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Early Land Plants Today (ELPT): How many liverwort species are there?

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Abstract

Estimates of extant liverwort species range from 4,500 to 9,000, with estimates in the past decade converging on 5,000 to 6,000. Potential problems and pitfalls of deriving species estimates are addressed, including binomial accumulation, the impact of synonymy, taxonomic inflation, the impact of unrevised species-rich genera, species concepts and cryptic species. We present a revised mean estimate of 7,500 for the number of liverwort species based on estimating rates of synonymy in a sample of recently monographed and revised taxa. This estimate does not include infraspecific names and may underestimate global diversity as a result. We also present a databased estimate of about 8,500 species derived from the Early Land Plants Today data set. We argue higher estimates are supported by: 1) the number of published species has not reached a plateau and new species continue to be discovered; 2) not all regions have been thoroughly explored and with equal intensity, with survey effort being historically biased toward northern temperate regions; 3) synonymy rates are not uniform across taxonomic groups; 4) novel discovery of species outpaces new species derived from elevation in rank (taxonomic inflation); and 5) species numbers are not necessarily distorted by large unrevised genera. A standardized global worldwide liverwort checklist with strong community participation coupled with the critical need for ongoing monographs and revisions, will aid in arriving at a clearer estimates of liverwort diversity. We promote and encourage interest in the topic using an evidence-based approach and quantitative data.

Key words: biodiversity, estimation, liverworts, species numbers

Introduction

"How many species are there on Earth?" (May 1988). This question transcends the discipline of taxonomy, reaching across science through conservation to the media as well as politics (Erwin 1991). Estimates of global species diversity are fundamental descriptors of life on Earth (Gaston & Hudson 1994). Measuring biological diversity often concerns enumerating species (Diamond 1985; May 1988), and biodiversity estimates are typically based on raw counts of currently recognized named species (Alroy 2002). An understanding of the extant number of species has an important bearing on a countless range of studies including extinction (Alroy 2002), conservation, land-use planning, management and policy (Pitman & Jørgensen 2002; Mueller & Schmit 2007), global biodiversity and biodiversity hotspots (Myers *et al.* 2000), bio-prospecting (Wilson 2000), and ecosystem function (May 1990).

A number of recent papers investigate various aspects of global species richness patterns (e.g., Isaac *et al.* 2004; Bebber *et al*. 2007; Kier *et al.* 2005, 2009)) and estimate global numbers for many major groups of organisms, including seed plants (e.g., Scotland & Wortley 2003; Govaerts 2003; Wortley & Scotland 2004),

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insects (e.g., Gaston 1991; Gaston & Hudson 1994; Ødegaard 2000; Ferrington 2008), birds (e.g., Orme *et al.* 2005), tiger beetles (Pearson & Cassola 1992), and fungi (Hawksworth 2001; Hyde *et al.* 2007; Mueller *et al.* 2007). However, similar studies have not been conducted for liverworts.

There are several key problems and pitfalls of estimating global diversity. Barriers to estimates of the number of living species include, but are not limited to: 1) uneven taxonomic coverage leading to poor knowledge of highly diverse taxonomic groups and geographic regions; 2) the lack of standardized sampling schemes and the disproportionate effort in exploring as well as under-explored regions of the world; 3) problems in extrapolating diversity counts; 4) multiple names for a single biological entity, i.e., synonymy; 5) taxonomic inflation, i.e., are the majority of new species from elevation in rank rather than novel discovery?; 6) the quality of underlying data; 7) the vast and scattered literature; and 8) the number of undescribed species (Gaston & Mound 1993; Patterson 1996; Solow *et al.* 1995; Govaerts 2001; Alroy 2002; Isaac *et al.* 2004; Mace 2004; von Konrat *et al.* 2008a,b).

In seed plants, recent estimates of the number of described species have varied by as much as 62% (Scotland & Wortley 2003). For example, Govaerts (2001) and Bramwell (2002) estimated the global diversity for seed plant species to be 422,127 and 421,968, respectively. These are much higher than other published estimates: 346,527 (Wortley & Scotland 2004), 300,000–320,000 (Prance *et al.* 2000), and 260,000 (Thorne 2000a,b, 2002). The variance in estimate for plants is in stark contrast to smaller groups of animals, such as birds, where estimates of the global number of species range between nine and ten thousand (e.g., Dickenson 2003).

