ORIGINAL ARTICLE

Attaching Names to Biological Species: The Use and Value of Type Specimens in Systematic Zoology and Natural History Collections

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Abstract

Biological type specimens are a particular kind of voucher specimen stored in natural history collections. Their special status and practical use are discussed in relation to the description and naming of taxonomic zoological diversity. Our current system, known as Linnaean nomenclature, is governed by the International Code of Zoological Nomenclature. The name of a species is fixed by its name-bearing type specimen, linking the scientific name of a species to the type specimen first designated for that species. The name-bearing type specimen is not necessarily a typical example of the species, while establishment of the boundaries of a species requires empirical taxonomic studies. The International Code of Zoological Nomenclature allows for the naming of new species in the absence of preserved specimens. However, photos and DNA sequences should not function as primary type material, while new species should not be described and named without deposition of at least one type specimen in a collection. Philosophically, species are individuals, spatiotemporally restricted entities. Therefore, Linnaean species names are proper names, which do not define the taxon but serve as a label, providing an ostensive definition of a species. Paratypes have no name-bearing function but, nevertheless, are highly valued specimens in natural history collections. Paratypes should be restricted to those specimens originating from the same sample as the holotype. Diagnosis of a species taxon involves establishment of a connection between a Linnaean name and determination of the boundaries of the species. A first step in this process is the choice of an appropriate species concept. It is not the examination of holotypes and paratypes that necessarily provides the best estimate of the taxonomic boundaries of a species, but this is facilitated by a set of voucher specimens known as the hypodigm. Dissatisfaction with the present nomenclatural code led some researchers to propose emendations. Other taxonomists suggested abandoning Linnaean nomenclature and proposed the alternative PhyloCode, albeit that it relegates the naming of species taxa to the traditional nomenclatural codes.

Keywords Definition · Hypodigm · International Code of Zoological Nomenclature · Name-bearer · Ostensive definition · Photographic evidence · PhyloCode · Species concepts · Taxonomy · Type specimens

Introduction

It is generally acknowledged that both taxonomy and natural history collections play a crucial role in the inventory and documentation of the biodiversity on planet Earth. As a subdiscipline of the field of systematic biology, taxonomy is involved in the discovery, documentation, and naming of species, as well as in the construction of classifications. Despite its central role in the exploration of the world's biodiversity, taxonomy suffers from an image problem and also from a crisis in resources and expertise that has come to be known as the "taxonomic impediment." These misunderstandings and the underappreciation of the science of taxonomy have to be taken into account, as well as possible countermeasures (see Sluys 2013; Kemp 2015; Wheeler 2020), to ensure wide appreciation of the central contribution of taxonomists in the inventory of the world's species and, thus, to fully value the importance of the topics discussed in the present article.

Natural history museums are repositories of specimens that were once collected and were subjects of study and that after deposition in a museum collection remain available for reexamination. Deposition of such voucher specimens in natural history collections creates an invaluable record of the evolution of life and at the same time constitutes a

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resource base that can be used for all kinds of studies that, for example, provide windows into the past; inform about present biodiversity; monitor environmental change; contribute to public health through examining the evolution of viral pathogens extracted from, for example, preserved bat specimens; analyze complex biological systems, such as reproduction; analyze geographic variation; focus on population-level diversity and evolution; and examine epigenetic change across time (see Mayr 1969; Suarez and Tsutsui 2004; Wandeler et al. 2007; Pyke and Ehrlich 2010; Ożgo and Schilthuizen 2012; Kemp 2015; Dreyer et al. 2018; Schindel and Cook 2018; Hahn et al. 2020).

Curation of collections in natural history museums applies not only to biological specimens, including fossils, deep-frozen tissues, and DNA samples, but also to sediment samples, rocks, minerals, and meteorites. Deposition of geological samples also ensures that these are accessible for reexamination and remeasurement by future workers (Planavsky et al. 2020).

From the above, it is apparent that natural history collections can be used for a plethora of studies that go far beyond the original goal for which taxonomists have always used the voucher specimens in such repositories, i.e., permanent documentation of described species diversity, thus facilitating future species identification as well as reexamination and possible taxonomic reevaluation of the material. An accidental, albeit not unimportant, effect of the vast collections of biological specimens amassed over centuries is that they harbor unexamined and unidentified specimens that upon detailed study turn out to represent new species (cf. Kemp 2015, 2017).

This article focuses on a particular kind of voucher specimen stored in natural history collections, viz., biological type specimens. There are various kinds of type specimens, such as holotype, paratype, syntype, lectotype, neotype, and hapanotype. The value and status of such type specimens depends upon the scientific context in which they are assigned a specific function, which may be nomenclatural or taxonomic.

As the International Code of Zoological Nomenclature (ICZN 1999; hereafter: the Code) takes as its starting point a book published by Carl Linnaeus in 1758, our current system is known as Linnaean nomenclature, with the type method (see below) and the binomial names for species forming two of its cornerstones. The scientific names of species consist of two terms. For example, a duck species that occurs throughout large parts of the world, the mallard, carries the Linnaean name *Anas platyrhynchos* (within a text, it is customary to write species names in italics, in accordance with a General Recommendation in the Code).

Natural history museums take great pride in their collections of type specimens, which are generally advertised in special publications and catalogues (e.g., Smith 1970; Morgan 1987; Boyko 1996; van den Hoek Ostende et al. 1997; Dekker and Quaissar 2006; LeCroy 2010). In this way they fulfil Recommendation 72.F.4 of the Code by publishing lists of one very special kind of type specimen, viz., the nomenclatural or name-bearing types, i.e., holotypes, syntypes, lectotypes, hapanotypes, and neotypes.

