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Taxonomic Quality of Species Descriptions Varies over Time and with the Number of Authors, but Unevenly among Parasitic Taxa

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Abstract.—Although concerns are being raised about a potential shortage of taxonomists and systematists, recent analyses suggest instead that the number of researchers involved in taxonomic descriptions is higher than ever and that the average number of new species described annually per taxonomist has declined in recent decades. Here, using nine metrics of taxonomic quality, such as the number of morphological traits measured, the number of separate line drawings included, and whether or not gene sequences are provided, we explore variation in taxonomic quality as a function of the number of authors and other potential determinants across 2366 descriptions of parasitic helminths published in 1337 articles between 1980 and 2014. Taxonomic quality has generally increased over time, but unequally among different groups of helminths. For example, the number of scanning electron micrographs per description has risen significantly over time in cestodes and nematodes, but decreased for digeneans. For most metrics used, the greater the number of authors per species description, the higher its quality, suggesting not more taxonomists but more collaborations between taxonomists and experts from other fields to produce more comprehensive species characterizations. Re-descriptions of species were of higher quality than their original descriptions, and the improved quality correlated with the number of years elapsed between them. However, the extent of this improvement varied among helminth species with different host taxa. Overall, our findings provide a note of caution for anyone using trends in the number of species described per author to extrapolate the total number of extant species. They also reveal cultural differences among taxonomists working on different groups of parasites that can serve to identify areas for potential improvement. [Biodiversity; Cestoda; Digenea; integrative taxonomy; Nematoda.]

With much of the Earth's biodiversity yet to be discovered and described, several commentators have recently expressed concerns about the dwindling taxonomic workforce's ability to document remaining species within a reasonable time (Wheeler et al. 2004; Agnarsson and Kuntner 2007; Pearson et al. 2011). If this is true for free-living organisms, it must be even more so for the smaller symbionts and parasites living on or within them. Indeed, alarm bells regarding a likely shortage of well-trained parasite taxonomists and systematists have been sounded many years ago (Brooks and Hoberg 2000, 2001) and continue to echo today (Cribb 2016).

In contrast, recent studies show that for a wide range of taxa, the number of researchers involved in taxonomic descriptions is increasing faster than the number of new species described per year (Joppa et al. 2011; Costello et al. 2013; Tancoigne and Dubois 2013). The upshot is that the average number of new species described per taxonomist per year has been declining more or less steadily in recent decades. Some have argued that this provides evidence that new species are becoming harder to find and that our inventory of Earth's biodiversity is close to complete (Costello et al. 2013). However, this ignores the fact that more people and greater effort are needed to achieve increasingly thorough and comprehensive species descriptions. Also, an analysis focusing specifically on parasitic helminths revealed a very different pattern: the average number of new species described annually per author has risen steadily over the past three decades (Poulin 2014). This does not support the idea that the pool of missing species is diminishing. At the same time, the mean number of authors per new species described has also been increasing over the same period (Poulin 2014). Instead of indicating a rise in the number of taxonomists, as suggested by Costello et al. (2013), an alternative explanation is that species descriptions increasingly require the contribution of multiple experts with different skill sets. The old image of the taxonomist working alone to describe new specimens is rapidly fading. Parasite taxonomy has been greatly influenced by technological advances, in particular the rise of molecular genetics and the increasing availability of scanning electron microscopy to characterize subtle morphological features. Taxonomy does not consist merely of naming species; it is rigorous science treating the existence of new species as hypotheses to be tested (Sluys 2013). The new tools at the disposal of parasite taxonomists may have fuelled greater sophistication

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in species description and greater rigor in species delimitation. Thus, far from reflecting a large workforce with fewer species to document, or the author inflation in publications across the sciences (Bebber et al. 2014), the higher number of people involved in species descriptions may simply mirror the steadily rising standards expected from new descriptions, with non-taxonomists being co-opted to contribute their particular expertise.

Recently, Sangster and Luksenburg (2015) have demonstrated that the quality of taxonomic descriptions of bird species has increased markedly over the past century, in parallel with a rise in the number of authors per description. Several quality metrics, such as the numbers of specimens examined, the number of characters measured, and the number of taxa to which the new species has been compared, have all increased linearly as a function of time. In addition, many species require re-descriptions or revisions, because original descriptions are not always sufficiently detailed to allow correct species delimitation. Bird species that were subsequently revised or re-described had original descriptions of lower quality than those that were not, and the re-descriptions scored higher than the original descriptions on all quality metrics (Sangster and Luksenburg 2015). These findings suggest that greater time and effort go into recent species descriptions than went into older ones. This is true for birds, which are among the best-known animal taxa, but may not necessarily be so for lesser-known groups such as parasite taxa. There may exist “cultural” or idiosyncratic differences between taxonomists working on different taxa. For instance, even among parasitic helminths, the mean number of authors per new species described is generally higher for digeneans than for acanthocephalans (Poulin 2014). An assessment of changes in the quality of taxonomic descriptions of parasite species is needed to reconcile trends in the number of people participating in species descriptions with trends in the number of new species described annually.