As in seed plants, published estimates of liverwort species richness vary considerably, by as much as 50%, with estimates ranging from 4,500 to 9,000 (Table 1). With the exception of Forrest *et al.* (2006), no publication explains how estimates were derived. It is assumed they are based on subjective estimates derived from the experience of a particular taxonomic group or a particular geographical region and extrapolating to a global context. The estimate cited by Forrest *et al.* (2006) is based on figures from a survey of 97 data references (accessed at http://bryophytes.plant.siu.edu/general.html). However, although they present baseline data, their literature survey and resulting data set do not encompass a detailed survey of all taxonomic groups and across all geographic regions. This is unsurprising given the diffuse and highly dispersed nature of liverwort literature. For instance, the bibliographic library behind the Early Land Plant project (ELPT) databases is in the order of 13,500 references (von Konrat *et al.* 2010a). Until recently there was no single central source of data to arrive at such an estimate of all published names, let alone an estimate of accepted species (von Konrat *et al.* 2008 a,b, 2010a). Hence, despite 250 plus years of documentation of liverwort diversity there remains no worldwide checklist of accepted species, and as such very few contestable estimates of global species numbers. Yet, reliable figures of the global number of extant species are in great demand (Gaston & Hudson 1994). Our ability to provide an accurate answer is needed to understand the structure and composition of global biodiversity. An accurate species estimate will facilitate better answers to other important questions, such as the rate at which species are becoming globally extinct and the scale of the task faced by species conservation (Bebber *et al.* 2007).

Previous estimates have been cited in government documentation, e.g., the estimate of 4,000 to 6,000 noted in a US federal government document about national parks in Alaska (accessed at http://www.fs.fed.us/r10/tongass/maps/low_res_bryobrochure%20photo_names.pdf). Interestingly, large discrepancy in recent estimates of the number of seed plants has been negatively interpreted in the public sector (Wortley & Scotland 2004).

Estimates in the range of 5,000 to 6,000 liverwort species have been widely accepted, particularly in the last decade (see Table 1). This paper explores an evidential approach to re-derive an estimate of global liverwort diversity. In part, this serves as an independent test of previous estimates.

This paper has two key objectives. Firstly, to provide an estimate of the number of global liverwort species based on estimating rates of synonymy and presenting a data-based approximate calculation of liverwort diversity. In doing so we address 1) has binomial accumulation (species description) reached a plateau?; 2) have all regions been thoroughly and equally explored?; 3) how many binomials are there?; and

4) how many species might there actually be when all synonyms have been accounted for? Secondly, we discuss factors that impede or confound this endeavour, with particular emphasis on peculiarities unique to liverworts, including the impact of taxonomic inflation, species-rich unrevised genera, species concepts and cryptic species.

TABLE 1. Estimates of liverwort species numbers.

Estimate	Author/s
4,500–5,000	Forrest *et al.* (2006)
5,000	Crosby (1980); Gradstein *et al.* (2001); Gradstein & Costa (2003); Crandall-Stotler *et al.* (2008)
5,000–6,000	Heinrichs *et al.* (2005); Gradstein & Ilkiu-Borges (2009)
6,000	Schofield (1985); Heinrichs *et al.* (2007); Groombridge & Jenkins 2002
6,500–7,000	Schuster (1984)
6,000–8,000	Crandall-Stotler & Stotler (2000)
9,000	Pearson (1995)

With the Early Land Plants Today project (see von Konrat *et al.* 2010a) a synthesis of information and data is now available on a global scale. Ultimately, we contend that the development of a global web-based database will make possible a reliable measure and analysis of global liverwort species richness. Finally, we underscore the importance of monographic treatments and highlight under-collected regions. Although there are many challenges ahead to obtain high quality data, quantifying global liverwort diversity is a tractable, multi-faceted and scientifically important goal, and everyone stands to gain by fostering this endeavour (von Konrat *et al*. 2008b). The success in arriving at testable estimates will be founded on strong collaboration between institutions and the bryological community in general—a model the ELPT project is striving towards.

