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From Integrative Taxonomy to Species Description: One Step Beyond

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The first part of knowledge is getting the names right

(Chinese proverb)

Integrative taxonomy was formally introduced in 2005 as a comprehensive framework to delimit and describe taxa by integrating information from different types of data and methodologies (Dayrat 2005; Will et al. 2005). Even if debate remains about the hierarchy of the types of characters and criteria to use for species delimitation (Schlick-Steiner et al. 2009; Padial et al. 2010; Yeates et al. 2011), most, if not all, taxonomists agree that objectively evaluating several lines of evidence within a formalized framework is the most efficient and theoretically grounded approach to defining robust species hypotheses (Samadi and Barberousse 2006; de Queiroz 2007). The last 10 years have seen a renewal of taxonomy, illustrated by the increasing number of published articles related to species concepts, species delimitation methodology and its application.

In the early 1990s, many systematists began to suspect that the majority of species would remain undescribed (Erwin 1982; Mora et al. 2011; Costello et al. 2013a—but see Costello et al. 2013b) and that some of them will probably go extinct before we have a chance to describe them (Leakey and Lewin 1995; Pimm et al. 2006; Barnosky et al. 2011). The use of molecular data, and in particular molecular barcoding (Hebert et al. 2003), was presented as one answer to this "taxonomic impediment" (as defined in Rodman and Cody 2003), and welcomed as such by taxonomists. It thus adds to the toolkit of taxonomy, which continues its development as a synergic discipline involving morphological taxonomists, field ecologists, naturalists, and statisticians (Knapp 2008). Integrative taxonomy, used for many decades by taxonomists but only recently formalized concomitantly with the molecular revolution, is organised following a three-step workflow (see also Evenhuis 2007): first, we need to 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, that is, 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 (Schlick-Steiner et al. 2007; Patterson et al. 2010; Satler et al. 2013). 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.

Although 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 8 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 information (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 Supplementary material, available at http://dx.doi.org/10.5061/dryad.59jp0. Contingency tables were analyzed 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 animals 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 (Supplementary material 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 (Supplementary material 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 four 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), chondrichtyans (4), and crocodilians and turtles (one 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 with other groups in which there might be fewer—or more plastic—types of characters available to

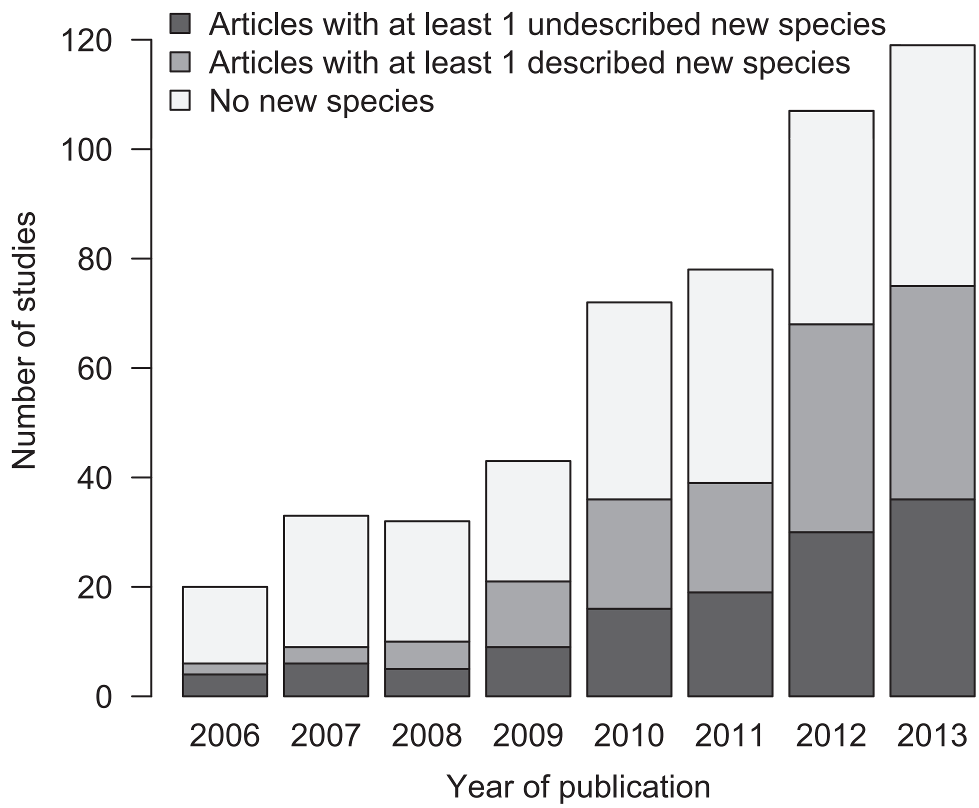

FIGURE 1. Number of articles (2006–2013) that did not delimit new species (dark gray), delimited new species without formally describing them (medium gray), and described newly delimited species (light gray).

