

Banning paraphylies and executing Linnaean taxonomy is discordant and reduces the evolutionary and semantic information content of biological nomenclature

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Received: 26 August 2015 / Revised: 12 October 2015 / Accepted: 13 January 2016
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The particular and the general problem

In a recent issue of *Systematic Entomology*, Ward et al. (2015) presented a new variant of the phylogeny of the huge and extremely diverse ant clade Myrmicinae. Their paper is a valuable contribution to understand the formation of major phylogenetic clades against a credibly evaluated time scale. The intention of our opinion paper is not to criticize particular “technical” aspects, such as selection of genes or number and selection of species considered to be representative for a tribe. Instead this opinion is of a very general nature: we express our growing concern about a severe reduction of the semantic content and functionality of zoological nomenclature and our doubts that phylogenetic classification can adequately reflect the information content

of evolution. The concern comes from the fundamental position of phylogenetic systematists of stringently translating the monophyly criterion into binominal nomenclature regardless of the consequences for practical research. This position was expressed by Ward et al. (2015):

“...The ultimate goal is a phylogenetic classification in which all higher taxa of a given rank (in this case, genus or tribe) are monophyletic and hence mutually exclusive...the classification proposed here goes some distance towards this ideal by substantially reducing the number of nonmonophyletic genera, and by ensuring that all tribes are monophyletic...”

We contend that banning all paraphyletic groups while simultaneously executing binominal Linnaean nomenclature

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results in a taxonomy going off the rails. This becomes apparent in the case of Myrmicinae. In a single strike, Ward et al. (2015) synonymized the socially parasitic ant genera *Myrmoxenus*, *Chalepoxenus* and *Protomognathus* with *Temnothorax*, and *Anergates* and *Teleutomymex* with *Tetramorium*. They also stated a paraphyly of *Tetramorium* Mayr, 1855 in relation with the socially parasitic genus *Strongylognathus* Mayr, 1853. Yet, they refrained from executing a nomenclatural change, because this would have meant that a genus containing more than 400 independent species would then carry a name applied for more than 160 years to a rather small and very distinct group of socially parasitic ants. Instead, they announced their intention to achieve a reversal of precedence by a ruling of the International Commission on Zoological Nomenclature.

Establishing the new system of Ward et al. will have severe consequences: practitioners studying biology of whole ant groups, comparing traits between related groups of species, studying mutualistic relations between these or simply making biodiversity studies in ecosystems or nature conservation will suffer from this reductionism. Being confronted with a multidimensional reality, they would be forced to use a language developed by a logical system knowing only two dimensions: time and phylogenetic splitting.

The damage from banning paraphyletic groups appears particularly striking in the example of socially parasitic ant genera and their host genera (Seifert 2007), but the generality of the problem within taxonomy as a whole is indicated by a series of publications advocating recognition of paraphyletic taxa (Cronquist 1987; Rieseberg and Brouillet 1994; Crisp and Chandler 1996; Ghiselin 1997; Brummitt and Sosef 1998; Brummitt 2002; Diggs and Lipscomb 2002, 2014; Hörandl 2006; Hörandl and Stuessy 2010; Flegr 2013; Stuessy and Hörandl 2014a, b; Willner et al. 2014). A paraphyly problem somewhat related to the particular ant case we are focusing here becomes also evident in recent discussions of the nomenclature of the lycaenid butterfly clade formed by *Phengaris* and *Maculinea* (Fric et al. 2007; Ugelvig et al. 2011). This clade contains species which parasitize societies of *Myrmica* ants.

