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Eric Pante, Charlotte Schoelinck, Nicolas Puillandre

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SPECIES DELIMITATION AND DESCRIPTION

**From Integrative Taxonomy to Species Description: one Step Beyond**

Pante E.<sup>1\*</sup>, Schoelinck C.<sup>2\*</sup>, Puillandre N.<sup>3</sup>

<sup>1</sup> *Littoral, Environnement et Sociétés (LIENSs) UMR 7266 CNRS, Université de La Rochelle, La Rochelle, France. pante.eric@gmail.com*

<sup>2</sup> *Fisheries and Oceans Canada, Aquatic animal health, 343, University Avenue E1C 9B6 Moncton N.B., Canada. schoelinck@mnhn.fr*

<sup>3</sup> *Muséum National d'Histoire Naturelle, Département Systématique et Evolution, ISyEB (UMR 7205 CNRS/UPMC/MNHN/EPHE), 43, Rue Cuvier, 75231 Paris, France. puillandre@mnhn.fr*

*Corresponding author: Nicolas Puillandre, Muséum National d'Histoire Naturelle, Département Systématique et Evolution, ISyEB (UMR 7205 CNRS/UPMC/MNHN/EPHE), 43, Rue Cuvier, 75231 Paris, France. puillandre@mnhn.fr. Tel: +33 1 40 79 31 73. Fax: +33 1 40 79 38 44*

*\* Both authors contributed equally to this work*

22    **Keywords**

23    Cryptic species, grey zone, impact factor, literature review, species complex, species  
24    delimitation, species hypotheses, taxonomic impediment.

25 *The first part of knowledge is getting the names right*

26 Chinese proverb

27  
28 Integrative taxonomy was formally introduced in 2005 as a comprehensive framework  
29 to delimit and describe taxa by integrating information from different types of data and  
30 methodologies (Dayrat 2005; Will et al. 2005). Even if debate remains about the hierarchy of  
31 the types of characters and criteria to use for species delimitation (Schlick-Steiner et al., 2009;  
32 Padial et al., 2010; Yeates et al., 2011), most, if not all taxonomists agree that objectively  
33 evaluating several lines of evidence within a formalized framework is the most efficient and  
34 theoretically-grounded approach to defining robust species hypotheses (Samadi and  
35 Barberousse 2006; de Queiroz 2007). The last ten years have seen a renewal of taxonomy,  
36 illustrated by the increasing number of published articles related to species concepts, species  
37 delimitation methodology and its application.

38 In the early 90s, many systematists began to suspect that the majority of species would  
39 remain undescribed (Costello et al. 2013a; Erwin 1982; Mora et al. 2011 – but see Costello et  
40 al. 2013b) and that some of them will probably go extinct before we have a chance to describe  
41 them (Barnosky et al., 2011; Leakey and Lewin, 1995; Pimm et al., 2006). The use of  
42 molecular data, and in particular molecular barcoding (Hebert et al., 2003), was presented as  
43 one answer to this “taxonomic impediment” (as defined in Rodman and Cody, 2003), and  
44 welcomed as such by taxonomists. It thus adds to the toolkit of taxonomy, which continues its  
45 development as a synergic discipline involving morphological taxonomists, field ecologists,  
46 naturalists, and statisticians (Knapp 2008). Integrative taxonomy, used for many decades by  
47 taxonomists but only recently formalized concomitantly with the molecular revolution, is  
48 organised following a three-step workflow (see also Evenhuis 2007): first, we need to  
49 accumulate data on numerous specimens (from various types of data: DNA, morphology,

ecology...); second, we need to circumscribe groups of organisms using concepts that ensure that these groups correspond to species (this second step may be coupled with the first, as biological data are continuously accumulated and species hypotheses re-discussed); and third, we need to provide a species description, i.e. a diagnosis and a name for the species recognized as new.

