Title: Holophyly and associated concepts if the unknown is unclassifiable

Subtitle: Holophyly and associated concepts

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Abstract

The current definitions of holophyly (monophyly *sensu stricto*) and paraphyly suggest a direct inclusion of ancestors in taxa. These ancestors are almost always unknown (undiscovered) in phylogenetics. Therefore, no one describes them as species and does not create other taxa for them. The organisms unknown to science can not be an object of the biological taxonomical classification. Here, the direct inclusion/exclusion of unknown ancestors was replaced with the ability/disability of the systematic group to include them (according to the definition of each specific group). In this way, the problem of incomplete division of the clade into subclades is solved compatible with holophyletic-only classification. The possible definitions of the main phylogenetic concepts for the views of dealing only with known group members were proposed. The system of "phyletic states" of the groups proposed here deals more carefully with ancestors as well as the fact that every two organisms of now-known life have a common ancestor (than the systems stemmed from Haeckel, who did not reject the possibility of multiple origins of known life). Inability to provide a concise definition of holophyly using the existing terms indicates the lack (or imprecision) of more basic concepts. These concepts (phylon, rendestor, inprestor, ancessure) were also proposed (or improved) here and holophyly was defined using them near the end of the paper.

Keywords: *enophyletic*; *merophyletic*; *kollitophyletic*; *schizophyletic*; *drade*; *skade*.

INTRODUCTION

Many biologists use a kind of model-dependent realism (Hawking and Mlodinow 2010a, b; Koonin 2011), where characters of known organisms serve as the base for the construction of a phylogenetic tree—a hypothesis, which in it turn becomes accepted as a reflection of phylogeny in each particular case. This reflection serves as the base for conclusions on groups' states and on features of some ancestors of different known organisms like the last common ancestor of known eukaryotes (Koonin 2010; Desmonda et al. 2011; O'Malley et al. 2019) or the last common ancestor of known eukaryotes plus known archaea (Forterre 2013; Doolittle 2020). It is the way by which undiscovered entities appear in scientific discussions. Despite the growing volume of predictions about them, these entities still can not enter the classification.

In natural sciences, the key criterion for proving the existence of an object (like a physical particle of a previously unknown kind, an atom of a previously unknown element or an organism of a previously unknown species) is its observation and/or observation of traces of the existence of this object (radiation, remains of vital activity etc.). Only objects that meet this criterion can be classified (e.g. introduced in the periodic table of elements or described as a species). Single unknown organisms or unknown species can not enter the classification. Despite this, the current system of phylogenetic concepts (holo-/monophyly, paraphyly, and polyphyly as they are currently defined) is not adapted to the separation of known and unknown organisms (as well as populations, species, etc.) including ancestral ones. The current definitions of holophyly and paraphyly suggest a direct inclusion of ancestors in taxa (Encyclopedia of Life Science—Cullen 2009, p. 91; PhyloCode—de Oueiroz and Cantino 2020, Article 2.1; Campbell biology — Urry et al. 2021 p. 560; etc.). These ancestors are almost always unknown in phylogenetics. Therefore, no one describes them as species and does not create other taxa for them. Unknown organisms can not be an object of biological taxonomical classification. Thus, we are deprived of direct manipulation of unknown organisms. With this in mind, the triad holo-, para-, and polyphyly can not function normally. The difference of holo- and paraphyletic groups from polyphyletic groups is whether the last common ancestor is a member of the group. Since almost always the last common ancestor can not be included in the taxon because this ancestor is unknown, nonsense and confusion arise. Current phylogenetic discussions require a system of more accurately defined concepts.

Unknown organisms are not considered members of groups (for example, new species are described as new, rather than already existing in the group). However, there is one problematic type of unknown organisms—the unknown ancestors of known organisms. For some reason, everything is not so simple with them. A remarkable feature of biological systematics and phylogenetics is that known descendants inevitably imply the existence of their ancestors, even if these ancestors are unknown. But this implication is not enough to "specify the identity" for each of the unknown ancestors. This can be compared to the following analogy from the judiciary. If the existence of some illegal organisation with a leadership management system is proven, then it certainly has a leader. However, this data is not enough to bring any person to trial. As in the case of unknown ancestors, a "vacancy" is known here, but not a specific identity. Despite all this, the non-classification of unknown organisms contradicts the current system of phyletic states and creates confusion in it.

Hennig (1950; 1965; 1966) was probably aware that only known organisms can be classified. At the same time, he considered the probability of finding an ancestor of any group so low that he did not stipulate the inclusion of ancestors in any way in his definitions of phyletic terms. Ancestors *de facto* were excluded from the groups. This theoretical inaccuracy led to the rapid inclusion of the last common ancestor by other authors in the definitions of the three "phyly". The inclusion was direct and unconditional. This lack of differentiation between known and unknown organisms has led to confusion among taxonomists (see Podani 2010 for review). Probably, both of the main types of the vision of phylogenetic trees shown by Podani (2009, Fig. 2; 2010, Fig. 1) are not completely correct and the consensus seems possible and necessary (compare aforementioned figures of Podani and Fig. 1, here).

Currently, there is some inconsistency in the phylogenetic practice. The phylogenetic terminology does not specifically stipulate the separation of known and unknown organisms. The definitions are widely used, but users often do not pay attention to unknown ancestral organisms regarding their obligatory inclusion in taxa, which the current definitions of *holo*- and *paraphyly* dictates. For example, they divide one clade into two subclades, supposedly without a remainder and use the wording "last common ancestor of X" disregarding the unknown organisms, which can be the part of X. If we assume that unknown organisms are not considered members of groups *a priori*, then arises the problem of demarcation of *holophyly* and *paraphyly* from *enophyly* and *merophyly* respectively (see below). Regardless of the user's views, the terms "last common ancestor" and "progenitor" are used like there are no unknown ancestors at all. Logically, the ancestor or progenitor of the group can not be (or even be able to be) a member of that group (Fig. 2).

To be consistent we should either directly include unknown ancestors in taxa somehow, describe species for them and introduce at least one paraphyletic subtaxon per taxon or not include them directly and amend the system of concepts. The differentiation between known and unknown organisms makes it possible to accurately and unambiguously define several phylogenetic terms, to avoid the problem of description of unknown organisms, and to make the cladistic systematics possible (i.e. a full division of one clade into two subclades). However, this differentiation makes necessary changes and additions in the system of concepts. The revised and supplemented system of concepts with definitions and comments is proposed below. It starts with the basic concepts (e.g. *phylon*, *inprestor*, *rendestor* and *ancessure*), which were used to define *enophyly*, *merophyly*, *holophyly*, *paraphyly*, and *schizophyly*, which follow after them.