Methods

The impact of synonymy

A key issue affecting estimates of described species is that of multiple names for a single biological entity, i.e., synonymy (Gaston & Mound 1993; Solow *et al* 1995; Patterson 1996; Govaerts 2001). There have been two approaches in recent estimates of the global number of seed plants (Crane 2004). One approach has used data derived from a geographical focus using information contained in regional floras and species checklists (Govaerts 2001; Bramwell 2002). A problem with this approach is that regional floras and checklists usually underestimate rates of synonymy and overestimate levels of endemism (Scotland & Wortley 2003). A second approach has focused on taxonomy and nomenclature based largely on data derived from recently monographed taxa (Thorne 2002; Scotland & Wortley 2003). Both approaches calculated the rate of synonymy from their data sets and applied the rate to the number of known published names for seed plants, extrapolating from this to arrive at an estimate of the number of species. The assumed number of known seed plant names is 1,015,000 in *Index Kewensis*, but this list is far from accurate due to a range of factors including duplicate and missing entries (Scotland & Wortley 2003). Scotland & Wortley (2003) briefly critiqued three recent estimates and the methodology used to infer the extent of synonymy in seed plants. In arriving at their own estimate of 223,300 they tested the synonymy rates predicted by all recent estimates against rates empirically derived from a sample of taxa for which they assumed synonymy rates are relatively accurate. This method was further revised by Wortley & Scotland (2004) with an increased sample size resulting in an overall synonymy rate of 65.9%, translating to 346,527 species of seed plants. We emulate this approach here.

Source database

The analysis and assessment is based on a combined data set maintained by Lars Söderström (Trondheim) and Anders Hagborg (Chicago), which forms the basis of the Early Land Plants Today project—hereafter referred to as the ELPT data set. This data set was used for the calculation of 1) binomial accumulation, 2) geographical distribution of new names over the past two decades, and 3) data-based estimates of total number of names, total number of accepted names, and total number of synonyms. von Konrat *et al.* (2010a) provide a thorough description of the data set, an assessment of the quality of the data, and quality control of the data. The authors of this paper can be contacted for access to the database, or portions thereof. The ELPT data set forms the basis for the development of a worldwide checklist of liverworts and has 21 taxonomists actively contributed to portions of the data set. The data set is derived from a pool of resources and cross-referencing, involving a combination of species checklists, annotated checklists with synonyms, monographs, revisions, specialists and broad taxonomic papers. The present working data sets includes a bibliography of 13,500 publications; approximately 35,000 published liverwort names (including "accepted" taxa, infraspecific ranks, synonyms, invalid and illegitimate names); over 400,000 geographical observations (a single observation is a record of one taxon from one geo-political unit); and almost 500 geo-political units, e.g., state, province, country. More than 3,500 journal articles and monographs have been used so far as input for this data. The tabulation of binomial accumulation (species description) over time is a modified version from von Konrat *et al.* (2008b) based on an updated ELPT data set as well as an annual account for each year over the past decade. The geographical units presented in the geographical distribution of new names (Fig. 2) follows Level-3 of the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001).

Synonymy rates

To estimate the impact of synonymy and assess the rate of synonymy, 26 monographs and revisions were surveyed. The 26 publications were selected on the basis that they represented relatively recent works from the last 13 years, a range of taxonomic groups, and different spatial scales from regional to global. These are summarized and listed in Table 4. We assume this is a representative sample of synonymy rates for all taxa. We followed the methodology used by Scotland & Wortley (2003) and Wortley & Scotland (2004) to infer the extent of synonymy in liverworts, and by deduction, the number of species. This simple method firstly calculates the mean rate of synonymy from the surveyed monographs and revisions; secondly, applies the mean rate to the total number of known published names for liverworts. Extrapolating from this figure an estimate of the number of synonyms and accepted species can be calculated. The total number of known binomial names used in our calculations is 25,637, which is derived from the ELPT database at the time of this publication. Confidence levels were calculated to assess upper and lower estimates and compare against other previously published estimates. Graphics and Confidence levels were produced and calculated using OpenOffice.calc and Statistics Open For All (SOFA).

