# Holophyly and associated concepts if the unknown is unclassifiable

- 3 Running title: Holophyly and associated concepts
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#### 8 Abstract

9 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 10 one describes them as species and does not create other taxa for them. The organisms unknown to science can 11 not be an object of the biological taxonomical classification. Here, the direct inclusion/exclusion of unknown 12 13 ancestors was replaced with the ability/disability of the systematic group to include them (according to the 14 definition of each specific group). In this way, the problem of incomplete division of the clade into subclades is 15 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 16 states" of the groups proposed here deals more carefully with ancestors as well as the fact that every two 17 18 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 19 20 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 21 22 near the end of the paper.

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

#### 24 INTRODUCTION

Many biologists use a kind of model-dependent 25 26 realism (Hawking and Mlodinow 2010a, b; Koonin 2011; similar to constructive empiricism of Van 27 28 Fraassen (1980)). Here, the objective reality and absolute truth exist and we have accessible signals 29 from the objective reality. The robustness of these 30 signals vary depending on the object of study. Along 31 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 values of models: their empirical adequacy; self-35 36 consistency; explanatory power; and parsimony. Concerning the phylogeny of life, this approach 37 manifests itself in the following chain: 1) characters 38 of known organisms serve as the base for the 39 construction of a phylogenetic tree; 2) this 40 phylogenetic tree becomes accepted as a reflection of 41 phylogeny in each particular case; 3) this reflection 42 43 serves as the base for conclusions on groups' states and on features of some ancestors of different known 44 organisms like the last common ancestor of known 45 eukaryotes (Koonin 2010; Desmond et al. 2011; 46 O'Malley et al. 2019) or the last common ancestor of 47 known eukaryotes plus known archaea (Forterre 48 2013; Doolittle 2020). It is the way by which 49 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.).

59 There is no natural or government law, which60 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

97 species are described as new, rather than already 98 existing in the group, as it is about the human 99 knowledge of biodiversity. Unknown organisms within the definitional border of a taxon are only its 100 101 potential members. 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*. 139 Hennig (1950; 1965; 1966) was probably aware 140 that only known organisms can be classified. At the 141 same time, he considered the probability of finding an 142 ancestor of any group so low that he did not stipulate 143 the inclusion of ancestors in any way in his definitions 144 of phyletic terms. Ancestors de facto were excluded 145 from the groups. This theoretical inaccuracy led to the 146 rapid inclusion of the last common ancestor by other 147 authors in the definitions of the three "phyly" (e.g. 148 Ashlock 1971). The inclusion was unconditional. 149 Likewise, the kind of members is not stipulated by the "connected-disconnected" (Kwok 2010) / 150 151 "continuous-discontinuous" (Aubert 2015) divide. 152 This lack of differentiation between known and 153 unknown organisms has led to confusion among 154 taxonomists (see Podani 2010 for review). Probably, 155 both of the main types of the vision of phylogenetic 156 trees shown by Podani (2009, Fig. 2; 2010, Fig. 1) are

157 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.

### 218 **CONCEPTS AND COMMENTS**

### 219 **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.

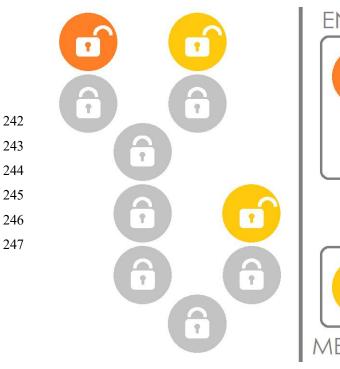
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**PHYLON** (/'faɪlɒn/; from Greek  $\varphi \tilde{v} \lambda ov$  [*phylon*] - tribe) — the ancestor plus all its descendants, or the set of a sole member having no descendants.