Naming new species is a fundamental step when describing biodiversity and is the only way to ensure that scientists are talking about the same entity, and that all the data linked to conspecific specimens but produced by different researchers (or amateurs) can be associated in a comparative analysis (Patterson et al., 2010; Satler et al., 2013; Schlick-Steiner et al., 2007). Not linking biological data (should they be molecular, morphological, or ecological) to a formal species name will result in these data losing tremendous value (Goldstein and DeSalle 2011). Indeed, when authors publish data on entities that are not defined within the framework of a referencing system (e.g. solely identified by an alphanumeric label), they make it very difficult for other authors to build on these data. The best example is the need for taxa to be named to have a chance to be listed in an endangered species list and to benefit from a conservation program: no name, no surviving (Mace 2004). Beyond the need for communication among scientists, names are also key to communicating with non-scientist audiences.

While it is now widely recognized that integrating several lines of evidence is the most efficient and theoretically grounded way to delimit new species (e.g. de Queiroz, 2007; Schlick-Steiner et al., 2009; Yeates et al., 2011), the formal naming of new entities may have become decoupled from species delimitation. Indeed, we noted that in several cases new delimited species were not accompanied by formal species description (see also Goldstein and DeSalle 2011). The aim of this article is therefore to test the hypothesis that integrative taxonomy, as defined in 2005 (Dayrat 2005; Will et al. 2005), and in particular the use of

molecular data, helped to alleviate the taxonomic impediment by delimiting *and* describing new species. We reviewed part of the “integrative taxonomy” literature of the last eight years (2006-2013) and tested if authors that delimit new species also name them. We also looked at how the number and type of characters used, across different taxa, varies across articles.

## **MATERIALS AND METHODS**

We performed a literature survey using the Web of Science research tool, limited to the scientific articles published between 2006 and 2013, and using the following keywords: “Integrative Taxonom\*” in TITLE OR TOPIC OR “Species boundar\*” in TITLE OR “Integrative delineation” in TITLE OR “Integrative delimitation” in TITLE OR “Species delineation” in TITLE OR “Species delimitation” in TITLE. This timespan (2006-2013) was chosen because it follows the formal introduction of modern integrative taxonomy. We acknowledge that older articles also include integrative taxonomic approaches (e.g. Hogan et al., 1993, and see Turrill, 1938), but the lower limit for the literature survey would have been chosen arbitrarily. The keywords helped limit the size of our survey while focusing on integrative taxonomy papers, as other keywords (e.g. “new species”) or options (e.g. “species delineation” in TOPIC and not only in TITLE) led to a much higher number of articles (several thousands).

From the resulting list of 666 articles, we removed 172 articles that did not fit the context of this review (i.e. methodological and theoretical articles, review studies that did not perform any species delimitation, studies that re-analyzed published data, and studies that focused on supra- or infra-species levels only). For the 494 remaining articles, we extracted data on the number of delimited species, the number of new species delimited, the number of new species described (and, when given, the reason(s) why new species were not described),

and the studied taxon. We did not attempt to interpret published results ourselves, but recorded the number of species (delimited, new and described) as reported by the authors of each paper. We also recorded the type of data and methods used to delimit species: molecular data, morphology (including anatomy, cytology...), ecology (including phenology, niche modelling...), cross tests, behavior (e.g. call songs) and other miscellaneous methods (e.g. caryology, chemical data, presence of endosymbionts, etc...). We considered the geographical distribution to be implicitly used in all articles. The resulting table is presented in Online Appendix 1. Contingency tables were analysed using Fisher's Exact Test, given the relatively small number of observations.

We investigated journal editorial policies on including formal taxonomic descriptions into articles. As a proxy for editorial policies, we recorded whether journals that published articles in which new animal species were delimited also published formal descriptions, within three time periods (1864-2004, 2005-2010, 2011-2013), using the "Systematics Controlled Terms" feature in the Zoological Records database (Online Appendix 2). We recorded the impact factor of these journals between 2005 and 2010 to investigate whether there is a link between the inclusion of formal descriptions in papers and impact factor (Online Appendix 2). Indeed, there is a strong incentive for researchers to publish in high-impact journals (e.g. Casadevall and Fang, 2014, and see Werner, 2006); if these journals do not welcome descriptions, authors may be tempted to submit their contributions without descriptions to high-impact journals rather than submitting their integrative work, including descriptions, to lower-impact journals. We chose these time periods as a trade-off between the number of articles published within time groups for each journal and the variance of the impact factor (the longer the time period, the larger the variance in impact factor). Also, we noted from personal experience that narrow time periods would be preferred as editorial policies may change relatively rapidly. We used a one-tail Wilcoxon test to evaluate the null

hypothesis that journals including formal species descriptions do not have lower impact factors than journals that do not. All statistical tests were performed in R (R Core Team 2014).

