Holophyly and associated concepts if the unknown is unclassifiable

- Running title: Holophyly and associated concepts
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Abstract

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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

25 Many biologists use a kind of model-dependent

26 realism (Hawking and Mlodinow 2010a, b; Koonin

27 2011; similar to constructive empiricism of Van

28 Fraassen (1980)). Here, the objective reality and

29 absolute truth exist and we have accessible signals

30 from the objective reality. The robustness of these

31 signals vary depending on the object of study. Along

32 with it, for many objects of study in each particular

33 time we have only a rating of models, but not the

34 single absolute truth. This rating is built based on four

35 values of models: their empirical adequacy; self-

36 consistency; explanatory power; and parsimony.

37 Concerning the phylogeny of life, this approach

38 manifests itself in the following chain: 1) characters

39 of known organisms serve as the base for the

40 construction of a phylogenetic tree; 2) this

41 phylogenetic tree becomes accepted as a reflection of

42 phylogeny in each particular case; 3) this reflection

43 serves as the base for conclusions on groups' states

44 and on features of some ancestors of different known

45 organisms like the last common ancestor of known

46 eukaryotes (Koonin 2010; Desmond et al. 2011;

47 O'Malley et al. 2019) or the last common ancestor of

48 known eukaryotes plus known archaea (Forterre

49 2013; Doolittle 2020). It is the way by which

50 undiscovered entities appear in scientific discussions.

51 In natural sciences, the key criterion for proving 52 the existence of an object (like an astronomical object of a previously unknown kind, an atom of a 53 previously unknown element or an organism of a 54 previously unknown species) is its discovery—an 55 56 observation of this object and/or observation of traces of its existence (radiation, remains of vital 57 58 activity etc.).

There is no natural or government law, which prohibits putting undiscovered (or even purely

hypothetical) entities into groups. As there is no such law, which prohibits the creation of systems of life composed exclusively of form-taxa. But is it better to do it one way or another?

If we consider the unknown organisms to be direct members of groups, then we must write right now that intelligent life is polyphyletic (and all life too), if somewhere in the endless universe there is (or was) intelligent life besides us. Any group with classical morphological definition can not be called holophyletic, as there always is a possibility of the existence of an undiscovered "member" of the same lineage which does not fit the definition. Also, if you consider unknown organisms classifiable, then no clade can be divided into subclades without a reminder (Cavalier-Smith 1993 p. 955; 1998 p. 211). In this case, we must introduce at least one paraphyletic group per holophyletic one (Cavalier-Smith, 1993; 1998). What do I put in taxa by putting undiscovered organisms into them? Probably, I put no more than sketchy pictures in my mind.

It seems premature to directly place the undiscovered into taxa (or create separate taxa for it) before its discovery. With the unclassifiable unknown, we can call life holophyletic until any independently occurring life is discovered (if it ever happens). Likewise, groups with classical morphological diagnoses may be called holophyletic until any member of the same lineage not matching the diagnosis is discovered. Also, the clades become fully divisible into subclades. Official nomenclatural codes seem to support this position. According to them, only discovered entities are taxonomically nameable (Articles 1.3.1, 72.3, 72.5 of ICZN; Principle II and Articles 7.1 and 8.1 of ICN[afp]; Principle 5 and Rule 15 of ICNCP; Articles 11.1, 11.4 of *PhyloCode*). New

species are described as new, rather than already 98 existing in the group, as it is about the human knowledge of biodiversity. Unknown organisms within the definitional border of a taxon are only its 100 potential members.

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102 Because of all this, the present work is dedicated 103 only to the approach where undiscovered is not directly classifiable. Among undiscovered organisms, 104 105 there is one special kind, which deserves a closer look. 106 It is the unknown ancestors of known organisms. A 107 remarkable feature of phylogenetics is that known descendants inevitably imply the existence of their 108 ancestors, even if these ancestors are unknown. 109 Nevertheless, this implication is not enough to 110 111 "specify the identity" for each of the unknown ancestors. This can be compared to the following 112 analogy from the judiciary. If the existence of some 113 114 illegal organisation with a leadership management system is proven, then it certainly has a leader. 115 116 However, this data is not enough to bring any person 117 to trial. As in the case of unknown ancestors, a "vacancy" is known here, but not an identity. 118

