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The Bold Taxonomic Hypotheses of Collins (1991): 23 Years Later

> "**Bold ideas,** unjustified anticipations, and speculative thought, are our only means for interpreting nature: our only organon, our only instrument, for grasping her. And we must hazard them to win our prize. Those among us who are unwilling to expose their ideas to the hazard of refutation do not take part in the scientific game." Popper (1959:280).

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In the pages of this journal in 1991, Joseph T. Collins published a set of bold hypotheses under an innocuous sounding title: "Viewpoint: A new taxonomic arrangement for some North American amphibians and reptiles." This paper proposed 55 hypotheses about species. Specifically, Collins proposed the elevation of 55 nominal subspecies to species based on the application of the evolutionary species concept (ESC). As defined by Wiley (1978:18), evolutionary species are "… a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." Wiley (1978:18–19) was quite explicit with regard to the development of hypotheses based on his definition, "The definition is empirical in that it permits hypotheses from which can be tested…For example, we may frame the hypothesis, 'these two populations (or groups of populations) maintain separate identifiable evolutionary lineages.' Evidence used to test such an hypothesis can come from a variety of sources depending on the nature of the organism and the genetic, phenetic, spatial, temporal, ecological, biochemical and/or behavioral evidence which is available to test the question. *Whether a group of organisms is or is not a species then becomes an hypothesis to be tested*" (emphasis added). In many ways, the above quote forms the foundation of this retrospective of Collins' (1991) proposals.

The year before, Frost and Hillis (1990) published an influential paper on the ESC and its application in herpetology. One of the conclusions that Frost and Hillis (1990:93) reached, and certainly the most relevant for Collins, was that "where allopatric populations have not been demonstrated to be parts of a monophyletic group of very similar populations (e.g., *Bufo m. microscaphus* and *B. m. californicus*), we consider them to be distinct evolutionary species and name them as binomials (i.e., *B. microscaphus* and *B. californicus*)." Frost and Hillis (1990) gave numerous other examples where allopatric populations had been investigated and found to be multiple species, which led them to predict (p. 94), "… most of the large 'polytypic' species left (such as *Ambystoma tigrinum*, *Necturus maculosus*, *Sceloporus jarrovii*, *S. undulatus*, *Diadophis punctatus*, *Pituophis melanoleucas*, *Lampropeltis getula*, *Tantilla rubra*, *Thamnophis sirtalis*, and *Crotalus durissus*) will be found to be composed of several evolutionary species." The claims of Frost and Hillis (1991) at that time were bold, and presumably emboldened Collins.

Applying the arguments of Frost and Hillis (1991; which were an extension of Wiley [1978]), Collins (1991:43) made the philosophical and operational leap to treat allopatric North American amphibian and reptile subspecies as species as lineages: "the following taxa exhibit two characteristics which reveal their specific distinctiveness: 1) They are mapped as allopatric (based on the best published evidence available), and 2) they are in some way morphologically (and presumably genetically) distinct." Of course, like all change, this leap was controversial and did not go unchallenged. Three response papers (Lazell 1992; Montanucci 1992; Van Devender et al. 1992) appeared in *Herpetological Review* that argued strongly against Collins's hypotheses (for many reasons) and these rebuttals were in turn answered (Collins 1992; Frost et al. 1992). The debates were lively and enlightening and led to an awakened interest in the nature of species among herpetologists.

My purpose here is not to rehash the debates and the battles already fought and, frankly, won by proponents of the ESC, but instead to ask the empirical question: How many of Collins' hypotheses have been falsified? In my opinion, answering this question should be an important addition to the debates. Was Collins' trust in the ESC justified? Were the theory and philosophy behind the ESC well-founded? If the predictions of Collins were not rejected, then the answers to these questions should be "yes."

To address the question of how many of Collins' 1991 hypotheses have been falsified, I took the list from Collins (1991) and reviewed the systematics literature for each species. Based on the literature since 1991 (with a couple exceptions), the hypotheses were designated as either (1) failed to falsify, (2) failed to falsify but different from proposed, (3) falsified, and (4) unstudied. Failed to falsify means the hypothesis of Collins (1991) was corroborated as originally proposed. Failed to falsify but different means that although Collins (1991) was correct in proposing multiple species present, the discovered patterns were different, and more complicated than he predicted. Falsified hypotheses mean that the allopatric subspecies were found to be part of a single species. Unstudied hypotheses are precisely that; no work has been done to address what Collins proposed.