In this article I explain, discuss, and comment on the special status, principles, and practical use of biological type specimens in relation to both the description and naming of taxonomic biodiversity. Because zoological taxonomy and nomenclature are disciplines that are independent and somewhat different from their botanical counterparts and are governed by a separate code of nomenclature, I shall restrict myself to zoology. However, because of the overlap with the principles and practice of botanical taxonomy, I believe that much of what will be treated below shall be of interest also for workers involved with plants, algae, fungi, or prokaryotes. In what follows I will focus on current methods and practices and will not consider the historical development of the concepts of type specimen and type method and of the current Code of zoological nomenclature, as accounts on this historical background are available elsewhere (e.g., Blackwelder 1967; ICZN 1999; Witteveen 2016).

The issues concerning the correct application of the rules of the Code and those related to type specimens are complex for the uninitiated, at times even for practicing taxonomists. However, in this contribution I shall focus on the essentials and avoid, as much as possible, any specialized jargon, thus, hopefully, providing a clear exposé of the topics at stake. A glossary with definitions of technical terms is provided at the end of this paper, with the aim of removing any remaining uncertainties.

Nomenclatural Types

The Type Method

In zoological taxonomy the type method for fixing the name of a certain group of organisms, or taxon, is applied at three levels of the taxonomic hierarchy and involves three basic types: (a) a family-group name is based upon that of its *type genus*; (b) a genus-group name is based upon the name of the *type species* for that genus; (c) the name of a species is fixed by its name-bearing *type specimen*. From these three kinds of types it is only the last one that involves tangible, material objects in the form of organismal specimens housed, preferably, in natural history museums. And these tangible name-bearing specimens and the species that they provide with a name form the subject matter of the present article.

That natural history museums are proud of their collections of type specimens resides in the fact that through the application of the type method in taxonomy the scientific

name of a particular species is linked, in principle for now and in eternity, to the type specimen that was designated for that species by the taxonomist who for the first time provided a description and a name for that species. Generally, this specific name-bearing specimen is called the holotype. Thus, this holotype is the specimen to which the scientific name of the species is permanently attached. And this is the only official, formal function of the holotype, i.e., it is a nomenclatural type. All kinds of issues that may arise when taxonomists have to decide which name should be used for a particular species (e.g., which name was assigned first and, thus, should be used; what should be done in case a holotype is not available; what is the correct spelling of the name?) are regulated by the Code (ICZN 1999) and by Amendments, Declarations, and Opinions published afterwards by the International Commission on Zoological Nomenclature. Such issues need not concern us here, as our focus is on the basic principles and methods applied to nomenclatural types in taxonomy.

Since the inception of the modern Code, the name-bearing type specimen formally performs only a single function, being a nomenclatural designator of the species name. Thus, the name-bearing type specimen, despite its name, is not a typical example, a prototype, or an archetype of the species to which it belongs and to which it affixes a name. The fact that a holotype is only a name-bearer (onomatophore or nomenifer; Simpson 1961; Heise and Starr 1968, respectively) and not an exemplary taxonomic representative of a species continues to confuse even professional taxonomists up to the present day. For example, Bahia and Schrödl (2018, p. 6), in an important revisionary taxonomic study of Brazilian polyclad flatworms, opined that examination of type material forms "a relevant way … to check a taxon hypothesis." In his epoch-making book *Phylogenetics*, in which he promoted the philosophy and method of phylogenetic systematics and also outlined taxonomic principles and procedures, Wiley (1981, p. 390) characterized type specimen(s) as "A single specimen or a series of specimens that comprise the type of a taxon of the species category or below." Even the great evolutionary systematist Ernst Mayr (1997, p. 148) wrote that, "The type of a species is a specimen," although this was in a popular book on the history and philosophy of biology, while he had expressed the correct notion about nomenifers or type specimens in many other publications (e.g., Mayr 1983, 1989). Four more examples will suffice to illustrate that the incorrect conception of a type specimen as being a paradigm of the species, as opposed to its correct function as a nomenclatural device, continues to bedevil not only philosophers of science but also professional systematists.

In a paper authored by no less than fifty taxonomists from all over the world, Amorim et al. (2016, p. 124) considered types to be the "timeless standards for species delimitation."

Philosopher of science Lorraine Daston wrote that, "The type specimen is not just the bearer of the species name; it is in principle the original of the species description," and that "botanists focus on one individual member, the holotype, side by side with its description, as the standard against which other specimens are measured" (Daston 2004, pp. 179, 181, respectively). A remarkable example concerns a publication by the International Commission on Zoological Nomenclature in the form of Declaration 45, which in its explanatory note states that, "Whenever feasible, new species-group taxa should be established on the basis of at least one preserved type specimen" (ICZN 2017, p. 96). In a similar vein, the Code itself obfuscates matters when it states in Article 72.1.1 "type series: all the specimens on which the author established a nominal species-group taxon" (ICZN 1999, p. 75).

In all of these examples provided above mention is made of a taxon, the delimitation of which would be effectuated by the type specimen. According to the Code, a taxon is "A taxonomic unit, whether named or not: i.e. a population, or group of populations of organisms which are usually inferred to be phylogenetically related and which have characters in common which differentiate … the unit… from other such units" (ICZN 1999, p. 118). This implies that the delimitation of a taxon, e.g., establishing the boundaries of a species, requires empirical taxonomic studies, the results of which may be tested and refined by subsequent research but cannot be prescribed by the Code. Thus, the Code merely specifies a set of rules for scientific nomenclature and does not formulate taxonomic concepts nor regulate methods for establishing the boundaries of taxa. In other words, the Code is a nomenclatural code and not a code of taxonomy, the latter being nonexistent and philosophically undesirable. Taxonomy is an analytical, hypothesis-driven science (Sluys 2013) that needs to run its own course and should not be put into the straightjacket of a code prescribing operational rules and procedures. Through taxonomic research it is established which species exist, how these can be recognized, and how they are differentiated from one another. In contrast to nomenclature, in taxonomic research statements are made with biologically relevant content.

