Introduction

Alexandre K. Monro

Abstract.

This Systematics Association Special Volume is the result of a symposium entitled, ‘Cryptic taxa - artefact of classification or evolutionary phenomena?’ held on June 17 as part of the Association’s 10th Biennial Meeting 2019. I began to realise that the notion of, – and process of discovery for – cryptic species touches the heart of several major debates in biology, including, ‘what are species?’, ‘how should we recognize them?’, the notion of punctuated equilibria and that of morphological stasis in the fossil record. In addition, in the midst of a biodiversity crisis the phenomenon of cryptic species suggests that there may be a greater diversity of evolutionary lineages in need of conservation, than has been suggested by morphology alone. The chapters that emerged from the Symposium show clearly how the topic of 'species' remains central to biodiversity sciences and the subject of wide-ranging and lively debate. In almost every chapter there is a call for change, either of direction or for the inclusion of new developments and data, and their focus ranges from abandoning species altogether to highlighting the weaknesses in current taxonomic process suggesting that our representation of the biological universe remains superficial.

Cryptic species: a product of the paradigm difference between taxonomic and evolutionary species

Simon J. Mayo

Abstract.

Taxonomic and evolutionary species (T-species and E-species) can be viewed as distinct ontologically. Conventional taxonomic species are cognitive concepts, refined by biological theory, which tessellate the living world into comprehensible but imperfectly delimited units to provide an overview of biodiversity – the public domain status quo species system. A single named taxonomic species may consist of multiple species taxon concepts, each of which is objectified by the specimen sets used – Simpson's hypodigms. The resulting compound species taxon may thus be vague. Evolutionary species are predicted from evolutionary theory and serve as models for investigating evolutionary processes. They are tools for biologists to probe deeper into biological reality and generate hypotheses of patterns that lie beyond the confines of human cognition. Cryptic species result from the feedback to taxonomy of discoveries in evolutionary biology and may differ from species taxa in data, analysis method, or species criterion. Social conventions among biologists, especially systematists, are involved in their recognition as taxonomic species; they should be objectified as published taxon concepts using protocols including description, diagnosis, hypodigm and a correct name. The public domain taxon system would benefit if species taxon concepts were based on a system of online databases.

Species circumscription in cryptic clades: a nihilist's view

Richard M. Bateman

Abstract.

In this unashamed polemic I argue that most extant plant species currently represented by a Linnean binomial exist only at the most basic level of a primary hypothesis that has not yet been subjected to the crucial test of circumscription. Circumscription is the search for discontinuities in fundamental intrinsic properties through extensive sampling of individuals, ideally pursued in situ in their chosen habitats. Rigorous circumscription requires sampling of numerous populations across the full range

of a putative species and all of its supposed close relatives for several properties, including as essentials analytical morphology and genetics (increasingly expected to reflect next-generation sequencing), preferably supported by gene exchange experiments and autecological observations. Without such intensive study, here termed 'demographic monography', it is impossible to determine with confidence whether discontinuities in one or more of the properties studied are genuinely robust or merely metastable, perceptions changing substantially as sampling improves and additional categories of data are explored. In the absence of genuine, demonstrable discontinuities in at least one biologically meaningful property, perceived species boundaries remain entirely arbitrary, thereby hindering rather than assisting every kind of biological investigation. The term 'cryptic species' has many implied definitions, but in my opinion it simply boils down to the many situations where limited morphological and molecular differentiation leave the analyst unsure whether credible species boundaries exist among the representative individuals analysed. The lack of obvious discontinuities typically reflects ongoing gene-flow and/or low levels of extinction of intermediate lineages. Review of three case-studies of European orchid groups often accused of harbouring cryptic species – which collectively can be viewed as containing as many as 500 morphological species but also as few as 55 molecular species – reveals few shared properties other than recency of supposed divergence of the studied lineages. Such disparate biodiversity assessments within intensively studied, charismatic genera suggest that conventional taxonomic practices require radical revision, in order to focus on comprehension rather than mere documentation. At present, the status of a putative species is rarely subjected to critical appraisal through the lens of any specified species concept or evolutionary mechanism, despite the widely accepted primacy of species in systematic biology.

Multilevel organismal diversity in an ontogenetic framework as a solution for the species concept

Alexander Martynov & Tatiana Korshunova

Abstract.

The concept of ‘species’ is a persistent biological problem. In discussions about the species phenomenon, the ‘cryptic species’ concept currently prevails. We propose that the ‘cryptic species’ concept as it is currently understood strongly emphasizes the distinctions between morphological and molecular levels and obscures multiple other biological levels and the organism itself. Therefore we suggest, instead of the term ‘species’, a multilevel organismal diversity concept (MOD) as an alternative that is well-supported by numerous data. We also highlight the central role of ontogeny in a broad sense (one that encompasses all major properties of an organism as well as both genetic and epigenetic traits) for the future development of taxonomy and phylogenetics. Potential consequences of a new understanding of the species phenomenon for biological nomenclature are outlined. A general scheme for the future development of organism studies within the framework of MOD is presented.