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 nonintegrative 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 nonsignificantly 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 10 species, three 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 species for which names were available in the literature but never considered as a valid, such as forms, varieties or subspecies, were counted as new). In the remaining studies, 1346 new species were delimited

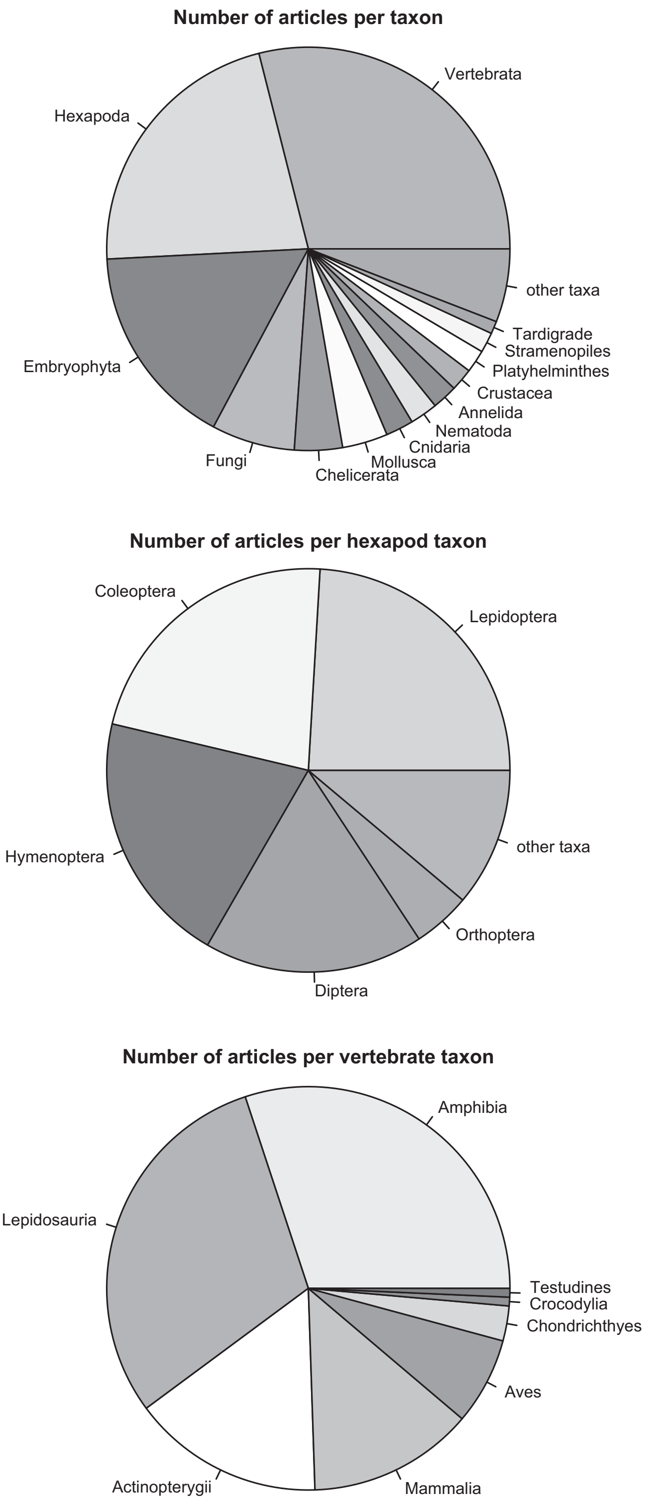

FIGURE 2. Number of articles per taxon (a), with emphasis on hexapods (b), and vertebrates (c). "Other taxa:" taxa for which fewer than five articles were analyzed.