119 Despite all this, the non-classification of unknown 120 organisms creates nonsense in the current system of 121 phylogenetic concepts. It (holo-/monophyly, paraphyly, 122 and polyphyly as they are currently defined) is not 123 adapted to the separation of known and unknown 124 organisms (as well as populations, species, etc.). The 125 difference of holo- and paraphyletic groups from 126 polyphyletic groups is whether the last common 127 ancestor is a member of the group (Encyclopedia of Life Science—Cullen 2009, p. 91; PhyloCode—de 128 129 Queiroz and Cantino 2020, Article 2.1; Campbell 130 biology —Urry et al. 2021 p. 560; Hawkswort 2010; and others). Almost always the last common ancestor 131 132 can not be included in a taxon because this ancestor is 133 unknown. This makes almost all groups polyphyletic 134 if take these definitions literally. Current phylogenetic 135 discussions require a system of more accurately 136 defined concepts. The inclusion of ancestors in taxa 137 can not be only direct as under current definitions of 138 holophyly and paraphyly.

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" (e.g. Ashlock 1971). The inclusion was unconditional. Likewise, the kind of members is not stipulated by the "connected-disconnected" (Kwok 2010) / "continuous-discontinuous" (Aubert 2015) divide.

Hennig (1950; 1965; 1966) was probably aware

151 152 This lack of differentiation between known and 153 unknown organisms has led to confusion among taxonomists (see Podani 2010 for review). Probably,

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155 both of the main types of the vision of phylogenetic 156 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). 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 high near the terminals of the Tree of Life. However, the inclusion of unknown organisms (including unknown ancestors) can not be direct and immediate.

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.

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 Cavalier-Smith (1993 p. 955; 1998 p. 211). Such definitions of the clade create problems in cladistic systematics. Cladistic systematics is the drive to constantly reduce non-holophyletic 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 PhyloCode (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. Well, let us go in search of "natural" groups' nature.

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 a 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 Zander's (2009) 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.

Phyletic states depending on the branching pattern of the group's actual content (of discovered members)

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

MEROPHYLETIC group (/mɪrə(υ)fʌɪˈlɛtɪk/; from Greek μέρος [méros] - 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 (/pɒlifʌɪˈlɛtɪk/; 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 within the cosmological horizon).



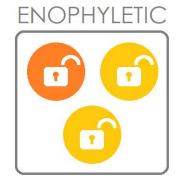




Figure 1. The tree of ancestor-descendant relationships. Circles with open locks represent known elementary units of classification, circles with closed locks represent unknown units.

This divide is sufficient and is the only possible one in case a set has no definition, but only the circumscription and the tree branching pattern. Along with it, the eno-mero divide is not enough for characterising a set as "natural" or not. A group of the former type must be at least kollitophyletic (cf. connected/continuous) or atomophyletic.

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". Both the progenitor and an ancestor of a group can not be members of that group. Also, an ancestor and a progenitor are unable to be included in the group (Fig. 2). The phrase "My mom is the ancestor of my mom, my sister and me" is not correct. So is this phrase if we replace the word "ancestor" with "progenitor". For systematic instance, eukaryotes are the first cell with (the thing posessing all character of) the true nucleus inside together with all that cell's descendants. Anything called (any) ancestor of eukaryotes is an ancestor of the first cell with a nucleus (i.e. was a prokaryote). It can not have a nucleus because of the meaning of the word "ancestor". Calling something an ancestor rules out its ability to become a member of the group of which it is said to be an ancestor.

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 words "concestor" and "cenancestor" are the different names of the same concept as the last common ancestor.) The absence of the concept was the reason for the introduction of inprestor. The wording "first common ancestor", which is sometimes used (e.g. Koumandou et al. 2013; Dacks et al. 2016; Eme et al. 2017) stands even less criticism. Literally, the first common ancestor 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 (/'mprɛstə/; 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 ἴδῖος - pertaining to self, one's own, private (as opposed to public); Greek πρώτα [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.

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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.

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

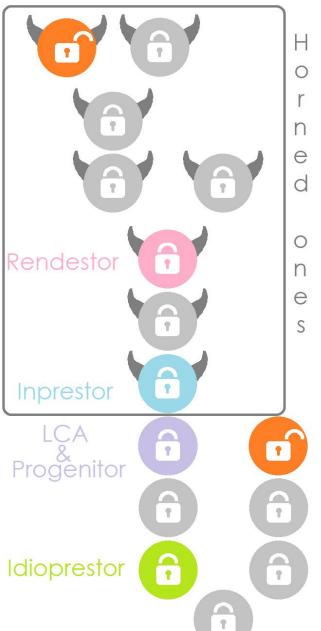


Figure 2. The tree of ancestor-descendant relationships illustrating the different identities of rendestor, inprestor, idioprestor and last common ancestor (LCA) and progenitor. The grey frame is the definitional borders of the group based on the apomorphy of horns.

