

Towards integrative taxonomy

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Delineating species boundaries correctly is crucial to the discovery of life's diversity because it determines whether or not different individual organisms are members of the same entity. The gap in communication between the different disciplines currently involved in delimiting species is an important and overlooked problem in the so-called 'taxonomy crisis'. To solve this problem, it is suggested that taxonomy become integrative, and this integration is seen as the real challenge for the future of taxonomy. 'Integrative taxonomy' is defined as the science that aims to delimit the units of life's diversity from multiple and complementary perspectives (phylogeography, comparative morphology, population genetics, ecology, development, behaviour, etc.). Some workers have already collaborated and successfully adopted an integrative approach to taxonomy. However, it is now time for the whole discipline to evolve. A radical change in mentality is needed concerning the creation of names in order to achieve this integration and to prevent the over-abundance of both synonyms and names of doubtful application from worsening. Integrative taxonomy gives priority to species delineation over the creation of new species names. Furthermore, it is emphasized that describing morphological diversity, referred to as 'morphodiversity', does not require the naming of any single set of specimens. Seven guidelines are proposed to help integrative taxonomists recognize cases when species are supported by broad biological evidence and therefore are deserving of an official name. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 407–415.

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INTRODUCTION

Recently, several scientists have pointed out that taxonomy is facing a crisis and that we need to determine what the future of taxonomy will be (e.g. Gewin, 2002; Godfray, 2002; Mallett & Willmott, 2003; Wilson, 2003; Wheeler, Raven & Wilson, 2004). Given that an estimated 10 million species remain to be discovered (Wilson, 2004), it is well worth debating our approach to describing life's diversity. In doing so, we must clearly distinguish the nature of the different tasks of taxonomy. Two of these tasks are scientific: delineating and classifying species. Two others are services to the community: naming species and providing tools to identify them. These distinctions aid in the realization that the various tasks may need different kinds of improvements.

Taxonomists currently treat the two scientific tasks of taxonomy (i.e. delimiting and classifying species) in very different ways. On the one hand, the vast majority of taxonomists use phylogenetic methods for classifying species. Indeed, most taxonomists consider themselves phylogeneticists, which makes sense because they wish to reconstruct natural relationships among living beings. Introducing rigorous phylogenetic methods into taxonomy was a challenge in the 1970s (e.g. Nelson, 1971; Felsenstein, 1979), but this goal has now largely been achieved. On the other hand, most taxonomists would not consider themselves population biologists, phylogeographers or molecular ecologists, although they share similar goals: delimiting the units of life's diversity. For the most part, taxonomists have paid little attention to methods developed during the last 15 years for delimiting species (e.g. Avise & Ball, 1990; Avise, 2000; Sites & Marshall, 2003). Many non-taxonomist biologists are now frustrated by the 'old-fashioned' typological

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approach with which taxonomists still describe species. I believe that this frustration is one of the most overlooked aspects of the 'taxonomy crisis'. By species, I refer to cohesive genealogical lineages. The notion of lineage is a common component of all views of species proposed during the last 50 years (de Queiroz, 1999, 2005). It also is close to the evolutionarily significant units (ESUs) of Moritz (1994). Addressing how species are to be delineated is the real scientific challenge for the future of taxonomy. It is important to note that in practice some species may be very difficult to delineate.

ON IDENTIFICATION

Ideally, identification should be easy and efficient because different users, such as pharmacologists, physiologists, conservation biologists and ecologists, need to identify species. The need for simple and reliable identification tools helps solve the recent quarrels over 'DNA barcoding' (e.g. Baker *et al.*, 2003b; Hebert *et al.*, 2003; Lipscomb, Platnick & Wheeler, 2003; Scotland *et al.*, 2003; Seberg *et al.*, 2003; Stoeckle, 2003; Tautz *et al.*, 2003; Blaxter, 2004; Gaston & O'Neill, 2004; Will & Rubinoff, 2004). Proponents of DNA barcoding (e.g. Hebert *et al.*, 2003; Tautz *et al.*, 2003; Blaxter, 2004; Gaston & O'Neill, 2004) have argued that one should use DNA sequences of one (or a few) particular gene(s) to identify species, based on the idea that every species has its own 'diagnostic' sequence, i.e. a unique set of base pair mutations, acknowledging that there may be some variation around a single sequence. In cases where it is demonstrated that sequences of particular molecular markers provide faster, more reliable identifications than morphological features, there is no reason not to use them (e.g. Baker *et al.*, 2003b; Proudlove & Wood, 2003). However, in instances where it is shown that morphological features provide faster, more reliable identifications, there is no reason to discard them. These two systems of identification should not be seen as competing against each other or exclusive, but rather as approaches to the same goal which simply differ in the characters they consider. One system or the other may be favoured for particular cases depending on the results it provides, but they also can be used concurrently. It is very likely that what will work best for identification will depend on the particular species being considered, even among closely related species. Science progresses by transmitting, transforming, increasing and challenging knowledge, but certainly not by ignoring it, and the achievements of centuries of research in comparative morphology must not be ignored.