## RESULTS

The 494 articles were published in 150 different journals, over half of which published a single article from our list, and 4 of which (Molecular Phylogenetics and Evolution, Zootaxa, PLOS ONE and the Zoological Journal of the Linnean Society) published over 20 articles. The number of articles published each year steadily increased from 2006 (20 articles) to 2013 (118 articles) (Fig. 1). Most major lineages of organisms are represented, but the number of articles varies greatly among groups (Fig. 2a). Among hexapods, hymenopterans, lepidopterans, coleopterans and dipterans were the taxon of interest for 19-26 articles each (Fig. 2b); among vertebrates, amphibians (43 articles) and lepidosaurians (43) are the most studied taxa, followed by actinopterygians (22), mammals (19), birds (10), chondrichthyans (4), and crocodilians and turtles (1 each) (Fig. 2c). In all taxonomic groups represented by more than five articles, molecular data were analyzed in 100% of the articles, except for embryophytes (71.6%), vertebrates (88.8%), chelicerates (94.7%), hexapods (92.6%) and annelids (90%). One possible explanation for the lower prevalence of molecular data in these taxonomic groups is that morphological characters may generally be more easily formalized, and congruent with molecular data (compared to other groups in which there might be fewer -or more plastic- types of characters available to taxonomists, such as some cnidarians, e.g. McFadden et al., 2010).

Almost half (47.2%) of the studies based their species delimitation on two types of characters (DNA and morphology in 89.7% of them), 15.2% three types of characters and



only 2.2% four types of characters. More surprisingly, 35.4% of the studies used only one type of character (molecular data for 74.9% of them). This reflects a bias in our survey (the keywords we choose also targeted non-integrative taxonomy), but also an inappropriate use of the “integrative taxonomy” terminology by some authors. Indeed, the “integrative” aspect of the approach is restricted in these articles to the use of different methods and/or criteria of species delimitation, and not to the use of different types of characters. The number of types of characters used varied significantly according to the year of publication when all studies were considered, and non-significantly when only studies with new species delimitations were considered, suggesting a weak tendency toward more integrated species delimitation over the years (Fisher’s Exact Test:  $p=0.019$  and  $p=0.16$ , respectively; Table 1). A trend toward using preferentially two types of characters in 2012-2013 was detected among papers describing at least one new species (Fisher’s Exact Test:  $p=0.0002$ ; Table 1). A concurrent decline in the number of studies using a single type of character was detected, the prevalence of such studies falling from 44.7% between 2006 and 2010 to 29.3% between 2011 and 2013 (Fisher’s Exact Test:  $p=0.0005$ ). Finally, the proportion of articles using molecular data and/or morphological data did not vary significantly from 2006 to 2013 (Fisher’s Exact Test:  $p=0.99$ ; Table 2).

We then focused on comparing studies that did not delimit any new species, studies that delimited new species without describing all of them, and studies that delimited new species and described at least one of them. We decided to compare the number of studies in these categories, rather than the number of delimited and described species, because the number of species delimitation and description per study was highly variable. Indeed, among the 139 studies that described at least one species, 135 described fewer than ten species, 3 described between 10 and 16 species, and one described 101 species (Riedel et al., 2013).