(for studies providing a range of putatively new species, we used the lower number reported by the authors), representing 18.7% of the total number of delimited species in the 494 studies (7205). Among the studies that delimited new species, 125 delimited but did not describe at least one new species and 139 described at least one new species (in 10 studies some new species were described and others not). The ratio of Described over Undescribed Species (hereon called the "DUS" ratio, more specifically calculated as the number of studies that delimited new species and described at least one new species divided by the number of studies that delimited new species and did not describe at least one new species) was ~1.11 for the whole dataset and did not change significantly from 2006 to 2013 (Fisher's exact test: $P = 0.91$). The DUS ratio varies nonsignificantly among taxa: when considering only the taxa represented by more than five studies, the ratio varied from 0.44 for molluscs to 4 for platyhelminthes (these differences are largely driven by small sample sizes; Fisher's exact test: $P = 0.67$; Table 3). Finally, the DUS ratio also varies with the number and the type of characters analyzed. The ratio is 0.29 when only one type of character is analyzed, 1.54 with two types of characters, and 1.70 with three types of characters (only four studies found new species with four different types of characters; DUS = 1.33). Studies describing new species were more likely to use two types of characters or more, compared with studies that delimited new species without describing all of them (Fisher's exact test: $P < 0.001$), confirming that taxonomists prefer to have multiple sources of information to describe species. The DUS ratio is 1.05 when molecular data (alone or among other types of data) are analyzed, 1.87 when morphological data are analyzed, and 1.22 when other types of characters are analyzed, and these differences were statistically 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 toward 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,

TABLE 1. Number of studies (percent of total, per year) analyzing one, two, three, or four types of characters for delimiting species

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

TABLE 2. Number of studies (percent of total, per year) that included molecular data or morphological data for each year (2006–13)

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

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. Pons et al. 2006; Puillandre et al. 2012; Ratnasingham and Hebert 2013; Zhang et al. 2013; Kekkonen and Hebert 2014. 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

TABLE 3. Number of studies (percent of total, per taxon) without new species, with at least one delimited but undescribed new species, and with at least one described species in each taxon considered

	Articles without new species	Articles with ≥1 undescribed new species	Articles with ≥ 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

Note: The DUS ratio corresponds to the ratio of columns 3 and 2.

because many might be in "gray 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 by 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 gray zone (reviewed in Fujita et al. 2012; Camargo and Sites 2013; Carstens et al. 2013; and see Leaché et al. 2014). In any case, species are and remain, by definition (Samadi and Barberousse 2006; de Queiroz 2007), 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 delimitated, 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 their 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 (Minelli 2003; Bertrand et al. 2006; Jansen et al. 2011), including names proposed in an old and antiquated literature, sometimes not written in English (Godfray 2002; Balakrishnan 2005). 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 (Schindel and Miller 2010; Ratnasingham and Hebert 2013), to, at least partly, solve the difficulties linked to describing new species and to reduce "shelf life" (Fontaine et al. 2012). However, none of these alternate referencing systems has 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, six of them have never published species descriptions, based on Zoological Records, and six did not publish species descriptions after 2004; on average, journals including descriptions had a lower impact factor than the journals that do not. Due to 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 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.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.59jp0.

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REFERENCES

Agnarsson I., Kuntner M. 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. Syst. Biol. 56:531–539.

Balakrishnan R. 2005. Species concepts, species boundaries and species identification: a view from the Tropics. Syst. Biol. 54:689–693.

Barnosky A.D., Matzke N., Tomiya S., Wogan G.O.U., Swartz B., Quental T.B., Marshall C., McGuire J.L., Lindsey E.L., Maguire K.C., Mersey B., Ferrer E.A. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–57.

Bertrand Y., Pleijel F., Rouse G.W. 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. Syst. Biodivers. 4:149–159.

Camargo A., Sites J.J. 2013. Species delimitation: a decade after the renaissance. In: Pavlinov Y.I., Rijeka (HR), editors. The species problem - ongoing issues. INTECH, p. 225–247.

Carstens B.C., Pelletier T.A., Reid N.M., Satler J.D. 2013. How to fail at species delimitation. Mol. Ecol. 22:4369–4383.

Casadevall A., Fang F.C. 2014. Causes for the persistence of impact factor mania. mBio 5:e00064–14.

Chapman A.D. 2009. Numbers of living species in Australia and the World, 2nd ed. Canberra, Australian Government, Department of the Environment, Water, Heritage, and the Arts.

Cook L.G., Edwards R.D., Crisp M.D., Hardy N.B. 2010. Need morphology always be required for new species descriptions? Invertebr. Syst. 24:322–326.

Costello M.J. 2009. Motivating online publication of data. BioScience 59:418–427.

Costello M.J., May R.M., Stork N.E. 2013a. Can we name Earth's species before they go extinct? Science 339:413–416.

Costello M.J., Wilson S., Houlding B. 2013b. More taxonomists describing significantly fewer species per unit effort may indicate that most species have been discovered. Syst. Biol. 62:616–624.