From the actual content of a group of organisms coupled with a phylogenetic reconstruction, one can only conclude whether the group is *enophyletic* or *merophyletic* (see below). To get more than two variants when any two organisms have a common ancestor and to determine whether a group is *holo-, para-*, or *schizophyletic*, we are forced to conclude about a certain part of ancestors of known members of a group (*inprestral ancessure*, see below): 1) is the definition of this group capable of ensuring the inclusion of all *inprestral ancessure* members in the theoretical case, if all of them become known; 2) whether the *inprestral ancessure* of the given group gave rise to any known organisms outside the given group.

CONCEPTS AND COMMENTS

THE CORE CONCEPT

Before distinguishing known and unknown organisms fitting the definitions of groups it is needed to introduce the core concept using no such distinctions. This concept (*phylon*) can serve as the frame for this distinguishing and has a definition similar to one currently widely used for an holophyletic group (monophyletic group *sensu stricto*; clade) with the addition allowing a singleton to be a phylon. Nevertheless, it is just the logically starting point having a direct practical sense only when the ancestor and all its descendants together are discovered (such a group can be named <u>Zander's (2009)</u> term euphyletic). The form "*phylon*"—the direct transliteration from Greek—is chosen here to avoid confusion with the phylum—the taxonomic rank.

PHYLON (/'faɪlɒn/; from Greek $\varphi \tilde{v} \lambda o v$ [phylon] - tribe) — the ancestor plus all its descendants, or the set of a sole member having no descendants.

ENOPHYLETIC group ($/\epsilon$ nə(υ)farˈlɛtɪk/; from Greek $\epsilon \nu \delta \tau \eta \tau \alpha$ [enótita] - unity) — a set of known organisms, for which at least one phylon exists, all known members of which they are.

MEROPHYLETIC group (/mɪrə(v)fʌɪˈlɛtɪk/; from Greek $\mu \acute{e} \rho o \varsigma$ [$m\acute{e} ros$] - part, portion) — a set of known organisms of common descent for which no phylon exists, all known members of which they are; or a set of a sole known member having known descendants.

POLYPHYLETIC group (/pplifʌɪˈlɛtɪk/; from Greek πολύς [polús] - many, much) — a set of known organisms, which have no common ancestor; descendants of different ancestors (an exclusively theoretical concept in the present state of knowledge of life in the universe).



Figure 1. The tree of ancestor-descendant relationships.

Circles with open locks represent known elementary
units of classification, circles with closed locks represent
the unknown units.





ANCESTOR AND PROGENITOR ARE MISUSED CONCEPTS, REPLACEMENTS

There is a logical and semantical problem with both the wording "last common ancestor" and the word "progenitor" without adding "of the known members of the group". The progenitor of a group can not be a member of that group. Likewise, an ancestor of a group can not be a member of that group. Also, an ancestor and a progenitor are *unable to be included* in the group (Fig. 2). The phrase "My granny is the ancestor of my granny, my mother and me" is not correct. So is this phrase if we replace the word "ancestor" with "progenitor". The last common ancestor of eukaryotes could not have a nucleus. Otherwise, it will be one of the eukaryotes but not their ancestor. The same is with the concepts "concestor" (simple contraction from "common ancestor" coined by Nicky Warren and popularised by Dawkins (2004); see p. 7 in op. cit.) and "cenancestor" (originally coined by Fitch and Upper (1987)). This issue and the cumbersomeness of the wording "the last common ancestor of the known members of the X" as well as the un-pronounceability of possible abbreviation LCAKM were reasons for the short term (rendestor), which would not be burdened with pre-existing other definitions. The absence of the concept was the reason for the introduction of *inprestor*. The wording "First Common Ancestor" (FCA), which is sometimes used (e.g. Koumandou et al. 2013; Dacks et al. 2016; Eme et al. 2017) stands even less criticism. Literally, the FCA of any group goes to the origin of known life. This indicates the need for the concept of *idioprestor*.

RENDESTOR of a group (/'rɒndɛstə/; from French *rendezvous* - a meeting at an agreed time and place, and the ending *-estor*, like in the word *ancestor*) — the last in natural history common ancestor of all (two or more) known members of the group except this ancestor itself if this ancestor is known and is a member of the group.

INPRESTOR of a group (/'inprestə/; from *in*, Greek $\pi\rho\omega\tau\alpha$ [*próta*] - first, and the ending -*estor*, like in the word *ancestor*) — the first in natural history ancestor of all known members of the group (except this ancestor itself if this ancestor is known and is a member of the group), which is able to be included (or *is* included) in the given group.

IDIOPRESTOR of a group (/ɪdɪˈə(ʊ)prɛstə/; from Ancient Greek ἴδἴος - pertaining to self, one's own, private (as opposed to public); Greek $\pi \rho \dot{\omega} \tau \alpha$ [próta] - first, and the ending -estor, like in the word ancestor) — the first in natural history ancestor of all known members of the group (except this ancestor itself if this ancestor is known and is a member of the group) and no known organisms outside the group.

Supporting concept: an ancestral link

The basic criterion, which gives us *eno-* and *merophyly*, is not dealing with unknown organisms, including unknown ancestors. Unknown ancestors are matter that can not be completely divided into discrete units (e.g. could not be divided into a number of species). Although inside it some positions can be distinguished (such as the *rendestor*, the *inprestor*, the *idioprestor*), these are not specific identities. In each given moment of the time, some ancestors of known members of a group appear as a solid functional unit with an ancestor of all known members of the group (e.g. *rendestor* or *inprestor*). The common term for this unit seems highly suitable.

Ancessure of a group (/anses'juə/; contraction from ancestor and commissure) — a usually branching continuous sequence composed of at least one ancestor of all known members of the given group (except this ancestor itself if this ancestor is known and is a member of the group) as well as (if any) all descendants of this ancestor, which also are ancestors of known members of the group.

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INPRESTRAL ANCESSURE of a group — the inprestor of the given group plus (if any) all the inprestor's descendants, which also are ancestors of known members of the given group.