Taxonomy and systematics are cornerstones of parasitology, as they underpin all efforts at targeting the *right* species of parasite or vector to control diseases of humans, livestock and wildlife (Littlewood 2011). So, what is the status of parasite taxonomic research? In this article, we document temporal changes in the quality of taxonomic descriptions of parasitic helminths belonging to three large taxa with complex life cycles and infecting all vertebrate classes: Cestoda, Digenea, and Nematoda. Specifically, we test the following five predictions: (1) species descriptions have become more elaborate over time as measured by several quality metrics; (2) the rise in quality of species descriptions is not equal among the three helminth taxa; (3) more authors per description leads to higher taxonomic quality; (4) original descriptions of species that are subsequently re-described are of lower overall quality than those that are not re-described; and (5) the improvement in the quality of re-descriptions relative to original descriptions is proportional to the number of years elapsed between them. Our findings complement recent recommendations for the description of new parasite species (Slapeta 2013; Blasco-Costa et al. 2016), by highlighting the drive toward higher quality descriptions and its uneven application among helminth taxa.

Methods

Data Compilation

We retrieved all species descriptions that appeared in either *Journal of Parasitology* or *Systematic Parasitology* between 1980 and 2014 by systematically reviewing each issue published during that period. These two journals have been, and continue to be, major outlets for species descriptions of parasitic helminths, and thus provide a representative cross section of taxonomic studies over the 35-year period. Because by convention parasitic helminths are generally only named based on adult specimens, we excluded descriptions of larval or juvenile stages alone; these are usually assigned to a genus or family only. We made an exception in the case of trypanorhynch cestodes, where new species are sometimes described based on juvenile specimens only because these change very little as they develop into adults. All species descriptions in our database consisted of either a newly named species accompanied by a morphological diagnosis, or a previously named species being re-described (and possibly transferred to another genus, split, or lumped/synonymized with another species) with a different or expanded diagnosis.

For each species description, we recorded the species name, the higher taxon to which it belonged (Digenea, Cestoda, or Nematoda), whether it was an original description or a re-description (including change of name if assigned to different genus), the taxon serving as definitive host (fish, herptiles, birds, or mammals) or sole host (invertebrates, in the case of several nematodes), the year and journal of publication, and the number of authors of the description. In the case of re-descriptions, we also noted the year in which the original description was published. If the original description was among the studies in our main data set (i.e., published in one of our two target journals between 1980 and 2014), it was used to determine whether original descriptions of species that are subsequently re-described are of lower quality than those published at the same time that were not re-described. If the original was not part of our main data set, it was retrieved whenever possible (depending on availability via the University of Otago library), to create a new data set, hereafter referred to as the re-description data set, consisting of pairs of original and revised descriptions. This second data set was used to test whether the improvement in the quality of re-descriptions relative to the originals is proportional to the number of years elapsed between them.

We scored each description or re-description on the basis of the following nine quality metrics: (1)

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the number of specimens on which morphological measurements were taken, with the highest number used here in the few cases where different numbers were used for different traits; (2) the number of morphological traits measured, taken here as the number of traits for which quantitative data are given; (3) the number of named taxa to which the new species has been formally compared; (4) the number of separate line drawings provided in addition to a drawing of the whole body; (5) whether light microscope images were provided, and if so how many; (6) whether scanning electron micrographs (SEMs) were provided, and if so how many; (7) whether gene sequences were provided, and if so, how many individuals were sequenced and which genes were characterized; (8) whether or not ecological data on both prevalence and intensity of infection were provided; and (9) whether or not at least one larval or juvenile stage (other than eggs) was also described morphologically. When considering genetic information, we excluded enzyme electrophoretic data, because those were used mostly for species delimitation rather than species description. Also, analyses of genetic data were restricted to species descriptions published from 1999 onward, because this was the year in which DNA sequences were first included among the studies we surveyed. Information was not always available for all nine quality metrics in every species description covered here. For further details regarding the above quality metrics and how they were scored, see Supplementary Appendix 1 (available on Dryad at http://dx.doi.org/10.5061/dryad.j4j7q).

Data Analysis

All analyses were conducted in JMP v. 11.0 (SAS Institute Inc., Cary, NC, USA). Using the main data set, simple correlations (Spearman's rho, r_S) between year of publication and annual means (for count data) or proportion of descriptions per year providing certain data, were used to assess temporal trends in quality metrics. Pairwise correlations were also computed between quality metrics (count data only) across all descriptions of helminth parasite species, to determine how the different metrics covaried with each other.

Subsequently, we tested the influence of several factors on quality metrics across all descriptions using generalized linear models, with Poisson error distributions for count data (number of specimens measured, number of morphological characters measured, number of taxa compared, number of line drawings, number of light microscope images, number of SEM images, number of individuals sequenced) and binomial error distributions for binary data (whether ecological data are provided, whether juvenile or larval stages are described). The fixed factors were the higher helminth taxon (Digenea, Cestoda, or Nematoda) to which a species belonged, the host taxon (invertebrates, fish, herptiles, birds, or mammals), whether it was an original description or a re-description, the year of publication, and the journal in which it appeared. Because one of our central aims was to test whether the temporal improvement in the quality of species descriptions differs among the three helminth taxa, we also included the interaction between helminth taxon and year of description.

The link between the number of authors of a species description and its taxonomic quality was assessed as part of the correlation analyses mentioned above. In addition, we determined whether the inclusion of either SEM images, genetic data, ecological data, or descriptive data on larval or juvenile stages, was associated with more authors. For this, we used generalized linear models, with Poisson error structure and number of authors as response variable, and both helminth taxon and the binary variable corresponding to the inclusion/exclusion of the above descriptive data as fixed factors.