Dayrat B. 2005. Towards integrative taxonomy. Biol. J. Linn. Soc. 85: 407–415.

Dayrat B., Cantino P.D., Clarke J.A., de Queiroz K. 2008. Species names in the PhyloCode: the approach adopted by the international society for phylogenetic nomenclature. Syst. Biol. 57:507–514.

de Queiroz K. 2007. Species concepts and species delimitation. Syst. Biol. 56:879–886.

Erwin T.L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopt. Bull. 36:74–75.

Evenhuis N.L. 2007. Helping solve the "other" taxonomic impediment: completing the eight steps to total enlightenment and taxonomic Nirvana. Zootaxa 1407:3–12.

Fonseca G., Derycke S., Moens T. 2008. Integrative taxonomy in two free-living nematode species complexes. Biol. J. Linn. Soc. 94: 737–753.

Fontaine B., Perrard A., Bouchet P. 2012. 21 years of shelf life between discovery and description of new species. Curr. Biol. 22:R943–R944.

Fujita M.K., Leaché A.D. 2011. A coalescent perspective on delimiting and naming species: a reply to Bauer et al. Proc. R. Soc. B 22:490–492.

Fujita M.K., Leaché A.D., Burbrink F.T., McGuire J.A., Moritz C. 2012. Coalescent-based species delimitation in an integrative taxonomy. Trends Ecol. Evol. 27:480–488.

Gaston K.J., May R.M. 1992. Taxonomy of taxonomists. Nature 356: 281–282.

Godfray H.C.J. 2002. Challenges for taxonomy. Nature 417:17–19.

Goldstein P.Z., DeSalle R. 2011. Integrating DNA barcode data and taxonomic practice: determination, discovery, and description. Bioessays 33:135–147.

Hebert P.D.N., Cywinska A., Ball S.L., deWaard J.R. 2003. Biological identifications through DNA Barcodes. Proc. R. Soc. B 270: 313–321.

Hogan K.M., Hedin M.C., Koh H.S., Davis S.K., Greenbaum I.F. 1993. Systematic and taxonomic implications of karyotypic, electrophoretic, and mitochondrial-DNA variation in *Peromyscus* from the Pacific Northwest. J. Mammal. 74:819–831.

Isaac N.J.B., Mallet J., Mace G.M. 2004. Taxonomic inflation: its influence on macroecology and conservation. Trends Ecol. Evol. 19:464–469.

Jansen M., Bloch R., Schulze A., Pfenninger M. 2011. Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. Zool. Scr. 40:567–583.

Kekkonen M., Hebert P.D.N. 2014. DNA barcode-based delineation of putative species: efficient start for taxonomic workflows. Mol. Ecol. Resour. 14:706–715.

Knapp S. 2008. Taxonomy as a team sport. In: Wheeler Q.D., editor. The new taxonomy. p. 33–53.

Knapp S., Lughadha E.N., Paton A. 2005. Taxonomic inflation, species concepts and global species lists. Trends Ecol. Evol. 20:7–8.

Leaché A.D., Fujita M.K., Minin V., Bouckaert R. 2014. Species delimitation using genome-wide SNP data. Syst. Biol. 63: 534–542.

Leakey R.E., Lewin R. 1995. The sixth extinction: patterns of life and the future of humankind. New-York, Doubleday.

Leliaert F., Verbruggen H., Wysor B., Clerck O.D. 2009. DNA taxonomy in morphologically plastic taxa: algorithmic species delimitation in the *Boodlea* complex (Chlorophyta: Cladophorales). Mol. Phylogenet. Evol. 53:122–133.

Mace G.M. 2004. The role of taxonomy in species conservation. Philos. Trans. R. Soc. B 359:711–719.

McFadden C.S., Sanchez J.A., France S.C. 2010. Molecular phylogenetic insights into the evolution of Octocorallia: a review. Integr. Comp. Biol. 50:389–410.

Miller S.E. 2007. DNA barcoding and the renaissance of taxonomy. Proc. Natl Acad. Sci. USA 104:4775–4776.

Minelli A. 2003. The status of taxonomic literature. Trends Ecol. Evol. 18:75–76.

Mora C., Tittensor D.P., Adl S., Simpson A.G.B., Worm B. 2011. How many species are there on Earth and in the ocean? PLoS Biol. 9:e1001127.

Padial J.M., Miralles A., De la Riva I., Vences M. 2010. The integrative future of taxonomy. Front. Zool. 7:16.