Results

Rate of binomial accumulation

1) HAS BINOMIAL ACCUMULATION (SPECIES DESCRIPTION) REACHED A PLATEAU? Figure 1 depicts the number of novel liverwort species, excluding new combinations, which have been described over the last 290 years. von Konrat *et al.* (2008b) provided an account of the major peaks corresponding to works of several early 19th century botanists, including K. M. Gottsche, J. B. W. Lindenberg, C. G. Nees von Esenbeck, W. Mitten, J. D. Hooker and T. Taylor, and the late 19th and 20th century works of V. Schiffner, F. Stephani, R. M. Schuster, H. Inoue, and S. Hattori.

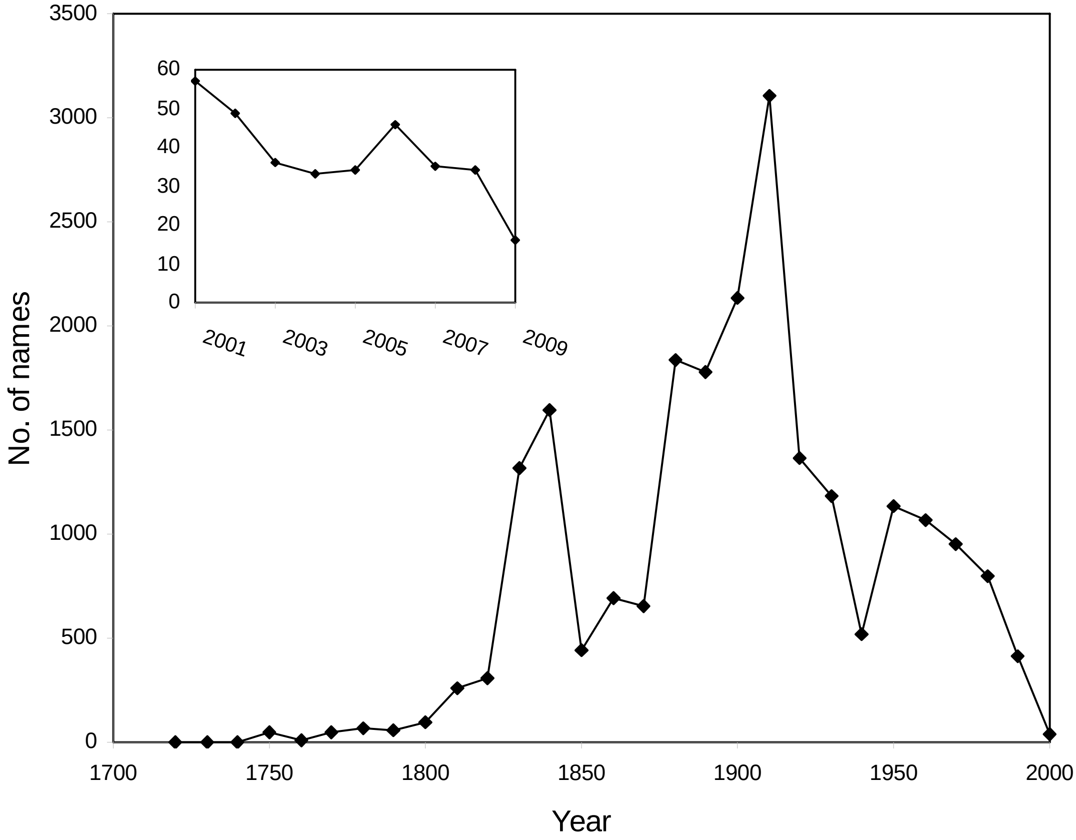

FIGURE 1. Number of novel liverwort species, excluding new combinations, which have been described over the last 250 years, with an inset of the number described from 2001–2009.

The first two major peaks, with over 1,300 and 1,500 described species respectively, correspond to the works of several early 19th century botanists, including Synopsis Hepaticarum by Gottsche *et al.* (1844–1847). The highest two peaks throughout the history of description of new species, of 2,137 and 3,105 between 1900 and 1920, corresponds largely to the plethora of taxa described by Stephani (1898-1924) in his monumental work Species Hepaticarum. With the exception of the 1940's, it was not until between 1970 and 1979 that the number of described species per decade dropped below 1,000. Another significant decline appeared in the 1990's when only 414 species were described compared to 794 the decade before. At least 376 species have been described since the year 2000.