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Diagnosability and cryptic nodes in Angiosperms: a case study from Ipomoea

Pablo Muñoz-Rodríguez, John. R. I. Wood & Robert W. Scotland

Abstract.

Three important properties associated with a classification of any group of organisms are diagnosability, monophyly and resolution. In this chapter we explore the interrelationships between these three properties in the context of cryptic taxa, here defined as a clade with no obvious diagnostic morphological support. We present the view that the number of nodes on a phylogenetic tree of all flowering plants that have morphological diagnostic support is less than five percent; as such, cryptic nodes are much more common than non-cryptic nodes. Because of this, we suggest that the phrase ‘cryptic nodes’ is a preferable description as opposed to cryptic taxa because taxa in the sense of traditional classifications are generally diagnostic. By reference to a global taxonomic study of the genus Ipomoea, we discuss the role of diagnosability at various scales including major infrageneric clade, genus and species. We demonstrate that the level of diagnosability for Ipomoea is relatively low, therefore making cryptic nodes the rule and not the exception. We provide several examples of such cryptic nodes, detail how we discovered them and place them in a wider conceptual framework of diagnosability in angiosperms.

Connecting micro- and macro-evolutionary research – extant cryptic species as systems to understand macro-evolutionary stasis

Torsten H. Struck & José Cerca

Abstract.

‘Cryptic species’ are nowadays commonplace in systematics, and, with the application of barcoding approaches, increasing numbers of species are shown to be supposedly cryptic. However, the use of the term is inconsistent in the literature. Moreover, processes associated with the formation of cryptic species are generally not taken into account. These processes comprise (I) recent divergence, (II) parallel or (III) convergent phenotypic evolution, or (IV) phenotypic stasis. This causes confusion and imprecision in attempting to resolve the origins, evolutionary trajectories and ecological importance of cryptic species.

Here, we will briefly present these four processes based on a recently proposed conceptual framework for the definition of cryptic species. The four categories differ from each other in their temporal scale, phylogenetic context, and underlying selection. In focusing on the phenomenon of stasis, that is the absence of change over long geological periods, we discuss the overlap between stasis seen in the paleontological record and as observed in cryptic species, and we further consider that the challenge of integrating stasis into current evolutionary thinking is due to several different factors. These include microevolutionary research findings in extant species that seem to indicate abundant variation in both genetic markers and quantitative traits and development. Hence, there are contradictions between micro- and macroevolutionary scales. Cryptic species can provide study systems of extant species, which make it possible to bridge the gap between micro- and macroevolutionary research. Here we discuss this potential and provide an outlook on future research directions exploiting cryptic species.

Coexisting cryptic species as a model system in integrative taxonomy

Cene Fišer & Klemen Koselj

Abstract.

Species are fundamental units in which we describe nature and reflect on its diversity. The development of molecular delimitation methods has shown that many species cannot be diagnosed on the basis of morphological traits. Despite the warnings that have deemed such species the most challenging segment of the Linnean taxonomy, we suggest that they represent an opportunity for progress in taxonomy. Here we examine what can be learned from the cryptic species pairs that overlap in their ranges and occupy the same habitat. Their joint occurrence is possible under two conditions. First, these species should be isolated reproductively. Second, the effects of interspecific competition on population growth must be neutralised. Identifying the functional traits that contribute to solving of these two biologically meaningful challenges and integrating them into taxonomy could strengthen species delimitation. We first examine the mechanisms of cryptic species origin. Then we review some well-documented cases of reproductive isolation between cryptic species, focusing on prezygotic isolation mechanisms mediated by premating recognition and communication. We move to examples of co-occurring cryptic species, focusing on ecological niche differentiation and habitat choice. We conclude that both mate recognition and habitat choice importantly depend on species' sensory ecology, and argue that the field of sensory ecology should become more often included into integrative taxonomy. Moreover, if we do not attempt to understand sensory worlds of cryptic species, a large part of the existing diversity will remain hidden, misunderstood and unprotected in this time of rapid anthropogenic global change.

Non-monophyletic species are common in plants: an ecological evolutionary perspective

Matt Lavin & R. Toby Pennington

Abstract.

The delimitation of species does not require the coalescence (monophyly) of multiple genetic samples representing a single taxonomic species, as long argued, especially by botanists. However, when a plant clade includes many species, including cryptic ones, with each represented by coalescing conspecific genetic samples, this could be revealing of underlying mechanisms that promote genetic coalescence. Such mechanisms potentially include low effective population sizes due to either population or genomic attributes, adaptation to dispersal-limited habitats, or long evolutionary persistence of populations. We suggest that coalescence or monophyly of conspecific genetic samples occurs more commonly in animal than plant clades, which implies that plant species are more likely to have some combination of larger effective population sizes from a population or genomic perspective, a predilection to less dispersal limited habitats, or average evolutionary younger ages. For woody plant species, we suspect adaptations to dry environments are more dispersal limiting than adaptations to wetter environments. We give examples that suggest coalescence of conspecific plant samples likely occurs more often among genetic samples taken from isolated populations that are phylogenetically niche conserved to seasonally dry tropical forests and woodlands (the succulent biome). This is in comparison to conspecific genetic samples taken from isolated plant populations that are niche conserved to tropical wet forests. However, these suggested patterns will be context dependent. For example, recency of evolution, large effective population sizes, or polyploid genomes could work against detecting coalescent patterns of conspecific genetic samples in plant taxa that are niche conserved to seasonally dry tropical forests and woodlands.

