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The meaning of categorical ranks in evolutionary biology

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Abstract Despite having been utilized for over 250 years, Linnaean ranks are periodically dismissed by some systematists and evolutionary biologists. Here, we discuss recent criticisms and point out that they are often the result of a misunderstanding of both the meaning and the intent of such ranks. Although arbitrary in some cases, ranks contain meaningful taxonomic information, facilitate communication, and serve as proxies for a fully resolved and correctly dated tree of life. Ranks favor communication and evolutionary comparisons, but they do not make assumptions about equal age or diversity for any two taxa with the same Linnaean category.

Keywords Taxonomy · Classification · Linnaean ranks · Systematics

Taxonomic ranks and classification systems have been an integral part of the life of systematists and other evolutionary biologists, but Linnaean ranks (e.g., phylum, family, genus) have lost credit among some users in the community and alternatives or hybrid systems are constantly being proposed (e.g., Minelli 2000; Kluge 2005; Naomi 2014). In a recent opinion note, Lambertz and Perry (2015) criticize a proposal for a new classification system of chordates by Satoh et al. (2014), who elevated three "subphyla" of the "phylum" Chordata—Urochordata, Cephalochordata, and Vertebrata—to the rank of phylum, in turn making Chordata a superphylum. In fact, some authors had already treated these three taxa as phyla (e.g., Nielsen 2012). The debate over whether Chordata is a phylum or a superphylum is ultimately futile because it does not alter anything about our knowledge or interpretation of the phylogeny and evolution of chordates. No single character or combination of characters makes a taxon a phylum or a class; nor is there a prize for erecting a phylum—although it is true that novel body plans receive especial attention. Lambertz and Perry [1] conclude that "The major problem with the rank-based classificatory system is the lack of any objective criteria to assign them." For the great majority of systematists, however, taxa have an objective basis because of the requirement of monophyly. Although by itself, this requisite does not confer any particular rank (Hennig 1950), the hierarchy of monophyletic groups within more inclusive monophyletic groups is efficiently retrieved from a ranked classification, if that classification has been derived from such a hierarchy and that hierarchy is resolved.

Lambertz and Perry (2015) discuss the rank of *phylum* and what makes a phylum—which we agree could be somewhat arbitrary. But if they or we were to discover a new deuterostome group that were phylogenetically placed outside both Chordata and Ambulacraria, that taxon could be described as a new animal phylum, as opposed to discovering a new sea urchin, which could not be described as a new phylum. They question whether Placozoa should receive the same rank as Chordata or Arthropoda because they have a different number of species. This suggests that their problem is not with the rank of phylum per se (in that example), but rather with the amount of diversity a phylum contains. They also state that "[t]he only at least theoretically viable objective criterion

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would be to assign equal ranks to sister taxa only." Here, they misinterpret Hennig's principle of every taxon having only one sister taxon. This is not the same as saying that every rank can only be a sister taxon to the same rank. As practicing systematists have observed over the decades in which this debate has ensued, no system could function that way, yet Lambertz and Perry propose as a solution a hypothetical scenario that "would require an almost infinite number of different qualifying prefixes (such as 'supra-' or 'infra-') and/or a similar quantity of completely new ranks to even be able to assign one to chordates." This is unnecessary because no system would be efficient if it needed to name (with or without a rank) all clades.