The difference between nomenclature and taxonomy surfaces also in the two following situations. As a result of a systematic biological study of a group of organisms, frequently involving an analysis that results in a phylogenetic tree expressing the genealogical relationships between the operational units at the tips of the tree, a researcher may recognize a great number of taxa. However, for several reasons the same researcher may decide to coin names for only a few of these taxa and to make reference to the other, non-named taxa only in an informal way. Thus, one may scientifically distinguish a taxon but refrain from coining a name for it that fulfils the requirements of the Code; by definition (see

above) a taxon is either a named or an unnamed group of organisms.

The other situation in which the difference between taxonomy and nomenclature becomes apparent emerges from the fact that the same Linnaean scientific name may be used for differently circumscribed taxa (Costello 2020; Minelli 2020). As our knowledge on biodiversity increases and changes as a result of systematic biological studies, phylogenetic trees and the taxonomic classifications based on these trees change as well. As a consequence, our perspectives on the content and delimitation of taxa change over time. This not only concerns higher level taxa such as genera and families but also holds true at the species level. But as a consequence of the rules of zoological nomenclature, the Linnaean name remains attached to a particular taxon, irrespective of its taxonomic content and extension. Hence, the application of a name may change over time, thus illustrating the divorce between nomenclature and taxonomy. From this perspective, Linnaean taxon names may become unstable (Mayr 1969; Minelli 2019) and thus seem to fail the goals set by the Code, viz., "stability and universality in the scientific names of animals and to ensure that the name of each taxon is unique and distinct" (ICZN 1999, p. 2). However, in another way stability in nomenclature is actually achieved because the Linnaean name is affixed, in principle indefinitely, to a certain taxon. The particular name that should be used in reference to a taxon is regulated by the principle of priority, which thus effectuates nomenclatural stability.

The principle of priority establishes that when two or more names have independently been created for the same taxon, in general the oldest one should be used. This oldest name, which was published first, then becomes known as the valid name or senior synonym, while the younger names are assigned the status of junior synonyms, the usage of which is suppressed.

The type method promotes nomenclatural stability on the species level also when the name-bearing type specimen, such as the holotype, is deposited in the collections of a natural history museum. This practice ensures that in cases of doubt about the usage of a Linnaean name for a particular species, a taxonomist can check the ultimate standard of reference, i.e., the type specimen to which the name is permanently attached. Therefore, it makes perfect sense that the current Code requires workers to explicitly designate type specimens, but it makes no sense that it does not rule at the same time that these types be deposited in a collection (ICZN 1999, Article 16.4, p. 20). In its current version the Code merely rules in Article 16.4.2 that in the original publication a worker should express a "statement of intent" that type specimens will be deposited in a specified collection and advises in Recommendation 16C that such important standards of nomenclatural reference should be deposited in institutions with proper facilities. Both Article 16.4.2 and Recommendation 16C boil down to the fact that when in the end no type specimens of a new species are deposited in a museum collection the new name, nevertheless, is available for use, albeit that absence of a tangible specimen prevents future workers from performing the ultimate check on the correct usage of the name (recommendations in the Code are merely advisory, nonmandatory statements).

Photographic Evidence

In line with Article 16.4.2. and Recommendation 16C, the Code has always tolerated and sanctioned the naming of new species in the absence of preserved specimens, as it only specifies mandatory rules as well as recommendations in case such material specimens are available (Dubois 2017a); however, it excludes naming hypothetical concepts (ICZN 1999, Article 1.3.1). This opens up the possibility of basing Linnaean species names on non-tangible objects, such as photographs, drawings, or nucleic acid sequences. In recent literature there has been a great deal of discussion whether photography-based type specimens and nomenclature are appropriate, adequate, and inevitable or violate the spirit of the Code (cf. Dubois 2017a and references therein). For a proper understanding it is important to make a distinction between what is presently allowed under the current Code and what would be desirable from a scientific perspective.

Species have been named on the basis of a photograph-based description and in the absence of preserved specimens because the type specimen escaped or the authors refrained from collecting and preserving any specimens from a population on the verge of extinction. In several of such cases the actual animal in the photo was considered to be the holotype, albeit no longer available. This is in accordance with Articles 72.5.6 and 73.1.4 of the Code. In the case of a new species of land iguana from the Galapagos islands, *Conolophus marthae*, a tracking device was implanted under the skin of the holotype before its release (Gentile and Snell 2009). Thus, in principle, it might be possible to retrieve the specimen after its death and deposit it in a collection. But this represents an unusual situation as in most cases in which photos and/or videos form the basis of the description and illustrate the holotype, as in the land iguana, the specimen will be irretrievably lost for science. When in future studies absence of a material type specimen causes taxonomic and nomenclatural problems, because the actual name-bearer cannot be reexamined, taxonomists' last resort is the designation of a neotype, i.e., a new type. A neotype may be selected from an already available series of specimens, such as the paratypes, but may be chosen also from a set of newly collected animals, as long as there is a high degree of likelihood that the neotype belongs to the same species as the original type specimen.

Some workers have suggested going one step further by proposing that in the absence of material type specimens the images or videos used in the description of a new species become the actual primary name-bearers (Garraffoni and Freitas 2017). The plea of these workers for revision of the current Code mainly concerned soft-bodied meiofaunal organisms. These animals generally live in the interstitial spaces of benthic sediments, such as beaches, and are so small that during the identification process the type material is lost. Apart from the fact that the short Letter of Garraffoni and Freitas (2017) suffered from the two misconceptions that (a) the Code forbids the naming of species without preserved specimens having been deposited in a museum, and (b) that there exists a taxonomic code, their publication raises four issues. One concerns the question whether the Code should be modified to facilitate the nomenclatural procedures for a taxonomically poorly delimited group such as the meiofauna, which is usually loosely defined as comprising those animals that will pass through a 1 mm mesh but will be retained by a 45 µm mesh. Secondly, instead of adapting the Code for a particular group of organisms to the exclusion of all others, a better option may be that the Code implement a procedure for individual workers to call on a dedicated international committee, installed by the International Commission on Zoological Nomenclature, to evaluate and, subsequently, rule on individual cases. It may well be the case that preservation of type specimens may not only be difficult or impossible for meiofaunal organisms but also for other soft-bodied animals, such as comb jellies or ctenophores. A dedicated committee, working with the principles of a modified Code, could decide that for such animals in particular cases photographic material functions as the name-bearer. However, before modifying, or not, the Code two related questions need to be answered, viz., whether it is good scientific practice (a) to provide only photographic evidence, and (b) to refrain from depositing at least one holotype specimen in a museum collection.

