

# From Integrative Taxonomy to Species Description: one Step Beyond

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1 SPECIES DELIMITATION AND DESCRIPTION

2

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

4

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21

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,

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

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

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

75 molecular data, helped to alleviate the taxonomic impediment by delimiting *and* describing  
76 new species. We reviewed part of the “integrative taxonomy” literature of the last eight years  
77 (2006-2013) and tested if authors that delimit new species also name them. We also looked at  
78 how the number and type of characters used, across different taxa, varies across articles.

79

## 80 **MATERIALS AND METHODS**

81

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

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

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

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

125 hypothesis that journals including formal species descriptions do not have lower impact  
126 factors than journals that do not. All statistical tests were performed in R (R Core Team  
127 2014).

128

## 129 **RESULTS**

130

131           The 494 articles were published in 150 different journals, over half of which  
132 published a single article from our list, and 4 of which (Molecular Phylogenetics and  
133 Evolution, Zootaxa, PLOS ONE and the Zoological Journal of the Linnean Society) published  
134 over 20 articles. The number of articles published each year steadily increased from 2006 (20  
135 articles) to 2013 (118 articles) (Fig. 1). Most major lineages of organisms are represented, but  
136 the number of articles varies greatly among groups (Fig. 2a). Among hexapods,  
137 hymenopterans, lepidopterans, coleopterans and dipterans were the taxon of interest for 19-26  
138 articles each (Fig. 2b); among vertebrates, amphibians (43 articles) and lepidosaurians (43)  
139 are the most studied taxa, followed by actinopterygians (22), mammals (19), birds (10),  
140 chondrichthyans (4), and crocodylians and turtles (1 each) (Fig. 2c). In all taxonomic groups  
141 represented by more than five articles, molecular data were analyzed in 100% of the articles,  
142 except for embryophytes (71.6%), vertebrates (88.8%), chelicerates (94.7%), hexapods  
143 (92.6%) and annelids (90%). One possible explanation for the lower prevalence of molecular  
144 data in these taxonomic groups is that morphological characters may generally be more easily  
145 formalized, and congruent with molecular data (compared to other groups in which there  
146 might be fewer -or more plastic- types of characters available to taxonomists, such as some  
147 cnidarians, e.g. McFadden et al., 2010).

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



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

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

173 A total of 240 studies did not delimit any new species, but confirmed the current alpha  
174 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:  $p=0.009$ ).

200           Among the 150 journals of our sample, 84 delineated new species. Our Impact Factor  
201 analysis, using Zoological Record, focused on 73 zoological journals. Among these journals,  
202 90.4% published descriptions from 1864 to 2013, 9.6% never published descriptions within  
203 that period, and 16.4% stopped publishing descriptions within that period (either from 2005  
204 onward, or from 2011 onward). The average impact factor of journals with species  
205 delimitation but without descriptions was significantly higher than that of journals publishing  
206 formal descriptions during the 2005-2013 periods (one-tail Wilcoxon:  $n=50$ ,  $W = 72$ ,  $p =$   
207  $0.038$ ).

208

## 209 **DISCUSSION**

210

211           As reported previously (Gaston and May 1992), taxonomy studies are strongly biased  
212 towards vertebrates (here, they accounted for 29% of the articles we reviewed), even though  
213 this taxon accounts for only ~3% of the described diversity on earth (Chapman 2009; Zhang  
214 2011) and probably has the highest ratio of described over undescribed species. Most of the  
215 studies on vertebrates actually focus on groups that still encompass high levels of unknown  
216 species, such as amphibians or lepidosaurians. Integrative taxonomy and molecular taxonomy  
217 are linked in 90% of the studies, confirming that the formal definition of integrative taxonomy  
218 in 2005 is probably linked to the concomitant molecular revolution (as explained in the  
219 introduction). In the literature, both have often been associated with an inflation in the number  
220 of new species, artificial or not (Isaac et al. 2004; Knapp et al. 2005; Sangster 2009). Our  
221 results suggest that this is not always true: 48.7% of studies did not detect new species, and  
222 some authors actually proposed to reduce the number of valid species in their taxon of  
223 interest.

