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The unappreciated, fundamentally analytical nature of taxonomy and the implications for the inventory of biodiversity

Ronald Sluys

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Abstract Several ways have been suggested to improve the poor status of taxonomy as well as to overcome the taxonomic impediment and thus to speed up species discovery and documentation, such as: DNA barcoding, creation of databases of taxa and identification tools, online quantum contributions, standardization of morphological features, training of a new generation of taxonomists. The paper comments on the desirability and effectiveness of these presumed remedies. It is argued that the analytical, hypothesis-testing nature of taxonomic research is not well understood or appreciated and forms a major constraint on the rate of taxonomic descriptions. The various components of the taxonomic method, such as exploration, data, analysis, and results, interact in a complex manner that resembles the erratic, bouncing behaviour of a pinball machine. Species hypotheses probably are the most tested hypotheses in the natural sciences. The introduction of cybertaxonomy instrumentation and infrastructure will not alleviate the time-consuming, intrinsically analytical and hypothesis-testing process underlying the description and/or identification of each taxon. Long-term survival of the discipline of taxonomy, thus guaranteeing the future cumulative taxonomic output of amateurs and professionals, is endangered by a diminishing workforce of adequately trained professional systematists. The only way to increase the pace of a well-documented and scientifically useful taxic inventory of the world's biodiversity is to increase the number of professional taxonomists.

Keywords Biodiversity · Cybertaxonomy · DNA barcoding · Hypothesis-testing · Inventory · Methodology · Nature conservation · Species delimitation and description · Taxonomic impediment

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Introduction: the status of taxonomy

Taxonomy is the subdiscipline of systematic biology involved in species discovery and documentation, and in the construction of classifications. The number of papers lamenting the poor status of taxonomy among the natural sciences, objecting to the all too-frequent and easy portrayal of this discipline as merely descriptive (and hence its poor reception among universities and funding agencies), are already too numerous to cite in full. The publications that discuss the poor status of this discipline range from papers in scientific journals (e.g. Wheeler 2004, and references therein) to governmental and institutional reports (e.g. BION 1993; House of Lords 2008). Numerous papers have also pointed out the discrepancy that exists between the poor reception of the discipline of taxonomy among the natural sciences and its highly insufficient funding and dwindling number of professional specialists on the one hand, and on the other hand the desire of society to make a taxic inventory of the world's biodiversity, thus resulting in a crisis in taxonomic resources and expertise that has become known as the "taxonomic impediment." Several routes have been suggested as potential ways to overcome both this taxonomic impediment and the Cinderella status (cf. Padial and de la Riva 2007) of taxonomy, such as DNA barcoding, the creation of databases of taxa and identification tools, online quantum contributions, standardization of morphological features, and the training of a new generation of taxonomists.

In this paper I endeavour to make some annotations and connotations on the effectiveness or desirability of these presumed remedies. Further, I elaborate on an aspect of taxonomy that has received much less attention in recent literature and that will have a long-lasting effect on the inventory of biodiversity, i.e. the analytical procedure that is inherent in the every-day practice of taxonomists.

The end-user mode

Traditionally, taxonomists have not spared any effort to construct and publish identification keys, field guides, and distribution atlases, either as conventional publications or in digital form. They have been successful to such a degree that often the discipline is considered to be merely descriptive and to provide only a service, albeit valuable, to interested end-users such as nature conservationists, biodiversity scientists, forensics specialists, agricultural scientists, and field ecologists (Ebach et al. 2011a, b).

This perception of the discipline of taxonomy as being merely descriptive frequently results in suggestions of overcoming the taxonomic impediment and accelerating the slow pace of new species descriptions by implementing web-based bioinformatics devices (e.g. Maddison et al. 2012). However, making basic data on the morphology of presumably new-, but still unnamed, species more quickly available to a broad audience does not automatically imply an increased speed of species discovery and documentation.

