

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**

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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

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

	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)

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 ≥ 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

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.