RENDESTRAL ANCESSURE of a group — the rendestor of the given group plus (if any) all the rendestor's descendants, which also are ancestors of known members of the given group.

An *ancessure* is not always just the minimal ligament between known members of a group through ancestors. Only the *rendestral ancessure* is this minimal ligament. Any *non-rendestral ancessure* can include not just the *rendestor* but also "a tail" to (and including) an earlier common

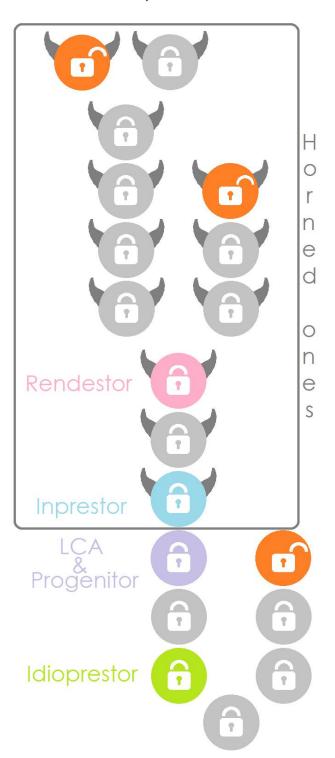


Figure 2. The tree of ancestor-descendant relationships illustrating the different identities of rendestor, inprestor, idioprestor and last common ancestor (LCA) and progenitor. The grey frame is the definitional borders of the group based on the apomorphy of horns.

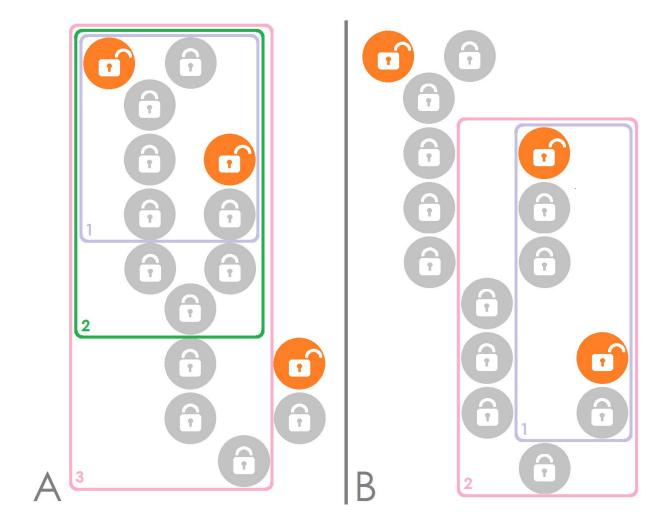


Figure 3. Possible definitional borders for the equivalent sets of two known organisms: enophyletic (A) and merophyletic (B). The groups A1 and B1 are schizophyletic. A2 is holophyletic. A3 and B2 are paraphyletic. ancestor of all known members of a group (e.g. *inprestor* in the case of *inprestral ancessure*; see Figs. 2

ancestor of all known members of a group (e.g. *inprestor* in the case of *inprestral ancessure*; see Figs. 2 and 4). An *ancessure* can include known, unknown organisms or a mixture of both and can consist of only one ancestor (if all known members of the group are its direct descendants). Using the *ancessure* concept, it is possible to define the following basic duet of the phyletic states (Fig. 4).

PHYLETIC STATES DEPENDING ON THE ABILITY TO INCLUDE ENTIER ANCESSURE

KOLLITOPHYLETIC group (/kəlaɪtə(υ)fʌɪˈlɛtɪk/; from Greek κολλητός [kollitós] - glued) — a set of known organisms, which has the non-zero inprestral ancessure and is able to include all its members (according to the definition of the group) and no unknown ancestors of known organisms outside the group unless these ancestors are the members of the inprestral ancessure or the continuous sequence of immediate descendants of the inprestral ancessure.

SCHIZOPHYLETIC group (/skitsə(v)fai'lɛtik/; from Greek $\sigma \chi i \zeta \omega$ [skhízō] - split) — a set of known organisms, which is unable to include all members of its inprestral (if it is non-zero) or rendestral (in all other cases) ancessure (according to the definition of the group) or able to include unknown ancestors of known organisms outside the group if these ancestors are not the members of the inprestral ancessure and not the continuous sequence of immediate descendants of the inprestral ancessure.

A kollitophyletic group has the potential to include unknown members of its inprestral ancessure but does not include them before they are known. A kollitophyletic group is usually able to include the rendestor (as it is usually the part of the inprestral ancessure; the only exception is some singleton sets, see below) and always has the inprestor (the rendestor and the inprestor are the same ancessure member in the case of minimal clades). Usually, schizophyletic groups have no single inprestor, although their parts have their own inprestors. Also, schizophyletic groups are usually unable to include the rendestor.

PHYLETIC STATES DEPENDING ON WHETHER GROUP'S INPRESTRAL ANCESSURE GAVE RISE TO DISCOVERED ORGANISMS OUTSIDE THE GROUP

Having the two basic phyletic dichotomies it is finally possible to define the duet of phyletic variants emerging at the intersection of *kollitophyly* with *eno-* and *merophyly* (Fig. 4). It is *holophyly* and *paraphyly*.

HOLOPHYLETIC (monophyletic *sensu stricto*)* group (/hɒlə(υ)fʌɪˈlɛtɪk/; from Greek ὅλος [hólos] whole) — a kollitophyletic group, the inprestral ancessure of which did not give rise to any known organism outside the group; or a set of a sole member having zero inprestral ancessure and no known descendants.

PARAPHYLETIC group (/pɛɹə(v)fʌɪˈlɛtɪk/; from Greek $\pi\alpha\rho\alpha$ [pará] - beside, near, alongside) — a kollitophyletic group, the inprestral ancessure of which gave rise to at least one known organism outside the group; or a set of a sole member having zero inprestral ancessure and known descendants.

An *inprestral ancessure* may give rise to known organisms outside the given group either directly (immediate descendant(s) of a member of the *ancessure*) or indirectly through a series of generations separating the member of the *ancessure* and known organism(s) outside the group. In this series of generations, there may be known member(s) of the group.