224           When new species are discovered, however, they are not systematically described (in  
225 46.1% of the articles), thus leaving the new species unnamed. In these cases, several  
226 justifications for not describing have been put forth by the authors, and we propose a few  
227 more. The first reason is the lack of support for the species hypotheses (given in 72.2% of the  
228 articles that do provide a justification). In taxa for which the proportion of unknown species is  
229 greater than the number of described species, difficulties are linked to the fact that nobody has  
230 ever proposed species hypotheses. Exploratory methods are therefore needed, either based on  
231 traditional morphological characters or on molecular markers (several DNA-based methods  
232 are now available: e.g. (Kekkonen and Hebert, 2014; Pons et al., 2006; Puillandre et al., 2012;  
233 Ratnasingham and Hebert, 2013; Zhang et al., 2013). This exploratory step is generally  
234 efficient to detect highly divergent lineages that most probably correspond to different  
235 species. However, it is more difficult to estimate the number of species in clades with many  
236 closely-related species because many might be in “grey zones” (i.e. parts of the tree of life  
237 where the speciation process is ongoing and where different types of characters and criteria  
238 will not provide the same answer, as defined in de Queiroz, 2007). This situation is  
239 encountered in well-studied groups (e.g. some vertebrates and flowering plants), for which  
240 what was easy to recognize as species has been described, and challenging species complexes  
241 remain to be disentangled (e.g. in orchids, Pessoa et al., 2012). Several multi-locus and  
242 coalescent-based methods now exist to help delimit species in the grey zone (reviewed in  
243 Camargo and Sites 2013; Carstens et al. 2013; Fujita et al. 2012, and see Leaché et al., 2014).  
244 In any case, species are and remain, by definition (de Queiroz 2007; Samadi and Barberousse  
245 2006), only hypotheses, and these hypotheses can be more or less supported. In an integrative  
246 context, the number of arguments, data and criteria (including the need for additional  
247 specimens) needed for defining new species and their hierarchy can vary depending on the  
248 taxon considered or the approach applied, and turning species hypotheses into a formally

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

254         However, in other cases, the species hypothesis is highly supported by numerous lines  
255 of evidence, but remains undescribed. Consequently, other reasons should be invoked. For  
256 example, it could be the choice of the author to not describe the species in the article where it  
257 has been delimited, but in a forthcoming article (reason given in 24.1% of the studies  
258 providing a justification for not describing). This can be motivated by the fact that the authors  
259 wish to present additional data that are beyond the scope of the present article (e.g. Pante et  
260 al., 2014). It can also be explained by the pressure of publishing more papers, driving many  
261 authors to publish in several articles what could be published in one (i.e. submitting their  
262 work as “least publishable units”). Then, taxonomists might refrain from describing a species  
263 if no morphological differences were found with its sister-species, although there is no reason  
264 to think that all “good” species will exhibit morphological differences (Fujita and Leaché  
265 2011). Diagnosing a new species using only DNA characters is possible, but not yet  
266 widespread (Cook et al. 2010), especially in animals, although molecular data are increasingly  
267 included in species descriptions (Goldstein and DeSalle 2011). Actually, a substantial part  
268 (35.4%) of the articles we reviewed delimited species with only one type of character.  
269 However, even if only one type of character is used, it generally remains associated with the  
270 use of different loci, or different methods, or different criteria (phenetic – genetic distances,  
271 phylogenetic – reciprocal monophyly, reproductive isolation – independent molecular  
272 markers).

273 Another reason for not naming new species is the unwillingness of some scientists  
274 (e.g. molecular systematists) to describe species (Satler et al., 2013). A formal description  
275 should follow strict nomenclatural rules dictated by the codes of nomenclature, and writing a  
276 species description is in itself an exercise that necessitates training that is rarely proposed in  
277 modern biological classes (Pearson et al. 2011). Fonseca et al. (2008) and Leliaert et al.  
278 (2009) also highlighted the need of sequencing type-specimens to correctly attribute available  
279 species names or name new species (Puillandre et al 2011). Furthermore, proposing a new  
280 name necessitates, at the very least, a literature review of all the species-level names available  
281 (Bertrand et al. 2006; Jansen et al. 2011; Minelli 2003), including names proposed in an old  
282 and antiquated literature, sometimes not written in English (Balakrishnan 2005; Godfray  
283 2002). Naming new species also necessitates comparison with existing type material, often  
284 requiring visits to museums. Non-taxonomists are often frustrated by the over-abundance of  
285 redundant species names (i.e. species that have multiple synonymous names) as well as  
286 doubtful names (Dayrat, 2005), which makes the assignation of species names to well-  
287 delineated entities even more difficult. Once again, this exercise requires excellent knowledge  
288 of the group, contrary to a genetic approach which is basically the same in mammals and in  
289 plants, and can be time consuming (Miller 2007). Other systems have been proposed, some  
290 designed to replace the Linnean System (Dayrat et al. 2008; Vences et al. 2013), others only  
291 proposing interim systems before full description following the Linnean System  
292 (Ratnasingham and Hebert 2013; Schindel and Miller 2010), to, at least partly, solve the  
293 difficulties linked to describing new species and to reduce “shelf-time” (Fontaine et al. 2012).  
294 However, none of these alternate referencing systems have been as widely accepted and  
295 applied as the Linnean system.