In these days of high-quality digital photography with its numerous possibilities, e.g., making 3D images, one may wonder whether the day has not come that photographs replace material specimens. Similarly, one may wonder why a large number of taxonomists have argued against images as type specimens, as well as against the naming of species without deposition of at least one specimen, the holotype, in a research collection (cf. Ceríaco et al. 2016; Amorim et al. 2016; Rogers et al. 2017); as discussed above, the present Code allows for the second possibility.

The major problems with photos, or images in general, are of course that (1) they are merely representations of reality, derivatives of the actual organism, (2) their content is selected by the original author and thus influenced by subjectivity, and (3) they can easily be modified or misinterpreted (cf. Dubois 2017a; Krell and Marshall 2017, and

references therein). That images are selected representations of reality is obvious from scientific illustrations, which usually include a component of interpretation. But this interpretation by the original authors may have been incorrect, which can be resolved only when future workers have access to the type specimen. For example, in planarian flatworms one needs to make complex three-dimensional reconstructions of the copulatory apparatus by examining numerous histological sections; the reconstructions are expressed in two-dimensional drawings. It may happen that upon reexamination of the type material such interpretations of the structure of the copulatory complex appear to be incorrect. Such was the case in the marine planarian *Synsiphonium ernesti*, which upon reexamination of the type material, as well as additional specimens, was even removed from its original genus to its present genus (Sluys 1989).

Although photos are usually presumed to form objective documentation, they may equally suffer from misinterpretation, not only by future workers but even by the original authors. Photographs subjectively document parts of the morphology of a type specimen, with the authors selectively adding labels to point out the various anatomical structures. However, incorrect structures may have been discerned and labelled, a situation that will become apparent only when there is a possibility of reexamining the type specimen.

Apart from the fact that photos present a selection of the characteristics of a specimen, while in future studies the non-documented data may become important, it is generally impossible to verify the authenticity of an image because its digital photographic format has not been deposited (Aguiar et al. 2017). Evidently, modification of photographs has always been possible, even in the old days when with the help of a special set of retouching paint black-and-white photographic prints could be altered. Clearly, modification of digital images is almost unlimited. As counterargument against objections to use photographs either as the sole basis of documentation in the absence of tangible type specimens or even as primary name-bearers, it has been noted that specimens too can be manipulated. There are several well-documented cases in which feathers of birds or the coat of monkeys were dyed, whereafter photos were used to describe new species (Krell and Marshall 2017 and references therein). Although these cases were brought to light and resolved through expert knowledge, it is clear that when type specimens had been deposited in a collection any knowledgeable taxonomist would have been able to discover this malpractice.

In view of the importance of nucleic acid sequences (DNA, RNA) as a data source in many modern systematic-biological studies, one might be tempted (a) to identify and name new species solely on the basis of differences in molecular sequences and only preserve molecular samples, either as genomic DNA or in other form (blood, tissues), and

(b) to deposit as holotype preserved genomic DNA. In point of fact, both of these routes have been taken in contemporary systematic studies. However, nucleic acid sequences suffer from many of the same problems that adhere to photographs as scientific evidence of type specimens. DNA and RNA sequences must be interpreted within the context of a particular study and in this respect do not differ from other kinds of data. Furthermore, nucleic acid sequences do not provide information on anatomical structures or any other kind of organismal features. In conclusion, photos and DNA sequences should preferably not function as primary type material and new species should not be described and named without deposition of at least one type specimen in a natural history collection.

Apart from the reasons detailed above, Recommendation 73B of the Code has been used as another argument against the use of photographs as the only basis for the description and naming of species (Amorim et al. 2016). This Recommendation states that, "An author should designate as holotype a specimen actually studied by him or her, not a specimen known to the author only from descriptions or illustrations in the literature" (ICZN 1999, p. 80). But in several of the cases criticized by Amorim et al. (2016) the authors actually studied the holotype, although they did not preserve the specimen because it escaped, for example, and subsequently documented the specimen by means of photographs. Thus, in such cases Recommendation 73B does not apply. It does apply to cases in which the authors did not make observations on the actual specimen but only examined images. An example is the elevation of a geographic form of the polyclad flatworm *Leptoplana tremellaris* to the full species *Leptoplana mediterranea*. This special form from the Mediterranean Sea was first suggested by Lang (1884) but the name *mediterranea* was only proposed by Bock (1913) after having studied Lang's account and illustrations. Although type specimens were unavailable, Gammoudi et al. (2012) elevated the form *mediterranea* to species level and used Bock's name for it as the specific epithet. Although this goes against Recommendation 73B, it does not invalidate their nomenclatural act as recommendations of the Code are nonbinding, advisory statements.

As a result of these discussions on non-preserved type specimens, the International Commission on Zoological Nomenclature has recently issued a Declaration specifying four additional Recommendations (73 G–J) in an attempt to promote good taxonomic practice. A Declaration is a provisional amendment of the Code. It is noteworthy that these Recommendations, among others, do not concern nomenclature as such but indeed try to stimulate proper taxonomic procedures that will ease the resolution of nomenclatural problems. In short, Recommendations formulated in this Declaration 45 (ICZN 2017) state that when species taxa are named, the Linnaean name should be based on at least one preserved type specimen, but that, nevertheless, photo-based descriptions and names are Code-compliant but are discouraged. Apart from the fact that these Recommendations are nonbinding, they additionally do not guarantee that the preserved holotype specimen will be available for future workers, as the Code merely requires a statement of intent that the type material will be deposited in a collection accessible by researchers (see above).