Sets of a sole member with a zero *inprestral ancessure* (i.e. having no *inprestor* in accordance with the definition of a given set) can not be *kollitophyletic* or *schizophyletic*. At the same time, such singleton sets can be *eno-* and *holophyletic* (if descendants of the sole member are unknown) or *mero-* and *paraphyletic* (if descendants of the sole member are known). *De facto* there are not two but three phyletic states in the row *kollitophyletic* groups – *schizophyletic* groups. These sets of a sole member having zero *inprestral ancessure* are the third state in this row—*atomophyletic* groups (Fig. 5). *Kollitophyletic* groups always have both *rendestral* and *inprestral* ancessures. For a *schizophyletic* group always at least a *rendestral ancessure* exists. For an *atomophyletic* groups neither *inprestral* nor *rendestral ancessures* exist (there is neither *inprestor* nor *rendestor*). Singleton sets, the definition of which allows the inclusion of the ancestors of the only member, have a linear *inprestral ancessure* (i.e. from the *inprestor* to the member of the group; Fig. 5). Therefore, such groups can be divided into *kollitophyletic* and *schizophyletic*, depending on whether or not the group is capable of including all members of the *inprestral ancessure* if they became known (Fig. 5).

*The term *holophyletic* was preferred here because of the number of meanings of the term *monophyletic*, both definitional and etymological. As <u>already noted</u>, a monophyletic group defined as "the ancestor plus all its descendants" has the very limited application if we take the definition literally—only the groups having more than one member where both the ancestor and all its descendants are discovered (monophyletic group *sensu strictissimo*/euphyletic group). Actually, phylogenetic taxonomists use it in the more loose sense (monophyle *sensu stricto*), probably the same as *holophyletic* group as it was defined here. Evolutionary taxonomists use it probably in the same sense as *kollitophyly* (monophyly *sensu lato*). As there was no differentiation between known and unknown organisms relatively to the phyletic states before, additional confusion arose. This confusion allows the term *monophyly* to be treated as a synonym of *enophyly* or *kollito-enophyly* or to cover both *eno-* and *merophyly*. It is quite attractive to treat *monophyly* in the latter sense ("descendants of one ancestor"/"belonging to a single phylon"; *sensu latissimo*) opposite to *polyphyly*, although it extremely reduces the term's usefulness. Haeckel, who introduced the concepts *monophyly* and *polyphyly* (Haeckel 1866), also used them as antonyms and, notably, did not reject the possibility of multiple origins of known life (e.g. Haeckel 1866 p. 198; 1868 p. 347; 1873 p. 371; 1894 p. 89; see Dayrat 2003 and Rieppel 2010 for review). In such views the terms *polyphyly*, as it was defined here, and *monophyly*, as its antonym, were applicable. Despite all this, it is still possible to treat *monophyly* as the synonym of *holophyly* (as the latter was defined here) and

the definition of holophyletic group used here can also be treated definition of monophyly [sensu stricto]. Although, the term, then, became misleading and the etymology is violated. It can not be deduced from Ancient Greek μ óvo ς [mónos] ("one", "alone", "only", "sole", "single") like in the cases of monophyletic group sensu strictissimo (it is exactly one phylon) or sensu latissimo (members of the group belong to one phylon) as the meaning of the term is exactly "whole", "entier" (Ancient Greek ŏλο ς [hólos]) both in relation to known organisms and in relation to unknown members of the ancessure.

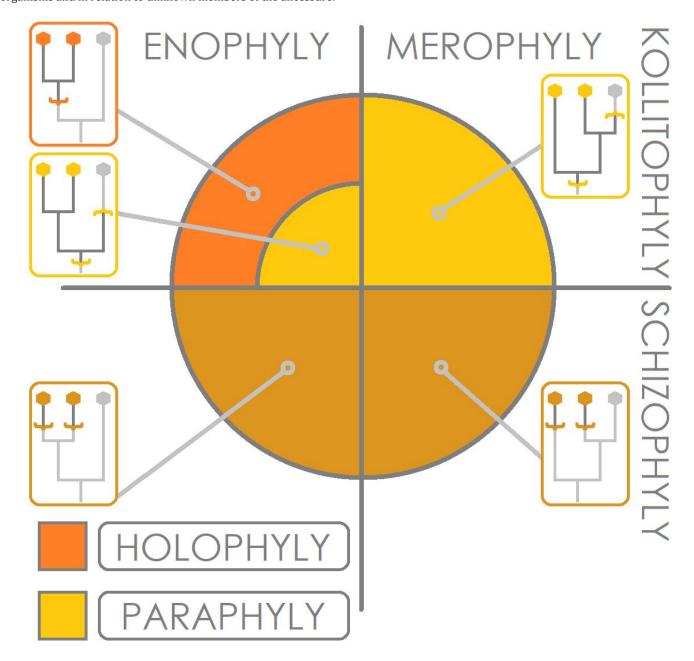


Figure 4. The diagram of the relationships of phyletic states among themselves. Coloured hexagons represent known group members. Grey hexagons represent the known organisms outside the group. The groups: on all three trees on the left are enophyletic; on all two trees on the right are merophyletic; on all three trees above are kollitophyletic; on all two trees below are schizophyletic. Atomophyly is not shown. The colour of the hexagons and borders around each tree matches the colour of the segment of the vertical half of the diagram. Examples of five types of groups shown: holophyletic—mammals (Mammalia), birds (Aves); para-enophyletic—choanomonads (Choanomonada; as the rendestor of choanomonads and metazoans had a collar and was a monad, i.e. is inside the definitional borders of choanomonads); schizoenophyletic—TSAR grouping (see below); para-merophyletic—reptiles (Reptilia); schizo-merophyletic—warm-blooded animals (Homotherma).

THE "-ADE" TERMS

The distinct entities of *enophyletic* and *holophyletic* groups raise the question of to what kind of groups the term *clade* should be ascribed. Although *merophyletic* groups now are not generally considered *clades*, there are still three options left of what the *clade* can be considered (Fig. 4):

1) an *enophyletic* group, 2) a *kollito-enophyletic* group or 3) a *holophyletic* group. As the etymology of the term *clade* (from Greek $\kappa\lambda \acute{\alpha}\delta o\varsigma$ [*kládos*] - shoot, branch) minds the inclusion of an *ancessure* and no breaks in the branch, here the term *clade* was applied only to *holophyletic* groups as they were defined here.

