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Letter

Cryptic Species –
Conceptual or
Terminological Chaos?
A Response to Struck
*et al.*Michael Heethoff^{1,*}

In a recent article, Struck *et al.* [1] aimed at finding evolutionary processes hidden in cryptic species. They provided a broad overview on the different usage of the term ‘cryptic species’ and called for a more rigorous definition by comparing phenotypic (morphological) disparity with the degree of genetic differentiation. They conclude ‘if biologists cannot even agree on what to consider different species, then how can we reach consensus on what represents cryptic species?’ I argue that there is only one solution to both of these issues and that cryptic species represent nothing more than an incompatibility of species ‘concepts’ in applied taxonomy. Hence, ‘cryptic species’ can neither be defined nor are they outcomes of an evolutionary process like ‘cryptic speciation’.

Species delimitation has been confused with species conceptualization, leading to

a controversy on what the species category is and how species can be delineated [2]. The evolutionary species concept [3] represents a general primary concept, however, without much value for applied taxonomy. Applied taxonomy mostly refers to the morphological species concept, although there is no clearly defined workflow for species delineation [4]. In this context, Struck *et al.* suggest that ‘morphological variation needs to be explicitly quantified’, and I could not agree more. The biological species concept [5] is often used to confirm or reject morpho-species hypotheses, but is only applicable to sexually reproducing organisms. Using genetic differences for species delineation has also been proposed (e.g., [6]), and has recently been applied to split giraffes into four distinct species despite them interbreeding in captivity [7]. Hence, whether a species is cryptic or not depends on nothing else than the underlying species concept. Struck *et al.* implicitly used the morphological species concept and ‘tested’ it against genetic divergence. Hence, they compared two classes of species concepts (morphological vs. genetical) regarding their compatibility (i.e., supporting the same boundaries of species), and ‘define’ species to be cryptic when they are morphologically similar but genetically distinct (which is here taken as a proxy for ‘reduced gene flow’ and ‘reproductive isolation’ and would thus confirm the biological species hypothesis). This approach prioritizes the ‘evolutionary truth’ of genetic over morphological species concepts – probably a valid approach in many if not most cases. Ten years ago, Bickford and colleagues defined cryptic species as ‘two or more distinct species classified as a single species’ [8], rendering ‘cryptic’ species as nothing more than grouping artifacts. I agree and conclude that cryptic species do not exist as a concept, but that the term ‘cryptic’ is only used to prioritize one species concept over others. Eventually,

it may turn out that cryptic species are not so cryptic at all [9].

Hence, we should not aim at defining what ‘cryptic species’ are, but what species concept we believe to represent evolutionary entities that we can use as fundamental units in biology – even if such a concept may lack clear instructions for applied taxonomy.

¹Ecological Networks, Technische Universität Darmstadt, Schnittspahnstraße 3, 64287 Darmstadt, Germany

*Correspondence:

heethoff@bio.tu-darmstadt.de34 (M. Heethoff).
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Letter

Cryptic Species –
More Than
Terminological Chaos:
A Reply to Heethoff

Torsten H. Struck,^{1,*}
Jeffrey L. Feder,²
Mika Bendiksbj, ^{1,3}
Siri Birkeland,¹ Jose Cerca,¹
Vladimir I. Gusarov,¹
Sonja Kistenich,¹

Karl-Henrik Larsson,¹
Lee Hsiang Liow,^{1,4}
Michael D. Nowak,¹
Brita Stedje,¹ Lutz Bachmann,¹
and Dimitar Dimitrov^{1,5}

Recently we discussed problems and challenges associated with inconsistent definitions and methods used to identify cryptic species, and how these hamper studies of their evolutionary significance. We proposed a conceptual framework that is focussed on evolutionary processes and advocated for a shift from pattern- to process-driven research concerning cryptic species, in order to circumvent these issues [1]. In his response, Heethoff [2] argued that cryptic species are merely a reflection of the limitations of applied taxonomy. He stated that cryptic species 'represent nothing more than an incompatibility of species "concepts" in applied taxonomy'. As such, he rejected our proposed framework as an approach that 'prioritizes the "evolutionary truth" of genetic over morphological species concepts'. In our opinion Heethoff's conclusions are based on his misconceptions about the proposed framework.

