

PERSPECTIVE

Cladistic species definitions can lead to under-representation of biodiversity from adaptive radiations.

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Abstract: Many species are paraphyletic, but current taxonomic practices often do not recognise this, and attempts are made to apply a monophyletic species concept. While allowing the recognition of ecomorphologically equivalent, or even phenotypically indistinguishable allopatric taxa as species, this often leads to combining distinctive local forms (such as cave-adapted populations) or even whole adaptive radiations (often in lakes) with widespread paraphyletic species to force species monophyly. It is suggested that this has negative consequences for our documentation and understanding of biodiversity, as well as for conservation, through issues such as lack of IUCN redlisting.

Short header: Problems with cladistic species definitions.

Description of new species remains fundamental to many key processes in the documentation of biodiversity, both for academic research, such as ecological correlates of species richness and functional explanations for rates of lineage diversification (Faurby et al. 2007) and for information underlying practical conservation (Garnett & Christidis 2017), for example in obtaining an IUCN red-listing, archiving of range information on GBIF etc. Definitions of species remain contentious (e.g. de Queiroz 2007). In practice, many species are now being described based on molecular phylogenetics, either exclusively (e.g. Pons et al. 2006; Limeira Filho et al. 2024) or in combination with morphological traits (e.g. Delicado et al. 2024).

A number of opinion pieces have suggested that adoption of evolutionary or phylogenetic species models in preference to those based around morphology or reproductive isolation have led to ‘taxonomic inflation’ with geographically isolated but ecologically equivalent and morphologically little different populations being described as species, particularly in charismatic taxa of conservation concern (Isaac et al. 2004; Zachos et al. 2013). Other authorities have disputed this, citing improving taxonomic investigation (Sangster 2009). An issue which appears to have generated little discussion is one that I feel is particularly relevant to studies of adaptive radiations, including issues of conservation, namely the reluctance of taxonomists to formally recognise narrowly-distributed endemic taxa as species, even when they are clearly morphologically and ecologically distinct, and often extremely vulnerable.

I was recently discussing captive breeding programmes and reintroductions of threatened species with staff at Chester Zoo, and was impressed by the lengths to which they had gone to breed the Omani blind cavefish, *Garra barriemiae*, which I felt must surely be a very rare and valued species, only to be informed that it was in fact Least Concern on the IUCN red-list (Harrison 2015). A cave-dwelling fish in a desert country, Least Concern? The reason turned out to be that the cave-population is regarded as conspecific with the widely distributed surface population. Indeed, a recent revision of the group has split the surface population into 6 allopatric species, subtly differentiated in colour pattern and little else (one pair of species differ in gillraker counts). However, this left the cave fish as conspecific with the local surface population, now *Garra longipinnis* (Kirchner et al. 2020). By contrast, the cave fish are phenotypically highly distinct: unpigmented, blind and showing reduced squamation (Banister 1984). Its retention as conspecific with surface populations seems to be largely on the basis of molecular phylogenetic analysis (Kirchner et al. 2021). It was not explicitly stated why the cave form was not raised to species level, with one phylogeny suggesting it could have been a sister species to the surface *G. longipinnis*, but perhaps it was considered that it simply lacked sufficient genetic divergence (Kirchner et al. 2020). In other analyses, it would seem to risk rendering the local surface population genetically paraphyletic (Kirchner et al. 2021). It appears that there is little or no gene flow into the cave populations, although there is considerable evidence for hybridisation between surface forms recognised as distinct species (Kirchner et al. 2021). Likewise, recent studies have indicated that the cave phenotype of the Mexican cave tetra appears to have evolved several times independently from the surface form, and thus recognising the cave forms as distinct species would render the surface form paraphyletic, or force the creation of a host of essentially indistinguishable allopatric reciprocally monophyletic species. Presently all – surface and cave forms- are recognised as the single species *Astyanax mexicanus* (Garduño-Sánchez et al. 2023). However, at the time of writing, the IUCN red listing had not yet incorporated this, and the cave forms were still listed as *Astyanax jordani*, and as Endangered (Ornelas García 2019). Presumably, if they were synonymised into *A. mexicanus*, they would inherit its ‘Least Concern’ status (NatureServe 2013).

