Title: Holophyly and associated concepts if the unknown is unclassifiable

Subtitle: Holophyly and associated concepts

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ACKNOWLEDGEMENTS

The author is grateful to Vasily V. Zlatogursky for the language corrections.

Abstract
The current definitions of holophyly (monophyly) 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 (enophyly, merophyly, kollitophyly, schizophyly, paraphyly, holophyly) 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 life). Inability to provide a concise definition of holophyly using the existing terms indicates the lack (or imprecision) of more basic concepts. These concepts (phyla, 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 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 group's states and on features of some reconstructed 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 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. 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 "establish 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 (2010) are not completely correct and the consensus seems possible and necessary (compare Fig. 1 in Podani, 2010 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 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. phyla*, *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 draw conclusions 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

PHYLETIC CONCEPTS USING NO UNKNOWN ANCESTORS

PHYLON (/ˈfaɪlə/; from Greek *φῦλον* [*phylon*] - tribe) — the ancestor plus all its descendants, or the set of a sole member having no descendants.

ENOPHYLETIC group (/εnə(ʊ)fʌɪˈlεtɪk/; from Greek *ενότητα* [*enótita*] - unity) — a set of known organisms, for which at least one phyla exists, all known members of which they are.

MEROPHYLETIC group (/mɪrə(ʊ)fʌɪˈlεtɪk/; from Greek *μέρος* [*méros*] - part, portion) — a set of known organisms of common descent for which no phyla exists, all known members of which they are; or a set of a sole known member having known descendants.

POLYPHYLETIC group (/pɒlifʌɪˈlεtɪk/; 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).

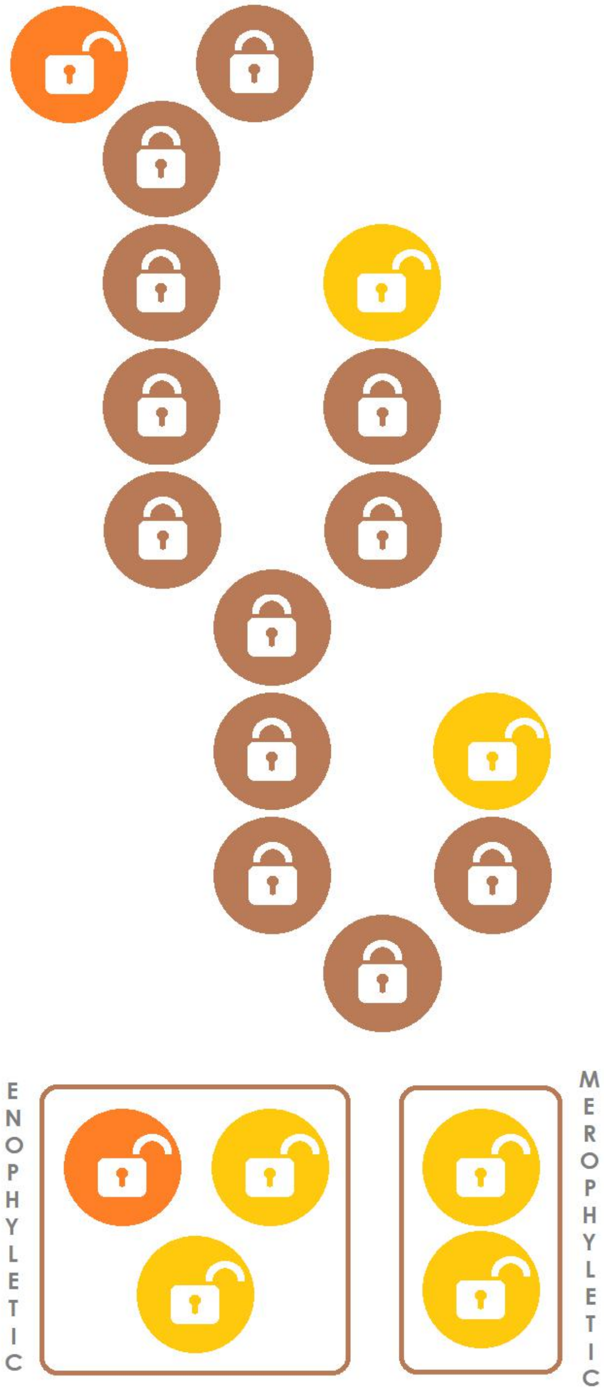

Figure 1. ***The tree of ancestor-descendant relationships. Circles with open locks represent known organisms, circles with closed locks represent unknown organisms.***

CONCEPTS FOR UNKNOWN ANCESTORS

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, FCA of any group goes to the origins of life. This indicates the need for the concept of *idioprestor*.