Table 2 provides a synopsis of the top 25 authorities who have described the most number of liverwort taxa in the history of liverwort taxonomy. During the course of his life time, Stephani described the most number of taxa totaling over 5,200. The next nine most prolific authors each described over 300 taxa. It is noteworthy that Schuster (with 301) and Engel (with 94) are the only two in the top 25 remaining alive and actively publishing. Equally informative as the number of described taxa is the rate of synonymy. Over the course of time, Colenso has had over 80% of his described taxa reduced to synonymy. This is followed by Stephani (with 62%) and Horikawa (with 72.5%). Workers such as Stephani and Colenso are well known for having described numerous erroneous species (Gradstein 2006).

TABLE 2. The top 25 authorities who have described the most liverwort taxa, including infraspecific taxa, as derived from the ELPT data set. The table includes the total number of taxa described, the total number of taxa that remaining accepted in the literature, the synonymy rate, and first and last dates of publication (all according to the ELPT dataset).

Name	ELPT data set	Remain accepted	Synonymy rate	Publication dates	
				First	Last
Stephani (1842–1927)	5,261	2001	62.0%	1883	1928
Herzog (1880–1961)	595	256	57.0%	1916	1961
Gottsche (1808–1892)	571	331	42.0%	1843	1882
Spruce (1817–1893)	524	286	45.4%	1847	1899
Lindenberg (1781–1851)	496	313	36.9%	1829	1852
Nees (1776–1858)	382	239	37.4%	1817	1847
Taylor (1775–1848)	365	215	41.1%	1836	1854
Mitten (1819–1906)	362	235	35.1%	1851	1891
Schiffner1862–1944)	317	155	51.1%	1896	1964
Schuster (1921–)	301	240	20.3%	1949	
Hattori (1915–1992)	287	207	27.9%	1941	1994
Lehmann (1792–1860)	221	161	27.1%	1829	1857
Colenso (1811–1899)	207	40	80.7%	1881	1890
Tixier (1918–1997)	205	162	21.0%	1958	1995
Montagne (1784–1866)	198	123	37.9%	1835	1860
Grolle (1934–2004)	197	163	17.3%	1959	2005
Horikawa (1902–1976)	193	53	72.5%	1929	1952
Hooker fil. (1817–1911)	191	124	35.1%	1844	1847
Arnell (1895–1970)	175	82	53.1%	1944	1965
Inoue (1932–1989)	174	97	44.3%	1954	1989
Evans (1868–1959)	143	96	32.9%	1891	1938
Pearson (1849–1923)	140	58	58.6%	1878	1931
Austin (1831–1880)	128	65	49.2%	1867	1879
Engel (1941–)	94	92	2.1%	1971	
Jovet-Ast (1914–2006)	92	80	13.0%	1947	2003
	11,819	5,874	49.7%		

2) Have all regions been thoroughly and equally explored and inventoried? Figure 2 illustrates the geographic distribution of the 667 new species described from 1990 to 2009. The most prominent region for new species is New Zealand where 81 species have been described in the last twenty years. South central China and New Guinea, each with 32 species, have also seen a significant number of new species described in the past 20 years as has Venezuela with 24 described species. The rate of species description over the past two decades has been far lower in most areas, including North America, Europe, many parts of Africa and South America, southeast Asia, Indonesia, and the islands of the Pacific. In fact, in many of these areas no species have been described in the past 20 years.