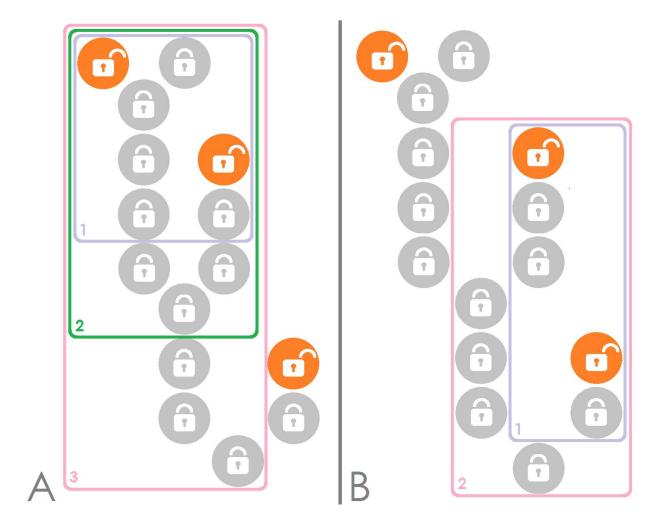


Figure 3. Possible definitional borders for the equivalent sets of two known organisms: enophyletic (A) and merophyletic (B). The groups A1 and B1 are schizophyletic. A2 is holophyletic. A3 and B2 are paraphyletic.

ancestor of all known members of a group (e.g. *inprestor* in the case of *inprestral ancessure*; see Figs. 2 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 $\zeta\omega$ [skhizo] - 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*.

The kollitophyly is enough to conclude that a set is "natural" only for ones who accept paraphyly in systems. For others, a set of the former type must be holophyletic (cf. previous definitions of holophyly and monophyly).

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*; see the next paragraph) 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* by 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* group, 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).

HOLOPHYLY OR MONOPHYLY?

The term *holophyletic* was preferred here because of the number of meanings of the term *monophyletic*, both definitional and etymological. As already noted, 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 (monophyly *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.

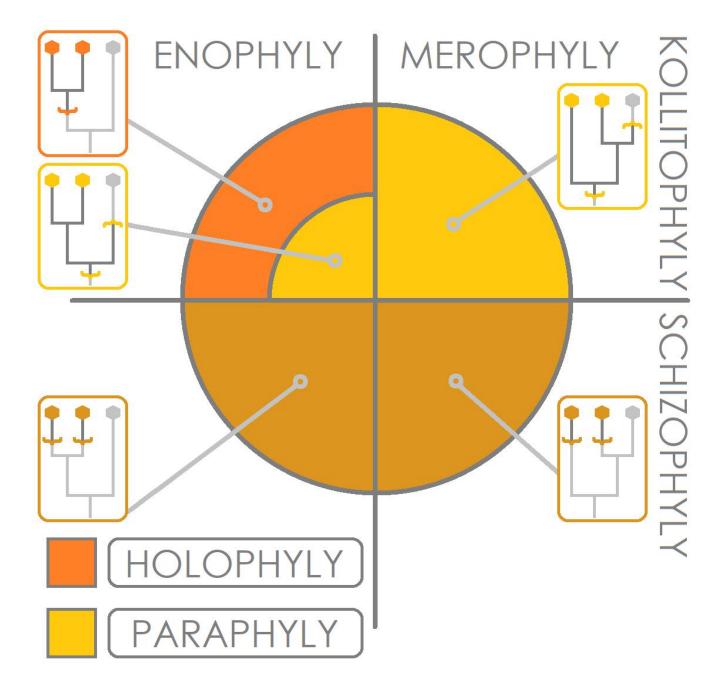


Figure 4. The diagram of the relationships of phyletic states among themselves. Coloured hexagons represent known group members. Grey hexagons represent the known organisms outside the group. The groups: on all three trees on the left are enophyletic; on all two trees on the right are merophyletic; on 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: 1) HOLOPHYLETIC—mammals (Mammalia), birds (Aves); 2) 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); 3) SCHIZO-ENOPHYLETIC—"photokaryotes" of Cavalier-Smith 1999 in the case if his (Cavalier-Smith 2018) hypothesis on the single origin of plastids in Chromista is true (as then there are two independent origin points: plastid aquisitition at the base of Archaeplastida and of Chromista; cf. schizoenophyletic "photokaryotes" and holophyletic Diaphoretickes), TSAR grouping (see below), probably (see Fowke and Pickett-Heaps 1969; Sawitzky and Grolig 1995) charophytes with phragmoplasts (Phragmoplastophyta); 4) PARA-MEROPHYLETIC—reptiles (Reptilia); 5) SCHIZO-MEROPHYLETIC—warm-blooded animals (Homotherma); Protista (including Myxozoa).