Thus, we have clear cases where phenotypically dramatically distinct cave fish are presently not recognised as species, leading to lack of recognition as units of significant conservation value, resulting at least in part, because of their rendering of other taxa as paraphyletic-effectively ‘ancestral’ - taxa, which are not allowed under cladistic principles where every speciation event results in the formation of two new sister species. Yet, there are clear examples where paraphyletic species are explicitly recognised, as in the Caribbean anoles, where, for example, *Anolis roquet* on Martinique is considered ancestral to *A. extremus* on Barbados (Thorpe et al. 2018). In this case, it appears that the colonisation of Barbados took place while Martinique was divided into a number of precursor islands, which have later joined, permitting subsequent gene flow, although there is still a strong signal of differentiation among them, allowing the Western and Central Martinique populations to be more divergent from each other than the Central populations are from the Barbados species (Thorpe et al. 2018).

Similar scenarios may be common for continental species. For example, the separation of the western continental populations of the European Grass snake into a distinct species, *Natrix helvetica*, is supported by its monophyly and the narrowness of the hybrid zone, suggesting strong selection against hybrids with the eastern populations retained in *Natrix natrix*. However, resulting mitochondrial phylogenies render *N. natrix* paraphyletic (Kindler et al. 2017). Notably, *N. natrix* extends over a much larger geographic area- from the Netherlands to eastern Mongolia (Schöneberg et al. 2023), and it would not be surprising if *N. helvetica* is more closely related to western *N. natrix* than western *N. natrix* is to its distant eastern conspecifics although there may be no actual barriers to gene flow across its ~8,000km west-east range.

How does this affect how we treat adaptive radiations? There seems to be considerable variation in practice. In situations like the African great lake cichlids, vast numbers of species, and indeed genera, are described (Turner 2007), but much less is known about the status of the sister/ancestral taxa, which are often assumed to be long since extinct. Lake Malawi presents an interesting exception to this, with the widespread riverine *Astatotilapia calliptera* being resolved as nested within the Lake Malawi radiation (Malinsky et al. 2018). It is hypothesised that this lineage remained in its shallow weedy habitat niche in both rivers and lakes (including Lake Malawi), with continuing exchange of genes between multiple lake and river systems – presumably intermittently, as some of these water bodies are currently unconnected. During this time, it is estimated to have budded off three species in Lake Malawi which have gone on to diversify into the current 800+ endemics, all currently confined to the Lake Malawi catchment (Malinsky et al. 2018). Similarly, an endemic radiation of *Bathyclarias* catfishes co-exists in Lake Malawi with its ‘ancestor’, the widely distributed *Clarias gariepinus*, which appears from a mitochondrial phylogeny, both nested inside the endemics and as a sister taxon, depending on geographical proximity (Agnès & Teugels 2001).

Perhaps a more common situation is where diversification within lakes or islands takes place, while the ancestral species remains allopatric, but persists over a wider geographic range. For example, radiations of mouthbrooding cichlids in Lakes Barombi Mbo and Ejagham both seem to be derived from populations of the widely distributed *Sarotherodon gallilaeus*, which is thereby rendered paraphyletic (Richards et al. 2018). Likewise, the radiations of *Coptodon* species in Lakes Bermin (Stiassny et al. 1992) and Ejagham (Poelstra et al. 2018), may be derived from the widespread and likely paraphyletic *C. guineensis* (but see Dunz et al. 2013).

In general, sympatric species flocks are widely accepted and named as such in tropical lakes, perhaps because of the extreme species richness and phenotypic diversity of headline examples, such as the cichlids of Lakes Malawi, Tanganyika and Victoria. However, this is less clear-cut with temperate lake radiations, where ecomorphologically divergent taxa have traditionally been referred to as ‘sympatric morphs’ (Turner 1999; Skúlason et al. 2019) or ‘ecotypes’ (Lucek et al. 2014). In consequence, local endemic taxa, often forming sympatric species flocks have not been identified as distinct species, but are subsumed into widely distributed ‘least concern’ taxa. To some extent, this may reflect the relative recency of divergence (Lucek et al. 2014; Wund et al. 2008), with similar terminology (ecotypes) used for situations like adaptation of marine sticklebacks to freshwater habitats- which has likely occurred thousands of times, often over very short time-scales, and often showing a major role for phenotypic plasticity, perhaps along with soft sweeps – selection shifting gene frequencies from standing variation (Hu & Barrett 2023). Granting species status to numerous likely ephemeral taxa would seem unwarranted.