RENDESTOR of a group (/ˈrɒndɛstə/; from French ***rende****zvous* - 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 (/ˈɪnprɛstə/; from ***in***, Greek *πρώτα* [***pró****ta*] - 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 (/ɪdɪə(ʊ)ˈprɛstə/; from Ancient Greek ἴδῐος - 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.

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* of a feature-based group (*e.g.* apomorphy-gainer), the *inprestor* of a maximal clade), 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 (/ansɛsˈjʊə/; 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

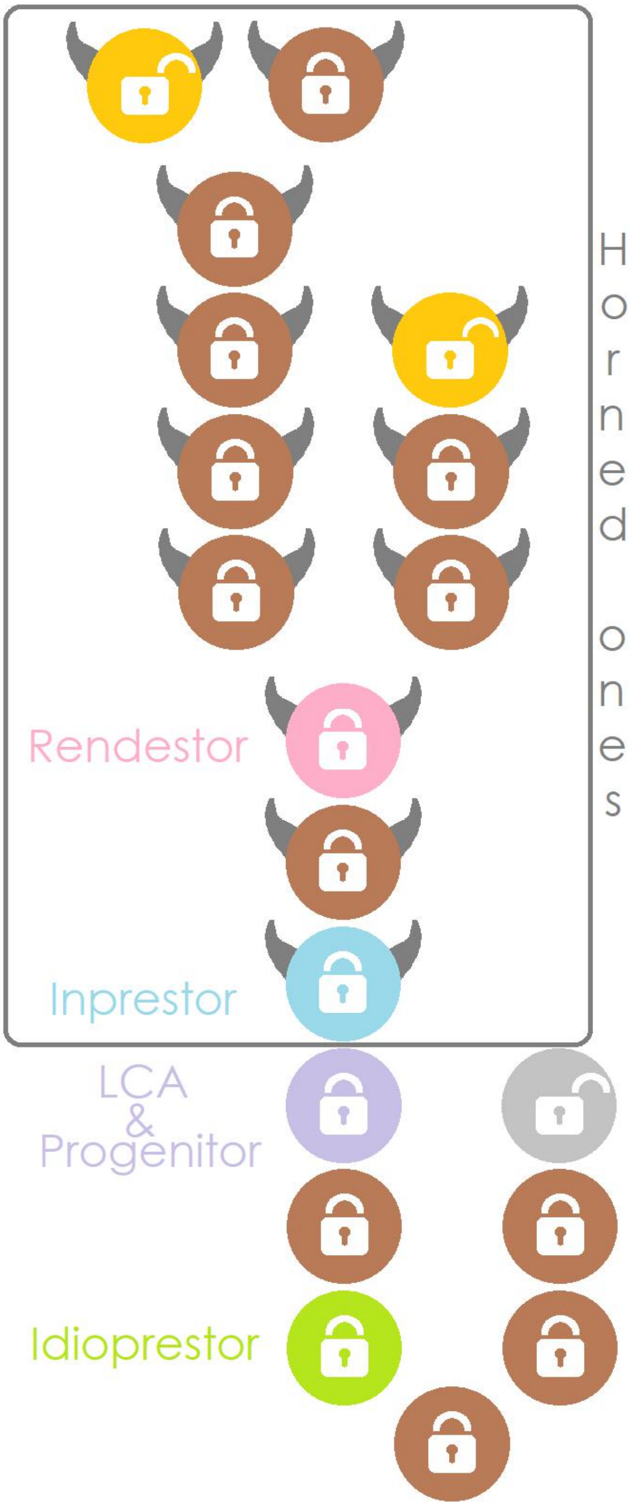

Figure 2. ***The tree of ancestor-descendant relationships illustrating the different identities of* rendestor, inprestor, idioprestor *and* last common ancestor *(LCA) and* progenitor*. The grey frame is the diagnostic borders of the group based on the apomorphy of horns.***