Guerrilla taxonomy and discriminating cryptic species – is quick also dirty?

Paul H. Williams

Abstract.

Our grasp of biodiversity, and especially of cryptic species, is fine-tuned through revisionary taxonomy. If species exist in nature and can be discovered with available techniques, then revisions should converge on broadly shared interpretations of species. Here species are recognised using integrative assessment, focussing on whether there is corroboration between evidence from coalescents in the COI gene and evidence from morphological divergences. Retrospective analysis of progress between 2011–2019 in global analyses of bumblebees (genus Bombus) in two contrasting groups (the subgenera Alpinobombus and Melanobombus) examines convergence on stable solutions within each group as samples were accumulated. Results show that convergence was slow to be achieved because of initial under-representation of rare species despite directed sampling to increase evenness of representation. Filtering out short sequences with ambiguous data had limited value for improving convergence. Filtering to retain only unique alleles (UAF) was more successful in reducing the over-sampling effects that can promote acceptance of false cryptic species and this did improve convergence. In addition, results for discriminating polytypic and cryptic species when using UAF are better supported by patterns in genetic divergence with geographical distance . Consequently, the UAF approach was better able to clarify the distinction for long-problematic cases of cryptic bumblebee species. In summary, these results show that reliable taxonomic revision may be difficult to achieve quickly, even when large numbers of data can be acquired rapidly from gene sequences, unless broad geographical coverage of even the rarest species can also be achieved, which will usually need a long time and broad international collaboration.

Cryptic lineages among Seychelles herpetofauna

Jim Labisko, Simon T. Maddock, Sara Rocha & David J. Gower

Abstract.

An expansion of the use of molecular data in the 21st Century has accompanied a greatly increased number of amphibian and reptile species descriptions. Some of the newly discovered or recognised diversity has been considered ‘cryptic’. Islands, and island-endemic taxa, represent worthwhile systems to address questions about cryptic species—i.e. phenotypically similar but genetically distinct lineages. Among islands, cryptic-species studies have typically been limited to recently emergent islands and/or rapid radiations. Being comprised of multiple islands of partly Gondwanan origin, the Seychelles Archipelago in the western Indian Ocean offers the opportunity to address crypsis for a biota comprised of both deep-time vicariant and more-recent overwater dispersed forms. Here we summarise current knowledge on the diversity and distributions of Seychelles herpetofauna (frogs, caecilians, snakes, lizards, turtles) of the Inner (granitic) Islands. We focus on the history of discovery, taxonomy, inter- and intraspecific variation, and phylogeography. Most recent studies investigating intraspecific variation in Seychelles herpetofauna have identified (often similarly) geographically structured, genetically divergent populations, and we note the potential of Seychelles herpetofauna to aid understanding of lineage crypsis more generally. We attempt to assess why some lineages have remained cryptic for so long; whether recently discovered lineages are truly cryptic and/or distinct taxa; and if ecology (namely vagility) and/or length of time on the islands can explain variation in lineage crypsis. Few or patchy data currently limit interpretations that can be made. Detailed ecological and environmental data, population genetic assessments, reconstruction of phylogeographic histories, and integration of phenotypic trait data will all aid future assessments. These approaches will enhance current understanding of regional and global patterns and processes of evolution in amphibians and reptiles, and also serve to inform mitigation efforts for the anthropogenic threats they currently face.

Cryptic diversity in European terrestrial flatworms of the genus Microplana (Platyhelminthes, Tricladida, Geoplanidae

Marta Álvarez-Presas, Eduardo Mateos, Ronald Sluys & Marta Riutort

Abstract.

In Europe, native terrestrial flatworms are a paradigm of the cryptic edaphic fauna in humid forests because they are small, difficult to collect, and externally very similar. Their Neotropical counterparts are good biodiversity indicators in the assessment of the conservation status of their habitat. While the diversity of terrestrial planarians in the Neotropics is high, the diversity of European microplanid land flatworms is comparatively scarce. Nonetheless, recent molecular barcoding studies have uncovered an increasing diversity. Furthermore, for Microplana terrestris (Müller, 1774) it was shown that its recent evolutionary history was mainly driven by Pleistocene climatic events. Intensive sampling throughout Europe revealed that nominal M. terrestris consists of a complex of cryptic species, sharing similar external appearance but differing at molecular and anatomical levels, thus constituting a prime example of zoological crypsis. Since these species can be differentiated on the basis of anatomical features, they do actually form pseudo-cryptic species. Temperate European forests show a comparatively high diversity of terrestrial flatworms, although never reaching the biodiversity level of the Neotropics. A better understanding of their ecological role and adequate measures to protect these land planarians depend on an increased effort to properly detect these organisms in their environment.