First of all, one may wonder who will provide the necessary high quality input for such devices (Ebach et al. 2011a). It is not to be expected that any biologist other than one who dedicates at least part of her time to detailed examination of frequently microscopic features (the major part of biodiversity being small, uncharismatic invertebrates) will be able to contribute scientifically useful and rigorous data. Second, the mere presence of images of all kinds of potentially useful taxonomic features, although easily collected and cheap in web-based repositories, does not represent taxonomic data. In order to become taxonomically meaningful the observation or image has to become part of an empirical

statement and subsequent interpretation in the context of similar features in other taxa and the species hypothesis under consideration (Vogt et al. 2010). In other words, a taxonomic character is a theory or hypothesis that two or more attributes, which appear different to some degree in two or more specimens or taxa, are actually the same (Platnick 1979). A clear example of the difference between images and data, and one that relates to my own field of expertise, is given by Vogt et al. (2010) concerning the interpretation of histological sections. As an experienced flatworm morphologist I am able to distinguish between histological preservation and processing artefacts and true structural features that may baffle an inexperienced observer. Unfortunately for end-users of taxonomic information, there is no replacement, web-oriented or otherwise, for knowledge that is based on years of observation, comparison, and experience (Ebach et al. 2011b).

DNA barcoding represents another example that was initially hailed as a possible panacea to the taxonomic impediment that would eventually provide everybody, professional as well as completely inexperienced users, easy access to species names (Hebert and Gregory 2005; Godfray 2007). That this claim runs foul of several theoretical and empirical problems has been amply discussed in the literature (cf. Will et al. 2005; Meier 2008). Some problematic issues concern the (1) simple character set provided by the single DNA sequence (COI), (2) organelle capture and the hitchhiking of organelle DNA with cytoplasmic symbionts (cf. Chat et al. 2003; Hurst and Jiggins 2005; Whitworth et al. 2007; Stegemann et al. 2013), (3) empirical fact that the desired universal marker gene COI is less suitable in land plants (in which *MatK* and *rbcL* are better markers), fungi (for which ITS was proposed as a standard marker; cf. Schoch et al. 2012; Gross 2012), and several groups of invertebrates (cf. Shearer et al. 2002; France and Hoover 2002, and references therein), (4) appropriate species concept to be used (Will and Rubinoff 2004), (5) frequent use of neighbour-joining trees for sequence identification (Taylor and Harris 2012). In addition to these issues it has recently been shown that the DNA barcoding enterprise falls short of its own targets, in that current species coverage is sparse, while growth rates are low (Kwong et al. 2012; Boykin et al. 2012). From this perspective, therefore, it is also questionable whether DNA barcoding will be able to overcome the taxonomic impediment.

And even in the unlikely case that many of the theoretical and empirical problems with DNA barcoding will be solved eventually, there are two aspects of biodiversity research that will remain paramount and underscore the never-ending need for competent taxonomists. One concerns the fact that the effectiveness of DNA barcoding is limited by the availability of reference sequences originating from voucher specimens identified by qualified taxonomists (Lücking 2008; Taylor and Harris 2012). That this verification part of the barcoding enterprise represents a major obstacle for its purported fast and easy assessment of biodiversity is apparent from the situation that a vast majority of publicly available barcodes has only very approximate identifications, merely specifying a taxon above the species level (Kwong et al. 2012).

The second paramount side of taxic biodiversity studies is that in “.... principle ... our task is not to name species but to know them...” (Ball 1980, p. 235). From that perspective, a DNA barcode merely points to a phenetic difference in a small stretch of DNA but does not provide more in-depth information on organismal divergence, either genetic (e.g. nuclear) or morphological (Wheeler 2004; Will et al. 2005; Taylor and Harris 2012). It is only whole organism description and knowledge that will enable us to frame and test scientifically interesting and relevant hypotheses on the evolution of structures, adaptations, functional morphology, behaviour, and life history.

Hypothesis-, and discovery-driven science

All too frequently, taxonomy is portrayed as a merely descriptive, non-analytical science that at best may provide valuable data, i.e. identifications, for other fields of inquiry. This view of taxonomy as a mere service industry is implicit, at the least, in papers promoting DNA barcoding as a replacement tool for classical species identification, discovery, and delimitation. However, such a view rests on a caricature of taxonomy and signals complete unfamiliarity with the methodology of this scientific discipline.

Implicit in this characterization of taxonomy as merely descriptive is the allegation that the field, thus, would be non-analytical and non-experimental. That the field is more observational and non-experimental cannot be considered as a disqualifying condition under any of the current philosophies of the natural sciences. Taxonomy is not the only natural science in which the test implications of an hypothesis can only be checked against new observational, empirical and non-experimental data (Hempel 1966). Furthermore, also in taxonomy there are situations in which the results of experiments form the test for previously formulated predictions (e.g. Aanen and Kuyper 1999).