Such an interpretation of the term *clade* borns the issue with the groups formed by a simple listing of their members or subgroups. Many such groups are unable to include their entire *rendestral ancessures* and therefore are *schizophyletic*. For example, the wordings "Sar+Telonemia clade" or "Telonemia formed the clade with Sar" or "TSAR clade" will not be correct since the *rendestral ancessure* is not able to be fully included here (see Strassert et al. 2019 for the phylogeny). TSAR were defined as "Telonemia + Sar grouping" (Strassert et al. 2019, p. 761). Wherein, Telonemia were defined on the complex of morphological traits (Shalchian-Tabrizi et al. 2006, p. 1840) and Sar were defined with the minimal-clade definition (Adl et al. 2012, p. 431). Therefore, this group is *schizophyletic* although *enophyletic* (*schizo-enophyletic*; see Fig. 4, 6). For such purposes, a short term for "*enophyletic* group" seems needed.

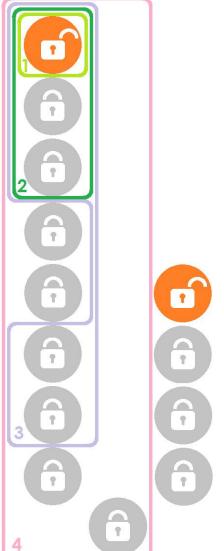


Figure 5. Possible diagnostic borders for the same singleton set (of one known organism): atomophyletic and holophyletic (1), holophyletic (2), schizophyletic (3), paraphyletic (4). All sets pictured are enophyletic. Sets 2 and 4 are kollitopyletic. All they could be merophyletic if the only included known organism had known excluded descendant(s). Sets 1 and 2 in this case would be paraphyletic. Atomophyly of the set 1, kollitophyly of the sets 2, 4, schizophyly of the set 3 and paraphyly of the set 4 would be unchanged.

DRADE (/dleid/; from the two first letters of the semantic core in L. *polydrupa*—the type of fruit to which raspberries belong, bramble fruit, the type of aggregate fruit easily separable from the receptacle—and the ending *-ade*, like in the terms *grade* and *clade*) — an enophyletic group.

CLADE (/kleid/; from Greek κλάδος [kládos] - shoot, branch) — a holophyletic group.

The short term for paraphyletic groups also seems necessary there. The term [evolutionary] *grade* does not mean "a paraphyletic group". Grades can also be *holophyletic* and *schizophyletic* as these terms were defined here (see <u>Huxley 1957</u>; 1958; 1959).

SKADE (/skeid/; from Greek σκαλών [skalón] - flight of stairs) — a paraphyletic group.

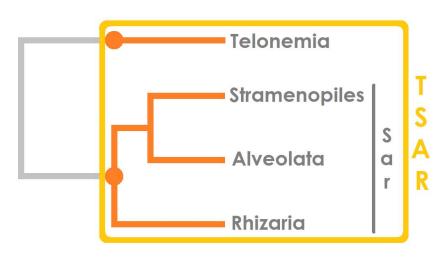


Figure 6. Schematic phylogenetic tree of Telonemia, Stramenopiles, Alveolata, and Rhizaria illustrating schizophyly of the union of Telonemia with Sar (TSAR drade). Definitional borders of TSAR are shown in yellow. Unincluded part of the rendestral ancessure is shown in gray. Inprestors of Telonemia and of Sar are shown with orange circles. As Sar are the minimal-clade, the inprestor, in this case, is the same identity as the rendestor.

CONCLUSIONS

- 1) Every two currently known organisms are descendants of one ancestor. Therefore, true *polyphyletic* groups do not exist in the current scientific reality.
- 2) Regardless of the likelihood of discovering each specific ancestor, a good system of concepts should be designed for the case when ancestors are found. The likelihood of this is very high near the terminals of the Tree of Life. However, the inclusion of unknown organisms (including unknown ancestors) can not be direct and immediate.
- 3) A group having the same composition may have different "phyletic states", depending on how this group is defined. Only *eno-* or *merophyly* reflects the composition and the branching pattern of the group. All other "phyletic states" depend on the definition of each specific group.
- 4) *Rendestor* is a short and correct term for what is now misleadingly and confusingly called a last common ancestor, almost always without adding "of the known members of X". Please note that

<u>Dawkins (2004)</u> also used the analogy with rendezvous, although he did not create the term on this base using instead the term *concestor* (to reduce "last common ancestor").

- 5) In discussions about the origin of a group (for example, about eukaryogenesis), we are talking primarily about the *inprestor* of this group.
- 6) *Ancessures* of groups is a hitherto unnamed component of phylogenetic trees, usually shown simply by lines. Members of an *ancessure* are almost always unable to be included in taxa as they are unknown. Nevertheless, definitions of that taxa, which are considered *holophyletic* or *paraphyletic* (i.e. *kollitophyletic* taxa) should have the potential to include all members of their *inprestral ancessures*, although do not include them directly. In other cases, we can only talk about *enophyly* or *merophyly*.
- 7) The demarcation between *enophyly*, *kollito-enophyly*, and *holophyly* is the Achilles' heel of existing systems of phylogenetic concepts.
- 8) The difference of *holophyletic* and *paraphyletic* groups (i.e. *kollitophyletic* groups) from *schizophyletic* groups is the ability to include the entire *inprestral ancessure* (see also <u>Kwok (2010)</u>, who used the terms "connected group" and "disconnected group", although he does not distinguish between known and unknown organisms).
- 9) The difference between *holophyletic* and *paraphyletic* groups is whether the *inprestral ancessure* of the group gave rise to any known organism outside the group.
- 10) Definitions of the term *clade*, which do not use the separation of known and unknown organisms do not allow any clade to be completely divided into subclades—at least the *rendestor* will remain. This has been emphasised, for example, by <u>Cavalier-Smith</u> (1998 p. 211). Such definitions of the *clade* create problems in cladistic systematics. Cladistic systematics is the drive to constantly reduce nonholophyletic groups to only unknown organisms. However, such a definition of the clade (like the one given here for the *phylon*) is widespread and adopted, for example, by the <u>PhyloCode</u> (de Queiroz and Cantino 2020, Article 2.1). Regardless of how acceptable we think *paraphyletic* groups are, cladistics is possible only in the views adopted here and *paraphyletic* groups can be reduced to cases with known ancestors.