Pante E., Abdelkrim J., Viricel A., Gey D., France S., Boisselier M.C., Samadi S. Forthcoming 2014. Use of RAD sequencing for delimiting species. Heredity, doi:10.1038/hdy.2014.105.

Patterson D.J., Cooper J., Kirk P.M., Pyle R.L., Remsen D.P. 2010. Names are key to the big new biology. Trends Ecol. Evol. 25:686–691.

Pearson D.L., Hamilton A.L., Erwin T.L. 2011. Recovery plan for the endangered taxonomy profession. BioScience 61:58–63.

Pessoa E.M., Alves M., Alves-Araújo A., Palma-Silva C., Pinheiro F. 2012. Integrating different tools to disentangle species complexes: a case study in Epidendrum (Orchidaceae). Taxon 61:721–734.

Pimm S., Raven P., Peterson A., Sekercioglu C.H., Ehrlich P.R. 2006. Human impacts on the rates of recent, present, and future bird extinctions. Proc. Natl Acad. Sci. USA 103:10941–10946.

Pons J., Barraclough T.G., Gomez-Zurita J., Cardoso A., Duran D.P., Hazell S., Kamoun S., Sumlin W.D., Vogler A.P. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Syst. Biol. 55:595–609.

Puillandre N., Lambert A., Brouillet S., Achaz G. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Mol. Ecol. 21:1864–1877.

Puillandre N., Macpherson E., Lambourdière J., Cruaud C., Boisselier-Dubayle M.-C., Samadi S. 2011. Barcoding type specimens helps to identify synonyms and an unnamed new species in *Eumunida* Smith, 1883 (Decapoda: Eumunididae). Inv. Syst. 25:322–333.

R Core Team. 2014. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.

Ratnasingham S., Hebert P.D.N. 2013. A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. PLoS One 8:e66213.

Riedel A., Sagata K., Surbatki S., Tänzler R., Balke M. 2013. One hundred and one new species of *Trigonopterus* weevils from New Guinea. Zookeys 280:1–150.
Rodman J.E., Cody J.H. 2003. The taxonomic impediment overcome: NSF's partnerships for enhancing expertise in taxonomy (PEET) as a Model. Syst. Biol. 52:428–435.
Samadi S., Barberousse A. 2006. The tree, the network, and the species. Biol. J. Linn. Soc. 89:509–521.
Sangster G. 2009. Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. Proc. R. Soc. B 276:3185–3191.
Satler J.D., Carstens B.C., Hedin M. 2013. Multilocus species delimitation in a complex of morphologically conserved trapdoor spiders (Mygalomorphae, Antrodiaetidae, *Aliatypus*). Syst. Biol. 62:805–823.
Schindel D.E., Miller S.E. 2010. Provisional nomenclature: the on-ramp to taxonomic names. In: Polaszek A., editor. Systema naturae 250 – the Linnaean ark. London, UK: CRC Press, p. 109–115.
Schlick-Steiner B.C., Seifert B., Stauffer C., Christian E., Crozier R.H., Steiner F.M. 2007. Without morphology, cryptic species stay in taxonomic crypsis following discovery. Trends Ecol. Evol. 22: 391–392.
Schlick-Steiner B.C., Steiner F.M., Seifert B., Stauffer C., Christian E., Crozier R.H. 2009. Integrative taxonomy: a multisource approach to exploring biodiversity. Annu. Rev. Entomol. 55: 421–438.
Turrill W.B. 1938. The expansion of taxonomy with special reference to Spermatophyta. Biol. Rev. 13 :342–373.
Vences M., Guayasamin J.M., Miralles A., De La Riva I. 2013. To name or not to name: criteria to promote economy of change in Linnaean classification schemes. Zootaxa 3636:201–244.
Werner Y.L. 2006. The case of impact factor versus taxonomy: a proposal. J. Nat. Hist. 40:1285–1286.
Will K.P., Mishler B.D., Wheeler Q.D. 2005. The perils of DNA Barcoding and the need for integrative taxonomy. Syst. Biol. 54: 844–851.
Yeates D., Seago A., Nelson L., Cameon S.L., Joseph L., Trueman J.W.H. 2011. Integrative taxonomy, or iterative taxonomy? Syst. Entomol. 36:209–217.
Zhang J., Kapli R., Pavlidis P., Stamatakis A. 2013. A general species delimitation method with applications to phylogenetic placments. Bioinformatics 29:2869–2876.
Zhang Z.Q. 2011. Animal biodiversity: an introduction to higher-level classification and taxonomic richness. Zootaxa 3148:7–12.