Ostensive Definitions

It is perhaps counterintuitive that when our systematic-biological knowledge about the evolutionary relationships between species increases, nomenclature remains stable, due to application of the principle of priority. One would expect that changes in our systematic and taxonomic concepts are reflected in nomenclatural changes. That this is not the case is the result of two philosophical theses, viz., that species should be seen as representing individuals, and that species names are defined by ostension.

Starting in the late 1960s, the view has crystalized among philosophers of science and systematic biologists that species taxa are not classes composed of members sharing a particular defining property, but philosophically should be considered to constitute individuals. Two major arguments have been advanced in support of this claim. First, and foremost, is the notion that species are historical, genealogical entities that have evolved and are restricted to both a particular period of time and a certain region of the world. In other words, species are spatiotemporally restricted entities, in contrast to classes, which are unrestricted. Species, being individuals, can go extinct, whereas classes cannot. A second argument in favor of the individuality thesis is that species form cohesive entities because their members experience processes, such as geneflow and homeostasis, while they are exposed also to common selective forces. Such cohesion or evolutionary unity does not apply to classes. For further explication of the individuality thesis and for additional arguments, as well as counterarguments, I refer to Rosenberg (1985), Ghiselin (1997), Ereshefsky (2001), Brogaard (2004), and Lowe (2014).

By extension of the thesis that species are individuals, it is immediately clear that their Linnaean names are proper names, which do not define the taxon by listing a series of properties but merely serve as a label by means of which we indicate a particular species. In the parlance of philosophers, the name is an ostensive definition, through which we point to an individual of a species taxon carrying that name (Ghiselin 1997; Ereshefsky 2001). One could say that with the help of an ostensive definition, i.e., the Linnaean name, the species is baptized.

Paratypes and Other Material

Thus far I have discussed nomenclatural type specimens and issues related to such material. Name-bearing specimens concern holotypes, syntypes, lectotypes, neotypes, and hapanotypes. In their catalogues of type specimens, natural history museums frequently also document other so-called "type" specimens in their collections, in particular paratypes (cf. Smith 1970; Morgan 1987; Boyko 1996; van den Hoek Ostende et al. 1997; Dekker and Quaissar 2006; LeCroy 2010), although these have no name-bearing function. Usually, paratypes include all the remaining material that was examined by the author(s) of a new species, after a holotype has been selected, and that were designated as such.

The popularity of paratypes among taxonomists and museum curators is partly due to the fact that this material is generally considered to be a kind of duplicate(s) of the holotype (Blackwelder 1967). That is one of the reasons that frequently several paratypes are deposited in other collections than the holotype. In this way, researchers may be able to study paratypes when they are unable to examine the holotype, for one reason or the other. In case the holotype is lost, a neotype may be selected from among the series of paratype specimens (Article 72.4.5 and Recommendation 75A of the Code), which may be another reason for their popularity among collection managers and the generally acknowledged importance of paratypes.

It is good practice among curators of natural history collections to provide holotypes (and also syntypes, lectotypes, and neotypes) with a label—usually red—indicating their taxonomic importance, thus fulfilling Recommendations 72D and 73A of the Code. In a similar vein, Recommendation 73D of the Code suggests clearly labelling the paratypes, so that these can always be identified as forming part of the original series of specimens examined by the author(s). Some collection managers use red labels for paratypes, others use yellow, green, or pale blue labels.

Generally, when zoologists describe a new species, they select a holotype and relegate all remaining specimens to paratypes. This may result in the situation that the paratypes form a heterogeneous group of specimens, in that these may come from another sample than the holotype or even from several other samples, obtained at different locations and collected at different periods of time. I have always considered this to be an undesirable procedure and have adopted the strategy to restrict type material to those specimens originating from the same sample as the holotype, thus having been collected at the same site and at the same time. Specimens that were used in the description of the new species but formed part of other sample(s) I ranked under headings such as "Other material examined,"

thus expressly excluding these specimens from the type series, in accordance with Article 72.4.6 and Recommendation 72B of the Code. The reasons for this are as follows.

As mentioned above, if a holotype is lost, a neotype may be selected from the paratypes. But in some cases the paratypes may comprise such a heterogeneous assemblage of specimens that the particular paratype selected, i.e., the neotype, (a) does not belong to the same species as the holotype, and/or (b) does not come from the same locality as the holotype. One may wonder whether a competent taxonomist would make such a major error as choosing a specimen as neotype that does not belong to the same species as the lost holotype. But, as science is a basically human enterprise, errors cannot be excluded.

The distinct possibility of paratypes not belonging to the same population and species as the holotype can be graphically illustrated. In natural populations of organisms, quantitative genetic variation (for example, wing length in birds, number of bristles on the abdomen of flies) usually fits a normal distribution or curve. This becomes apparent when the frequencies in which features occur in a population are plotted against the particular character states recognized by the taxonomist (e.g., number of bristles). Often, the frequency distributions of natural populations show overlap. This is here illustrated for two theoretical populations, representing two different species (A and B) that occur at geographically nonoverlapping localities (X and Y) (Fig. 1). The holotype sits at the left tail of the curve, as it may well be an atypical specimen (see below). As paratypes the taxonomist included specimens from a different sample, collected at locality Y, and presumed that these specimens would fall within the bell-shaped curve of species A. Unfortunately, these presumed paratypes of species A concerned animals of species B that sit on the left side of the normal distribution curve of the latter. It is clear that the probability of such an error is greatly reduced when holotype and paratypes come from exactly the same sample.