ORIGINS OF THE TERMS

The number of terms used here was introduced by other authors with different definitions and/or applications. The terms *monophyly/monophyletic* and *polyphyly/polyphyletic* originated from Haeckel (1866). The terms *paraphyly/paraphyletic* originated from Hennig (1962). The terms *holophyly/holophyletic* originated from Ashlock (1971). The terms *merophyly/merophyletic* originated from Ghiselin (1981; probably having a priority: "Winter", the first *Paleobiology* issue of the year) or Bernardi (1981; probably later: the fourth *Revista Brasileira de Entomologia* issue of the year). The terms *schizophyly/schizophyletic* and *euphyly/euphyletic* originated from Zander (2009). The term *clade* originated from Cuénot (1940).

Although the aforementioned authors clearly applied their terms to the states of groups of organisms, some of the terms seem to have a prehistory of different applications. The wording "holophyletische Wirkung" appeared in Boas 1949 (p. 79). Kühn (1935 p. 131) used "paraphyletische Variation" and the wording "paraphyletic process" appeared in The Madras Agricultural Journal (Editor[s] of this journal 1949 p. 283). I have not been able to figure out the exact meaning of these uses.

Also, the term "monophylie" (the same spelling is used for "monophyly" in French and German—the native language of Haeckel and Hennig) appears in some digitalised versions of some French

dictionaries of the early XIX century (Bosc in Sonnini et al. 1803 p. 541; Poiret in Lamarck and Poiret 1804 p. 168; Lunier 1805, p. 94; Loiseleur Deslongchamps in Lacroix et al. 1821, p. 47; Richard in Audouin et al. 1825, p. 538). Nevertheless, all of these sources contain the imprecisely digitalised/printed word "monophylle" (confer the different links under each aforementioned source in the References section)—the adjective used for the type of construction of a flower calyx (or what was taken for it).

The terms *enophyly/enophyletic*, *kollitophyly/kollitophyletic*, *drade*, *skade*, *idioprestor*, *inprestor*, *rendestor*, and *ancessure* are believed by the author to be new.

CONFLICT OF INTEREST

None declared.

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600 601

603

604

611

614

REFERENCES

- Adl, S.M., Simpson, A.G., Lane, C.E., Lukeš, J., Bass, D., Bowser, S.S., Brown, M.W., Burki, F., Dunthorn, M., Hampl,
- V., Heiss, A., Hoppenrath, M., Lara, E., Le Gall, L., Lynn, D.H., McManus, H., Mitchell, E.A., Mozley-Stanridge, S.E.,
- Parfrey, L.W., Pawlowski, J., Rueckert, S., Shadwick, L., Schoch, C.L., Smirnov, A., Spiegel, F.W., 2012. The revised
- classification of eukaryotes. J Eukaryot Microbiol 59(5), 429–493.
- https://doi.org/10.1111/j.1550-7408.2012.00644.x
- Erratum in: J Eukaryot Microbiol. 2013, 60(3), 321. https://doi.org/10.1111/jeu.12033
- Ashlock, P.D., 1971. Monophyly and Associated Terms. Systematic Biology 20(1), 63–69.
- https://doi.org/10.1093/sysbio/20.1.63
- Audouin[, J.V.], Bourdon, I., Brongniart, A., De Candolle[, A.P. (Sr.)], D'Audebard de Férussac[, A.É.], Deshayes[,
 - G.P.], Eudes Deslon[g]champs[, E.], Desmoulins, A., Drapiez[, P.A.J.], Dumas[, J.-B.-A.], Edwards[, H.M.?/W.F.?],
 - Fée, A., Flourens[, M.J.P.], Geoffroy Saint-Hilaire[, É.], Geoffroy Saint-Hilaire, I., Guérin[, F.É.], Guillemin[, J.B.A.],
- De Jussieu, A., Kunth[, C.S.], Delafosse, G., Lamouroux[, J.V.F.], Latreille[, P.A.], Prévost[, C.], Richard, A., Bory de
- Saint-Vincent[, J.-B.G.M.], 1825. Dictionnaire classique d'histoire naturelle. Tome huitième. H-Inv. Paris. Rey et
- 607 Gravier, Libraires-Éditeurs, Quai des Augustins, n° 55; Badouin Frères, Libraires-Éditeurs, Rue de Vaugirard, n°
- 608 36.
- 609 https://archive.org/details/dictionnairecla19audogoog
- 610 https://www.biodiversitylibrary.org/item/100480
- Bernardi, N., 1981. Parentesco filogenético, grupo monofilético e conceitos correlatos: novas definições. Revista
- Brasileira de Entomologia 25(4), 323–326.
- Boas, F., 1949. Dynamische Botanik eine Physiologie einheimischer Pflanzen für Biologen, Ärzte, Apotheker,
- 616 Chemiker, Landwirte, Gärtner. Vol. 3. Carl Hanser Verlag München.
- 617 https://www.google.com/books?id=1rdTAAAAMAAJ