Of the 55 subspecies-to-species elevations proposed by Collins (1991), 40 (73%) had been studied by other investigators as of March 2014. Of those 40, 23 of Collins's hypotheses were corroborated (or were not rejected), six others had more complicated patterns of species distributions than predicted, and 11 were falsified (Table 1). Several of the decisions were not straightforward; it was not my intention to reinterpret the work of others, but simply to tally results. Some had actually been proposed as species prior to the publication of Collins's (1991) viewpoint. For example, Packard (1971) argued that regardless of reproductive compatibility, the disjunct population of *Anaxyrus* [then *Bufo*] *hemiophrys* recognized as *A. h. baxteri* was evolving independently of *A. h. hemiophrys* and should be recognized as a distinct species. Recognition of *A. baxteri* was supported later by Smith et al. (1998). *Thamnophis couchii gigas* is a similar case, where Rossman and Stewart (1987) previously had shown *T. gigas* to be a diagnosable lineage separate from *T. couchii*. These cases were included in the tally simply because Collins (1991) included them.

Is there any meaning that can be ascribed to only 11 hypotheses (out of the 40 tested) being falsified? Yes. Collins (1991) is an important paper because it challenged all of us to deal with the practical application of evolutionary science to taxonomy. Collins (1991) also strongly promoted further discussion on the nature of subspecies and their importance/relevance in understanding biodiversity. As circumstantial evidence, consider that from 1956 to 1990 (34 years), the number of subspecies recognized in nominal species of reptiles and amphibians in the USA dropped by 61, but from 1990 to 2012 (22 years), the number of subspecies dropped by 165 (Collins 1990; Conant et al. 1956; Crother 2012). Was this dramatic decline in the number of recognized subspecies caused by Collins (1991)? As noted above, Collins' (1991) polarizing paper was an empirical extension of the arguments of Frost and Hillis (1990), and coincident with the rise of molecular phylogenetics (e.g., Hillis and Moritz 1990), which provided new data and tools that spurred on phylogenetic research of North American amphibians and reptiles. While it can be argued that the philosophical and methodological advancements played a more important role in the decline of recognized subspecies, if Collins (1991) did not contribute to that decline, he certainly saw it coming (Collins 1991:42): "Besides providing recognition of the real species diversity in nature, a rigorous application of the evolutionary species concept (as discussed in Frost and Hillis 1990) would also reduce the number of arbitrarily defined subspecies dramatically…"

Collins (1991) exposed the false worry that nomenclatural instability may lead to chaos (see Pauly et al. [2009], Crother [2009], and Frost et al. [2009] for a recent debate of this issue); this "chaos" actually reflects the shock of change within the taxonomic community (Hedges 2013). Rarely considered, but of significance nonetheless, the results of the tests of Collins' hypotheses reflect the seeming fact that geographic disjunction, both allopatric and peripatric, are important drivers of speciation (Mayr [1963] was arguably the key work that solidified this orthodoxy). In the same vein, the results also supported a prediction of the ESC (Frost and

Table 1. Status of subspecies elevated by Collins (1991). 1 = Failed to falsify, 2 = multiple lineages but different than hypothesized, 3 = falsified, 4 = unstudied. See text for further explanation.* = determined there was not enough evidence to support or reject (C. Austin, pers. comm.).