That a taxonomic study is hypothesis-driven and analytical from its very beginning is not obvious to the uninitiated. However, empirical morphological observations on an unidentified, unknown organism immediately inspire the taxonomist to formulate a hypothesis about the identity of the organism. Such a scientific hypothesis results from the broad knowledge that the taxonomist has acquired after years of dedicated study of his favoured group of species, in combination with creative reflection on the possible taxonomic status of the organism under study. It is usually glossed over that already this first step of the taxonomic process can only be taken when one has acquired an intimate knowledge on numerous and often minute morphological characteristics of a generally sizeable group of species. It is not a skill and depth of knowledge that a novice in the field will quickly acquire, as is well-known to any taxonomist who endeavours to train a new generation of specialists.

The initial hypothesis that is formulated on the possible taxonomic status of the specimen under study is tested by comparing its morphological, anatomical, karyological, chemical, behavioural, and/or molecular details with those of species taxa or higher taxa already known to science. The results of such a comparative study will either corroborate or falsify the initial hypothesis on the taxonomic status. Portrayed in this way it seems to be a simple, linear process of scientific progress. Recently, Scotland and Wood (2012) presented a more complex and somewhat less linear flow chart for the taxonomic process. However, a more or less linear flow is rarely the case in any branch of science and certainly not in taxonomy. The various components of the taxonomic method, such as exploration, data, analysis, and results, interact in a complex manner that looks more like the erratic, bouncing behaviour of a pinball machine than a linear trajectory (Fig. 1). And this entire testing process is not only done once but again for each new specimen encountered (Wheeler 2004; Lücking 2008). Because of the ever-present variability in nature each new specimen of a presumed new species is slightly different from all others known thus far. The extent of this variation has to be evaluated and its possible implication for the taxonomic status of the specimen has to be tested against the background knowledge on the characteristics of the entire group of species or clade to which it might belong. This needs to be repeated indeed for every new specimen because an in-depth and comparative analysis may reveal that superficial similarity to a certain species actually obscures the real evolutionary and taxonomic affinity of a particular specimen. This implies that the amount