### 229 **PHYLETIC STATES DEPENDING ON THE BRANCHING PATTERN OF THE GROUP'S ACTUAL CONTENT (OF** 230 **DISCOVERED MEMBERS)**

231	<b>ΕΝΟΡΗΥLETIC</b> group (/εnə(υ)fʌɪ'lɛtɪk/; from Greek ενότητα [enótita] - unity) — a set
232	of known organisms, for which at least one phylon exists, all known
233	members of which they are.
234 235 236 237	<b>MEROPHYLETIC</b> group (/mɪrə(ʊ)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.
238	<b>POLYPHYLETIC</b> group (/pplifAI'lɛtık/; from Greek $\pi o\lambda \dot{v} \varsigma$ [polús] - many, much) — a set
239	of known organisms, which have no common ancestor; descendants of
240	different ancestors (an exclusively theoretical concept in the present
241	state of knowledge of life within the cosmological horizon).



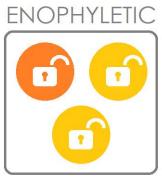


Figure 1. The tree of ancestordescendant relationships. Circles with open locks represent known elementary units of classification, circles with closed locks represent unknown units.



248 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

250 "natural" or not. A group of the former type must be at least kollitophyletic (cf. connected/continuous) or

atomophyletic.

### 252 ANCESTOR AND PROGENITOR ARE MISUSED CONCEPTS: REPLACEMENTS

There is a logical and semantical problem with both the wording "last common ancestor" and the word 253 "progenitor" without adding "of the known members of the group". Both the progenitor and an ancestor of a 254 group can not be members of that group. Also, an ancestor and a progenitor are *unable to be included* in the 255 group (Fig. 2). The phrase "My mom is the ancestor of my mom, my sister and me" is not correct. So is this phrase 256 if we replace the word "ancestor" with "progenitor". For systematic instance, eukaryotes are the first cell with 257 (the thing posessing all character of) the true nucleus inside together with all that cell's descendants. Anything 258 called (any) ancestor of eukaryotes is an ancestor of the first cell with a nucleus (i.e. was a prokaryote). It can 259 not have a nucleus because of the meaning of the word "ancestor". Calling something an ancestor rules out its 260 ability to become a member of the group of which it is said to be an ancestor. 261

This issue and the cumbersomeness of the wording "the last common ancestor of the known members of 262 263 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 264 265 "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 266 sometimes used (e.g. Koumandou et al. 2013; Dacks et al. 2016; Eme et al. 2017) stands even less criticism. 267 Literally, the first common ancestor of any group goes to the origin of known life. This indicates the need for the 268 269 concept of *idioprestor*.

270	<b>RENDESTOR</b> of a group (/'rɒndɛstə/; from French <i>rendezvous</i> - a meeting at an agreed time and
271	place, and the ending - <i>estor</i> , like in the word <i>ancestor</i> ) — the last in natural history
272	common ancestor of all (two or more) known members of the group except this
273	ancestor itself if this ancestor is known and is a member of the group.
274	<b>INPRESTOR</b> of a group (/'inprestə/; from <i>in</i> , Greek $\pi\rho\dot{\omega}\tau\alpha$ [ <i>próta</i> ] - first, and the ending
275	- <i>estor</i> , like in the word <i>ancestor</i> ) — the first in natural history ancestor of all
276	known members of the group (except this ancestor itself if this ancestor is known
277	and is a member of the group), which is able to be included (or <i>is</i> included) in the
278	given group.
279	<b>IDIOPRESTOR</b> of a group (/ɪdɪˈə(ʊ)prɛstə/; from Ancient Greek ἴδἴος - pertaining to self, one's
280	own, private (as opposed to public); Greek πρώτα [próta] - first, and the ending
281	-estor, like in the word ancestor) — the first in natural history ancestor of all
282	known members of the group (except this ancestor itself if this ancestor is known
283	and is a member of the group) and no known organisms outside the group.