To test whether original descriptions of species that are subsequently re-described are of lower quality than those that were not re-described, we used data on the 22 species which had both an original description and a re-description published in our main data set (i.e., published in one of our two target journals between 1980 and 2014). To generate fair comparisons, each of these 22 original descriptions was matched with other original descriptions of parasites from the same higher taxon published in the same year and the same journal. In one instance where no other original descriptions of parasites in the same taxon had been published in the same journal and year, we used all other original descriptions from that journal and year for comparison. Each matched set of descriptions was given an ID number. We then used generalized linear mixed models for each quality metric, with Poisson error distributions for count data. The fixed factor was a binary variable indicating whether the species had been re-described or not, and matched set ID was used as a random factor, to control not only for non-independence among the species descriptions in the data set, but also to account for any idiosyncrasies associated with particular combinations of helminth taxon, journal and year of publication. There were too few descriptions providing DNA sequences, ecological data or information of juvenile/larval stages, among both those re-described later and those not re-described, to allow formal analysis.

For the analysis of the re-description data set, we first computed measures of the "improvement" in taxonomic quality for each pair of original description and re-description, as the difference in metric value between them. This was only possible for four quality metrics: number of specimens measured, number of morphological characters measured, number of taxa compared, and number of line drawings (see 'Results' section). Positive differences indicate a higher quality metric value in the re-description than in the original, and vice versa for negative values. These differences were then used as response variables in generalized linear models; the fixed factors were the higher helminth taxon (Digenea, Cestoda, or Nematoda) to which a

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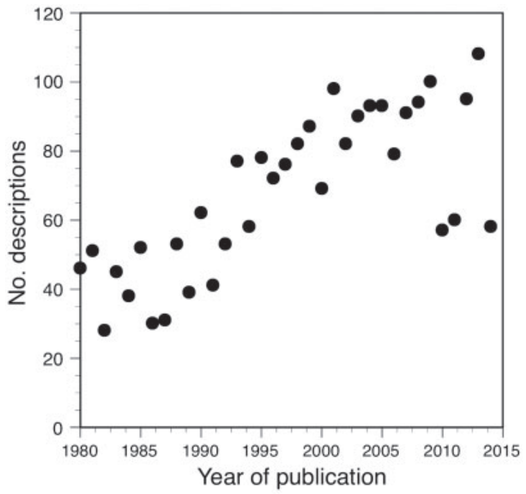

FIGURE 1. Number of descriptions of helminth parasite species (cestodes, digeneans, or nematodes) published annually in either *Journal of Parasitology* or *Systematic Parasitology* in the period 1980–2014.

species belonged, the host taxon (invertebrates, fish, herptiles, birds, or mammals), the time difference (in years, log-transformed) between publication of the original description and the re-description, and the journal in which the re-description appeared.

RESULTS

The main data set consisted of 2366 descriptions of helminth parasite species obtained from 1337 articles published between 1980 and 2014, comprising 651 descriptions of cestodes, 865 of digeneans, and 850 of nematodes; it is publicly available on Dryad http://dx.doi.org/10.5061/dryad.j4j7q. The number of descriptions published annually shows a steady increase over time; there are approximately twice as many descriptions published nowadays than there were in the early 1980s, though the annual output has been highly variable in recent years (Fig. 1). Overall, 1449 descriptions were of new species and 917 were re-descriptions (including revisions and name changes) of previously known species. Finally, there were more descriptions published in *Systematic Parasitology* than in *Journal of Parasitology* (1486 from 716 articles vs. 880 from 621 articles) during the period surveyed.

Temporal Trends in Taxonomic Quality

On average, sampling effort, quantified either as the number of specimens measured or the number of individuals used to obtain gene sequences, did not improve over time in any helminth taxon (Table 1). Similarly, the annual proportion of descriptions providing information on larval or juvenile stages has also remained unchanged over time. In contrast, the mean number of morphological characters measured, the mean number of light microscope images and the proportion of descriptions providing ecological data have all increased over time in all three helminth taxa (Table 1). This remains true for cestodes after exclusion of trypanorhynchs ($r_s = 0.428$, $P = 0.0103$), for which details provided on all proboscis hooks tend to inflate the number of morphological traits measured. The remaining quality metrics, however, show temporal patterns that differ among helminth taxa. For example, the mean number of other taxa to which a species is compared during description has doubled for cestodes and tripled for nematodes from 1980 to 2014, but has not changed significantly for digeneans (Fig. 2). Similarly, the mean number of SEM images included per description has risen from less than 1 to 4–5 in cestodes and nematodes, but remained unchanged for digeneans. Surprisingly, the mean number of line drawings supporting species descriptions has tended to decrease over time for digeneans and nematodes, though not for cestodes (Table 1, Fig. 2).

Determinants of Taxonomic Quality

There were significant positive or negative correlations among several pairs of quality metrics (Supplementary Table S1 in Supplementary Appendix 1 available on Dryad http://dx.doi.org/10.5061/dryad.j4j7q). However, this is mostly due to the high statistical power resulting from large numbers of observations, as the correlations among quality metrics are all very weak (all $r_s < 0.2$). Thus, a species description scoring well on a given quality metric does not necessarily also score well on other metrics. It is therefore appropriate to treat the various metrics as roughly independent measures of description quality.