By contrast, some taxa, such as the arctic charr morphs in Thingvallavatn, Iceland and Loch Rannoch, Scotland, or the brown trout in Lough Melvin, Ireland are ecomorphologically well-differentiated and these may deserve to be treated as distinct species flocks (Kottelat & Freyhof 2007). Although some old names are available for some of these taxa, they are still not in widespread use and many remain undescribed (Kottelat & Freyhof 2007). However, those taxa lucky enough to have pre-existing older names have sometimes been given an IUCN redlisting, such as *Salvelinus struanensis*, the ‘vulnerable’ Loch Rannoch planktivorous charr (Freyhof & Kottelat 2007). By contrast, whitefish (*Coregonus* sp. and relatives) appear to be readily assigned to formal species, with numerous sympatric taxa currently named and more being described recently (Hudson et al. 2011; Selz et al. 2020; Selz & Seehausen 2023). It is not clear why this is (a productive research group that also works on Lake Victoria cichlids?), but it does not seem to have been consistently applied, as, although Hudson et al. (2007) review data from over 200 whitefish radiations (each presumably of more than one taxon), only 95 valid species are listed in FishBase (Froese & Pauly 2024).

So, the Zoological and Botanical communities (prokaryote taxonomists necessarily use molecular-based methods: Meier-Kolthoff et al. 2013) seem to be content with a species concept somewhere between the classic Evolutionary Species Concept (Simpson 1961) and De Queiroz’s (2007) separately evolving metapopulation lineages. If we like, we can define reciprocally monophyletic ecologically equivalent allopatric populations as species (e.g. Buckley-Beaton et al. 2006). We can use narrow contact zones as an indication of limited gene flow (e.g. Chambers & Hillis 2020)- there seems to be an acceptance of a certain amount of hybridisation both in sympatry and allopatry. There is also often an acceptance of paraphyletic species- units which are descended from a single common ancestral taxon, but do not contain all of its descendants. However, this is often unstated, with rare exceptions such as the Martinique Anole (Thorpe et al. 2018). As paraphyletic taxa are prohibited under cladistic principles, some authors have expressed discomfort at the idea of paraphyletic species, mistakenly believing that formal taxonomic codes preclude them (e.g. Grube & Kroken 2000)- in fact there is no requirement for monophyly in any of the generally accepted taxonomic codes (Freudenstein et al. 2017). Even the attempt at creating an entirely new ‘rank-free’ cladistically-based classification system, Phylocode (de Queiroz & Gauthier 1994; de Queiroz 2006), has balked at insisting on monophyly at the species level and indeed

apparently does not deny the existence of non-monophyletic supraspecific taxa- it seems it just doesn't fit with them (de Queiroz 2006).

There are relatively few explicit discussions of the virtues of recognising paraphyletic species. For example, Rieseberg & Brouillet (1994) believe that paraphyletic species are likely to be common in plants, while Rieppel (2010) proposes that species can never be truly monophyletic. Freudenstein et al. (2017) explicitly state that they believe that paraphyletic species exist and can be accommodated in a definition compatible with de Queiroz's (2007) species concept, in which both lineage and ecological role are emphasised. They are, however, clear that they do not propose to accept polyphyletic species, i.e. species comprised of more than one (meta-)population which has evolved similar phenotypes and roles in parallel. These works, although generally reasonably well-cited, do not seem to have penetrated much into the theoretical literature nor indeed the adaptive radiation literature. I suggest that it is about time that they did.