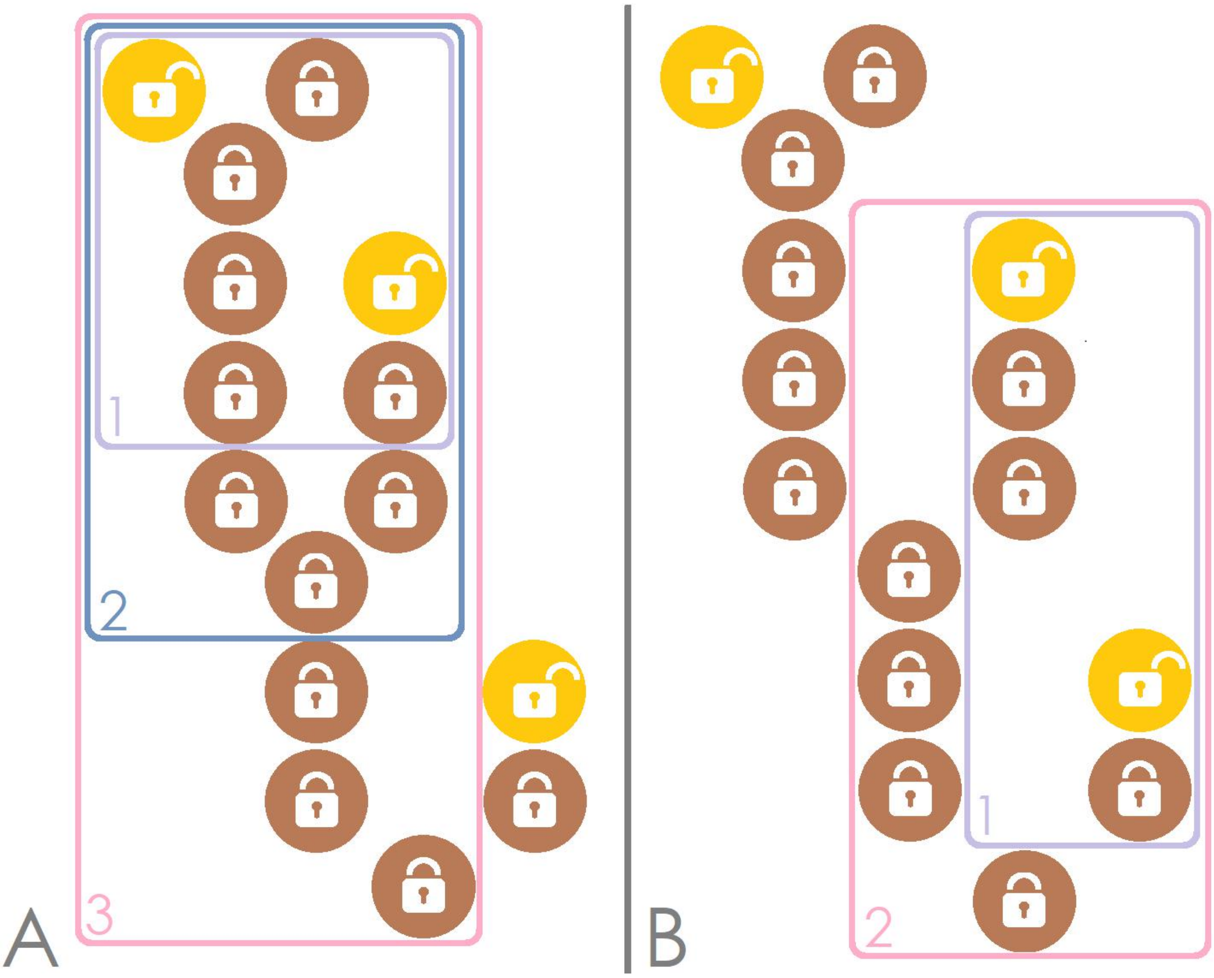

Figure 3. ***Possible diagnostic borders for the same set of two known organisms: enophyletic (A) and merophyletic (B). The groups A1 and B1 are schizophyletic. A2 is holophyletic. A3 and B2 are paraphyletic.***

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 CONCEPTS USING UNKNOWN ANCESTORS

KOLLITOPHYLETIC group (/kəlaɪtə(ʊ)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 (/skɪtsə(ʊ)fʌɪˈlɛtɪk/; from Greek *σχίζω* [*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*.

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 group (/hɒlə(ʊ)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(ʊ)fʌɪˈlɛtɪk/; from Greek *παρά* [*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 (if a term is needed there). *Kollitophyletic* groups always have both *rendestral* and *inprestral* ancessures. For a *schizophyletic* group always at least a *rendestral ancessure* exists. For an a*tomophyletic* 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). 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.

The term *holophyly* was preferred here because of the number of meanings of the term *monophyly*, both definitional and etymological. Evolutionary taxonomists use it probably in the same sense as *kollitophyly*. Phylogenetic taxonomists use it in the stricter sense, probably the same as *holophyly* as it was defined here. As there was no differentiation between known and unknown members relatively to the phyletic terms 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”) 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 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).

