Species concepts and speciation of fishes: concluding remarks

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Abstract

The definition of the species category has stimulated more debate than perhaps any other topic in the biological sciences. There are currently more than 22 different species concepts and the debate continues on which concepts apply to all organisms, which concepts are operational and which concepts should be used in specific circumstances. The first major division of the types of concepts depends on whether one views species as constructs that exist for ordering biodiversity and information retrieval (i.e. classes), or views species as ontological individuals that exist in nature. If species are categories that can be defined, then theoretically, a single species can arise more than once in different places or at different times. If, on the other hand, species are individuals, then they are historical events, monophyletic and each species is unique.

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Introduction

The goal to define the species category has provoked more discussions and arguments than perhaps any other topic in comparative or evolutionary biology (Eldridge 1995). Darwin (1859) recognized the difficulty in delimiting species when he noted that many forms considered by competent scientists as varieties are ranked as species by other competent researchers. The debate continues. Mayden (1997) lists 22 different species concepts. Subsequently, Nelson (1999) combined parts of the Evolutionary Species Concept (Simpson 1951; Wiley 1978) and the Biological Species Concept (Mayr and Ashlock 1991) to form the Evolutionary Biological Species Concept, which is defined as 'groups of interbreeding populations that, under natural conditions, are reproductively isolated, or at least potentially so, from other such groups and as such are evolutionary lineages separated by irreversible discontinuities' (Nelson 1999, p. 278). In 1999, *Reviews in Fish Biology and Fisheries* published a special issue on species concepts in fish biology.

The species category

It would appear that the first step in defining the species category is based on one's philosophical outlook (Ghiselin 1969). Nominalists argue that individual organisms exist as separate entities, but taxonomic categories (e.g. class, family, genus, and species) are constructs that exist for ordering biodiversity and information retrieval (Gilmour 1940; Haldane 1956; Ehrlich and Holm 1963). At the other extreme, other scientists (e.g. Mayr 1949, 1963, 1996; Simpson 1961; Hennig 1966; Ghiselin 1969; Dobzhansky 1970; Grant 1971; Hull 1976; White 1978) state that species are not merely categories for a taxonomist's convenience, but exist in nature. The latter view is endorsed by three papers in this issue (Ghiselin 2002; Mayden 2002; Wiley 2002).

Ghiselin (2002) states that classes (not to be confused with classes in the Linnaean hierarchy) are abstractions that can be defined. As such, their properties exist because of the laws of nature. Laws of nature permit prediction (i.e. periodic table of the elements), they describe what must happen, and they do not tell us what happened in terms of historical fact (Ghiselin 2002). In contrast, individuals, in this case species, exist because of historical events – depending upon a series of events, a different result, other than the one we now observe, could have occurred. Wiley (2002) elaborates on this when he states that species are not invented or defined, but require discovery. Mayden (2002) further notes that individuals change over time and space so that they cannot be defined, but must be described or diagnosed. If species were classes or sets, they would be defined by their membership, and if a particular organism were to die and another born, the set would change (Ghiselin 2002). Furthermore, classes have very distinct definitions and are, in effect, immutable (Mayden 2002). Individuals, unlike classes, can change over time and yet remain the same object (Ghiselin 2002; Mayden 2002; Wiley 2002). In effect, species as individuals can participate in descent with modification; if, on the other hand, species are regarded as a category, then they cannot evolve.

Supraspecific taxa

The same philosophical arguments apply to supraspecific taxa. If one regards them as classes, then they are abstract, but if one views them in the ontological sense as individuals, they are concrete. If supraspecific taxa are individuals, then how do they differ from the species taxon? Species participate in the processes of descent with modification (Mayden 2002); the historical entities that we term clades do not (Ghiselin 2002). All monophyletic supraspecific taxa originated as a single species; hence, the only cohesion that exists among the members of a supraspecific taxon is historical. With the exception of special cases of introgression, there are no tokogenetic relationships among or between members of a supraspecific taxon.

Alpha taxonomy

If one accepts the argument that species are individuals (*sensu* Ghiselin) then we cannot rigorously define them. Instead, we have to be satisfied with a diagnosis of a biological species; hence the boundaries among them tend to be fuzzy (Barlow 2002; Mayden 2002, this issue). Certainly, species evolve at different rates (see Mayden, this issue, for a brief discussion of molecular clocks) and acquire different morphological, genetic and behavioural attributes. Thus, we can diagnose a particular species, but we cannot define it. Furthermore, the practising taxonomist must be able to diagnose and describe species within some operational species concept. Historically, morphology has played an important role in describing fish species, and many fish species were delimited by meristic and univariate morphometric analysis based on one or two specimens. More recently, systematists have been able to qualify and quantify the shapes of organisms to determine variation within and between populations and species (see Stauffer and McKaye 2001; Stauffer *et al*. 2002, this issue, for a review). Subsequently, allozyme data (Sage *et al*. 1984), mtDNA (Kornfield 1978), microsatellites (Markert *et al*. 1999) and amplified fragment length polymorphisms (AFLP) (Albertson *et al*. 1999) have been successfully used to diagnose species and higher taxonomic relationships (see Ghiselin 2002; Turner 2002, this issue, for a brief discussion of gene trees vs. species trees). Behavioural data have also played an important role in diagnosing fish species (see Barlow 2002, this issue, for a review) and Stauffer *et al*. (2002, this issue) gives specific examples of how behaviour can be used to diagnose both sympatric and allopatric populations.

Conclusions

As Mayden (2002, this issue) eloquently states 'Species are the basic currency of biodiversity worldwide'.

Thus, it is important to be able to identify particular species so that we can account for this diversity. If we view species as being ontological individuals (Ghiselin 2002; Mayden 2002; Wiley 2002, this issue) then we must consider the fact that they are historical events and are monophyletic. Turner (2002, this issue) asks whether a single species can arise more than once in different places or at different times; he further speculates on speciation and extinction through hybridization. Biology is not an exact science; thus, the outcomes of biological processes are difficult to predict. As stated in the introduction, the definition of the species category has stimulated more discussion than any other topic in the biological sciences; we predict that it will continue to elicit discussions, arguments and debates well into the future.

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