Subspecies	Proposed Species	Status	Key Publications
Caudata			
Ambystoma macrodactylum croceum	*Ambystoma croceum*	4	NA
Cryptobranchus alleganiensis bishopi	*Cryptobranchus bishopi*	2	Tonione et al. (2010), Crowhurst et al. (2011)
Gyrinophilus palleucus gulolineatus	*Gyrinophilus gulolineatus*	1	Niemiller et al. (2008)
Necturus maculosus louisianensis	*Necturus louisianensis*	1	Chabarria et al., unpubl. data
Plethodon dorsalis angusticlavius	*Plethodon angusticlavius*	1	Highton (1997)
Plethodon vandykei idahoensis	*Plethodon idahoensis*	1	Howard et al. (1993)
Pseudotriton montanus diastictus	*Pseudotriton diastictus*	4	NA
Taricha torosa sierrae	*Taricha sierrae*	1	Kuchta (2007)
Anura			
Anaxyrus [*Bufo*] *hemiophrys baxteri*	*Anaxyrus baxteri*	1	Packard (1971), Smith et al. (1998)
Anaxyrus [*Bufo*] *microscaphus californicus*	*Anaxyrus californicus*	1	Gergus (1998)
Pseudacris streckeri illinoensis	*Pseudacris illinoensis*	1	Moriarty and Cannatella (2004)
Lithobates [*Rana*] *areolatus capito*	*Lithobates capito*	1	Young and Crother (2001)
Lithobates [*Rana*] *sylvaticus maslini*	*Lithobates maslini*	4	NA
Scaphiopus holbrooki hurteri	*Scaphiopus hurteri*	4	NA
Testudines			
Kinosternon flavescens arizonense	*Kinosternon arizonense*	1	Serb et al. (2001)
Kinosternon flavescens spooneri	*Kinosternon spooneri*	3	Serb et al. (2001)
Pseudemys concinna gorzugi	*Pseudemys gorzugi*	1	Seidel (1994), Spinks et al. (2013)
Pseudemys concinna suwanniensis	*Pseudemys suwanniensis*	3	Spinks et al. (2013)
Squamata: Lizards			
Aspidoscelis [*Cnemidophorus*] *burti xanthonotus*	*Aspidoscelis xanthonotus*	4	NA
Crotaphytus insularis vestigium	*Crotaphytus vestigium*	1	McGuire (1996)
Plestiodon [*Eumeces*] *egregius insularis*	*Plestiodon insularis*	1	Branch et al. (2003)
Plestiodon [*Eumeces*] *gilberti arizonensis*	*Plestiodon arizonensis*	3	Richmond and Reeder (2002)
Plestiodon [*Eumeces*] *septentrionalis obtusirostris*	*Plestiodon obtusirostris*	*	Fuerst and Austin (2004)
Holbrookia lacerata subcaudalis	*Holbrookia subcaudalis*	4	NA
Ophisaurus attenuatus longicaudus	*Ophisaurus longicaudus*	4	NA
Sceloporus graciosus arenicolus	*Sceloporus arenicolus*	1	Wiens and Reeder (1997)
Sceloporus graciosus vandenburgianus	*Sceloporus vandenburgianus*	1	Wiens and Reeder (1997)
Uta stansburiana stejnegeri	*Uta stejnegeri*	1	Upton and Murphy (1997)
Xantusia vigilis utahensis	*Xantusia utahensis*	3	Sinclair et al. (2004)
Squamata: Snakes			
Arizona elegans occidentalis	*Arizona occidentalis*	4	NA
Carphophis amoenus vermis	*Carphophis vermis*	4	NA
Cemophora coccinea lineri	*Cemophora lineri*	4	NA
Coluber constrictor mormon	*Coluber mormon*	2	Burbrink et al. (2008)
Coluber [*Masticophis*] *bilineatus lineolatus*	*Coluber lineolatus*	3	Camper and Dixon (1994)
Diadophis punctatus acricus	*Diadophis acricus*	2	Fontanella et al. (2008)
Diadophis punctatus amabilis	*Diadophis amabilis*	2	Fontanella et al. (2008)
Drymarchon corais couperi	*Drymarchon couperi*	1	Wüster et al. (2001)
Pantherophis [*Elaphe*] *vulpinus gloydi*	*Pantherophis gloydi*	2	Crother et al. (2011)
Farancia erytrogramma seminola	*Farancia seminola*	4	NA
Lampropeltis triangulum taylori	*Lampropeltis taylori*	3	Ruane et al. (2013)
Lampropeltis calligaster occipitolineata	*Lampropeltis occipitolineata*	4	NA
Lampropeltis pyromelana infralabialis	*Lampropeltis infralabialis*	3	Burbrink et al. (2011)
Lampropeltis zonata multifasciata	*Lampropeltis multifasciata*	1	Rodríguez-Robles et al. (1999), Myers et al. (2013)
Lampropeltis zonata parvirubra	*Lampropeltis parvirubra*	3	Rodríguez-Robles et al. (1999), Myers et al. (2013)
Lampropeltis zonata pulchra	*Lampropeltis pulchra*	3	Rodríguez-Robles et al. (1999), Myers et al. (2013)
Micrurus fulvius tener	*Micrurus tener*	1	Campbell and Lamar (2004)
Nerodia harteri paucimaculata	*Nerodia paucimaculata*	1	Densmore et al. (1992)
Pituophis melanoleucus catenifer	*Pituophis catenifer*	1	Rodríguez-Robles and de Jesús-Escobar (2000)
Pituophis melanoleucus ruthveni	*Pituophis ruthveni*	1	Reichling (1995)

Table 1. Continued.

Subspecies	Proposed Species	Status	Key Publications
Tantilla relicta pamlica	*Tantilla pamlica*	4	NA
Tantilla rubra cucullata	*Tantilla cucullata*	2	Dixon et al. (2000)
Tantilla rubra diabola	*Tantilla diabola*	3	Dixon et al. (2000)
Thamnophis couchi gigas	*Thamnophis gigas*	1	Rossman and Stewart (1987)
Thamnophis sirtalis dorsalis	*Thamnophis dorsalis*	4	NA
Virginia valeriae pulchra	*Virginia pulchra*	4	NA

Hillis 1990; Frost and Kluge 1994; Wiley 1978): if two populations are disjunct, and diagnostically distinct, the evidence suggests that they are on independent evolutionary trajectories and thus are species. And finally, Collins (1991) implicitly embraced Popperian (Popper 1959, 1962, 1972, 1983) logic by not waiting for the slow accumulation of inductive statements before proposing his hypotheses, but instead was bold in his proposals and risked the "hazard of refutation" (Popper 1959:280) with his hypotheses.

Although many of Collins's predictions were correct, this kind of taxonomy is not encouraged. I do not advocate nomenclatural changes that are not based on data (see Kaiser et al. 2013). However, it would advance our knowledge of biodiversity if biologists were less reticent about naming discovered lineages they identify in their phylogenies. After all, the phylogenetic system was originally developed for the specific purpose of classification (Hennig 1966; Wiley 1980).

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