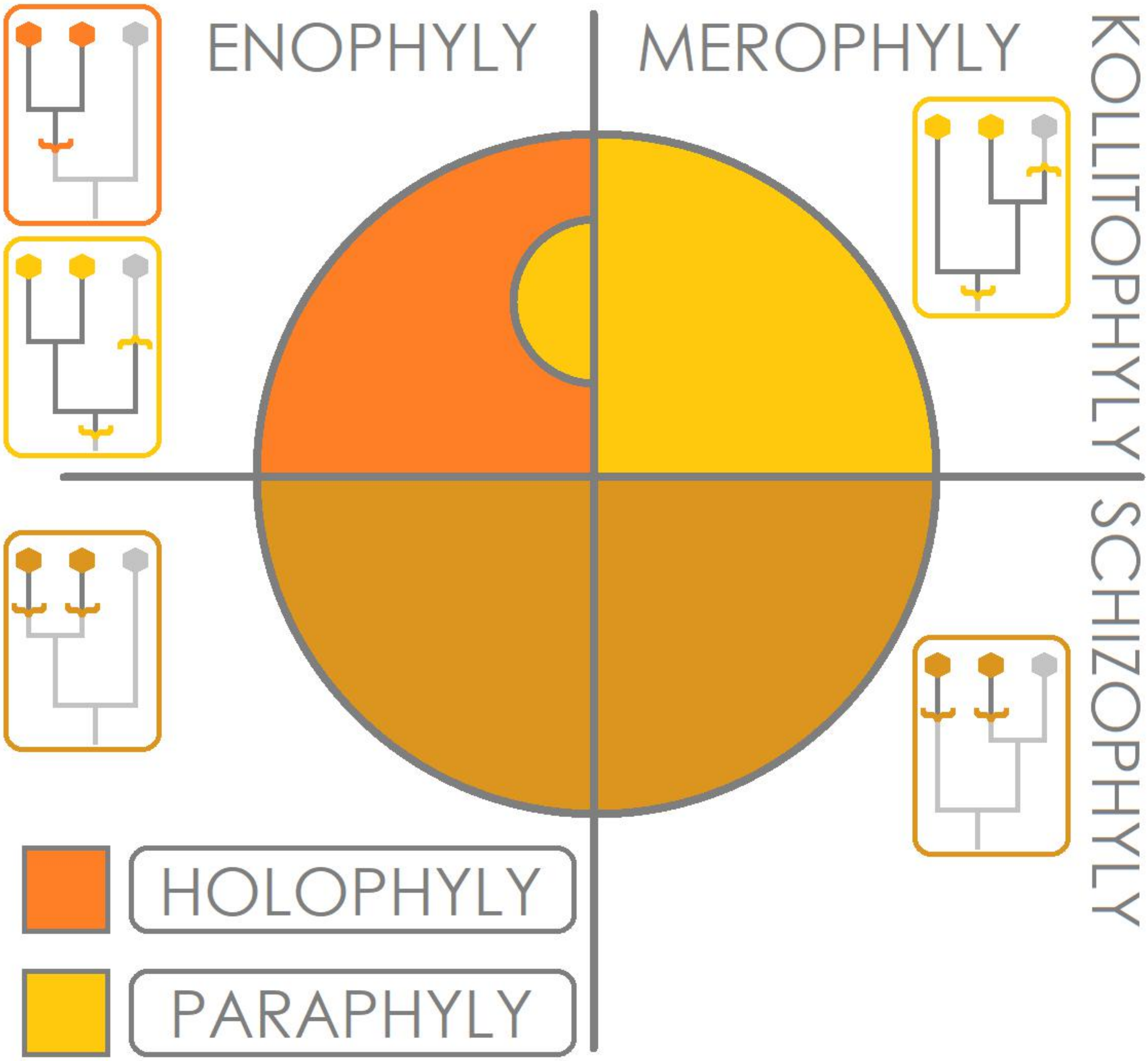

Figure 4. ***The diagram of the relationships of "phyly" among themselves. Coloured hexagons represent known group members. Grey hexagons represent the known organisms outside the group. The groups: on all three trees on the left are enophyletic; on all two trees on the right are merophyletic; on all three trees above are kollitophyletic; on all two trees below are schizophyletic. The colour of the hexagons and borders around each tree matches the colour of the segment of the vertical half of the diagram.***

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 *κλάδος* [*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). Therefore, this group is *schizophyletic* although *enophyletic* (*schizo-enophyletic*; see Fig. 4). For such purposes, a short term for "*enophyletic* group" seems needed.

DRADE (/dɹeɪd/; from the two first letters of the semantic core in L. *poly***dr***upa*—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 (/kleɪd/; 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 Huxley 1957; 1958; 1959).

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

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 knowing 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" described here 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 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").

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 Kwok (2010), 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 Cavalier-Smith (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 *phyla*) is widespread and adopted, for example, by the PhyloCode (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 application. The terms *monophyly*/*monophyletic* and *polyphyly*/*polyphyletic* originated from Haeckel (1866). The terms *paraphyly*/*paraphyletic* originated from Hennig (1965). The terms *holophyly*/*holophyletic* originated from Ashlock (1971). The terms *merophyly*/*merophyletic* originated from Bernardi (1981). The term *clade* originated from Cuénot (1940).

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

CONFLICT OF INTEREST

None declared.

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