Moreover, a DNA-based system of identification can only work if all the species have their 'diagnostic'

sequence(s) present in the database. An incomplete database will simply allow users to determine whether a given sequence is different from the others already stored. Such a result will not identify the specimen in question *per se*, and it will not automatically imply that the specimen is a member of a new species. This is not an argument against barcoding initiatives, but simply a reminder that, at all stages (e.g. collecting efforts, sorting specimens, curating collections of vouchers, providing names), the construction of a centralized DNA-based system of identification would depend in part on the expertise of 'non-DNA' taxonomists.

However, the most fundamental question of taxonomy is not how to identify species, but rather how to delineate them. Species delineation is fundamental to the discovery of life's diversity because it determines whether or not we can recognize when different specimens are members of the same cohesive lineage.

FROM TRADITIONAL TO INTEGRATIVE TAXONOMY

There is a critical need for rigorously delineated species not only for producing accurate species inventories, but more importantly because most questions in evolutionary biology (e.g. speciation), ecology (e.g. ecosystem development), conservation biology (e.g. conservation priorities) or biogeography (e.g. diversification processes) depend in part on those species inventories and our knowledge of species. Erroneous species boundaries or diversity estimates may lead us to provide incorrect answers to those questions, exactly as phylogenetic trees must be reconstructed rigorously and analysed critically because they are a first step toward discussing broader questions.

Part of the problem of species delineation is the fact that morphology, as an approach for delimiting species, has some limits. Traditional morphology-based taxonomy only discriminates what Cain (1954) called 'morphospecies', i.e. species exclusively established on morphology. Note that the term morphospecies has been used recently in a different manner by some conservation biologists (e.g. Oliver & Beattie, 1996). Traditional morphology-based taxonomy is not the study of life's diversity *per se*, but rather the study of one of its multiple facets, morphological diversity, which I refer to as 'morphodiversity'. This does not mean that morphospecies are never valid species, but rather that morphospecies are hypotheses that should be tested via different approaches and with different kinds of data.

Several new methods for delineating species and testing species hypotheses have been developed during the last 15 years (e.g. Avise & Ball, 1990; Avise,

2000; Sites & Marshall, 2003). Nothing illustrates their contribution better than the discovery of cryptic species and their help in cases with high intra- and interspecific morphological variation. Some scientists have already successfully combined these methods with traditional, morphology-based taxonomy for studying species diversity (e.g. Boisselier-Dubayle & Gofas, 1999; Shaw & Allen, 2000; Williams, 2000; Drotz & Saura, 2001; Lessios, Kessing & Pearse, 2001; Schaal & Leverich, 2001; Baker *et al.*, 2003a; Fall *et al.*, 2003; Marcussen, 2003; Meyer, 2003a, 2004; Parmakelis *et al.*, 2003; Finlay, 2004; Malhotra & Thorpe, 2004). Integrating different perspectives is a standard procedure for groups such as mammals, where the vast majority of the species are already known (e.g. Wada, Oishi & Yamada, 2003), or in groups where morphological features are limited, such as bacteria (e.g. Oren, 2004). There is not a single kind of taxonomic practice, but rather multiple practices depending on which taxon is considered: for example, an entomologist and an ornithologist would probably have different opinions concerning the current problems of taxonomy. However, an integrative approach to taxonomy should now become general.