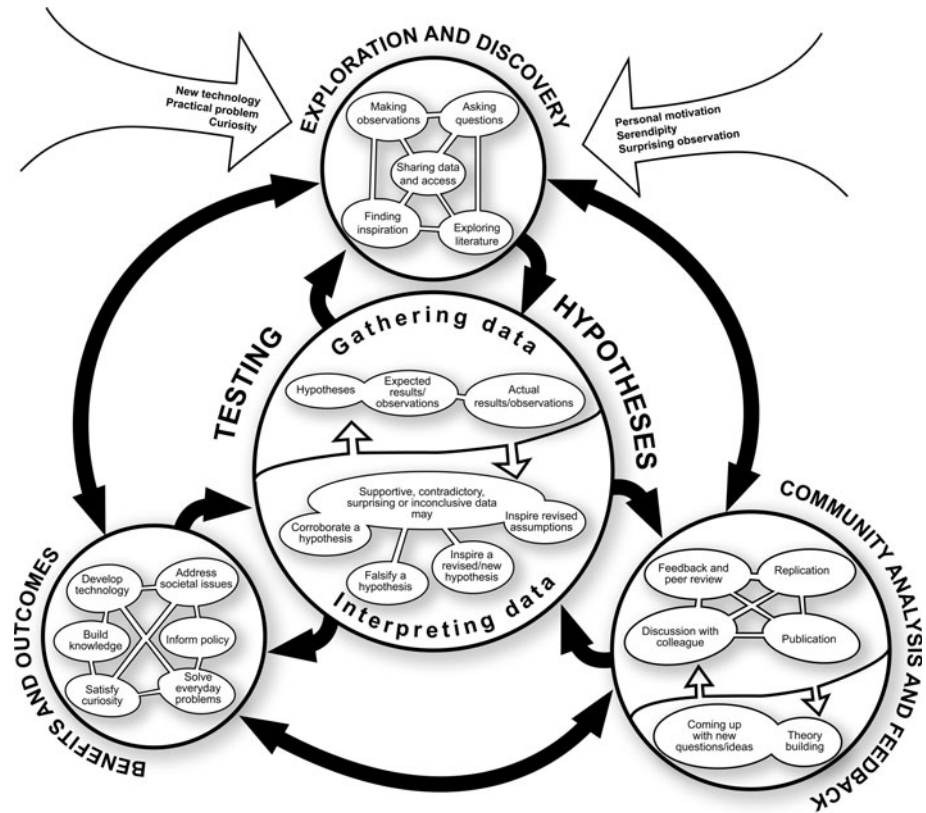


Fig. 1 Pinball machine methodology in taxonomy (after: California Academy of Sciences 2013). Starting with Exploration and Discovery and the formulation of a preliminary hypothesis on species identity, during each step the process bounces more or less erratically between Gathering Data, Interpreting Data, Community Analysis and Feedback until a stable species hypothesis can be formulated that can be incorporated into the existing knowledge and be used in scientific and societal contexts (Benefits and Outcomes) and also reflects on future rounds of Exploration and Discovery. A stable hypothesis on species identity is only a scientific fact as long as it survives new rounds of testing when further data becomes available, which implies that taxonomic work is never finished

of hypothesis testing done in taxonomy exceeds that of any other biological discipline and probably also any other branch of science (Lücking 2008; Padial and de la Riva 2010).

Although species hypotheses probably are the most tested hypotheses in the natural sciences, this does not imply that the species names once attached to particular organisms are immutable facts. A species name once assigned remains a scientific fact as long as it continues to be corroborated by subsequent tests, but it is falsified when the species hypothesis fails the test (Fig. 1). Basically, species names are hypotheses of evolutionary, genealogical relationships, which may change when tested against new data (de Carvalho et al. 2007). From this perspective it might be useful if a taxonomist would be able to provide some information on the probable stability of a species name, i.e. on the degree of its corroboration (Padial and de la Riva 2010). This is also one of the major reasons that generally taxonomists are reluctant to describe a new species solely on the basis of the examination of a single specimen. Nevertheless, scarcity and/or uniqueness of the material

at hand may induce a taxonomist to coin a new species name after having studied only one specimen (cf. Sluys and Kawakatsu 2001; Grant et al. 2006). However, there is some merit to this strategy, since a newly proposed name that turns out to be a synonym of a known species can easily be suppressed. But if a specimen is assigned to an incorrect species, the misidentification may linger in the literature for many years (Ross 1974).

In similar vein, the perception of taxonomy, and systematic biology in general, by other scientists would be improved by a more rigorous objectification and standardization of some of its procedures and data. The fact that one of the leading systematists of the 1930s–1960s, George Gaylord Simpson, characterized taxonomic classification as an art (Simpson 1961, p. 107) continues to cast a shadow over the entire field of taxonomy until the present day. However, since Simpson's time the field of systematic biology has experienced several revolutions that attempted to objectify particular aspects of its methodology and practice. The most famous of these revolutions, and one that continues to exert its influence until the present day, is the phylogenetic systematics or cladistics movement (cf. Williams and Ebach 2008; Wiley and Lieberman 2011, and references therein). In short, phylogenetic systematics objectified the reconstruction of evolutionary trees, and its philosophy implicitly or explicitly underlies every phylogenetic inference study published in current primary literature. The majority of these studies is based on molecular data because morphological data are inherently more complex and subject to greater operational and interpretational ambiguities. However, recent ramifications of the cladistic revolution have taken on the standardization and objectification of morphological character delineation, coding, and scoring, as well as the databasing of morphological features (cf. Sereno 2009; Vogt et al. 2010; O'Leary and Kaufman 2011). In the future this new movement will result in standardized morphological data that will facilitate communicability and comparability across disciplines and present usable data for taxonomic studies and for evolutionary comparative analyses in a next generation of phyloinformatics programs (cf. Deans et al. 2012; Vos et al. 2012).

The pace of taxonomic description

Recent studies have downplayed the taxonomic impediment alluded to in so many publications (e.g. Giangrande 2003; Wheeler et al. 2004) and that stimulated the U. S. National Science Foundation to launch the PEET programme, with its goal to overcome some of the problems residing under this generalized label (cf. Rodman and Cody 2003; Agnarsson and Kuntner 2007). Notably Joppa et al. (2011a) showed that for a number of organismal datasets the rates of species description has increased exponentially over the period 1950–2000, as did the number of taxonomists (see also Costello et al. 2012; Costello et al. 2013). These results run counter to an earlier study that identified a long and persistent decline since the 1950s in both professional and amateur entomological output, as well as number of active workers in entomology (Hopkins and Freckleton 2002; see also Drew 2011).