Fortunately, taxonomy does not work like that—but see Sibley and Ahlquist (1983) for a failed attempt—and we were puzzled that researchers debating the current taxonomic system apparently have such a misunderstanding of it. One genus can be the sister group of two or more genera; one phylum, like Placozoa, can also be the sister group to many phyla, or even to a clade composed of all other animal phyla. A strength of taxonomy is that it does not attempt to equate ranks—i.e., it does not imply that two phyla or two families are equally old or that they must have the same diversity because they have the same rank (although this is misunderstood by many users of taxonomy; see a discussion about this below). It only asks that an equal or higher rank cannot be subsumed under a lower rank—e.g., a *phylum* cannot be nested within a *class*, as it would render that class paraphyletic. The Linnaean system is in fact robust to accommodating new organisms, unlike the "ideal" system proposed by Lambertz and Perry (2015), which would force re-ranking everything once a new organism is discovered or named. As Farris (1976: p. 275) succinctly summarized, a phylogenetic classification requires "that each monophyletic group be a taxon, each taxon be a monophyletic group, and the natural inclusion relationships of monophyletic groups must be retained by the taxa." The notion that sister taxa need to have an equal rank was indeed proposed by Hennig, but this was already discussed and resolved by Farris (Farris 1976): "Hennig apparently considered the equivalence of rank of sister groups to be necessary in order that the classification correctly express phylogenetic relationships. In fact, the monophyletic groups of a phylogenetic system can be correctly represented in a classification without the necessity of requiring that sister groups have the same rank." We consider that Lambertz and Perry (2015)'s view is a misinterpretation of how biological classification operates in practice.

Lambertz and Perry (2015) further see fossils as throwing ranked classifications into chaos, asking "[W]hat if new fossils are found and they are nested somewhere down the stem line? What about fossils in general? In a consistent system, it would require taking into account all taxa, including extinct ones, and a re-ranking whenever something new is discovered." Alternative systems have been proposed to accommodate fossils (e.g., Wiley 1981: p. 214 and onwards), but apart from the stem-/crown-group distinction, these have not been widely adopted. Paleontologists have made cogent arguments for the merits of ranked classifications for many of the same reasons as neontologists (Benton 2007), and despite the incessant discovery of new fossils, the predicted chaos shows no sign of eventuating.

Other common misinterpretations of ranked Linnean classifications come from evolutionary biologists who attempt to equate taxonomic rank with sequence divergence, e.g., genera differ X% in gene *A*, families diverge Y%, or those trying to assign ranks based on divergence times, such as genera originated in the "X-ocene", families in the "Y-ocene" (something Willi Hennig himself considered). Others use ranks to explore general ecological or evolutionary patterns, such as how many genera occur at a certain latitude or at a certain depth. Some of these applications can be bold (just thinking about establishing ranks based on genetic distances).

Many systematists use ranks to refer to and compare taxa. Otherwise, it would be impossible to communicate easily and to convey concepts, as crude as they may be, as to whether Arthropoda is the most diverse animal *phylum* or that Coleoptera is the most diverse insect *order*. There is no other way to convey such information, which attempts to compare diversity between more or less comparable clades of organisms. Some may question whether such information is relevant at all; but arthropod and beetle workers often use such information, and we consider that it points to an evolutionary pattern and the concomitant asymmetric success of different clades that begs for an explanation. Attempts to convey such information without recurring to ranks are cumbersome and futile—i.e., Arthropoda is the largest animal clade excluding those groups of which it is a part, Coleoptera is the most diverse clade of Insecta excluding those groups of which it is a part. For many evolutionary questions, ranks may not be needed; "Coleoptera is monophyletic" does not require stating that it is an order in the Linnaean hierarchy of insects. But this does not mean that ranks are useless in every situation.

We have ourselves named many clades, some using formal Linnaean ranks and others using rankless labels, and it may be the case that in some instances, it is not needed to specify ranks when they are supported by a phylogenetic tree. But when the new taxa are to be accommodated into a pre-existing classification system (e.g., a new species that cannot be placed phylogenetically within any known genus or family), there is little one can do than to utilize such ranks. This necessity contrasts with what many criticize, as in the case that triggered Lambertz and Perry (2015)'s response, an arbitrary assignment of a taxon to a given rank that it is not required.