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

298 when they are numerous and long (the number of pages is generally very limited in these  
299 journals). In this study, we showed that among the 23 journals that included at least one study  
300 in which new species were delimited but not described, 6 of them have never published  
301 species descriptions, based on Zoological Records, and 6 did not publish species descriptions  
302 after 2004; on average, journals including descriptions had a lower impact factor than the  
303 journals that do not. Because of the publication pressure, authors will almost automatically  
304 prefer to publish in high impact factor journals, even at the price of removing the species  
305 descriptions (Agnarsson and Kuntner, 2007; Costello 2009). Scientists all know the  
306 importance in the current system to have articles in journals with high-impact factors, and  
307 thus most of them do not spend their time in writing articles that will not be rewarded (Minelli  
308 2003).

309

## 310 **CONCLUSION**

311

312 The increase in the number of articles recorded between 2006 and 2013, and the large  
313 range of journals represented in our review reflects the high dynamism of the taxonomic  
314 community. In addition, the increase in the proportion of papers using multiple lines of  
315 evidence underlines the success of the modern integrative taxonomy approach, as defined in  
316 2005. The positive relationship between the number of different types of characters used for  
317 delimitation, which can be seen as a proxy of the degree of integration, and the DUS ratio also  
318 supports the idea that integrative taxonomy contributes to a better understanding of  
319 biodiversity. However, the 446 species described in the reviewed articles are only a drop in  
320 the ocean of new species described in the same period (85,000, if considering a mean of  
321 17,000 new species described each year – <http://www.esf.edu/species/SOS.htm>).

322 Nevertheless, this sample reflects the fact that modern integrative taxonomy as formalized in

323 2005 (thus not considering the pre-2005 articles that delimited and described species using an  
324 integrative taxonomy-like approach), is, at least for the moment, not a very efficient solution  
325 to the taxonomic impediment. Most new species seem to be described without applying an  
326 integrative taxonomy approach, and most new species are still described without the help of  
327 molecular data: a screening of 200 articles published in 2013, obtained with the keywords  
328 “Taxonomy” in TOPIC AND “sp nov” in SYSTEMATICS in Zoological Records revealed  
329 that only 18 of them mentioned the use of molecular data in the abstract. This would suggest  
330 that most species are thus still described using morphological characters only. The “molecular  
331 revolution” that was announced after the renewal of the taxonomy in the early 2000s, largely  
332 associated with the emergence of the integrative taxonomy approach, has apparently not  
333 happened yet. We are convinced that integrative taxonomy, when associated with formal  
334 species description, is a good way to improve the quality of species hypotheses and associated  
335 descriptions, and should therefore be encouraged. However, and contrary to a barcoding  
336 approach that can perhaps accelerate the rate of species discovery (but not improve the quality  
337 of the species hypotheses nor the rate of species description; e.g. Will et al., 2005), integrative  
338 taxonomy did not accelerate the rate of species description between 2006 and 2013. Efforts  
339 must be made by authors to seek training or new collaborations to formalize their species  
340 delimitation, and to avoid delaying new species descriptions for reasons associated with  
341 impact factors. Editors may help the naming of newly delimited species by encouraging the  
342 publication of species descriptions. Editorial policies could, for instance, impose that new  
343 delimitation be either accompanied by formal descriptions or a strong justification for not  
344 describing. Research institutions and funding agencies may encourage the naming of newly  
345 delimited species by recognizing taxonomic work as a foundation of biological research, and  
346 refrain from putting too much emphasis on impact factors when evaluating scientists.

347



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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*

<b>Nb of characters</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>Total</b>
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*

<b>Nb of characters</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>Total</b>
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*

<b>Nb of characters</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>Total</b>
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

	<b>Articles without new species</b>	<b>Articles with <math>\geq 1</math> undescribed new species</b>	<b>Articles with <math>\geq 1</math> described species</b>	<b>DUS ratio</b>
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.