When the neotype was collected from a different locality than the lost holotype, then the original type locality
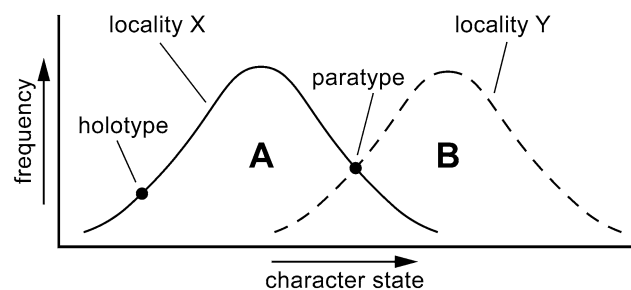
Fig. 1 Frequency distribution of character states in two populations of species A and B, distributed at nonoverlapping geographic sites X and Y, respectively. Position of holotype and paratype indicated

becomes obsolete and the place of origin of the neotype becomes the new type locality, according to Article 76.3 of the Code. However, taxonomically this is counterintuitive and undesirable as at one moment the type locality of a species is locality A, whereas at another moment the type locality of the same species is locality B. Thus, regulations of the Code cause the type locality of a species to be a variable geographic datapoint. However, subjects such as the type locality of a species concern taxonomic issues that should not be infringed upon by a nomenclatural code. The only argument that could be levelled against this interpretation is that the Code defines type locality merely as the place of collection of the name-bearing type. However, in my experience this is rarely the interpretation used by practicing taxonomists, who usually consider the type locality to be the place of the *population* from which the type was collected. Therefore, specimens collected at the type locality, at the time of description of the species or afterwards, are called topotypes. These specimens have no nomenclatural function, but topotypes serve a taxonomic purpose as they represent a population sample illustrating the range of morphological variation.

That the Code allows paratypes to be a heterogeneous set of specimens (see above) has another curious effect in regard to type localities. In case an author has not designated a holotype and thus, by definition, not paratypes either, the type series consists of a number of so-called syntypes, which collectively form the name-bearing type. But when the syntypes were collected from two or more localities, the Code stipulates that the type locality then encompasses all of these sampling sites (Article 73.2.3). This may have as effect, for example, that the type locality of a species comprises sites located in Denmark, Belgium, Germany, and Bulgaria.

Diagnosing Species

Mnemonic Names

As has been detailed above, the Linnaean names of species are proper names that have no semantic meaning, while type specimens achieve allocation of the name through ostensive definition. Therefore, the Code is an ostensional nomenclatural system (Dubois 2017b). "However language changes, or taxonomic groups get shuffled, when anyone sees an animal and says 'that is an aardvark [*Orycteropus afer*]', the true meaning is: 'that is the same kind of animal as the aardvark [*O. afer*] holotype'" (Ashby 2017, p. 280; Linnaean names added). Although species names are merely labels, without any empirical, biological content, it is good practice among taxonomists to devise names that convey some information about the new species. In particular this applies to the second part of the binomial name of a species, i.e., the specific

epithet. But when the new species also represents a new genus, the generic name may be constructed in such a way that it references certain features of its component species. Generally, the name refers to morphological or anatomical characters, or to the geographical range of a species. In this way, Linnaean names function as mnemonic devices, quickly reminding the taxonomist of its salient features. In the scientific publication the derivation of the name is specified in a particular paragraph on etymology.

Evidently, there are innumerable examples of species names pointing to peculiar biological features. I shall only give one example from my own work on planarian flatworms. In 1988 I described a new species of marine triclad flatworm that possesses a highly pointed penis papilla, as compared with congeneric species, for which I coined the specific epithet *acuminata*, "taper-pointed." At the same time, I created a new genus to which I assigned this new species *acuminata*, as well as several others. Members of this new genus have a strongly muscular penis papilla, and, therefore, I named it *Obrimoposthia*, derived from the Greek *obrimos*, "strong" and *posthe*, "penis" (Sluys and Ball 1988; Sluys 1989).

In a way, this practice of coining mnemonic names harks back to the pre-Linnaean period when species names were polynomial, i.e., consisted of three or four or even more words detailing the characteristics of the species. For example, in the 17th century the name of the honeybee was *Apis pubscens, thorace subgriseo, abdomino fusco, pedibus posticis glabris utrinque marginae ciliatis*, literally meaning "furry bee, greyish thorax, brownish abdomen, hind legs smooth with hair on both sides" (Ohl 2018).

Although the names may thus have a useful mnemonic function, the fact remains that currently they formally do not have any empirical connotation. As type specimens merely fix the reference to a species name but do not define or diagnose the species taxon, taxonomists have to face the two problems of (a) establishing a connection between the name and the taxon, and (b) determining the sense, extension, or boundaries of that species taxon. This does not concern only the species newly described by an author but applies also to already known species when the taxonomist has to evaluate which of the already available species names should be used for a series of specimens collected at a particular site. These two problems are tackled with specific taxonomic operations and procedures.

Species Concept

The first step in these taxonomic operationalizations is the choice of an appropriate species concept. From about 30 available concepts (Zink 1997; Zachos 2016) the taxonomist has to select that species concept that fulfils the needs of his or her research program (Sluys and Hazevoet 1999; Conix

2019) and, subsequently, explicitly document which species notion is adopted and for what reasons. It has been argued that in a taxonomic context the preferred species concept should be one of the so-called taxic concepts, i.e., a species concept that relates to observable characters of animals (Sluys and Hazevoet 1999). The inevitable pluralism in species concepts (Sluys and Hazevoet 1999) may lead some workers to despair when they cannot foresee a consensus and lament that such pluralism may result in several, equally valid biological classifications (e.g. Minelli 2020). However, this assessment is overly pessimistic and does not take into account that presently a conceptual agreement is emerging among biologists in which species are viewed as independently evolving metapopulation lineages. This notion is known as the General Lineage Species Concept, which subsumes other concepts in that the latter are considered to be recognition criteria instead of concepts (de Queiroz 1998). These various recognition criteria are used as different lines of evidence to delineate independently evolving lineages, i.e., species (de Queiroz 2007; Frankham et al. 2012). In the present context it suffices to realize that in one way or another taxonomists operationalize their preferred species concept in the description of a new species or during the identification of a series of specimens, that is, during the process of species recognition.