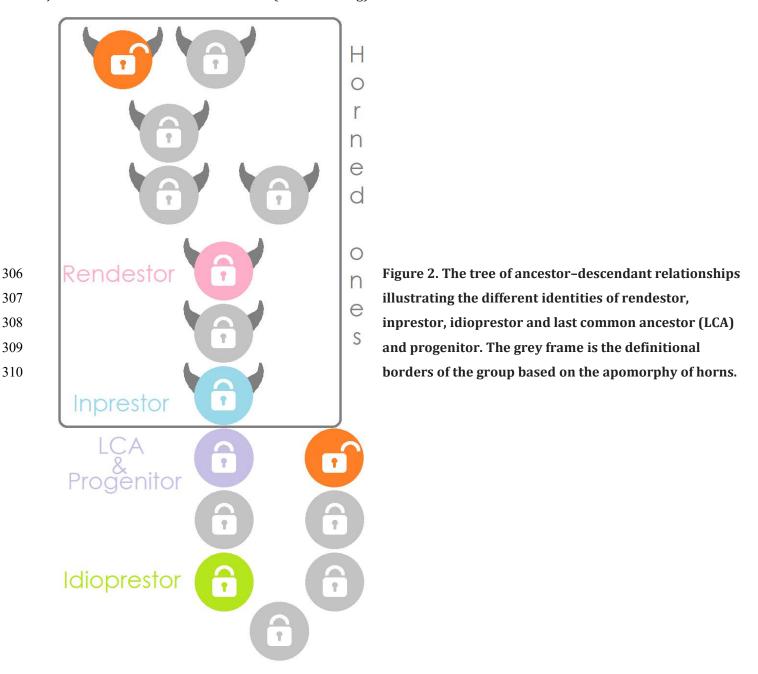
### 284 SUPPORTING CONCEPT: AN ANCESTRAL LINK

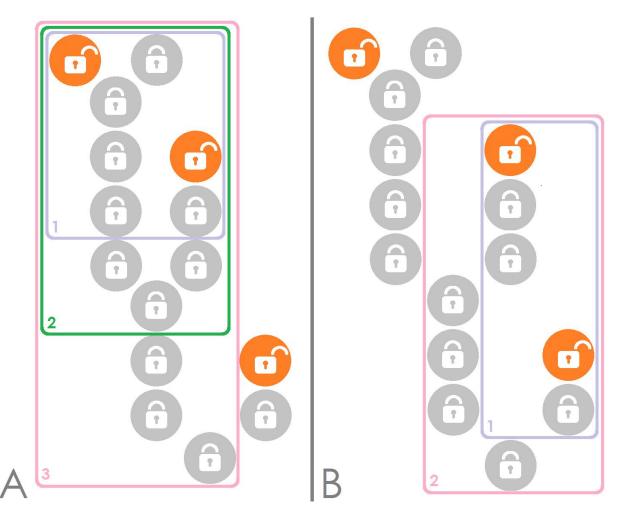
The basic criterion, which gives us *eno-* and *merophyly*, is not dealing with unknown organisms, including unknown ancestors. Unknown ancestors are matter that can not be completely divided into discrete units (e.g. could not be divided into a number of species). Although inside it some positions can 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.

292	ANCESSURE of a group (/ansɛs'jʊə/; contraction from ancestor and commissure) — a usually
293	branching continuous sequence composed of at least one ancestor of all known
294	members of the given group (except this ancestor itself if this ancestor is known and
295	is a member of the group) as well as (if any) all descendants of this ancestor, which
296	also are ancestors of known members of the group.
297	<b>INPRESTRAL ANCESSURE</b> of a group — the inprestor of the given group plus (if any) all the
298	inprestor's descendants, which also are ancestors of known members of the given
299	group.
300	<b>RENDESTRAL ANCESSURE</b> of a group — the rendestor of the given group plus (if any) all the
301	rendestor's descendants, which also are ancestors of known members of the given
302	group.