In general, generalized linear models (GLMs) on individual descriptions supported the temporal trends shown by the above analyses of annual averages (Supplementary Table S2 in Supplementary Appendix 1 available on Dryad http://dx.doi.org/10.5061/dryad.j4j7q). They also revealed significant differences among the three higher helminth taxa with respect to all quality metrics, and a significant interaction between helminth taxon and year of publication also indicated that all quality metrics (except the number of individuals sequenced) did not change over time in the same way in the three helminth taxa (Supplementary Table S2 available on Dryad). For example, the number of SEM images per description has risen significantly over time in cestodes and nematodes, but actually decreased for digeneans (Fig. 3). A simple explanation for these differences may come from the fundamental differences in structural anatomy that exist between cestodes, digeneans, and nematodes. For example, it has become de rigueur to compare the microtriches of cestodes using SEM pictures, whereas the external features of digeneans are not widely adopted as taxonomically useful. The number and nature of distinguishing structures can determine how many morphological traits can (or need to) be measured, and how useful various imaging

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TABLE 1. Temporal trends in measures of quality and in number of authors of species descriptions of parasites in three helminth taxa, estimated as the correlation (Spearman's rho, r_s) between annual means (for count data) or proportion of descriptions and year of publication (1980–2014). Significant correlations are highlighted in bold.

		Cestodes		Digeneans		Nematodes	
	N (years)	r_s	*P*	r_s	*P*	r_s	*P*
Specimens measured (number)	35	0.135	0.4384	−0.160	0.3596	−0.099	0.5736
Morphological characters measured/counted (number)	35	0.429	**0.0102**	0.793	< **0.0001**	0.750	< **0.0001**
Taxa compared (number)	35	0.711	< **0.0001**	0.167	0.3386	0.797	< **0.0001**
Line drawings (number)	35	0.269	0.1179	−0.473	**0.0041**	−0.345	**0.0421**
Light microscope images (number)	35	0.468	**0.0046**	0.633	< **0.0001**	0.510	**0.0018**
SEM images (number)	35	0.834	< **0.0001**	−0.223	0.1978	0.738	< **0.0001**
Individuals sequenced (number)[a]	16	−0.144	0.7578	0.037	0.9151	−0.014	0.9655
Ecological data (proportion)	35	0.510	**0.0017**	0.793	< **0.0001**	0.848	< **0.0001**
Description of larvae/juveniles (proportion)	35	0.314	0.0661	−0.002	0.9892	−0.131	0.4530
Authors (number)	35	0.699	< **0.0001**	0.857	< **0.0001**	0.807	< **0.0001**

Notes: [a]Measured only across studies that presented DNA sequences and starting since the first use of DNA sequences (1999–2014).

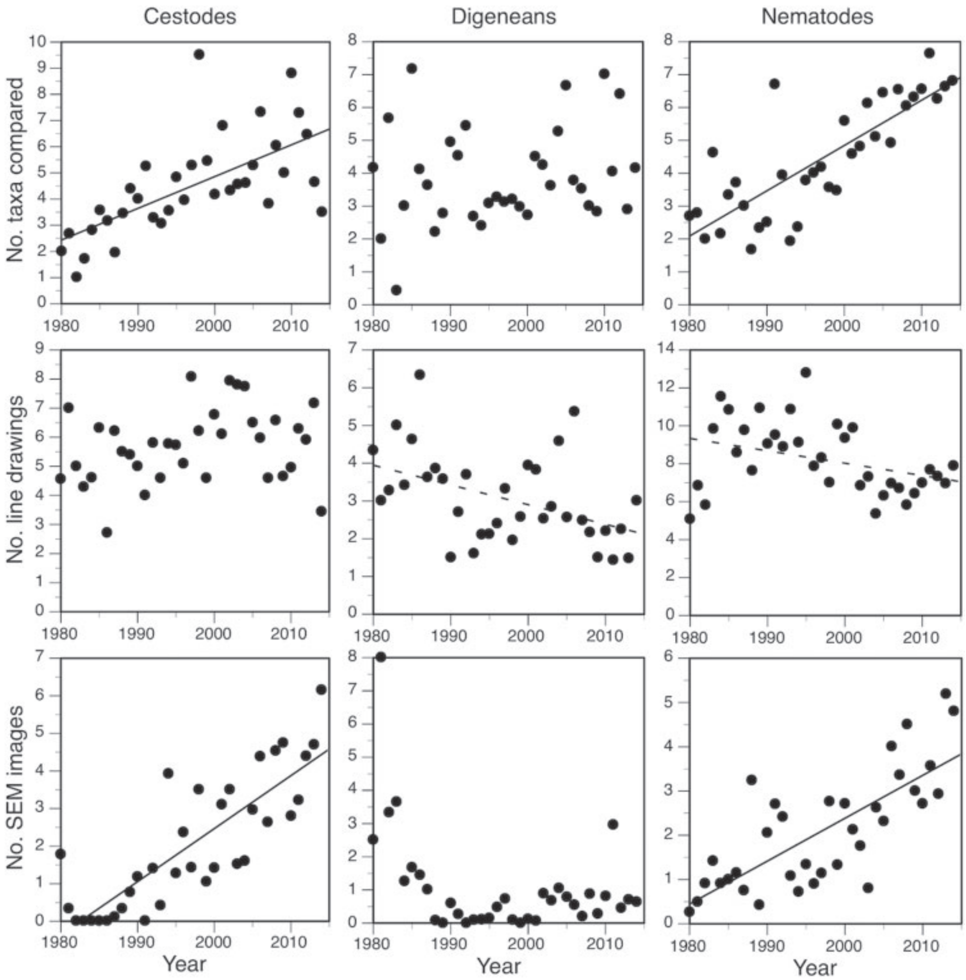

FIGURE 2. Temporal trends (1980–2014) in three measures of taxonomic quality (number of taxa to which the species is compared, number of line drawings, and number of SEM images), expressed as annual means, in species descriptions of parasitic helminths, shown separately for cestodes, digeneans, and nematodes. Trend lines indicate the significance of the correlation: solid, $P < 0.0001$; broken, $P < 0.05$; no line, non-significant.