Bibliometric analyses of the number of active taxonomists, their cumulative effort, and their taxonomic output, in the form of documented new species, although valuable in principle, appear to be fraught with difficulties and to yield contradictory results. The problems already start with the appropriate classification of authors of species descriptions. Some studies distinguish between professionals and amateurs and class an author as an amateur if the associated address is a private residence, grouping all others with an affiliation at an institution as professional taxonomists (cf. Hopkins and Freckleton 2002).

In this context it is important to realize that non-paid taxonomic workers often use the address of a professional institution. They do this because the organization may have facilitated part of the study, for example by providing access to collections of specimens, in the case of natural history museums, and/or because such workers hold an honorary position at the institution. Other studies consider as professional taxonomists only those authors who hold a paid job to do taxonomy, while as amateurs are classified all other workers, including the frequently very active retired taxonomists (cf. Fontaine et al. 2012b). In the most inclusive categorization a taxonomist is any author who contributes a species description (Costello et al. 2012, 2013). It would be interesting to know whether the contribution of amateurs, or at least non-specialists, to the taxonomic output leads to a greater increase in synonyms. As an example I mention the description of five new Chinese wasps by Dong and coauthors (Dong 2001; Dong et al. 2002, 2004, 2005; Dong and Wang 2003) that not long thereafter were synonymized by Carpenter et al. (2011).

An example of a contradictory result between bibliometric analyses concerns the prediction by Costello et al. (2012) that soon it would become harder to find new species, excepting smaller invertebrates in the less explored areas and habitats. However, their prediction was already falsified before it had been made public because the results of Fontaine et al. (2012b) indicated that the species description curve for the European fauna shows no sign of approaching a plateau, in other words, that the inventory of this well-studied fauna is far from being complete. This holds true not only for small invertebrates but also for freshwater fishes (see also Giam et al. 2011).

The discrepancy between the notion that the number of taxonomists is not in decline (e.g. Costello et al. 2013) and the viewpoint that the opposite is true (e.g. Drew 2011) may well result from different perspectives and different concerns about what is necessary for a healthy future of the discipline of taxonomy. When one focuses only on current overall taxonomic output the situation may seem not so bleak. But the picture darkens considerably when one thinks about the necessary infrastructure (e.g. natural history museums, web-based databases) and about the equally necessary scientific framework of systematic biology, in which taxonomy lies embedded as a subdiscipline. If the current situation is such that many new species are described by amateur, non-paid taxonomists (Fontaine et al. 2012b) and that the number of tenured professionals is dwindling, a notion that keeps on surfacing within the community of professional taxonomists (cf. Drew 2011), one may indeed wonder who will train and facilitate the research of future generations of amateurs. Therefore, without an adequately-sized professional workforce and infrastructure the entire field of taxonomy, including amateurs as well as professionals, runs the risk of eventually, but inevitably, falling below the level of sufficiency.

The fact that taxonomic papers are increasingly multi-authored (Costello et al. 2012) does not necessarily imply an increased and healthy taxonomic workforce. Many of the co-authors will concern workers with a wide range of competency, only documenting species in the context of other studies but not dedicated to a comprehensive taxonomic and phylogenetic analysis of a group of species.

Furthermore, it is unsurprising that the number of taxonomists has increased considerably since 1800 (cf. Joppa et al. 2011a, Fig. 1C). Most likely a similar trend is present in many other branches of science, in view of the increased overall size of the global scientific community. But this increase in absolute numbers does not nullify the situation that (1) universities and funding agencies all too often weaken or even completely discontinue their support for taxonomy (Wheeler 2004; Kozłowski 2008; Drew 2011), (2) even an increased number of taxonomists is currently insufficient to provide a good and timely account of still undiscovered species (Bacher 2012). A recent example of the first-mentioned situation

is the discontinuation of the Zoological Museum of the University of Amsterdam (ZMA) in 2011, after having existed for almost 175 years (cf. Reitsma 2012). Fortunately, the collections of the ZMA and its highly reduced number of staff members were incorporated in the restructured Naturalis Biodiversity Center.