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 μόνος [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 ὄλος [hólos]) concerning both known organisms and unknown members of the ancessure.

THE "-ADE" TERMS

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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 $\kappa\lambda$ άδος [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 by definition although enophyletic (schizo-enophyletic; see Fig. 4, 6). For such purposes, a short term for "enophyletic group" seems needed.

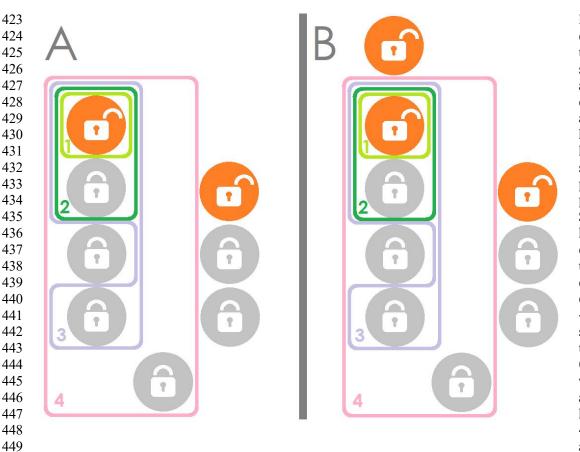


Figure 5. A. Possible diagnostic borders for the equivalent singleton sets (i.e. containing one and same known organism): atomophyletic and holophyletic (1), holophyletic (2), schizophyletic (3), paraphyletic (4). All sets pictured are enophyletic. Sets 2 and 4 are kollitopyletic. All they could be merophyletic if the only included known organism had known excluded descendant(s) —see B. Holophyly of the sets 1 and 2 in this case turned to paraphyly. Other states of all sets would be unchanged: atomophyly of the set 1, kollitophyly of the sets 2. 4, schizophyly of the set 3 and paraphyly of the set 4.

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 $\kappa\lambda\alpha\delta\delta\sigma$ [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 Huxley 1957; 1958; 1959).

SKADE (/skeid/; from Greek $\sigma \kappa \alpha \lambda \dot{\omega} \nu$ [skalón] - flight of stairs) — a paraphyletic group.

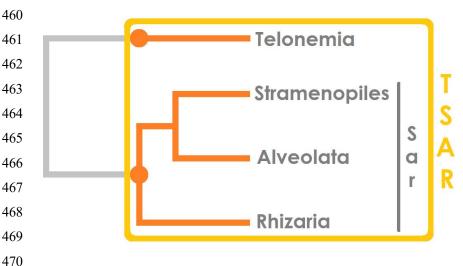


Figure 6. Schematic phylogenetic tree of Telonemia, Stramenopiles, Alveolata, and Rhizaria illustrating schizophyly of the union of Telonemia with Sar (TSAR drade). Definitional borders of TSAR are shown in yellow. Unincluded part of the rendestral ancessure is shown in grey. Inprestors of Telonemia 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) 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.
- 3) *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 Dawkins (2004) 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").
- 4) In discussions about the origin of a group (for example, about eukaryogenesis), we are talking primarily about the *inprestor* of this group.

- 5) *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.
- 486 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*.
- 6) The demarcation between *enophyly, kollito-enophyly*, and *holophyly* is the Achilles' heel of existing systems of phylogenetic concepts.
- 490 7) 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 Kwok (2010),
 - who used the terms "connected group" and "disconnected group", although he does not distinguish
 - between known and unknown organisms).
- 494 8) The difference between holophyletic and paraphyletic groups is whether the inprestral ancessure of
- the group gave rise to any known organism outside the group.

ORIGINS OF THE TERMS

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- 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
- 505 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.
- The term *concestor* was coined by Nicky Warren and popularised by Dawkins (2004; see p. 7). The term
- "cenancestor" was coined by Fitch and Upper (1987).
- 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
 - and the desired and the second of the type of
- 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

521 None declared.

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