techniques are for characterizing species in a particular taxon. Other explanations are needed, however, to account for differences among the three higher helminth taxa in how many other taxa the species being described is compared to, or how frequently ecological data is provided. These point toward "cultural" differences among taxonomists specializing on different groups of parasites, setting up and perpetuating different levels of

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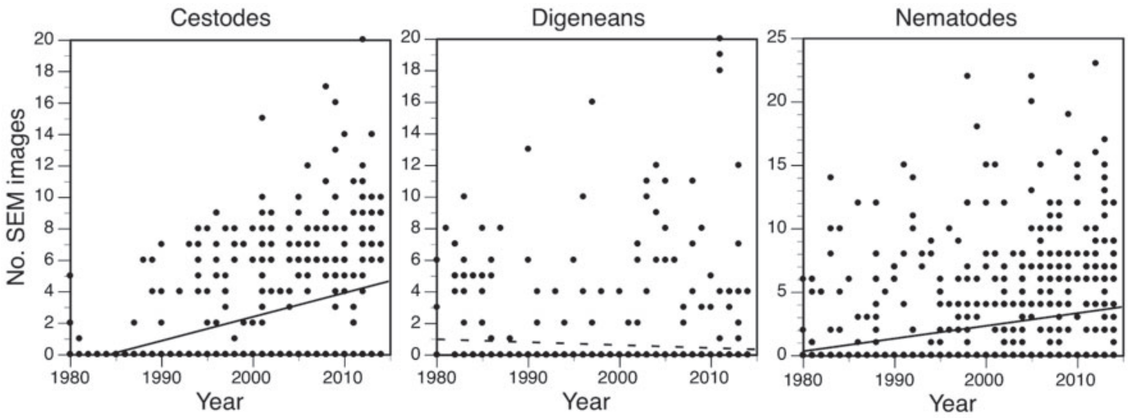

FIGURE 3. Number of SEM images per species description as a function of the year of publication, shown separately for cestodes ($N = 651$), digeneans ($N = 865$), and nematodes ($N = 850$). Note: multiple points are stacked on top of each other. Trend lines indicate the significance of the correlation: solid, $P < 0.0001$; broken, $P < 0.05$.

expectation for taxonomic quality instead of promoting uniformly high standards across all helminth parasite taxa.

Another clear pattern, also suggesting cultural differences among taxonomists, is the effect of the taxonomic identity of the host on all metrics of taxonomic quality considered here (Supplementary Table S2 available on Dryad). For example, the number of line drawings included in a description is about the same for nematodes and cestodes, except if the host is a mammal, in which case more drawings are provided for nematodes (Fig. 4). Descriptions of trichostrongylid nematodes parasitic in mammals traditionally come with several drawings of cross sections of the worms detailing the synlophe (a system of longitudinal cuticular ridges), which is important for taxonomy and species delimitation in this group. Similarly, ecological data is more often provided in descriptions of nematodes than those of digeneans or (in particular) cestodes, but ecological data is more than twice as likely to be given if the host of a nematode is a fish instead of a mammal (Fig. 4). And descriptive data on the larval or juvenile stages of a parasite is much more likely to be provided if the host is a bird, for all higher helminth taxa (Fig. 4). Restrictions applying to sampling wild vertebrates for parasite surveys have tightened over the years because of ethical concerns and conservation policies. This is particularly true for birds and mammals, and could affect the quantity and quality of helminth specimens available for description, and the subsequent quality of the descriptions themselves. For whatever reasons, the above patterns suggest that different subsets of parasite taxonomists, working on the same group of helminths but on species from different kinds of hosts, have developed cultural differences in the completeness and quality of the species descriptions they produce.

Finally, the GLMs also revealed significant differences in taxonomic quality between species descriptions published in *Journal of Parasitology* and those published in *Systematic Parasitology*, for most quality metrics (Supplementary Table S2 available on Dryad). In general, descriptions published in *Journal of Parasitology* scored higher than those in *Systematic Parasitology* for the number of specimens measured, the number of taxa to which the described species is compared, the number of light microscope images provided, the inclusion of ecological data and (for certain taxa) the inclusion of SEM images and descriptive data on larvae or juveniles (Supplementary Fig. S1 in Supplementary Appendix 1 available on Dryad http://dx.doi.org/10.5061/dryad.j4j7q). In contrast, descriptions published in *Systematic Parasitology* scored higher for the number of line drawings provided and the number of individuals sequenced. The journals differ in that the *Journal of Parasitology* has page charges and is a general journal covering all aspects of parasitology, whereas *Systematic Parasitology* has no page charges and specializes in parasite systematics and taxonomy. There is no evidence from our data that page charges in *Journal of Parasitology* force authors to limit the length of their manuscript and save money at the expense of taxonomic quality, or that the specialist journal *Systematic Parasitology* sets higher standards for each new species description than does the more general parasitology journal.