Why do we not want to apply the concept of Ward et al.? All these socially parasitic ants underwent a rapid evolution leading to dramatic differences from their hosts in morphology, physiology and behavior. The socially parasitic genera containing more than one species—*Myrmoxenus* (about 12 species), *Chalepoxenus* (4–9 species) and *Strongylognathus* (about 25 species)—are themselves monophyletic, well-circumscribed clusters each sharing several strong autapomorphies that distinguish them from their hosts [We use here the terminology of Hennig (1966)

but the “shared-deviating-characters” within socially parasitic genera are “syn-apo-morphies” in the true sense of the word]. These autapomorphies sensu Hennig are so striking that anyone without biological education could separate the parasite genera safely from the host genera. The host genera *Temnothorax* and *Tetramorium*, in contrast, each containing hundreds of species, did not experience a comparably rapid evolution. Their morphology, physiology and behavior remained relatively static—independent from their cladogenetic distance or proximity to one of the socially parasitic satellite genera. In other words, socially parasitic ants and their hosts provide good examples in which the degree of anagenesis is not correlated with divergence time measured by phylogenetic systematics.

Flegr (2013) discussed why, so often, in multicellular organisms a phenotypically distinct group of species appears as an internal clade of a phenotypically distinct and uniform group of species instead of being a sister clade of them. He concluded that the phenomenon is very likely related to the erratic nature of evolution. In fact, there is a lot of palaeontological evidence that the evolution of most multicellular species is to a larger degree punctuational than gradualistic (Eldredge and Gould 1972; Jackson and Cheetham 1999; Jablonski 2000; Eldredge et al. 2005; Gould 2002; Hunt 2010; Monroe and Bokma 2010). There are several, differing, explanations for the change between phases of slow and fast evolution. One group of related explanations is provided by genetic models supposing that the species are evolutionarily “frozen” under normal conditions (Carson 1968; Flegr 1998, 2010; Mayr 1963; Templeton 1980). Under variable conditions, for example during peripatric speciation, when exposed to a changed environment, or in sympatric speciation when a social parasite begins to parasitize a host (Buschinger 1986, 1990, 2009), they can turn to the plastic state in which they start a rapid response to selection. This transient plasticity can lead to extreme changes in morphology, behavior or metabolic pathways. In socially parasitic ants, these are outstanding morphological, ethological and biochemical adaptations to fighting, recruiting and scouting, development of powerful pheromonal systems securing adoption in host colonies, reduction of storage organs in queens, and many other changes (Buschinger 1986, 1990, 2009).

Having briefly described the situation and the problem, we present in the following three lines of argumentation why the original generic names of social parasites are needed in the scientific language. The first argument focuses on functionality and semantic content of biological nomenclature, the second on a severe disaccord of the Hennigian system with Linnaean classification and the third on the evolutionary information content of paraphyletic taxa.

Functionality and semantic content of names are crucial

Binominal nomenclature was created by Carolus Linnaeus first of all as a tool for practitioners of biodiversity research. It makes clear sense to give a genus name to well-circumscribed groups of related species which dramatically deviate from other evolutionarily conservative groups. The logic of constructing determination keys requires this, and further, teaching, nature conservation and science in general need these names for strong operational, semantic and mnemonic reasons.

The spontaneous protest of myrmecologists against Ward et al. is primarily based on a fear of the Babelian confusion which is caused by reducing the information content of language. Species lists would become invalid and all students of ants would have trouble reading “old” literature to figure out what now are the correct names and what are synonyms, greatly exacerbating an already existing problem. In order to avoid this confusion, Phil Ward (pers. comm. to Seifert, 5 February 2015) proposed that clarity may be achieved by combining a name with an explanatory appendix. Following his proposal, an example sentence in a future work of ants should be written as follows: “*Temnothorax* (formerly *Myrmoxenus*) *ravouxi*, *T.* (formerly *Myrmoxenus*) *kraussei* and *T.* (formerly *Myrmoxenus*) *stumperi* throttle the *Temnothorax* (formerly *Temnothorax* sensu stricto) host queens”. The alternative sentence needs less than 50 % of space and is more translucent: “*Myrmoxenus ravouxi*, *M. kraussei* and *M. stumperi* throttle the *Temnothorax* host queens”. We believe that the most effective way of transmitting and memorizing information is by a parsimonious language using words with an unambiguous semantics and high mnemonic value. A very similar position is expressed by Ghiselin (1997): “Systems with paraphyletic taxa may be simpler, better in accord with vernacular language, and more conveniently expressive of features deemed important (such as major changes in organization)”.