A total of 240 studies did not delimit any new species, but confirmed the current alpha taxonomy or extracted previously described species from synonymy (on the contrary, new

175 species for which names were available in the literature but never considered as a valid, such  
176 as forms, varieties or subspecies, were counted as new). In the remaining studies, 1346 new  
177 species were delimited (for studies providing a range of putatively new species, we used the  
178 lower number reported by the authors), representing 18.7% of the total number of delimited  
179 species in the 494 studies (7205). Among the studies that delimited new species, 125  
180 delimited but did not describe at least one new species and 139 described at least one new  
181 species (in 10 studies some new species were described and others not). The ratio of  
182 Described over Undescribed Species (hereon called the “DUS” ratio, more specifically  
183 calculated as the number of studies that delimited new species and described at least one new  
184 species divided by the number of studies that delimited new species and did not describe at  
185 least one new species) was approximately of 1.11 for the whole dataset and did not change  
186 significantly from 2006 to 2013 (Fisher’s Exact Test:  $p=0.91$ ). The DUS ratio varies non  
187 significantly among taxa: when considering only the taxa represented by more than five  
188 studies, the ratio varied from 0.44 for molluscs to 4 for platyhelminthes (these differences are  
189 largely driven by small sample sizes; Fisher’s Exact Test:  $p=0.67$  Table 3). Finally, the DUS  
190 ratio also varies with the number and the type of characters analyzed. The ratio is 0.29 when  
191 only one type of character is analyzed, 1.54 with two types of characters and 1.70 with three  
192 types of characters (only four studies found new species with four different types of  
193 characters;  $DUS = 1.33$ ). Studies describing new species were more likely to use two types of  
194 characters or more, compared to studies that delimited new species without describing all of  
195 them (Fisher’s Exact Test:  $p<0.001$ ), confirming that taxonomists prefer to have multiple  
196 sources of information to describe species. The DUS ratio is 1.05 when molecular data (alone  
197 or among other types of data) are analysed, 1.87 when morphological data are analysed, and  
198 1.22 when other types of characters are analysed, and these differences were statistically  
199 significant (Fisher’s Exact Test:  $p=0.009$ ).

Among the 150 journals of our sample, 84 delineated new species. Our Impact Factor analysis, using Zoological Record, focused on 73 zoological journals. Among these journals, 90.4% published descriptions from 1864 to 2013, 9.6% never published descriptions within that period, and 16.4% stopped publishing descriptions within that period (either from 2005 onward, or from 2011 onward). The average impact factor of journals with species delimitation but without descriptions was significantly higher than that of journals publishing formal descriptions during the 2005-2013 periods (one-tail Wilcoxon:  $n=50$ ,  $W = 72$ ,  $p = 0.038$ ).

## **DISCUSSION**

As reported previously (Gaston and May 1992), taxonomy studies are strongly biased towards vertebrates (here, they accounted for 29% of the articles we reviewed), even though this taxon accounts for only ~3% of the described diversity on earth (Chapman 2009; Zhang 2011) and probably has the highest ratio of described over undescribed species. Most of the studies on vertebrates actually focus on groups that still encompass high levels of unknown species, such as amphibians or lepidosaurians. Integrative taxonomy and molecular taxonomy are linked in 90% of the studies, confirming that the formal definition of integrative taxonomy in 2005 is probably linked to the concomitant molecular revolution (as explained in the introduction). In the literature, both have often been associated with an inflation in the number of new species, artificial or not (Isaac et al. 2004; Knapp et al. 2005; Sangster 2009). Our results suggest that this is not always true: 48.7% of studies did not detect new species, and some authors actually proposed to reduce the number of valid species in their taxon of interest.