Number of Authors versus Taxonomic Quality

The mean number of authors per species described has increased steadily over the period 1980–2014, in all three higher helminth taxa (Table 1). This confirms an earlier finding based on a different data set covering digenean and acanthocephalan parasites (Poulin 2014). Interestingly, the number of authors per description correlates positively with several quality metrics: the number of individuals measured or sequenced, the number of morphological traits measured, and the numbers of light microscope and SEM images included in a description (Supplementary Table S1 available on Dryad). These correlations, though statistically significant, are generally weak. In addition, generalized

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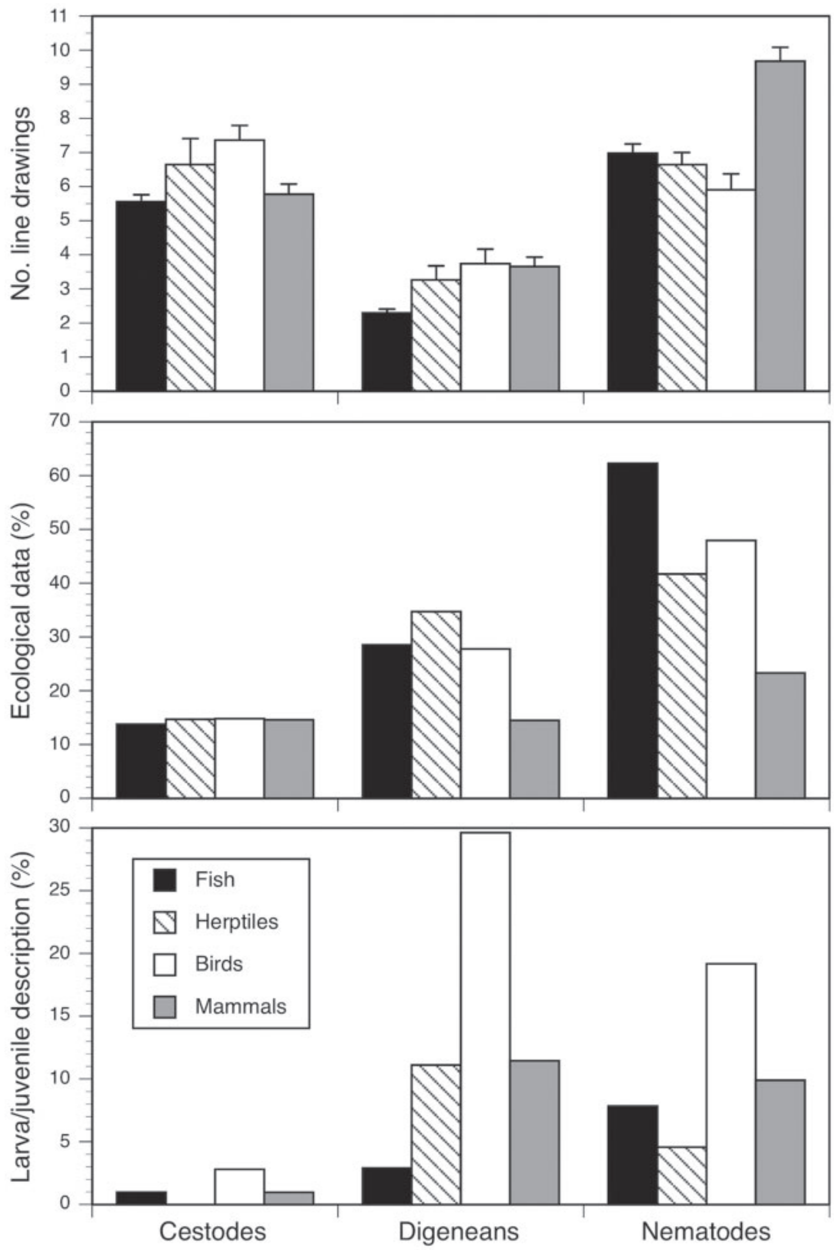

FIGURE 4. Numbers of line drawings (means ± SE) per species description, percentage of descriptions providing ecological data (prevalence and intensity of infection), and percentage providing some description of at least one larval or juvenile stage other than the egg, shown separately for cestodes, digeneans, and nematodes according to the type of vertebrate host in which they were found. Data on nematodes using invertebrates as their sole host are not shown.

linear models revealed that there were significantly more authors associated with descriptions including SEM images ($P = 0.0042$), genetic data ($P < 0.0001$), or ecological data ($P < 0.0001$) than with descriptions not including these useful data (Fig. 5). There was no difference in number of authors between descriptions with and without information on larval or juvenile stages ($P = 0.1824$). Overall, these findings suggest that the increasing number of authors per species description is not necessarily an indication that the number of taxonomists is increasing, as concluded by Costello et al. (2013), but rather that, as suggested by Poulin (2014), taxonomists are teaming up with experts in other fields, such as microscopy and molecular genetics, to achieve more thorough and extensive characterizations of parasite species.

It is also possible that the location of authors determines their access to resources such as an electron microscope or a genetics laboratory. For example, species descriptions from countries or institutions with lower financial means may score lower on several metrics. However, because (1) authors often change addresses,