Banning paraphyly while applying binominal nomenclature is discordant

The issue of discordance between these two logical systems has been thoroughly treated by others (Rieseberg and Brouillet 1994; Brummitt and Sosef 1998; Brummitt 2002, 2003; Flegr 2013). In a talk given at a symposium on Linnaean taxonomy at the Smithsonian Institution in 2001, Richard Brummitt addressed to the audience the provocative sentence: “If anybody here thinks they can draw a phylogenetic tree and divide it into families and genera without creating paraphyletic

families and genera, they are welcome to come up here and do so...” (Brummitt 2002). Opponents may say such trees can be drawn with ease without violating a stringent inner logic, but Brummitt stated later in the text that this proves true only if we are willing to accept systems as PhyloCode, to deny anything that has been proposed so far by binominal nomenclature as genus concepts, and to ignore the purpose of Linnaeus’ system. The sentence of Brummitt describes the discord that appears when the Hennigian monophyly criterion is applied to Linnaean nomenclature. The same ideas were already expressed by Rieseberg and Brouillet (1994): “Thus, many plant species are likely to be paraphyletic, and predictably a species classification based on the criterion of monophyly is unlikely to be an effective tool for describing and ordering biological diversity”¹. The argumentation of Brummitt (2003) can be condensed as follows “As soon as you put the apex of the tree (or indeed the apex of any sector of the whole tree) into a genus or family, this must be paraphyletic in relation to any other genus or family recognized among its progeny. If we are classifying all the products of evolution, every taxon we recognize (apart from the original one) must make another taxon paraphyletic. That is why...traditional taxonomy is incompatible with a system of only monophyletic taxa. Every monophyletic group would collapse into its original family, genus and species”. And later, Brummitt notes that “taxonomy must depend on characters related to lines of descent, not simply on lines of descent alone”. In this way he clearly expressed inalienability of phylogenetic research within a system that integrates cladogenesis and anagenesis.

When speaking of paraphyletic groups and genera, we should not forget the long-known problem that significant arbitrary components in fixation of supraspecific ranks are unavoidable. Sudhaus and Rehfeld (1992) quoted that “only pragmatic, consensus-based fixations of genera make a sense”. We conclude that there are only two clear options: If somebody insists on the monophyly criterion, the clade-based PhyloCode will provide the adequate logical framework but then we have no longer a binominal nomenclature. Those who want to continue with the use of binominal nomenclature or higher Linnaean ranks have to recognize at least those paraphyletic taxa which show a strong anagenetic divergence.

¹ For zoologists who find it problematic that botanists speak of “paraphyletic species”, we note that botanists have fundamental difficulties to say what a species is. The English speaking botanists do not have a special term for what by German botanists is called “Sippe” (=“clan”, “kin”). This usually describes a group of very closely related plant species (microspecies). Many botanists call such groups “species” whereas others say “taxon”.

Adding dimensions: paraphyletic taxa provide substantial evolutionary information content

We consider now the evolutionary aspects. Approaches strictly implementing the monophyly criterion suffer from a reduced dimensionality. Gene-based phylogenetic systematics translates sequence divergence, regardless of whether loci are neutral or under a dynamic selection, into a temporal sequence of phylogenetic splitting. Synapomorphies alone are relevant for them, and the information content provided by symplesiomorphy, conflicting characters or even autapomorphy, is obliterated (Hörandl 2014). Mental fixation on the lines of descent has caught phylogeneticists within the construct of logical inclusiveness.