303

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 304 just the rendestor but also "a tail" to (and including) an earlier common ancestor of all known members of a 305





- Figure 3. Possible definitional borders for the equivalent sets of two known organisms: enophyletic (A) and
- 312 merophyletic (B). The groups A1 and B1 are schizophyletic. A2 is holophyletic. A3 and B2 are paraphyletic.
- group (e.g. *inprestor* in the case of *inprestral ancessure*; see Figs. 2 and 4). An *ancessure* can include known,
- 314 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).

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### 317 **PHYLETIC STATES DEPENDING ON THE ABILITY TO INCLUDE ENTIER ANCESSURE**

318	<b>Κοιιιτορηγιετις</b> group (/kəlaɪtə(υ)fʌɪˈlɛtɪk/; from Greek κολλητός [kollitós] - glued) — a set
319	of known organisms, which has the non-zero inprestral ancessure and is able
320	to include all its members (according to the definition of the group) and no
321	unknown ancestors of known organisms outside the group unless these
322	ancestors are the members of the inprestral ancessure or the continuous
323	sequence of immediate descendants of the inprestral ancessure.
324	<b>SCHIZOPHYLETIC</b> group (/skɪtsə(υ)fʌɪˈlɛtɪk/; from Greek σχίζω [skhízō] - split) — a set of known
325	organisms, which is unable to include all members of its inprestral (if it is non-
326	zero) or rendestral (in all other cases) ancessure (according to the definition of
327	the group) or able to include unknown ancestors of known organisms outside
328	the group if these ancestors are not the members of the inprestral ancessure
329	and not the continuous sequence of immediate descendants of the inprestral
330	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).

### 340 PHYLETIC STATES DEPENDING ON WHETHER GROUP'S INPRESTRAL ANCESSURE GAVE RISE TO 341 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*.

344 345 346 347 348	<b>HOLOPHYLETIC</b> (monophyletic <i>sensu stricto</i> ; see the next paragraph) group (/hplə(u)fʌr'lɛtık/; from Greek $\delta\lambda o c$ [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.
349	<b>PARAPHYLETIC</b> group (/pε.iə(υ)fʌɪ'lɛtɪk/; from Greek παρά [pará] - beside, near, alongside) — a
350	kollitophyletic group, the inprestral ancessure of which gave rise to at least one
351	known organism outside the group; or a set of a sole member having zero
352	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 357 given set) can not be *kollitophyletic* or *schizophyletic*. At the same time, such singleton sets can be *eno-* and 358 holophyletic (if descendants of the sole member are unknown) or mero- and paraphyletic (if descendants of the 359 sole member are known). *De facto* there are not two but three phyletic states in the row *kollitophyletic* groups – 360 schizophyletic groups. These sets of a sole member having zero inprestral ancessure are the third state in this 361 row—atomophyletic groups (Fig. 5). Kollitophyletic groups always have both rendestral and inprestral 362 ancessures. For a schizophyletic group always at least a rendestral ancessure exists. For an atomophyletic group, 363 neither inprestral nor rendestral ancessures exist (there is neither inprestor nor rendestor). Singleton sets, the 364 definition of which allows the inclusion of the ancestors of the only member, have a linear *inprestral ancessure* 365 (i.e. from the *inprestor* to the member of the group; Fig. 5). Therefore, such groups can be divided into 366 *kollitophyletic* and *schizophyletic*, depending on whether or not the group is capable of including all members of 367 368 the *inprestral ancessure* if they became known (Fig. 5).