The second point mentioned above, i.e. the continued presence of the taxonomic impediment, has recently been questioned (Costello et al. 2013) but gets support from the generally long shelf life between the first collection of specimens of a new species and its formal description and naming in the scientific literature, with the average shelf life being 21 years (Fontaine et al. 2012a). This effective presence of the taxonomic impediment has resulted in suggestions to speed up the pace of taxonomic description through the implementation of new cyber technologies and non-conventional workflows (e.g. Maddison et al. 2012).

That taxonomy needs to implement and will profit from modernized practices and infrastructure is without any doubt. Evidently, constraints that may have slowed down progress in the past, such as availability of literature and access to specimens, need no longer exist (Wheeler 2010). However, it is questionable whether new technologies will greatly increase the number of adequately analyzed and documented species descriptions. It is clear that introduction of cybertaxonomy instrumentation and infrastructure will not alleviate the intrinsically analytical and hypothesis-testing process underlying the description of each new taxon, nor the identification of already known species. It is a scientific process that basically occurs in the minds of experienced taxonomists and forms the part and parcel of the comparative, hypothesis-driven methodology of taxonomy. As with any other branch of the natural sciences, speed of discovery, hypothesis testing, and scientific progress is constrained by the number of dedicated scientists.

It is also a misconception to think that the pace of taxonomic description will increase as we know more of biodiversity, with species description curves perhaps even approaching an asymptote, suggesting a diminishing pool of the so-called missing species (Joppa et al. 2011a, b). Only someone unfamiliar with the hard, complex, comparative, and analytical work involved in the discovery and description of new species could conclude that “... over time there has been easier circumscription of taxa owing to increasing numbers of species with which to compare ...” (Joppa et al. 2011a, p. 551). That precisely the opposite holds true is apparent from every taxonomic study. For example, description of a new species of freshwater flatworm of the genus *Dugesia* from South Africa entailed (1) comparison with all 75 species known to science, (2) redescription of several African species, and (3) re-assessment of the taxonomic status of some African *Dugesia* populations (Sluys 2007). All of that was necessary in order to properly establish the taxonomic status of animals from only one newly sampled population, representing a new species (see also Scotland and Wood 2012).

It is also obvious that as more becomes known of biodiversity, the amount of literature that needs to be consulted increases as well, as does the number of taxonomic synonyms (Costello et al. 2012). Again, evaluation of literature and synonyms can only take place in the mind of the qualified taxonomist and cannot be replaced or speeded up by new technologies.

In the present context I do also venture an alternative explanation for the asymptotically decreasing number of species descriptions per taxonomist, as found in some studies (Joppa et al. 2011a, b; Costello et al. 2012). The decreasing number of descriptions may not result from a diminishing pool of missing species, as suggested by Joppa et al. (2011a), but may simply signal the fact that the time needed for the entire analytical taxonomic process increases with an increased base of specimens and existing data. That in many taxa missing species will concern cryptic species among the smaller invertebrates (Costello et al. 2012;

Scheffers et al. 2012) will add another complicating and time-consuming factor to the taxonomic process.

Although molecular tools certainly will help in the discrimination of putative species, notably new cryptic species, these methods will not necessarily increase the discovery process and rate of description. One of the reasons for this is that integrative taxonomy is rapidly becoming the new conceptual framework for the formulation of stable species hypotheses. In an integrative approach to taxonomy several, independent data sources (e.g. morphology and DNA) are used to formulate and test species boundary hypotheses (cf. Schlick-Steiner et al. 2010). In practice, integration of the results from analyses of several datasets will actually slow down the discovery and documentation of fully described species and candidate species. This is simply due to the fact that performing more analyses takes more time and that cooperation between research groups with different competencies usually is accompanied by an expanded timetable for the project.

In conclusion, due to the analytical nature of taxonomy there is ultimately only one way to overcome the taxonomic impediment and to speed up the discovery and documentation of the world's undescribed species, viz. the training of more taxonomists. Currently, for many groups of organisms only one, or at best very few specialists, either professional or amateur, are available to resolve species identifications, while there is also a large number of taxa for which qualified expertise is insufficient or even completely lacking. It is of the utmost importance that a new generation of taxonomists is trained by professional specialists still active today before further erosion of the discipline has created a taxonomic cliff that cannot be overcome before the missing species have effectively gone extinct.

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