macroevolution. They determine the intrinsic ability of species, genera, lineages, and metalineages to survive millions of years of environmental challenge. Viewed through time, a metalineage is a scientifically real behemoth of structured timewise information that is modeled as a synchronogram and has a characteristic evolutionary trajectory powered by well-organized entropic digestion of Gibbs free energy. The descriptions of species, genera, lineages, and metalineages are all data tuples, being ordered sets at various scales [44], interpretable as informational bits that contribute to the statistical reality (two-sigma exclusion of uncertainty) and behavior (speciation, genusation, lineageation) of these natural taxa. Taxonomic ranks are quadrate in evolutionary topology, apparently associated with powers of four in that every rank is of 16 units derived from 4 units of the next smaller rank, as implied in actual curves of species per genus, genera per family, and families per order (Figure 1). Taxa and ranks are real groups in nature, held together by measurable forces related to evolutionary processes.

4.2. Macrogenera

What to do with massive genera? Certain genera are very large, with dozens or hundreds of species [18]. As an extreme, the genus *Astragalus* is the largest plant genus, with more than 3100 species, divided into about 230 taxonomic sections [68–70], leaving an average of 14 species per section. If this vascular plant genus is internally managed through time by processes similar to those described above, then there might be about

700 microgenera (minimally monophyletic groups) of about five species each that might be discernable with future study. Although this increases the number of genera to ca. 700, each minimally monophyletic set would be a scientifically real distinctive complex powerhouse of evolution with origins in the Miocene. The effect over time on the global environment of the *Astragalus* metalineage would be truly elephantine. On the other hand, there may be undiscovered macroevolutionary processes operating in such large genera, an opportunity for significant further research. Analysis with structural monophyly and evolutionary mechanics is scientifically rewarding, with much potential for new and effective evolutionary theory.

4.3. Neutral Evolution

Kimura's neutral evolution theory suggests that the majority of mutations observed should be neutral, that is, equal to the mutation rate with deleterious mutations strongly eliminated over time. Divergence between species is therefore not considered adaptive to those espousing this theory, although this has been criticized. Nowak [50] (p. 105), arguing for a middle ground, opined that most fixed molecular variation is indeed neutral, but "very occasionally advantageous mutations come into play." The present paper suggests that about four mutations of adaptive value are fixed in new species about every 22 to 26 million years and contribute in their small but important way to the survival of their ecosystems.

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Abbreviations

The abbreviations used in this manuscript are listed and described in Table 3.

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