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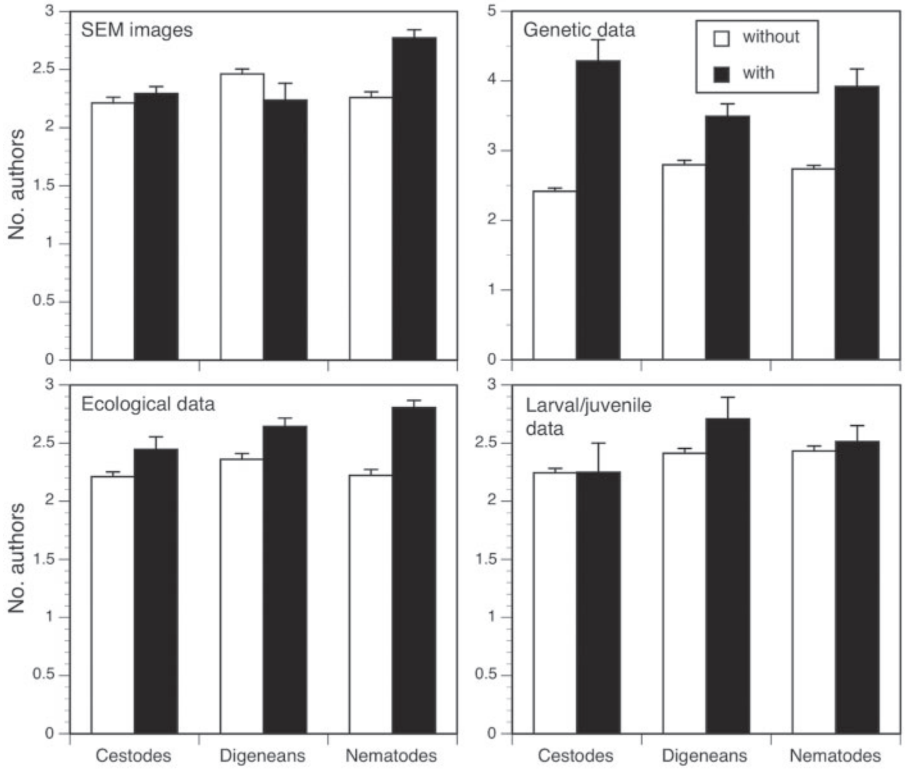

FIGURE 5. Numbers of authors (means ± SE) per species description, shown separately for cestodes, digeneans, and nematodes according to whether or not SEM images, genetic data, ecological data, or information on larval/juvenile stages are provided. Note that for genetic data, only descriptions published from 1999 onwards are included, as 1999 was the first year in which DNA sequences were included in helminth descriptions from our target journals.

(2) authors of species descriptions are often based in countries other than that where the species was discovered, and (3) multi-authored descriptions often involve an international team of authors, it is difficult to test for a geographical bias in description quality.

Quality of Original Descriptions versus Re-descriptions

Of the total number of descriptions in the main data set, 917 were re-descriptions, and the original descriptions of 22 of those species were also included in our data set. When those 22 original descriptions were matched against species from the same higher taxon originally described in the same year and same journal but that have not been the subject of re-description, we found no difference between them for any of the quality metrics (Supplementary Table S3 in Supplementary Appendix 1 available on Dryad). In other words, there is no evidence that species being re-described later were originally described more poorly than those not subject to re-description. Of course, it is likely that some of the species not re-described in our data set have been re-described in other journals, and therefore this conclusion is conservative. Nevertheless, this finding suggests that re-descriptions may be driven more by opportunity and the availability of new specimens than by a need for a more thorough characterization of previously described species.

In addition to the above 22 re-described species for which our main data set also included the original description, we tracked down original descriptions of further species subject to re-description. This produced a data set consisting of 574 pairs of original and revised descriptions, separated by 0–213 years; it is publicly available on Dryad http://dx.doi.org/10.5061/dryad.j4j7q. For analysis, we decided to consider only species whose original description appeared from 1950 onwards. Descriptions published before that date, especially those published before 1900, are often only verbal in nature; in contrast, helminth descriptions follow an increasingly standardized and quantitative format from about the 1950s. This more conservative data set consisted of 203 pairs of original and re-descriptions, separated by 0–61 years. Overall, the proportion of descriptions including light microscope images was higher among re-descriptions than among originals (5.5% vs. 2.9%); the same was true for inclusion of SEM images (21.7% vs. 4.9%), genetic data (4.9% vs. 0%), and ecological data (19.2% vs. 14.8%), but not for information on larvae or juveniles (7.9% vs. 10.3%). Only four quality metrics were obtained from sufficient descriptions for statistical analysis (Supplementary Table S4 in Supplementary Appendix 1 available on Dryad http://dx.doi.org/10.5061/dryad.j4j7q). Many of the early original descriptions did not specify how many specimens were measured, but most post-1950

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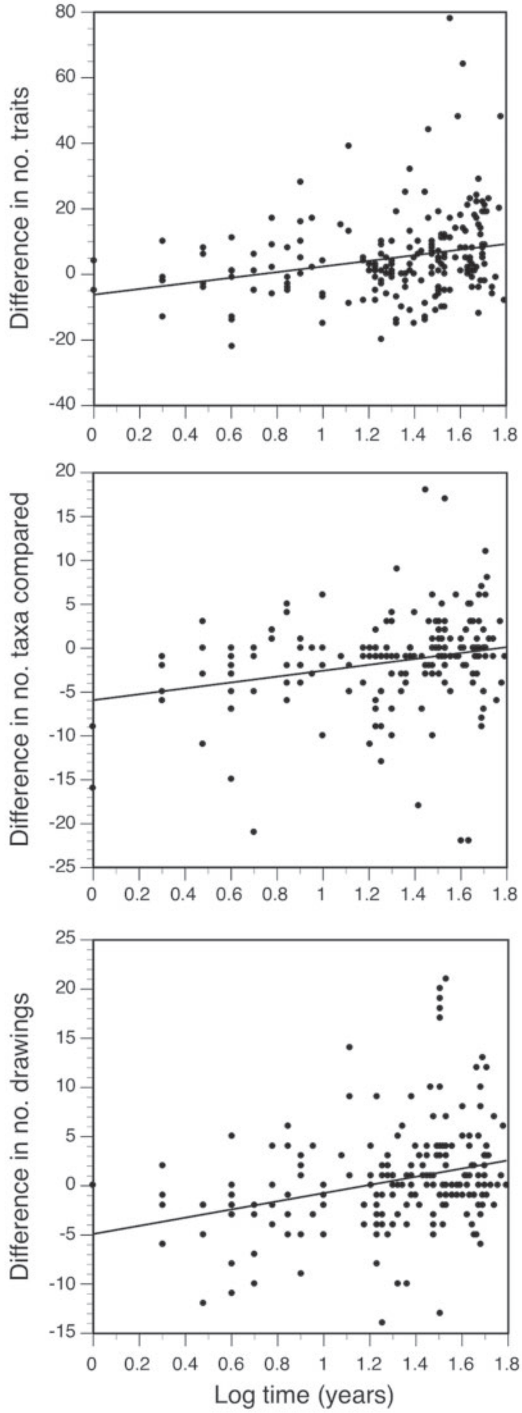