In essence, Heethoff repeats the often-cited opinion that cryptic species are only a temporary taxonomical formalization problem of species delineation [3,4] and not a natural phenomenon. He supports this view with examples of diverging species in the so-called grey zone of speciation [5,6], like the giraffe, and ignores many examples of good species with unusually high phenotypic similarity despite restricted gene flow, sometimes over long time periods [7–11]. Importantly, our survey of the literature revealed that there are as many old cryptic species reported as young ones [1]. However, the current taxonomic practice makes it difficult to differentiate between these two cases and to understand the evolutionary processes and mechanisms underlying their origins.

Thus, we proposed a framework that in contrast to previous approaches explicitly separated the two steps, that is, species delineation and assignment of the status cryptic. Specifically, we concluded that what is needed is a rigorous quantitative assessment of phenotypic similarity in an evolutionary context [1]. To this end, our framework provides explicit means of differentiating taxonomical errors from true cryptic biodiversity. The first basic requirement of our framework is to show that the lineages in question are clearly separate species [5]. This can be achieved by applying any species concept. We provided examples based on molecular approaches, but we did not advocate for any particular species concept, as presumed by Heethoff. In fact, our proposed call for proof of species being distinct is not different from any other species delineation attempt, and evidence should be based on as many sources of information as possible [5].

The second step of assigning the status cryptic implies that a null expectation (hypothesis) is to be formulated and tested. Specifically, it requires evidence for substantially higher degrees of phenotypic similarity between species in question than expected. This can, for example, be achieved by comparing evolutionary rates to other species pairs within the lineage. If the homogenizing effect of gene flow is shown to be low or absent, high phenotypic similarity becomes less likely with increasing divergence time. Hence, only species exhibiting statistically lower degrees of phenotypic disparity than expected for a given divergence time are accepted as cryptic in the proposed framework. Genetic divergence was proposed as a proxy, when actual divergence times cannot be determined with high confidence. This proposal offers further advantages because genetic divergence estimates can also serve as proxy for the degree of gene flow. However, this

does not mean that genetic divergence serves as a proxy for the biological species concept, as implied by Heethoff. Species delineation is done in the first step from the sum whole of information, including genetic data, before cryptic status is assigned.

Finally, it is important to note that we did not advocate that cryptic species are the outcome 'of an evolutionary process like cryptic speciation'. We clearly stated that this term is misleading and should not be used. When it comes to cryptic species, only recent divergence can be directly related to the speciation processes. Other processes such as convergence, parallelism, and stasis are not related to the speciation process itself, but describe macroevolutionary processes that have led to high phenotypic similarity as the outcome of evolution. We explicitly outlined the advantages of cryptic species as models for understanding these processes [1], an end goal of our proposed framework.

Responding to concerns raised by Heethoff [2], we conclude that they are the result of misconceptions about our framework. We reaffirm that our approach to evaluating whether species are cryptic is transparent, repeatable, and independent of taxonomic treatment (e.g., usage of species concepts and history of synonymies). We all make errors and overlook things sometimes, taxonomists included, but cryptic species are more than errors. If we take the time to define and quantify cryptic species with rigor, then they have potentially much to teach us about evolution beyond just learning from our mistakes.

¹Natural History Museum, University of Oslo, 0318 Oslo, Norway

²Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

³NTNU University Museum, Norwegian University of Science and Technology, 7491 Trondheim, Norway

⁴Centre for Ecological & Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, 0316 Oslo, Norway

⁵Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

*Correspondence: t.h.struck@nhm.uio.no (T.H. Struck).
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