An integrative approach to taxonomy is necessary because the complexity of species biology requires that species boundaries be studied from multiple, complementary perspectives. Also, our level of confidence in species supported by different kinds of data is much higher than for species supported by only one kind. A wide range of methods already exists for delimiting species, and the need for rigour in species delineation requires us to use those methods synthetically. Collaboration between disciplines such as phylogeography, comparative anatomy, population genetics, ecology and behavioural biology should become standard practice in taxonomy. All biologists who produce data that help delimit species boundaries are taxonomists, or at least 'integrative taxonomists'. Under the new paradigm of integrative taxonomy, morphologists could describe morphodiversity, analyse the variation of morphological features among individuals and propose hypothetical morphospecies. Then, those morphospecies – or some of them – could be submitted to the filter of other approaches and additional data (molecular, behavioural, developmental, ecological, etc.). In practice, one could establish priorities among morphospecies, because research is time-consuming and, unfortunately, limited financially. Morphospecies that are easily recognizable owing to a series of diagnostic morphological features could be investigated after more problematic species complexes.

The study of intra- and interspecific variation is the core of all disciplines involved in integrative taxonomy, and individual variation in morphology must be thoroughly addressed before morphospecies can be

proposed. More broadly, the study of variation helps to elucidate the processes that create diversity and maintain it (e.g. Masta & Maddison, 2002; Garcia-Paris *et al.*, 2003; Stepan, Zawadzki & Heaney, 2003). The issue of naming is discussed in more detail below.

Integration means multidisciplinary (Wake, 2003). I cannot emphasize strongly enough that the necessity of testing morphospecies does not mean that non-morphological approaches should replace morphological studies (Will & Rubinoff, 2004). Indeed, the non-morphological methods available to delineate species may present some problems, such as the fact that gene trees may differ from species trees. Also, even though morphology cannot be the unique approach for discovering species, it is a major and valuable component of our knowledge of life's diversity. Taxonomists are usually excellent field naturalists and morphologists, and know a great deal about the natural history of 'their' organisms. They must continue to publish descriptive and comparative morphological studies as well as general natural history data.

GUIDELINES FOR CREATING NAMES

In order to achieve this integration, which is desirable for the future of taxonomy, a radical change in mentality is needed concerning the creation of names. One of the main reasons why non-taxonomists are often frustrated by taxonomy is the over-abundance of redundant species names (i.e. species that have multiple synonymous names; see Godfray, 2002), as well as names of doubtful or unknown application, called *nomina dubia* by the *International Code of Zoological Nomenclature* (ICZN, 1999). The over-abundance of synonymous and doubtful names is an undeniable failure of past taxonomic practices. It greatly slows down the discovery of new species and complicates studies of recognized species and also makes the selection of names for well-delineated entities very difficult. Finally, it imperils the estimation of alpha-biodiversity as well as any science that depends on such estimates (e.g. community ecology, conservation biology, biogeography, etc.). Species names are a tool for communicating our knowledge of species diversity; they should make communication easier instead of impeding our scientific goals.

Nomina dubia arise when species are described based on a small number of specimens that are either entirely destroyed, uninformative or lost, and have original descriptions that are largely incomplete and do not provide characters needed for identification.

The over-abundance of synonyms has several causes. For example, a new species name may be introduced because the author(s) did not know that the same entity had already been named, which often happens in cases of arbitrary or unclear classification of

species within genera. Likewise, new species names can be introduced because the author(s) misinterpreted individual variants as members of new specific entities. This phenomenon, colloquially called ‘over-splitting’, is often related to the fact that some taxonomists evaluate their contribution to science by the number of species names they have introduced, and therefore create new names with the intention of seeing their own list of species names grow. Finally, synonymy may also occur by ‘lumping’ together species, i.e. by grouping several species into a single entity even though several species do exist. However, lumping is far less important than the two first causes for the abundance of synonyms.

Nomina dubia are actually more problematic than synonyms because they have no clear status. This is particularly striking when estimating or inventorying species diversity: an invalid synonym would not be counted, whereas it is difficult to decide how to handle *nomina dubia*.