618 Cavalier-Smith, T., 1998. A revised six-kingdom system of life. Biological Reviews 73, 203–266. 619 620 https://doi.org/10.1111/j.1469-185X.1998.tb00030.x 621 Cuénot, L., 1940. Remarques sur un essai d'arbre généalogique du règne animal. Comptes rendus 622 hebdomadaires des séances de l'Académie des sciences 210, 23-27. 623 https://gallica.bnf.fr/ark:/12148/bpt6k31623 624 625 Cullen, K.E., 2009. Encyclopedia of Life Science. Volume 1. Facts On File, New York. 626 https://google.com/books?id=wMpaAAAAYAAJ 627 628 Dacks, J.B., Field, M.C., Buick, R., Eme, L., Gribaldo, S., Roger, A.J., Brochier-Armanet, C., Devos, D.P., 2016. The 629 changing view of eukaryogenesis - fossils, cells, lineages and how they all come together. J Cell Sci 129(20), 630 3695-3703. https://doi.org/10.1242/jcs.178566 631 632 Dawkins, R., 2004. The Ancestor's Tale: A Pilgrimage to the Dawn of Life. Boston: Houghton Mifflin. 633 https://google.com/books?id=Tub-X6wydKgC 634 635 Dayrat, B., 2003. The Roots of Phylogeny: How Did Haeckel Build His Trees? Systematic Biology 52(4), 515–527. 636 https://doi.org/10.1080/10635150390218277 637 638 Desmonda, E., Brochier-Armanet, C., Forterre, P., Gribaldo, S., 2011. On the last common ancestor and early 639 evolution of eukaryotes: reconstructing the history of mitochondrial ribosomes. Research in Microbiology 162 640 (1), 53-70. https://doi.org/10.1016/j.resmic.2010.10.004 641 642 Doolittle, W.F., 2020. Evolution: Two Domains of Life or Three? Curr Biol 30(4), R177-R179. 643 https://doi.org/10.1016/j.cub.2020.01.010 644 645 Editor[s] of The Madras Agricultural Journal, 1949. W. Wouters — Contribution a l'etude Taxonomique et 646 Caryologique du Genre Gossiypium et application a l'amelioration du contonnier au Congo Belge. The Madras 647 Agricultural Journal 36(6), 282-285. 648 https://archive.org/details/in.ernet.dli.2015.25400 649 650 Eme, L., Spang, A., Lombard, J., Stairs, C.W., Ettema, T.J.G., 2017. Archaea and the origin of eukaryotes. Nat Rev 651 Microbiol 15(12), 711–723. https://doi.org/10.1038/nrmicro.2017.133 652 653 Fitch, W.M., Upper, K., 1987. The phylogeny of tRNA sequences provides evidence for ambiguity reduction in 654 the origin of the genetic code. Cold Spring Harbor Symposia on Quantitative Biology 52, 759–767. 655 https://doi.org/10.1101/sqb.1987.052.01.085 656

- Forterre, P., 2013. The Common Ancestor of Archaea and Eukarya Was Not an Archaeon. Archaea 2013(11),
 372396. https://doi.org/10.1155/2013/372396
 Ghiselin, M.T., 1981. The Metaphysics of Phylogeny. Phylogenetic Patterns and the Evolutionary Process. Niles
- Eldredge and Joel Cracraft. Paleobiology 7(1), 139–143.
 - https://doi.org/10.2307/2400649

666

669

671

672

673

675

677

679

680

681

683

686

689

692

- Haeckel, E., 1866. Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-
 - Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie. Erster
- Band: Allgemeine Anatomie der Organismen. Verlag von G. Reimer, Berlin.
- 668 https://doi.org/10.5962/bhl.title.3953
- Haeckel, E., 1868. Natürliche Schöpfungsgeschichte. Gemeinverständliche wissenschaftliche Vorträge über die
 - Entwicklungslehre im Allgemeinen nd diejenige von Darwin, Goethe und Lamarck, im Besonderen über die
 - Anwendung derselben auf den Ursprung des Menschen und andere damit zusammenhängende Grundfragen
 - der Naturwissenschaft. Berlin. Verlag von Georg Reimer.
- 674 https://google.com/books?id=C3ZGAQAAMAAJ
- Haeckel, E., 1873. Natürliche Schöpfungsgeschichte. Gemeinverständliche wissenschaftliche Vorträge über die
 - Entwickelungslehre im Allgemeinen und diejenige von Darwin, Goethe und Lamarck und Besonderen. Vierte
- 678 verbesserte Auflage. Berlin, Verlag von Georg Reimer. https://doi.org/10.5962/bhl.title.15259
 - Haeckel, E., 1894. Systematische Phylogenie. Entwurf eines Natürlichen Systems der Organismen auf Grund
 - ihrer Stammesgeschichte. Erster Theil: Systematische Phylogenie der Protisten und Pflanzen. Berlin, Verlag von
- Georg Reimer. https://doi.org/10.5962/bhl.title.3947
- Hawking, S., Mlodinow, L., 2010a. The Grand Design. Bantam Books (a division of Random House, Inc.). The USA.
- https://google.com/books?id=xKDnWSd5SC4C
- Hawking, S., Mlodinow, L., 2010b. The (Elusive) Theory of Everything. Sci Am 303(4), 68–71.
- https://doi.org/10.1038/scientificamerican1010-68
- Hennig, W., 1950. Grundzüge einer Theorie der Phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.
- 691 https://google.com/books?id=qJ0KAAAAMAAJ
- Hennig, W., 1962. Veränderungen am phylogenetischen System der Insekten seit 1953. pp. 29–42. In:
 - Sachtleben, H. (comp.) Bericht über die 9. Wanderversammlung Deutscher Entomologen, 6.–8. Juni 1961 in
- 695 Berlin. Tagungsberichte, Deutsche Akademie der Landwirthschaftswissenschaften №45. Berlin: Deutsche
- 696 Akademie der Landwirtschaftswissenschaften.
- 697 https://google.com/books?id=Ca8iAQAAIAAI

```
698
       https://google.com/books?id=FuIfAAAAIAAI
699
700
       Hennig, W., 1965. Phylogenetic systematics. Annual Review of Entomology, 10, 97–116.
701
       https://doi.org/10.1146/annurev.en.10.010165.000525
702
703
       Hennig, W., 1966. Phylogenetic systematics. University of Illinois Press, Urbana.
704
       Huxley, J.S., 1957. The three types of evolutionary process. Nature, 180(4584), 454–455.
705
       https://doi.org/10.1038/2F180454a0
706
707
708
       Huxley, J.S., 1958. Evolutionary processes and taxonomy with special reference to grades. pp. 21–39, in
709
       Hedberg, O. (ed). Systematics of To-day. Uppsala Universitets Arsskrift, Sweden.
710
       Huxley, J.S., 1959. Clades and grades. In: Cain, A.J. (Ed.), Function and Taxonomic Importance. The Systematics
711
       Association. London. UK. pp. 21–22.
712
       https://archive.org/details/functiontaxonomi0000syst
713
714
715
       Koonin, E.V., 2010. The origin and early evolution of eukaryotes in the light of phylogenomics. Genome Biol 11,
       209. https://doi.org/10.1186/gb-2010-11-5-209
716
717
       Koonin, E.V., 2011. The Logic of Chance: The Nature and Origin of Biological Evolution. FT Press Science (a
718
       division of Pearson Education, Inc).
719
720
       https://google.com/books?id=fvmv2kU6PrYC
721
       Koumandou, V.L., Wickstead, B., Ginger, M.L., van der Giezen, M., Dacks, J.B., Field, M.C., 2013. Molecular
722
       paleontology and complexity in the last eukaryotic common ancestor. Crit Rev Biochem Mol Biol. 48(4), 373-
723
       396. https://doi.org/10.3109/10409238.2013.821444
724
725
726
       Kühn, O., 1935. Geologisches zentralblatt. Palaeontologie. Abteilung B 5-6, 131.
       https://www.google.com/books?id=EoYQAAAAIAAI
727
728
       Kwok, R.B.H., 2010. Phylogeny, genealogy and the Linnaean hierarchy: a logical analysis. Journal of
729
       Mathematical Biology, 63(1), 73–108. https://doi.org/10.1007/s00285-010-0364-6
730
731
       Lacroix[, S.-F.], Chevreul[, M.E.], Brongniart[, A.], Brochant de Villiers[, A.-J.-F.-M.], DeFrance[, J.L.M.],
732
       Desfontaines[, R.L.], de Jussieu[, A.L.], Mirbel[, C.-F.], Cassini, [A.]H.[G.], Leman[, D.S.], Loiseleur Deslongchamps[,
733
       [.L.A.], Massey[, P.], Poiret[, [.L.M.], de Tussac[, F.R.], Cuvier, G., Geoffroi[, E.], Dumont[, C.H.F.], Lacépède[, B.G.],
734
       Dumeril[, A.M.C.], Cloquet[, H.], Leach[, W.E.], de Blainville[, H.M.D.], Turpin[, P.J.F.], de Humboldt[, A.], Ramond[,
735
       L.F.É.], de Candolle[, A.P. (Sr.)], Cuvier, F., 1821. Dictionnaire des sciences naturelles, dans lequel on traite
736
```

méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos

- connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les
- artes. Suivi d'une biographie des plus célèbres naturalistes. Tome XVIII. Ga-Gju. F. G. Levrault, Éditeur, à
- 740 Strasbourg, et rue des Fossés M. le Prince, n.° 33, à Paris. Le Noraunt, rue de Seine, N.° 8, à Paris.
- 741 https://archive.org/details/dictionnairedess18cuvi
 - https://www.biodiversitylibrary.org/item/74506

744

- Lamarck[, J.B.], Poiret, J.L.M., 1804. Encyclopédie méthodique, ou par ordre de matiere; par une société de gens
- de lettres, de savans et d'artistes. Tome cinquième. A Paris, Chez H. Agasse, Imprimeur-Libraire, rue des
- 746 Poitevins, n.° 18.
- 747 https://archive.org/details/bub_gb_xWrz6tlVx9wC
- 748 https://www.biodiversitylibrary.org/item/15263
- 749 https://www.biodiversitylibrary.org/item/104010

750

751

752

- Lunier, M., 1805. Dictionnaire des sciences et des arts. Tome II. A Paris, Chez Etienite Gide, Libraire, rue
- Christîne, n.° 5 et H. Nicolle et C.ie, rue des Petits-Augustins, n.° 35.
- 753 https://archive.org/details/dictionnairedess02luni
- 754 https://google.com/books?id=vPUOAAAAQAAJ
 - https://google.com/books?id=uyBCAAAAcAAJ

756

755

757

758759

- O'Malley, M.A., Leger, M.M., Wideman, J.G., Ruiz-Trillo, I., 2019. Concepts of the last eukaryotic common
- ancestor. Nat Ecol Evol 3, 338–344. https://doi.org/10.1038/s41559-019-0796-3
- 760 Podani, J., 2009. Taxonomy versus evolution. Taxon 58(4), 1049–1053. https://doi.org/10.1002/tax.584001

761

- Podani, J. 2010. Monophyly and paraphyly: A discourse without end? Taxon 59(4), 1011–1015.
- 763 https://doi.org/10.1002/tax.594002

764

- de Queiroz, K., Cantino, P.D., 2020. International Code of Phylogenetic Nomenclature (PhyloCode). CRS Press.
- 766 https://doi.org/10.1201/9780429446320

767

768

- Rieppel, O., 2010. Ernst Haeckel (1834-1919) and the monophyly of life. Journal of Zoological Systematics and
- Evolutionary Research, 49(1), 1–5. https://doi.org/10.1111/j.1439-0469.2010.00580.x

769770

- Shalchian-Tabrizi, K., Eikrem, W., Klaveness, D., Vaulot, D., Minge, M.A., Le Gall, F., Romari, K., Throndsen, J.,
- Botnen, A., Massana, R., Thomsen, H.A., Jakobsen, K. S., 2006. Telonemia, a new protist phylum with affinity to
 - chromist lineages. Proceedings. Biological sciences 273(1595), 1833–1842.
 - https://doi.org/10.1098/rspb.2006.3515

774775

777

- Sonnini[, C.-N.-S.], Virey[, J.-J.], Vieillot[, L.P.], Parmentier[, A.-A.], Huzard[,J.-B.], Bosc[, L.A.G.], Olivier[, G.-A.],
 - Latreille[, P.A.], Chaptal[, J.-A.], Cels[, J.P.M.], Thouin[, A.], Du Tour[de Salvert, A.A.], Patrin[, E.L.M.], Libes[, A.],

778	1803. Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, principalement à l'agriculture et à
779	l'économie rurale et domestique. Tome VIII. A Paris, Chez Deterville, Libraire, rue du Battoir, n.° 16.
780	https://www.google.com/books?id=SeVfAAAAcAAJ
781	https://www.biodiversitylibrary.org/item/260869
782	
783	Strassert, J.F.H., Jamy, M., Mylnikov, A.P., Tikhonenkov, D.V., Burki, F., 2019. New Phylogenomic Analysis of the
784	Enigmatic Phylum Telonemia Further Resolves the Eukaryote Tree of Life. Molecular Biology & Evolution 36(4),
785	757-765. https://doi.org/10.1093/molbev/msz012
786	
787	Urry, L.A., Cain, M.L., Wasserman, S.A., Minorsky, P.V., Orr, R.B., Campbell, N.A. (2021). Campbell biology. 12th
788	edition. Pearson, New York, NY.
789	https://www.pearson.com/store/p/campbell-biology/P100002940947/9780135988046
790	
791	Zander, R.H., 2009. Modern Evolutionary Systematics: Introduction. Res Botanica, a Missouri Botanical Garden
792	Web Site.
793	https://web.archive.org/web/20110130231823/https://mobot.org/plantscience/ResBot/EvSy/Intro.htm