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Paraphyly—again!? A plea against the dissociation of taxonomy and phylogenetics

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There is an infinite number of potential and useful classifications in biology, depending upon the context of the topic at hand. Organisms can be systematised according to size (e. g. small mammals vs. large mammals to highlight differences in physiology), diet (carnivores, omnivores, herbivores etc.), mating system (monogamous, polygynous, polyandrous etc.) and so forth. Each of these classifications is legitimate in its own right. However, there is one biological system that serves as a reference system for all other systems, and indeed for all of biology. It is this system that the biological discipline of systematics deals with, and since the acceptance of evolution (as opposed to divine creation) there has been a consensus that this system should reflect the phylogenetic relationships among taxa. Still, it took more than a century after Darwin until Willi Hennig introduced a truly scientific methodology of classification (Hennig 1966). The core concept that, for the first time, allowed for a rigorous and non-arbitrary designation of (supraspecific) taxa was monophyly (later sometimes called holophyly)—a natural (i. e. phylogenetically based) taxon may comprise *only* the descendants of a common ancestor and must at the same time comprise *all* of these descendants. While the first of these two conditions has met with general acceptance (i. e. polyphyletic groupings that are based on homoplasies are rejected), there has been an ongoing debate about the second one because many traditionally accepted taxa do not fulfil this condition. The classic textbook example is "Reptilia" which excludes the birds although they are the (extant) sister group of the crocodiles. These paraphyletic taxa are real die-hards in taxonomy, because despite their arbitrariness they have been forcefully defended by many systematists, most famously by Ernst Mayr (see his debate with Hennig on cladistic analysis vs. cladistic classification; Hennig 1974; Mayr 1974). The general line of reasoning behind what Mayr called evolutionary classification is that evolution comprises both cladogenesis (the branching of lineages) and anagenesis (change through time without branching) and that classification should reflect both aspects or processes by taking into account phylogeny (cladogenetic aspect) and the degree of divergence between sister groups or the different divergence of sister groups from their common ancestor (anagenetic aspect), thus reflecting not only descent but also evolutionary or adaptive "grades": „crocodilians are on the whole very similar to other reptiles, that is, they have developed relatively few autapomorph characters. They represent the reptilian 'grade', as many morphologists call it." (Mayr 1981, p. 513). Yet, this is a concept that is impossible to define non-arbitrarily (see below). Nonetheless, in a recent article published in Zootaxa (Flegr 2013), Flegr again argues in favour of paraphyly, this time by linking it with punctuated evolution sensu Eldredge and Gould (1972). He even claims that the acceptance of paraphyla is a sine qua non for the survival of taxonomy as a scientific discipline: „Otherwise, we might soon have to say farewell (…) to the whole taxonomic system." (Flegr 2013, p. 298) This apocalyptic warning should not remain unobjected as it is a step back in the long-lasting process of emancipating biological systematics from the remnants of pre-evolutionary thinking.

Flegr takes it for granted that punctuated equilibria and non-gradual evolution are the rule rather than the exception and that in a gradual world paraphyletic taxa (above the species level) would be rare. According to him, the punctuational nature of evolution can be used to define genera (gradual evolution within genera, punctuational evolution among genera) and is responsible for the fact that many derived groups are internal subclades of larger units rather than the sister group to the non-derived taxa. I do not subscribe to any of these views (except that punctuated evolution is probably a widespread phenomenon), but my main criticism is that the suggestions made by Flegr bypass the (in my opinion) fatal shortcomings of a system that accepts paraphyletic taxa. The same holds for the use of Linnean categories, but I will not deal with this as this is not the major topic of Flegr (for a treatment of the poverty of Linnean categories in an evolutionary framework see e. g. Ereshefsky 2001, Zachos 2011 and references therein). Instead, I will concentrate on paraphyly.

The debate about paraphyly in taxonomy has a distinctly logical/philosophical dimension, namely the question of

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separated from the then paraphyletic rest of a monophylum is not only arbitrary, but also random. I would argue that it is not. Instead, it is consistently groups that are considered to be "higher" or "more highly" evolved, leaving a paraphyletic "lower" group, e. g. fishes ("Pisces" vs. Tetrapoda), reptiles ("Reptilia" vs. Aves), primarily flightless insects ("Apterygota" vs. Pterygota), organisms without a cell nucleus ("Prokaryota" vs. Eukaryota) etc. When considering Sauropsida (the monophylum comprising reptiles and birds), why then are birds singled out and not the very aberrant turtles? To say that birds are more derived than turtles is difficult to substantiate because this is necessarily based on an (arbitrary) selection of certain characters from the infinite number of traits present, and surely, turtles are uniquely derived in their body plan as well. But birds are perceived as "higher" than turtles, implying an element of progress in evolution. However, while adaptation, differentiation and complexity are biologically real, progress is not (e. g. Dawkins 1992). It is again a human construct, and it is also anthropocentric as, not surprisingly, progress is gauged from the viewpoint of our own species. This is almost certainly a remnant of the very old concept of the great chain of being or scala naturae (see Lovejoy 1936, Rigato and Minelli 2013), a historically fascinating philosophical, but scientifically obsolete idea.

Paraphyletic taxa, Linnean categories and the concept of progress in evolution are ultimately based on a typological approach and logically and philosophically inconsistent with the theory of evolution. It is very peculiar indeed that Ernst Mayr, who considered population thinking and its victory over Platonic idealism (and thus typology) as the most important intellectual achievement in evolutionary biology and who also played a vital role in the process, never overcame typology in classification. However, if biological systematics and its methodology are to be viewed as rigorously scientific, then there is no room for arbitrary delineation of groups which will only introduce a schism into systematics between theoretically sound phylogenetics and only partly objective taxonomy. It is time that systematists at long last left behind the pre-evolutionary Linnean legacy!

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