Taxonomists often argue that species names are hypotheses and that therefore synonymy is not an issue. I disagree: although species names may be hypotheses, some are very poor hypotheses at best. For example, species names created without information about infra- and interspecific character variation are methodological mistakes, rather than rigorous hypotheses (see below *Guideline 2*), and names created without considering character variation are one of the main sources of synonyms. Most *nomina dubia* also are good examples of names that should probably not have been created, because neither the specimens on which the original descriptions were based nor the descriptions themselves can help people understand how those names apply.

In this context, the rules of the current nomenclatural codes have a somewhat surprising role: they were established to make sure that all species names will be permanently considered by taxonomists as long as they are ‘validly published’ (*International Code of Botanical Nomenclature*, ICBN, 2000) or ‘available’ (*ICZN*), and are not homonyms of earlier names. Indeed, the current codes only provide rules governing the use of names, and therefore protect all names, regardless of whether or not their creation was appropriate. Can we imagine a set of rules that would require physiologists, chemists or mathematicians always to cite articles whose experiments or equations were shown to be false or inaccurate? The current codes make taxonomy a peculiar discipline: all taxonomic work is permanent, regardless of its scientific rigour.

The 1999 edition of the *ICZN* includes an article (Article 79, *ICZN*, 1999: 89) that could help us deal with the over-abundance of existing synonymous or doubtful names: ‘An international body of zoologists... in consultation with the Commission may propose

that the Commission adopt for a major taxonomic field (or related fields) a Part of the *List of Available Names in Zoology*’. According to Article 79, species names that are not included in the *List* would be permanently suppressed. However, as pointed out by several authors (Scotland *et al.*, 2003; Vane-Wright, 2003) who commented on Godfray’s (2002) proposition that some names be permanently suppressed, no general clear-cut criteria exist to decide whether or not a name should no longer be regulated by the code. Godfray (2002) rightly pointed out that the determination of which names should be suppressed should be based on monographic revisions. However, I am afraid that even thorough revisions will not avoid intuitive and arbitrary decisions. Based on personal experience – I am currently completing a taxonomic monograph of the *Discodoris* sea slugs (Mollusca, Gastropoda, Nudibranchia, Doridina) – I certainly would not feel entitled to propose that the names I regard as synonyms or *nomina dubia* be suppressed, regardless of how many colleagues would agree with my results and decisions.

The debates concerning the suppression of existing species names help to emphasize that there needs to be a radical change in mind-set concerning the creation of new species names. It is time that taxonomists understand that creating species names is a serious responsibility, precisely because: (1) taxonomists are free to decide whether or not a set of specimens is part of a new species; and (2) species names are meant to be permanently present in the literature. In particular, we need to prevent the over-abundance of names from worsening in the future.

I propose a set of practical guidelines that should be followed for creating names in integrative taxonomy. These guidelines are based on personal taxonomic experience and on interactions with colleagues. I do not pretend that these guidelines must be followed. My primary goal is that they and alternatives be debated among taxonomists and non-taxonomist biologists on their merits in theory and in practice. I believe that these guidelines would help prevent the over-abundance of names from worsening, facilitate the integration that taxonomy needs, and ultimately produce better estimates of species diversity. These guidelines make a clear distinction between describing and naming species.

GUIDELINE 1

No new species names should be created in a given group unless a recent taxonomic revision has dealt with the totality of the names available for the group. Many synonyms are created because the absence of complete taxonomic revisions prevents taxonomists from taking all of the existing species names of a par-

particular group into account when they create a new name. This leads them to miss the name corresponding to the species that they think is 'new'. A thorough monographic revision of a taxon requires one: (1) to re-examine all type specimens available; (2) to read and examine critically the entire body of literature; and (3) to find all the species names that may have been misclassified by previous workers and that may belong to the group under study, by looking at additional type material, reading additional literature and performing phylogenetic analyses. Checklists of names or bibliographic searches, although very useful and necessary, cannot replace monographic revisions because supra-specific affinities are unfortunately often confusing. Revisions are the best way to establish a list of all the species names that belong to a particular taxon. Splitting taxonomic work into a multitude of short papers greatly reduces its rigour, and it is time the scientific community (including taxonomists) recognizes that global revisions are necessary, rigorous, and highly valuable scientific products.