### 369 HOLOPHYLY OR MONOPHYLY?

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370 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

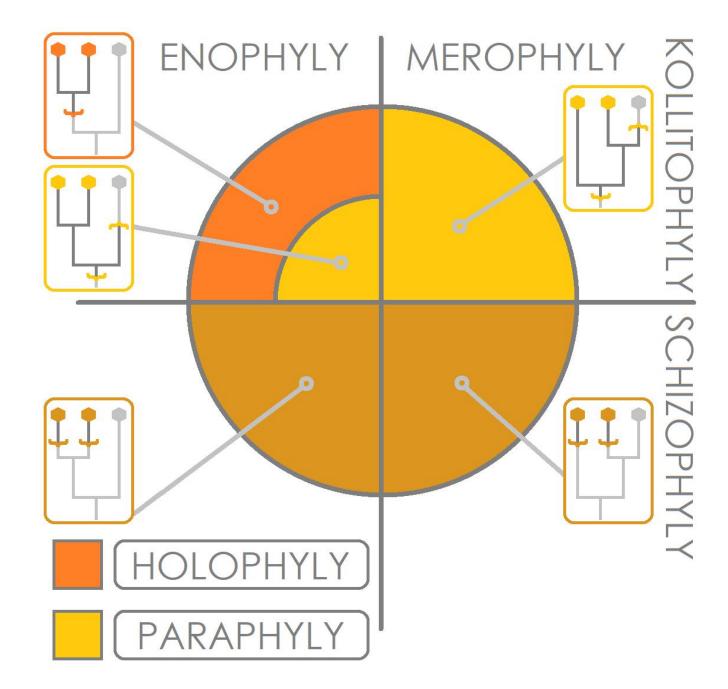
descendants" has the very limited application if we take the definition literally—only the groups having more

than one member where both the ancestor and all its descendants are discovered (monophyletic group *sensu* 

374 *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.



378 Figure 4. The diagram of the relationships of phyletic states among themselves. Coloured hexagons 379 represent known group members. Grey hexagons represent the known organisms outside the group. The 380 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. 381 The colour of the hexagons and borders around each tree matches the colour of the segment of the vertical 382 half of the diagram. Examples of five types of groups shown: 1) HOLOPHYLETIC—mammals (Mammalia), 383 birds (Aves); 2) PARA-ENOPHYLETIC-choanomonads (Choanomonada; as the rendestor of 384 choanomonads and metazoans had a collar and was a monad, i.e. is inside the definitional borders of 385 choanomonads); 3) SCHIZO-ENOPHYLETIC—"photokaryotes" of Cavalier-Smith 1999 in the case if his 386 (Cavalier-Smith 2018) hypothesis on the single origin of plastids in Chromista is true (as then there are two 387 388 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 389 390 Fowke and Pickett-Heaps 1969; Sawitzky and Grolig 1995) charophytes with phragmoplasts (Phragmoplastophyta); 4) PARA-MEROPHYLETIC—reptiles (Reptilia); 5) SCHIZO-MEROPHYLETIC— 391 warm-blooded animals (Homotherma); Protista (including Myxozoa). 392

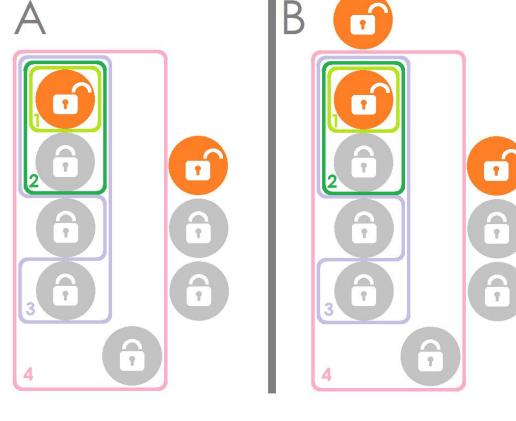
This confusion allows the term monophyly to be treated as a synonym of enophyly or kollito-enophyly or to 393 394 cover both *eno-* and *merophyly*. It is quite attractive to treat *monophyly* in the latter sense ("descendants of one ancestor"/"belonging to a single phylon"; sensu latissimo) opposite to polyphyly, although it extremely reduces 395 396 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 397 1866 p. 198; 1868 p. 347; 1873 p. 371; 1894 p. 89; see Dayrat 2003 and Rieppel 2010 for review). In such 398 views the terms *polyphyly*, as it was defined here, and *monophyly*, as its antonym, were applicable. Despite all 399 this, it is still possible to treat *monophyly* as the synonym of *holophyly* (as the latter was defined here) and the 400 401 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 402 μόνος [mónos] ("one", "alone", "only", "sole", "single") like in the cases of monophyletic group sensu strictissimo 403 (it is exactly one phylon) or *sensu latissimo* (members of the group belong to one phylon) as the meaning of the 404 405 term is exactly "whole", "entier" (Ancient Greek ὄλος [hólos]) concerning both known organisms and unknown 406 members of the ancessure.