When new species are discovered, however, they are not systematically described (in 46.1% of the articles), thus leaving the new species unnamed. In these cases, several justifications for not describing have been put forth by the authors, and we propose a few more. The first reason is the lack of support for the species hypotheses (given in 72.2% of the articles that do provide a justification). In taxa for which the proportion of unknown species is greater than the number of described species, difficulties are linked to the fact that nobody has ever proposed species hypotheses. Exploratory methods are therefore needed, either based on traditional morphological characters or on molecular markers (several DNA-based methods are now available: e.g. (Kekkonen and Hebert, 2014; Pons et al., 2006; Puillandre et al., 2012; Ratnasingham and Hebert, 2013; Zhang et al., 2013). This exploratory step is generally efficient to detect highly divergent lineages that most probably correspond to different species. However, it is more difficult to estimate the number of species in clades with many closely-related species because many might be in “grey zones” (i.e. parts of the tree of life where the speciation process is ongoing and where different types of characters and criteria will not provide the same answer, as defined in de Queiroz, 2007). This situation is encountered in well-studied groups (e.g. some vertebrates and flowering plants), for which what was easy to recognize as species has been described, and challenging species complexes remain to be disentangled (e.g. in orchids, Pessoa et al., 2012). Several multi-locus and coalescent-based methods now exist to help delimit species in the grey zone (reviewed in Camargo and Sites 2013; Carstens et al. 2013; Fujita et al. 2012, and see Leaché et al., 2014). In any case, species are and remain, by definition (de Queiroz 2007; Samadi and Barberousse 2006), only hypotheses, and these hypotheses can be more or less supported. In an integrative context, the number of arguments, data and criteria (including the need for additional specimens) needed for defining new species and their hierarchy can vary depending on the taxon considered or the approach applied, and turning species hypotheses into a formally

described species remains a taxonomist-dependent decision, sometimes difficult to make. It should also be noted that, even if test cross experiments are generally considered as the most robust criteria of species delimitation (following the conceptual framework established by de Queiroz 2007), it is rarely used (16 studies only), probably because of the difficulty to set up such tests for most non-model organisms.

However, in other cases, the species hypothesis is highly supported by numerous lines of evidence, but remains undescribed. Consequently, other reasons should be invoked. For example, it could be the choice of the author to not describe the species in the article where it has been delimited, but in a forthcoming article (reason given in 24.1% of the studies providing a justification for not describing). This can be motivated by the fact that the authors wish to present additional data that are beyond the scope of the present article (e.g. Pante et al., 2014). It can also be explained by the pressure of publishing more papers, driving many authors to publish in several articles what could be published in one (i.e. submitting their work as “least publishable units”). Then, taxonomists might refrain from describing a species if no morphological differences were found with its sister-species, although there is no reason to think that all “good” species will exhibit morphological differences (Fujita and Leaché 2011). Diagnosing a new species using only DNA characters is possible, but not yet widespread (Cook et al. 2010), especially in animals, although molecular data are increasingly included in species descriptions (Goldstein and DeSalle 2011). Actually, a substantial part (35.4%) of the articles we reviewed delimited species with only one type of character.

However, even if only one type of character is used, it generally remains associated with the use of different loci, or different methods, or different criteria (phenetic – genetic distances, phylogenetic – reciprocal monophyly, reproductive isolation – independent molecular markers).

Another reason for not naming new species is the unwillingness of some scientists (e.g. molecular systematists) to describe species (Satler et al., 2013). A formal description should follow strict nomenclatural rules dictated by the codes of nomenclature, and writing a species description is in itself an exercise that necessitates training that is rarely proposed in modern biological classes (Pearson et al. 2011). Fonseca et al. (2008) and Leliaert et al. (2009) also highlighted the need of sequencing type-specimens to correctly attribute available species names or name new species (Puillandre et al 2011). Furthermore, proposing a new name necessitates, at the very least, a literature review of all the species-level names available (Bertrand et al. 2006; Jansen et al. 2011; Minelli 2003), including names proposed in an old and antiquated literature, sometimes not written in English (Balakrishnan 2005; Godfray 2002). Naming new species also necessitates comparison with existing type material, often requiring visits to museums. Non-taxonomists are often frustrated by the over-abundance of redundant species names (i.e. species that have multiple synonymous names) as well as doubtful names (Dayrat, 2005), which makes the assignation of species names to well-delineated entities even more difficult. Once again, this exercise requires excellent knowledge of the group, contrary to a genetic approach which is basically the same in mammals and in plants, and can be time consuming (Miller 2007). Other systems have been proposed, some designed to replace the Linnean System (Dayrat et al. 2008; Vences et al. 2013), others only proposing interim systems before full description following the Linnean System (Ratnasingham and Hebert 2013; Schindel and Miller 2010), to, at least partly, solve the difficulties linked to describing new species and to reduce “shelf-time” (Fontaine et al. 2012). However, none of these alternate referencing systems have been as widely accepted and applied as the Linnean system.