Species Recognition

A misconception that remains pervasive up to the present day is that holotype and paratype specimens provide the ultimate characters for species recognition. For example, Bahia and Schrödl (2018, p. 6) wrote that examination of type material forms "a relevant way for contemporary and future researchers to check a taxon hypothesis," while Amorim et al. (2016, p. 124) considered types as "the timeless standards for species delimitation." In a similar vein it still happens that in their account on a new species authors focus on the description of the holotype and pay only scant attention to the paratypes and other available material. However, as we have seen, the primary function of a holotype is to attach a name to a zoological entity; it is not a paradigm representative of a species, exhibiting an accurate set of its characters. As Mayr (1969, p. 368) already wrote: "Description of a new species is based on the entire material available to the zoologist, including the type-specimen. It is *not* the function of the type to serve as the exclusive or primary base of the description" (italics in original). Apart from the nomenclatural aspect, the holotype merely being a name-bearer, it may be a completely atypical member of its species, falling in one of the tails of the normal distribution curve, and the same may be true of the paratypes (Fig. 1). Therefore, it is not the examination of holotypes and paratypes that necessarily provides the best insight and estimate of the boundaries of a

particular species taxon. It may well be that proper delimitation of a species is much better facilitated by the characteristics of specimens that were either not included in the type series by the original author (e.g., in the form of "Other material examined," see above) or became available later. During the process of taxonomic comparison, evaluation, and judgement, "A unique original specimen on which a species was first based has no more authority or weight for forming a valid concept of that species than has any one of a hundred specimens subsequently referred to that species and is no better as a standard of comparison" (Simpson 1980, pp. 162–3). Thus, during this taxonomic procedure the taxonomist has to take into account not only specimens referred to a species by its original describer, but also specimens that became available afterwards as a result of ongoing taxonomic studies. This set of voucher specimens, in principle all deposited in natural history collections, forms for a taxonomist the so-called hypodigm of that species (Simpson 1980), which is defined as follows:

> The hypodigm of a given taxonomist at a given time and for a given taxon consists of all the specimens personally known to him at that time, considered by him to be unequivocal members of the taxon, and used collectively as the sample on which his inferences as to the population are based (Simpson 1961, p. 185; in this quotation the reader is invited to replace "taxon" with "species," and "him/his" with a gender-neutral substitute).

That a holotype may not be the best voucher specimen from the hypodigm to be used in comparative taxonomic studies is obvious from cases in which certain features of this specimen are poorly developed or even absent. For example, in 1989 I described a new species of marine triclad, *Oregoniplana pantherina*, based on a series of histological sections of a specimen prepared by a taxonomist in the 1930s and on the notes and sketches left by this worker (Sluys 1989). Unfortunately, the glass slides with sections of the copulatory apparatus of this holotype were, and remain, missing. For this taxonomically important component of the anatomy I had to rely on the previously produced and not very detailed sketches. Many years later new specimens were collected that, subsequently, yielded perfect series of histological sections, which enabled us to provide a much more detailed account (Li et al. 2019). Evidently, in future taxonomic studies the latter material should play a much more prominent role than the holotype. Nevertheless, a holotype always belongs to the hypodigm of its species and falls within the range of variation of that species. Therefore, it is incorrect to claim that "type specimens do not help to define or reconstruct species" (Witteveen 2018, p. 457). Since type specimens are part of the hypodigm they may help in delimiting the boundaries of a species taxon, even

though sometimes they are not the best specimens for that purpose (see above).

As a result of ongoing taxonomic studies, specimens may become parts of the hypodigm or they may be removed from the hypodigm, which thus may be "subject to frequent change" (Simpson 1980, p. 162). As a consequence, "No one can ever guarantee that two specimens will always be placed in one hypodigm" (Simpson 1980, p. 163). That is precisely the reason that there can be only one name-bearing type as this will belong to only one species, irrespective of taxonomists' success in establishing the boundaries of that taxon, i.e., precisely diagnosing the species.

As amply discussed above, the Code provides no definition or diagnosis of species taxa as it is only concerned with the naming of species. Nevertheless, the Code requires that every new name is accompanied by a description or definition in which the characters are described that differentiate the new taxon from the already known taxa (Article 13.1.1). The Code recommends that such an account should include a diagnosis, that is, a summary of the differentiating characters (Recommendation 13A). It is indeed good practice among taxonomists to provide such a summary under the heading "Diagnosis." And in future taxonomic studies, generally, such diagnoses are consulted in order to get a quick overview of the differentiating features. However, this taxonomic function of a diagnosis is merely a fortunate side effect, as the only formal nomenclatural role of such diagnoses is to make the new names available, in the sense of the Code, and to ensure that these are based on real, non-hypothetical specimens (Dubois 2007, 2017b). This is a logical consequence of the fact that there is only a nomenclatural Code and no taxonomic code (see above).

Post-Linnaean Nomenclature

Over the years a good number of taxonomists have expressed their dissatisfaction with the current Code. These scholars and their respective sentiments can be categorized into two classes. One class is formed by taxonomists who unearth numerous uncertainties and inconsistencies in the principles, rules, and terminology of the Code and, therefore, propose to emend it. The other class comprises workers who have more basic, philosophical objections to the Code and argue that it falls short of achieving name stability and that it is based on outdated Linnaean, basically Aristotelian, principles.

A group of scholars belonging to the first class have pooled their efforts and recently published a large document specifying the so-called Linz Zoocode (Linz is the city in Austria where the group convened; Dubois et al. 2019). The document provides new text proposals for numerous articles and recommendations of the Code, with the aim of eventually incorporating these suggestions into a next version of

the zoological Code. In addition, Dubois et al. (2019) sketch the background information leading to the new text proposals. Despite their considerable criticism of the current Code, it is clear that these workers are of the opinion that Linnaean nomenclature is to be preferred.