FIGURE 6. Difference in the number of morphological traits measured ($N=203$), the number of taxa to which a species is compared ($N=195$), and the number of line drawings provided ($N=203$) between original descriptions and re-descriptions of the same helminth parasite species, as a function of the length of time between their publication. Positive differences indicate higher values in re-descriptions than in originals, and vice versa for negative values. Trend lines indicate significant relationships (all $P<0.001$).

descriptions did, and among those there was no effect of the number of years between the original description and the re-description on the difference in number of specimens measured (Supplementary Table S4 available on Dryad). However, the number of years between the original description and the re-description had a significant, positive effect on the difference in the number of morphological characters measured, the number of taxa compared, and the number of line drawings provided (Supplementary Table S4 available on Dryad, Fig. 6). In other words, the more time passed since the original description of a species, the greater the improvement in those metrics in its published re-description. Interestingly, although the helminth taxon to which the species belonged had no effects on the improvement in the quality of its description, the taxonomic identity of the host did in some cases (Supplementary Table S4 available on Dryad). This is seen as proportionately slightly greater improvements with time in the quality of descriptions of helminths parasitizing certain host taxa than others, again possibly hinting at different groups of taxonomists placing more or less value on particular aspects of species description depending on the organisms they study.

CONCLUSIONS

Parasite taxonomy has heeded the call to shift toward "integrative taxonomy", i.e., the use of multiple and complementary sources of data for species characterization and delimitation (Dayrat 2005). The recent application of molecular genetics to species identification has uncovered numerous cryptic species of parasites, i.e., genetically distinct species that are seemingly indistinguishable morphologically (Pérez-Ponce de León and Nadler 2010; Poulin 2011). However, reliance on genetic data alone is not a panacea for the diagnosis and delimitation of species, as different analytical methods can yield different results (Carstens et al. 2013). In contrast, the marriage of modern genetic approaches and traditional morphological characterization is widely promoted as the best taxonomical practice (Caira 2011; Perkins et al. 2011).

Recently, indices have been proposed to evaluate the quality of taxonomic publications (Valdecasas 2011; Pyke 2014). These indices are based on either the number of taxa described at different taxonomic level per publication, or the number of times described taxa are subsequently mentioned in the literature. We would argue that these do not in fact measure the quality of taxonomic publications, but instead their scope and impact. Taxonomic quality is independent of how many taxa are described and whether or not the rest of the scientific community mentions them frequently in the following years. Quality is multidimensional in nature, as reflected by the numerous metrics we used to quantify it, and it cannot be captured by a simple index. Quality refers to the level of effort and precision put into the full characterization and delimitation of species. Of course, quantitative metrics

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do not capture all aspects of taxonomic quality; although the formulaic style of species descriptions constrains the verbal and more subjective depiction of a new helminth, this is still an important component of the description, and it must also vary in quality in ways that cannot be measured. Nevertheless, the metrics used here provide a useful assessment of taxonomic effort and practices.

Our analysis has uncovered several trends. First, the taxonomic quality of species descriptions has generally improved over the past 35 years, but unequally among the three higher taxa of helminth parasites considered here. Combined with the fact that the identity of the host also affects most metrics of taxonomic quality, this suggests that there exist cultural differences among taxonomists working on different groups of parasites, such that they do not all make use to the same extent of the tools available for species description. This raises questions (e.g., why are not digenean taxonomists making greater use of scanning electron microscopy?) that may help the field to identify areas for potential improvement. Second, the number of authors per species description has also increased over time; however, a higher number of authors is associated with descriptions of greater quality. Contrary to Costello et al.'s (2013) argument that there are now more taxonomists than ever describing fewer species than in the past, our results support an alternative view: greater collaborations between the remaining taxonomists and experts from other fields to achieve more comprehensive species descriptions. We echo Sangster and Luksenburg's (2015) opinion that trends in the number of species described per author can in no way be used to extrapolate the total number of extant species. Third, the improvement in the quality of re-descriptions relative to original descriptions was roughly proportional to the number of years elapsed between them, although the extent of this improvement varied among helminth species with different host taxa. Again, this suggests possible cultural differences among taxonomists working on different organisms. Moreover, the results make it clear that most older descriptions of helminths that have not been re-described in recent years are probably in need of further characterization using modern descriptive tools if we are to achieve a comparable standard across all species. Overall, our findings indicate that even if their numbers may be shrinking (Brooks and Hoberg 2000, 2001), parasite taxonomists produce species descriptions of increasing quality, bringing in expertize from other fields to meet the principles of integrative taxonomy.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.j4j7q.

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