GUIDELINE 2

No new species names should be created if the infra- and interspecific character variation has not been thoroughly addressed. A second major source of synonymy is the fact that the individual variation of the 'taxonomically important' characters usually is not addressed: 'A thorough knowledge of all the possible forms of individual variation is necessary whenever the taxonomist is forced to make a decision as to whether certain specimens represent a different species or individual variants.' (Mayr, Linsley & Usinger, 1953: 81) As odd as it may seem, creating species names without addressing the individual variation of characters is not restricted to the old taxonomic literature; it remains a contemporary problem. Studying the individual variation of characters is essential not only for species delineation, but also for proposing diagnostic features for species identification: diagnostic features should be present in all specimens of a species, given that individual variation is taken into account. Species names created without information about character variation should not have been created. Not addressing infra- and interspecific character variation before creating new species names is a methodological error that must stop.

GUIDELINE 3

No new species names should be created based on fewer than a certain number of specimens (a number which specialists of each group could agree upon), and never with a single specimen. Otherwise infra- and interspecific character variation cannot be thoroughly

addressed. Also, the chance of making a mistake in an anatomical description is much higher with one than with many specimens (provided they are all examined). Finally, this allows future workers to check the original description, lest potential mistakes of observation become fixed permanently in the literature. More broadly, one should not confuse the necessity of having a typological species nomenclature with taxonomic practice. Although a species name is attached to a single name-bearing type (holotype, lectotype or neotype), or possibly a set of syntypes (note that some type specimens such as paratypes and paralectotypes do not have a name-bearing function), describing species requires the examination of multiple individuals in order to address character variation. Species nomenclature may be typological, but species description should not be typological.

GUIDELINE 4

A set of specimens differing in some regard from existing species can be described with the abbreviation 'sp.' (for 'species') and not with a real species name regulated by the codes of nomenclature. This guideline helps to emphasize that integrative taxonomy gives priority to species delineation, not the creation of new names. The solution proposed here is not new. Taxonomists have been using it for years, but certainly not enough. It presents the advantage of drawing attention to morphological differences observed in a set of specimens, which is always interesting if one suspects that it may have some evolutionary significance, without having to create a permanent name and thus take the risk of potentially increasing the list of synonymous or doubtful names. This solution is particularly useful in all uncertain cases where only partial information is available or when character variation cannot be addressed (e.g. because only a few specimens are known). More broadly, describing morphodiversity does not require the creation of new names for all sets of specimens differing from known species. An author who would describe a new morphospecies and designate it by the abbreviation 'sp.' would take the risk that another author might decide to create a new name for it. However, the *Code of Ethics* of the ICZN (1999: 24) clearly states that: 'A zoologist should not publish a new name if he or she has reason to believe that another person has already recognized the same taxon and intends to establish a name for it'. This recommendation, understood in a broad sense, urges taxonomists not to create new names for unnamed morphospecies (designated by the abbreviation 'sp.') unless additional data are provided. Bibliographic searches would not be jeopardized because one can always place unnamed morphospecies in supra-specific taxa. Ultimately, this guideline implies that

future biodiversity estimates may include different categories of entities, instead of just species names governed by the codes.

GUIDELINE 5

Ideally, names should only be created for species that are supported by broad biological evidence (morphology, genealogical concordance, ecology, behaviour, etc.). Species are always hypothetical, even when they are 'broadly supported', but our level of confidence is much higher for entities supported by different kinds of data than for entities supported by only one kind. Names could surely be created for morphospecies under certain conditions. However, guidelines 2, 3 and 4 imply that names should not be created without help from non-morphological data when morphology provides limited or ambiguous information.