Such is not the case with taxonomists in the second class, who propose to fully abandon Linnaean, typological nomenclature as it would not be compatible with our current evolutionary, non-typological, biological paradigm. In their perspective, names of groups of organisms, i.e., taxa, should be defined in relation to their position on a phylogenetic tree. The philosophy, principles, and methods of phylogenetic systematics, or cladistics, have made headway since the late 1960s and have pervaded and completely overturned the field of systematic biology (cf. Wiley 1981; Ax 1984; Wägele 2001; Wiesemüller et al. 2003; Schuh and Brower 2009; Wheeler 2012). Nomenclature is the last bastion of traditional systematic biology that has not yet crumbled under this phylogenetic avalanche. However, whether this is due to superiority of the Linnaean system or to mere stubbornness of its adherents is at this moment still undecided. Nevertheless, after 20 years of rather vehement discussions on the pros and cons of such phylogenetic nomenclature, this movement has recently culminated in the publication of the "International Code of Phylogenetic Nomenclature (PhyloCode)" as well as an accompanying book (de Queiroz and Cantino 2020; de Queiroz et al. 2020).

In the present context it serves no purpose to review the extensive literature on the pros and cons of phylogenetic nomenclature, particularly because the PhyloCode does not apply to species names. Draft versions of the PhyloCode still expressed the intention to also govern the names of species (e.g., PhyloCode version April 8, 2000). However, over the years it proved impossible to reach a consensus on how to deal with species names. Under the PhyloCode, all names are uninomial, in agreement with Mayr's (1969, p. 346) prediction that "there is little doubt that taxonomists will have to adopt some uninomial system sooner or later." Therefore, one of the early proposals of phylocodists involved putting a hyphen between the genus name and the specific epithet, thus creating a uninomial species name, e.g., *Anas-platyrhynchos.* Although Mayr (1969, p. 344) already wrote that, "Increasingly often the question is … asked whether the entire system of binomial nomenclature has not outlived its usefulness," it is the only available system for naming species taxa up to the present day. With respect to species names, a basic problem concerns the fact that PhyloCode names are tied to monophyletic groups or clades. And monophyly is precisely a notion that does not apply well to species taxa (Sluys 1991; Sluys and Hazevoet 1999). For these reasons the PhyloCode (de Queiroz and Cantino 2020) relegates the naming of species taxa to the traditional nomenclatural codes. Although through this exception incompatibilities

between PhyloCode names and Linnaean species names are evaded, this is not the case with names assigned to the same monophyletic groups recognized by both phylocodists and Linnaean taxonomists. In that respect, the existence of two nomenclatural codes governing zoological nomenclature may cause confusion (Sluys et al. 2004).

Glossary

Binomial name	A species name composed of two words, the generic part, beginning with an upper-case letter, and the specific part or epithet; for example, *Homo sapiens*
Character	Any observable attribute or feature that can have more than one form or expression in different organisms
Character state	One of the various conditions of a character
Clade	Any presumed monophyletic taxon or group of taxa
Cladistic, cladistics, cladism	A method analyzing evolutionary relationships between taxa through grouping by synapomorphies and by classifying taxa solely on the basis of their recency of common ancestry
Diagnostic	Refers to characters that allow recognition and identification of a taxon
Hapanotype	A special name-bearing type comprising one or more preparations consisting of directly related individuals at different stages of their life cycle; usually concerning protists
Holotype	The unique specimen designated to fix the Linnaean name of a species, a name-bearer
Hypodigm	All the specimens known and available to a taxonomist and considered to be unequivocal members of a species, and used collectively as the sample on which his or her taxonomic inferences are based
Lectotype	A representative specimen specimen designated from among a series of syntypes to serve as unique name-bearer
Linnaean name	A Latin or latinized name for a taxon designed and assigned according to the traditional nomenclatural codes, based on principles developed by Carl Linnaeus and elaborated by later workers
Monophyletic	A taxon or group of taxa all members of which have a common ancestor, including all descendants of that ancestor
Morphology	The study of the construction, shape, and appearance of the body of organisms, based on the recognition of characters related to external features or to the internal anatomy
Name-bearing type	The type genus, type species, holotype, lectotype, series of syntypes, or neotype, which provide an objective standard for the application of a scientific, Linnaean name
Neotype	A single specimen designated as name-bearing type when holotype, lectotype, or syntypes have been lost or destroyed
Nomenifer	A name-bearing type
Onomatophore	A name-bearing type
Ostensive definition	In general, connects a term to that to which it refers by "pointing" at it or one of its elements; in nomenclature, allocates and attaches the name of a taxon through pointing at one of its members, for example one of its constituent individuals in case of a species
Paralectotype	Each specimen of a former syntype series remaining after the designation of a lectotype
Paratype	Each specimen of a type series other than the holotype
Phylogenetic	Referring to evolutionary relationships based on a cladistic analysis

Priority	The rule in nomenclature that the Linnaean name first applied to a taxon is the valid name
Specific epithet	The second name in a binomial name
Synapomorphy	A derived or apomorphic character shared by two or more taxa, defining a group of taxa and thus indicating their common ancestry
Syntype	Each specimen from a type series from which neither a holotype nor a lectotype has been designated, collectively constituting the name-bearing type
Systematic, systematics	Recognizing taxa, determining the hierarchical relationships among taxa (usually on the basis of a phylogenetic, cladistic analysis) and analyzing their evolution, (historical) biogeography, and taxic diversity
Taxon (plural: Taxa)	Any definable group of organisms, whether named or not
Taxonomy	Subdiscipline of the field of systematic biology involved in the discovery, documentation, and naming of species, as well as in the construction of classifications
Topotype	A specimen collected at the type locality of a species and believed to belong to that species
Type series	All the specimens on which an author established a nominal species-group name
Type specimen(s)	A representative specimen term referring to holotype, lectotype, neotype, or any of the syntypes; also used generally for any specimen of the type series
Voucher specimen	A representative specimen retained as reference regarding the identity of the material studied

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