The psychological background and the consequences of any reductionism, wherever it occurs, can be elucidated by

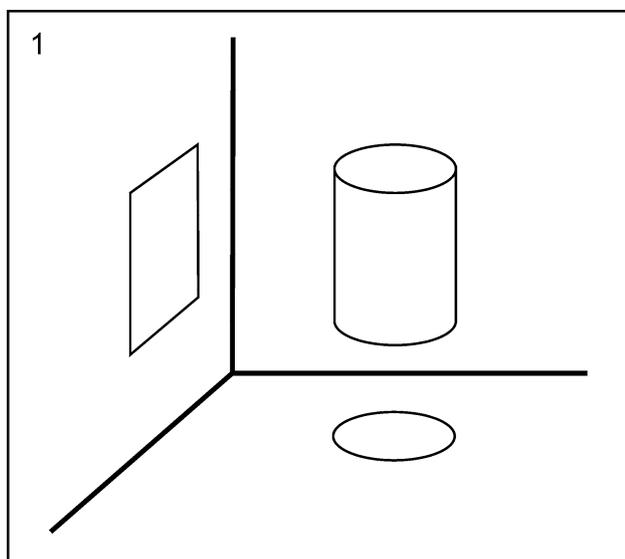
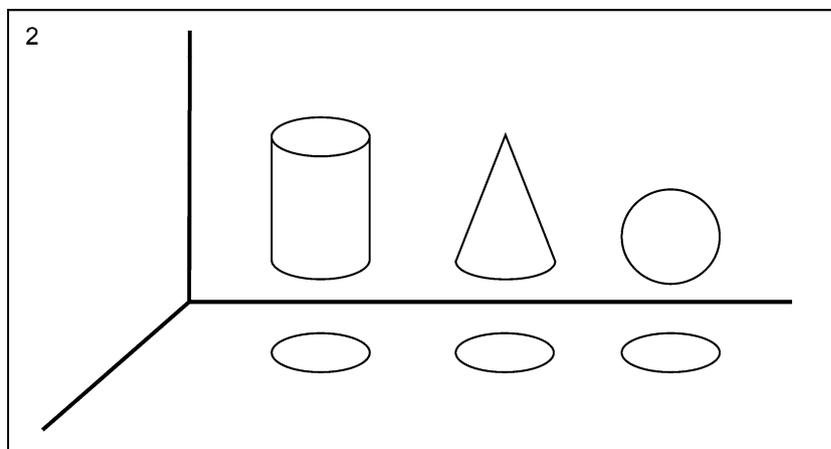


Fig. 1 Visualization of the first law of ontology of dimensions. Redrawn from Frankl (1953)

Fig. 2 Visualization of the second law of ontology of dimensions. Redrawn from Frankl (1953)



the laws of ontology of dimensions (Frankl 1953). The first law of ontology of dimensions tells us if one and the same phenomenon that is correctly identified by N dimensions may be interpreted in a contradictory way if visualized by $N-1$ dimensions (Fig. 1). The second law of ontology of dimensions tells us that different things correctly identified by N dimensions may be interpreted to be equal if visualized by $N-1$ dimensions (Fig. 2). These laws are crucial to understand divergent cognitive processes and disputes in natural science, psychology and everyday life. They explain why viewing under a reduced dimensionality will lead to misleading projections of reality. This is the case in phylogenetic systematics in its fundamental form as it was introduced by Hennig (1966). Felsenstein (2001) provided an interesting historical review of how the intellectual package of phylogenetic systematics got broadly accepted within exclusive circles of biological systematists by the end of the 20th century and which conflicts between different schools took place. It was explained above which essential dimension of evolutionary reality is ignored by phylogenetic systematics: it is anagenesis that in most multicellular species is not gradualistic but punctuational or erratic in nature.