Finally, Lambertz and Perry (2015) conclude that "the rank-based system is arbitrarily chosen, lacks any comparability and furthermore does not convey any scientifically relevant information.” They furthermore question: “What can we learn from these ranks? We can neither infer anything about the phylogenetic relations and position of a given taxon, nor anything about its biodiversity.” Again, the system may be arbitrarily chosen, but the other statements that these authors make are demonstrably incorrect. Linnaean ranks in fact convey vast sums of information about systematic relationships. As Norman Platnick elegantly put it (Platnick 2009) “Using the Linnaean hierarchy, when I identified the spider in John’s garden as a salticid, I was asserting that John’s spider is more closely related to any single species currently included within the Salticidae than it is to any single species that is currently excluded from that family… So by placing the animal as a salticid, the current Linnaean hierarchy allows me to make 158,290,416 three-taxon statements about it, within spiders alone.” This example illustrates a fundamental benefit of a nomenclatural system that requires the mutual exclusivity of equally ranked names (but see de Queiroz and Donoghue (2011) for a different perspective).

We must accept that we operate in a classification system that already uses ranks (and a majority would argue that it does so quite successfully (e.g., Schuh 2003)), where most species of eukaryotes are classified as members of genera and families and where new taxa must be inserted into a classification in which species are named following binomial nomenclature—attempts to avoid the binomial nomenclatural system in the original inceptions of the PhyloCode have been largely abandoned even by the original proponents. Such binomial nomenclature requires the acceptance of the genus as a rank. The same criticism made to phyla applies to genera and vice versa. Erecting new genera is not uncommon in groups of animals with numerous monotypic genera based on autapomorphic characters. This can be easily fixed with the current system by requiring appropriate phylogenetic analyses and by applying the principle of synonymy. Unnecessarily elevating groups to higher ranks when it is not needed (within a given clade making each of three *classes* their own *phylum*) should be avoided. But in other cases, it may be justified. We have seen phyla being erected for new animals discovered in the past few decades (Kristensen 1983; Funch and Kristensen 1995; Kristensen and Funch 2000), others being erected based on novel phylogenetic results (Ruiz-Trillo et al. 1999), and conversely many phyla being “demoted” due to causing paraphyly (i.e., Acanthocephala now in Rotifera; Echiura, Pogonophora, Sipuncula, and Vestimentifera now considered Annelida; Pentastomida now considered Arthropoda, etc.). So yes, while we may continue to argue whether Arthropoda, Onychophora, and Tardigrada constitute three phyla or one, and as in the case of Chordata, this is largely a matter of semantics. But in many other cases, it is not just semantics. Assignment of ranks might be arbitrary, and biologists should be aware of that, but they also constitute the best way of communication in the absence of the desired completely resolved *and* dated tree of life, and they contain a great deal of phylogenetic information. We know that any member of Salticidae does not belong to any other animal family, and the reason we can make such a statement, even before we examine any character data, is because a family is a Linnaean rank. If Salticidae were not recognized as a taxon that we call a family, but just as a clade, then we could not know that its members are excluded from another clade called Hominidae in the absence of a phylogenetic tree.

Our current biological classification system is far from perfect. Its hierarchical nature pre-adapted it to successfully incorporate the principle of monophyly, and the system has co-evolved with phylogenetic inference to integrate traditional ranks with clades that are useful to all biologists. Many use “supraphyletic” clades without ranks, e.g., Spiralia, Ecdysozoa, Bilateria, or “infraphylum” rankless clades such as Neodermata or Clitellata. They had no rank and it has not been found necessary to invent one, yet they are very useful clades to which to refer. But this is far from implying that we should adopt a rankless system.

Lambertz and Perry (2015) conclude by citing our esteemed colleague Peter Ax: “A consistent phylogenetic system can only be constructed by the eradication of all ranks, and accordingly has to be taught without ranks” (translated by Lambertz and Perry (2015)). While this may be possible for the “higher ranks” dealt with in Das System der Metazoa (Ax 1995, 1999, 2001), Ax did not get into the nitty-gritty details of the Linnaean system where >95 % of the potential ranks exist, at the genus and family levels.

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