Finally, publishing species descriptions in high impact factor journals is in general more difficult, because editors may be reluctant to publish species descriptions, especially

when they are numerous and long (the number of pages is generally very limited in these journals). In this study, we showed that among the 23 journals that included at least one study in which new species were delimited but not described, 6 of them have never published species descriptions, based on Zoological Records, and 6 did not publish species descriptions after 2004; on average, journals including descriptions had a lower impact factor than the journals that do not. Because of the publication pressure, authors will almost automatically prefer to publish in high impact factor journals, even at the price of removing the species descriptions (Agnarsson and Kuntner, 2007; Costello 2009). Scientists all know the importance in the current system to have articles in journals with high-impact factors, and thus most of them do not spend their time in writing articles that will not be rewarded (Minelli 2003).

## CONCLUSION

The increase in the number of articles recorded between 2006 and 2013, and the large range of journals represented in our review reflects the high dynamism of the taxonomic community. In addition, the increase in the proportion of papers using multiple lines of evidence underlines the success of the modern integrative taxonomy approach, as defined in 2005. The positive relationship between the number of different types of characters used for delimitation, which can be seen as a proxy of the degree of integration, and the DUS ratio also supports the idea that integrative taxonomy contributes to a better understanding of biodiversity. However, the 446 species described in the reviewed articles are only a drop in the ocean of new species described in the same period (85,000, if considering a mean of 17,000 new species described each year – <http://www.esf.edu/species/SOS.htm>). Nevertheless, this sample reflects the fact that modern integrative taxonomy as formalized in

2005 (thus not considering the pre-2005 articles that delimited and described species using an integrative taxonomy-like approach), is, at least for the moment, not a very efficient solution to the taxonomic impediment. Most new species seem to be described without applying an integrative taxonomy approach, and most new species are still described without the help of molecular data: a screening of 200 articles published in 2013, obtained with the keywords “Taxonomy” in TOPIC AND “sp nov” in SYSTEMATICS in Zoological Records revealed that only 18 of them mentioned the use of molecular data in the abstract. This would suggest that most species are thus still described using morphological characters only. The “molecular revolution” that was announced after the renewal of the taxonomy in the early 2000s, largely associated with the emergence of the integrative taxonomy approach, has apparently not happened yet. We are convinced that integrative taxonomy, when associated with formal species description, is a good way to improve the quality of species hypotheses and associated descriptions, and should therefore be encouraged. However, and contrary to a barcoding approach that can perhaps accelerate the rate of species discovery (but not improve the quality of the species hypotheses nor the rate of species description; e.g. Will et al., 2005), integrative taxonomy did not accelerate the rate of species description between 2006 and 2013. Efforts must be made by authors to seek training or new collaborations to formalize their species delimitation, and to avoid delaying new species descriptions for reasons associated with impact factors. Editors may help the naming of newly delimited species by encouraging the publication of species descriptions. Editorial policies could, for instance, impose that new delimitation be either accompanied by formal descriptions or a strong justification for not describing. Research institutions and funding agencies may encourage the naming of newly delimited species by recognizing taxonomic work as a foundation of biological research, and refrain from putting too much emphasis on impact factors when evaluating scientists.



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506

507 Online Appendix 1: List of the 494 articles reviewed and data extracted.

508 Online Appendix 2: List of the journals in which new species were delineated. Editorial

509 policies on including formal taxonomic descriptions to articles and impact factors were

510 investigated before 2005, between 2005-2010, and 2011-2014. Y=Yes, N=No, NA=Not

511 Available and IF=Impact Factor.



512 Table 1: Number of studies (% of total, per year) analysing 1, 2, 3 or 4 types of characters for  
513 delimiting species.  
514