GUIDELINE 6

No new species names should be created if type specimens deposited in a museum collection are preserved in a way that prevents any further molecular study. This guideline will not be applicable in palaeontology. Because it is critical that morphospecies be tested via other data and approaches (see Guideline 5), type specimens (or tissues of type specimens) of the newly described species should be preserved in a way that makes DNA extraction and sequencing possible. It is important that samples be taken from the types because it prevents identification mistakes from introducing confusion. This guideline presents a drawback: formalin-preserved as well as some old alcohol-preserved specimens may not be sufficient to describe new species. However, this issue could be addressed by collecting additional new specimens or by describing the available specimens without naming them formally. This guideline also stresses that future collecting efforts should preserve material both in formalin (which eases dissections of soft parts) and in a way that allows DNA extraction. In order to avoid DNA degradation, such 'DNA-types' could be deposited in a central institution in charge of immediately extracting the DNA and storing it properly. Not all taxonomic groups need be deposited at the same institution; aliquots of DNA could even be deposited in more than one institution. For example, Meyer (2003b) suggested that gastropod experts send alcohol-preserved or frozen specimens to a single facility in charge of undertaking an 'All Snails Initiative.' Meyer proposed that this facility could sequence a few markers for all unique gastropod species or morphospecies and thus, develop a population-level tree for the group to test all known and newly described species. Such taxon-specific, centralized facilities are the most cost-

effective and technologically efficient means to handle and process DNA-types of this kind.

GUIDELINE 7

All neotypes designated from now on should be preserved in a way that allows DNA extractions and sequencing. When the name-bearing type specimen(s) of a given species has (have) been lost or destroyed (this situation is not uncommon, even for well-known species), taxonomists can designate a 'neotype' that replaces the missing type(s). The designation of neotypes is an ideal occasion to preserve name-bearing types that can be used in molecular studies, and should not be missed. Concerning the species for which types still exist but cannot be used in molecular studies, there is no real solution other than to continue to deposit voucher specimens in museums for all published sequences so that identifications can be checked and morphological features can be compared and described.

A question of interest concerns the regulation of these or other guidelines. Introducing them as rules in nomenclatural codes would entirely change the nature of the codes, because they have always refused to deal with questions that are not strictly nomenclatural. Furthermore, I do not believe that a central 'authority' should force people to practice a particular kind of taxonomy.

Instead, taxonomy needs a change in mindset. We should accept that describing morphodiversity does not require the creation of a new species name for any single set of specimens. In that regard, the review process should play an important role. Furthermore, naming a species should not be seen as a strictly individual – and somewhat selfish – enterprise, but rather as the conclusion of a long process that may involve several people who have contributed to its delineation and study from multiple perspectives.

CONCLUSION

In the present paper, I have argued that an integrative approach is the best possible future for taxonomy. Indeed, because of its complexity, life's diversity needs to be studied from multiple and complementary perspectives. Therefore, taxonomists will display a regrettable lack of foresight for the future of taxonomy if we do not integrate all of the methods that are now available to delimit species boundaries into a synthetic approach. Some workers have already adopted an integrative approach to taxonomy. However, it is time that the discipline as a whole evolves and becomes integrative.

Realising integrative taxonomy will not be easy. It will require efforts from all sides. 'Non-taxonomist'

biologists will have to acknowledge that the accomplishments of traditional morphology-based taxonomy are immense, and that morphological studies are highly valuable and necessary, and 'taxonomists' will have to accept that a radical change in mentality is needed concerning the creation of new species names in order to prevent the over-abundance of *nomina dubia* and synonyms from worsening.

I am optimistic for several reasons, however, and think that taxonomy will eventually become an integrative discipline. First, the merits of integrative approaches are now widely recognized among biologists (e.g. Wake, 2003), and integrative biology has inspired me to coin the term 'integrative taxonomy.' Second, integrative taxonomy can solve two problems that otherwise would continue to grow: the frustration of non-taxonomists with how traditional taxonomists describe species and create new species names, and the feeling shared by many taxonomists that their discipline is isolated from the rest of the life sciences. Finally, the gap in communication among specialists from different disciplines is decreasing, and more and more researchers are already convinced that delimiting species should involve different perspectives. For example, several PhD students (e.g. Hayes, 2004; Kirkendale, 2004; Malaquias & Reid, 2004) presented studies based on both morphology and phylogeography at the World Congress of Malacology, July 2004, Perth, Australia.

Whether or not biologists with diverse training, competencies and perspectives will collaborate is a question that is probably more sociological than scientific. In that regard, funding agencies will have an important role in the future of taxonomy. I personally hope that they will encourage people to think about taxonomy in a different way, for example by inviting population biologists and morphological 'taxonomists' to write joint proposals on species diversity and taxonomic revisions. An integrative approach is the best possible future for taxonomy, and the sooner this future arrives the better.

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