### 407 **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):

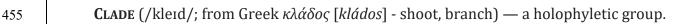
1) an *enophyletic* group, 2) a *kollito-enophyletic* group or 3) a *holophyletic* group. As the etymology of the term 411 *clade* (from Greek κλάδος [kládos] - shoot, branch) minds the inclusion of an *ancessure* and no breaks in the 412 413 branch, here the term *clade* was applied only to *holophyletic* 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 414 subgroups. Many such groups are unable to include their entire rendestral ancessures and therefore are 415 416 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 417 Strassert et al. 2019 for the phylogeny). TSAR were defined as "Telonemia + Sar grouping" (Strassert et al. 2019, 418 p. 761). Wherein, Telonemia were defined on the complex of morphological traits (Shalchian-Tabrizi et al. 2006, 419 p. 1840) and Sar were defined with the minimal-clade definition (Adl et al. 2012, p. 431). Therefore, this group 420 is schizophyletic by definition although enophyletic (schizo-enophyletic; see Fig. 4, 6). For such purposes, a short 421 422 term for "enophyletic group" seems needed.

450



**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** (/d.erd/; 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 .



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).

459

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

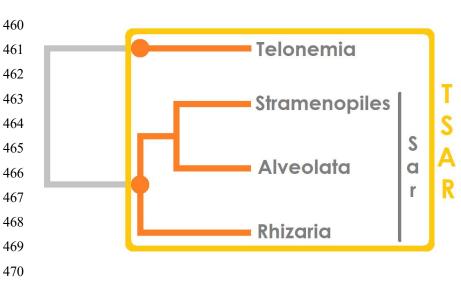


Figure 6. Schematic phylogenetic tree of Telonemia, Stramenopiles, Alveolata, and Rhizaria illustrating schizophyly of the union of Telonemia with Sar (TSAR drade). Definitional borders of TSAR are shown in yellow. Unincluded part of the rendestral ancessure is shown in grey. Inprestors of Telonemia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

### 471 **CONCLUSIONS**

472 1) Every two currently known organisms are descendants of one ancestor. Therefore, true
 473 *polyphyletic* groups do not exist in the current scientific reality.

474 2) A group having the same composition may have different "phyletic states", depending on how this
475 group is defined. Only *eno-* or *merophyly* reflects the composition and the branching pattern of the
476 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").

481 4) In discussions about the origin of a group (for example, about eukaryogenesis), we are talking 482 primarily about the *inprestor* of this group.

- 483 5) *Ancessures* of groups is a hitherto unnamed component of phylogenetic trees, usually shown simply
- 484 by lines. Members of an *ancessure* are almost always unable to be included in taxa as they are
- 485 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.
- 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
  495 the group gave rise to any known organism outside the group.

### 496 **ORIGINS OF THE TERMS**

497 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:

500 Asinock (1971). The terms *merophyly/merophyletic* originated from Ginselin (1981; probably having a price 501 "Winter", the first *Paleobiology* issue of the year) or Bernardi (1981; probably later: the fourth *Revista* 

502 Brasileira de Entomologia issue of the year). The terms schizophyly/schizophyletic and euphyly/euphyletic

503 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.

509 The term *concestor* was coined by Nicky Warren and popularised by Dawkins (2004; see p. 7). The term 510 *"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 of a flower calyx (or what was taken for it).

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

### 520 **CONFLICT OF INTEREST**

521 None declared.

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