Paraphyletic species exist: a widely distributed species can colonise isolated islands or lakes, radiate into a number of unique endemics, but continue to exchange genes across its 'mainland' range. In theory, it could do this a number of times. For example, *Astatotilapia calliptera*, as well as its role in founding the Malawi cichlid radiation, has also colonised a number of crater lakes to the north of Lake Malawi, where unique populations have evolved, several of which have clearly divergent male breeding colours (dark grey to black v yellow in the rivers: Malinsky et al. 2015; Turner et al. 2019). These male breeding colours are associated with mate preferences (Tyers & Turner 2013). In one lake, the colonising species has split into deepwater 'benthic' and inshore 'littoral' taxa which probably justify species status, differing in habitat preference, trophic morphology and male breeding dress (Malinsky et al. 2015). What holds for *A. calliptera*, holds equally for brown trout, arctic charr and 3-spined sticklebacks: we can recognise and name taxa in lacustrine species flocks, alongside widespread parapatric species. And it also holds for subterranean forms, such as the Omani cavefish and the Mexican blind tetra: these are clearly distinctive separately evolving lineages, diagnosable, worthy of conservation efforts. In the case of the tetra, each cave form would be a separate monophyletic species- evolved in parallel, but the wide-ranging surface form would be a single paraphyletic species.

Coda: The Limits of Cladistics.

The gist of the previous set of discussions is that I believe that evolution is not necessarily always best described by the cladistic model, and that over-rigorous employment of this model has negative repercussions for taxonomy, evolutionary biology and conservation. I agree that cladistics is a terrific clean, calculable null model, and an excellent way of constructing phylogenies, but it is basically just a set of proposals made by Willi Hennig (1966) - it is neither a set of laws deduced by the logic of mathematics, nor has it been induced from empirical observation to be a set of principles invariable in the natural world.

Clades undoubtedly exist, but so do paraphyletic taxa. Evolution often proceeds by dichotomous branching: sometimes the 'true' sequence is hard to determine, but sometimes theory suggests that the true sequence may not be dichotomous and hard polytomies may be real (Bolnick 2006), which is consistent with molecular evidence (e.g. Scherz et al. 2022). It may sometimes be convenient to regard a speciation event as producing two new daughter species, with the ancestral species going extinct (as required by cladistics). But sometimes this may be misleading and it might be more useful to consider an ancestral species as

persisting largely unchanged under stabilising selection and gene flow (as in *A. calliptera*: or the surface-living relatives of the cave fish), while budding off a number of geographically restricted and isolated daughter species. In addition, there is increasing evidence for introgression across the boundaries of stable and diagnosable species, indeed, often among non-sister species, most rampantly in the case of the cichlid fishes of Lake Victoria and neighbouring lakes (Meier et al. 2023). Conceptually, I feel this really ought to make clear that monophyly and the dichotomously branching cladistic tree is more of a null model, often a fuzzy approximation, as is the idea of species as ‘separately evolving lineages’.

Finally, this must inevitably raise the question of whether higher taxa can also be paraphyletic. Siefert et al. (2016) make an explicit plea to retain paraphyletic higher taxa, for example where current genera represent clearly distinctive ecomorphological groups. In the case of adaptive radiations, some of the lacustrine cichlid species flocks are presently considered to contain endemic genera (e.g. Lakes Victoria, Malawi, Barombi Mbo). So are the cottoid fish of Lake Baikal (Kontula et al. 2003). In theory, two or more lakes containing different endemic genera could be descended from the same ancestral riverine species, although I am not sure there is an example of this yet. At present, many riverine cichlids are assigned to the genus *Astatotilapia*, including relatives of the endemic cichlids of Lakes Malawi, Victoria, Kivu, Edward, Albert and Turkana (Meier et al. 2023). Not only are there no apparent diagnostic traits to break this genus up into monophyletic lineages, but there is clear evidence of massive introgression between distantly related lineages prior to the evolution of both the Malawi (Svardal et al. 2019) and Victoria region (Meier et al. 2023) radiations. A similar problem arises in the case of the Lake Baikal sculpins, where two endemic families and 11 endemic genera are resolved as being nested with the single widespread genus, *Cottus* (Kontula et al. 2003), and it gets even worse for the Baikalian gammarids (Naumenko et al. 2017).

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