The alternative: evolutionary classification plus binominal nomenclature

If it is not phylogenetic systematics, what then can make a classification system a truly evolutionary one and relatively stable in time? Finding the best quantitative procedures of integrating the dimensions, which are ignored by strictly phylogenetic systematists, will be a challenge for systematics in the twenty-first century. Some papers have shown how several aspects of phylogeny can be quantified and integrated (Estabrook 1986; Felsenstein 2004). More developed answers have been recently given by botanists

(e.g., Stuessy and Hörandl 2014a; Hörandl 2014) who are facing a more complicated situation due to the enormous impact of reticulate evolution and apomictic reproduction in plants. We encourage zoologists to be more open to the view of botanists—there is growing evidence that reticulate evolution is a significant component of evolution also in metazoa. Adaptive introgression of heterospecific alleles became a normal term in evolutionary genetics of Eukaryota (e.g., Mallet 2005; Arnold and Martin 2009; Abbott et al. 2013) and whole genome analyses are beginning to tell us in a fascinating way which alleles are transmitted between species and what are their functional consequences (e.g., The *Heliconius* Gene Consortium 2012; Martin et al. 2013).

Stuessy and Hörandl (2014a) plead for an evolutionary systematics that integrates the processes of descent (cladogenesis), modification (anagenesis) and reticulate evolution into a multidimensional concept. We basically agree that classification has to go this way to deserve the attribute “evolutionary”. The question of which procedures and algorithms are the best to incorporate the diversity of evolutionary patterns and processes into classification will be a matter of development for the next decades. The proposal of Stuessy and Hörandl to use shared descent as a primary grouping principle and to integrate degrees of divergence and similarity (cohesiveness of evolutionary features) appears as a sound basis for further discussion.

Evolutionary divergence in eukaryotes is largely driven by mutation and selection on nuclear regulatory and coding genes. This has effects on multiple levels of organismic organization—from the level of micro- or macromolecules up to the entire organism and its behavior. The vast majority of currently used DNA sequence markers are not chosen to depict the immediate working points of evolution. They appear as a random repertory of neutral and non-coding or selected regulatory or coding sequences. Everything that promises to provide some informative variation is used. In order to end this random fishing, genetics in classification of eukaryotic organisms has to comparatively assess the evolutionary significance of non-coding and coding nuclear genes. Non-coding sequences should largely reflect relatedness and the timing of cladogenesis whereas coding and regulatory sequences should determine anagenesis and fast evolution. There is a credible perspective that whole-genome scans will once provide the required insights into the evolutionary identity of organisms when all non-coding and coding nuclear genes will be mapped and annotated. The analyses will then allow identification, out of a mass of conserved genes, of just that tiny fraction of regulatory and coding genes responsible for dramatic changes in structural design, physiology and behavior as observed in our example of socially parasitic ants.

This ideal of genetic classification focusing on a balanced evolutionary view of non-selected and selected

sequences is only a vision at the moment. What we can do right now and what will always remain important for classification are advanced analyses of the expression products of nuclear genes. With decreasing proximity to nuDNA these are proteins, morphology, behavior, secondary natural products and ecology. External morphology, presenting the most obvious expression product of nuclear genes, should remain the backbone of binominal nomenclature. This is supported by the fact that phenotypic investigation, in contrast to genetics, allows a nondestructive investigation of type specimens of small arthropods—the vast majority of described organisms—and it is not limited by molecular degradation (Schlick-Steiner et al. 2007; Steiner et al. 2009).

Conclusion

Finally and after all argumentation on operational, logical and evolutionary reasons, we would add: There is no regulation in the current edition of ICZN demanding a naming of genera within big clades in a way that paraphyly is removed. No one is forced to follow the suggestions of Ward et al. (2015) and we ask that myrmecologists not too hastily adopt this proposal only for the reason that it is the newest variant of a phylogenetic system. As Felsenstein (2001) put it, phylogenies are central, but “it is nearly irrelevant how they are then used in taxonomy”. Knowledge of cladogenesis directs us to recognize which taxa could be constructed and knowledge of anagenesis is needed to recognize which taxa should be constructed. We propose a pragmatic, consensus-based use of phylogenies in taxonomy.

Acknowledgments We wish to thank Birgit Schlick Steiner and Florian Steiner, University of Innsbruck, Germany for constructive discussion and substantial improvement of the manuscript. All authors of this manuscript declare that there are no conflicts of interest.

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