*All articles*

Nb of characters	1	2	3	4	Total
2006	9 (45)	10 (50)	1 (5)	0 (0)	20
2007	14 (44)	10 (31)	8 (25)	0 (0)	32
2008	19 (59)	9 (28)	4 (13)	0 (0)	32
2009	15 (35)	20 (47)	6 (14)	2 (5)	43
2010	31 (44)	25 (36)	13 (19)	1 (1)	70
2011	18 (24)	42 (55)	14 (18)	2 (3)	76
2012	28 (27)	53 (51)	17 (17)	5 (5)	103
2013	41 (35)	64 (54)	12 (10)	1 (1)	118

*Articles with new species*

Nb of characters	1	2	3	4	Total
2006	1 (17)	5 (83)	0 (0)	0 (0)	6
2007	3 (38)	3 (38)	2 (25)	0 (0)	8
2008	4 (40)	3 (30)	3 (30)	0 (0)	10
2009	4 (19)	13 (62)	3 (14)	1 (5)	21
2010	12 (35)	10 (29)	11 (32)	1 (3)	34
2011	8 (22)	20 (54)	8 (22)	1 (3)	37
2012	11 (17)	38 (59)	12 (19)	3 (5)	64
2013	15 (20)	49 (66)	9 (12)	1 (1)	74

*Articles with described species*

Nb of characters	1	2	3	4	Total
2006	1 (50)	1 (50)	0 (0)	0 (0)	2
2007	1 (33)	1 (33)	1 (33)	0 (0)	3
2008	0 (0)	3 (60)	2 (40)	0 (0)	5
2009	2 (17)	6 (50)	3 (25)	1 (8)	12
2010	7 (35)	4 (20)	8 (40)	1 (5)	20
2011	1 (5)	13 (65)	6 (30)	0 (0)	20
2012	0 (0)	29 (76)	7 (18)	2 (5)	38
2013	1 (3)	31 (79)	7 (18)	0 (0)	39

515 Table 2: Number of studies (% of total, per year) that included molecular data or  
 516 morphological data for each year (2006-2013).

517

	<b>With / Without molecular data</b>	<b>With /Without morphological data</b>
<b>2006</b>	18/2 (90)	12/8 (60)
<b>2007</b>	25/7 (78)	21/11 (66)
<b>2008</b>	25/7 (78)	17/15 (53)
<b>2009</b>	38/5 (88)	32/11 (74)
<b>2010</b>	59/11 (84)	47/23 (67)
<b>2011</b>	71/5 (93)	57/19 (75)
<b>2012</b>	97/6 (94)	79/24 (77)
<b>2013</b>	110/8 (93)	77/41 (65)

518 Table 3: Number of studies (% of total, per taxon) without new species, with at least one  
519 delimited but undescribed new species, and with at least one described species in each taxon  
520 considered. The DUS ratio corresponds to the ratio of columns 3 and 2.  
521

	Articles without new species	Articles with $\geq 1$ undescribed new species	Articles with $\geq 1$ described species	DUS ratio
Vertebrata	59 (40)	46 (31)	44 (30)	0.96
Hexapoda	50 (46)	25 (23)	34 (31)	1.36
Embryophyta	63 (78)	7 (9)	11 (14)	1.57
Fungi	20 (59)	5 (15)	9 (26)	1.80
Chelicerata	11 (58)	4 (21)	4 (21)	1.00
Mollusca	6 (32)	9 (47)	4 (21)	0.44
Cnidaria	8 (73)	2 (18)	1 (9)	0.50
Nematoda	1 (9)	4 (36)	6 (55)	1.50
Platyhelminthes	1 (10)	3 (30)	6 (60)	2.00
Annelida	2 (20)	5 (50)	3 (30)	0.60
Crustacea	1 (11)	2 (22)	6 (67)	3.00
Stramenopiles	3 (38)	2 (25)	3 (38)	1.50

522 **Figure captions:**

523

524 Figure 1: Number articles (2006-2013) that did not delimit new species (dark grey), delimited  
525 new species without formally describing them (medium grey), and described newly-delimited  
526 species (light grey).

527

528 Figure 2: Number of articles per taxa (a), with emphasis on hexapods (b) and vertebrates (c).  
529 “Other taxa:” taxa for which fewer than five articles were analysed.