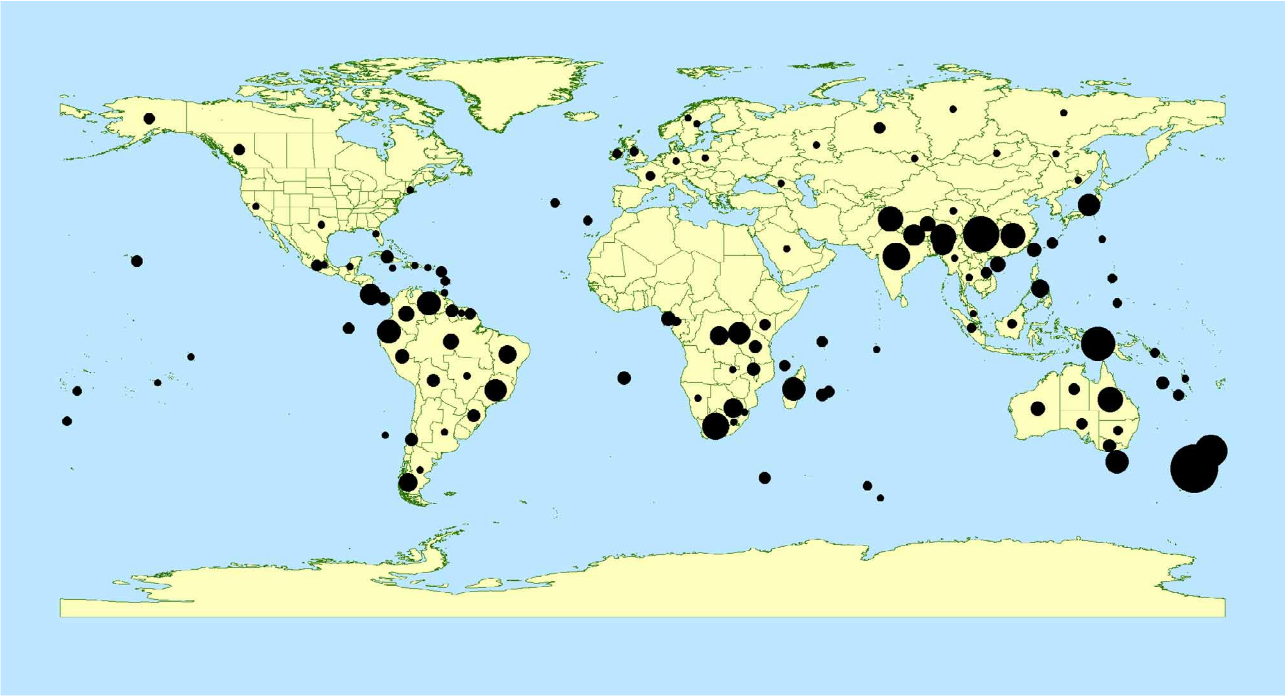

FIGURE 2. The geographical distribution of the almost 670 new species that have been described from 1990 to 2009. Dot size represents the number of new species in each area (maximum 81 in New Zealand).

Summary of the number of binomials derived from the ELPT data set

Table 3 provides a summary of preliminary numbers derived from the ELPT data set at the time of this publication. The strong utility of the data set is the application of a confidence level assessing our state of knowledge of a taxon. These are outlined and defined in von Konrat *et al.* (2010a). It is too early to give much weight to the confidence levels of these numbers as this continues to be in the developing phase of the data set. In summary, there is a total of 8,545 names that include 6,823 accepted binomials and 1,722 binomials representing conflicting views or a knowledge problem. Some of the 896 names representing a knowledge problem include invalid and illegitimate taxa according to ICBN (McNeill *et al*. 2006). Overall, there are 25,637 binomials including accepted names, synonyms, or those with a knowledge problem. If we extend the data set to include infraspecific taxa, there is a grand total of about 35,000 names. Of these, a total of 10,082 are regarded as accepted or have a knowledge problem where we are unable to confirm their status. This total of 10,082 excludes the rank of form, and includes only the ranks of variety and subspecies.

TABLE 3. Summary data from ELPT unpublished database as of May 02, 2010. Number in brackets equals the total number of names in the data set.

Confidence level	All binomials	All taxa
Doubtful or invalid	1,722	2,407
Currently accepted	6,823	7,675
Total	8,545 (25,637)	10,082 (35,000)

TABLE 4. Synonymy estimates for sample liverwort taxa.

Taxon	Monograph world/regional	All binomials	Accepted binomials	% synonyms
Anastrophyllum[1]	Australasia	16	10	38
Anastrophyllum[2]	Himalaya & W. China	18	7	61
Asterella[3]	Eurasia	139	16	89
Balantiopsis[4]	New Zealand and world	33	14	58
Ceratolejeunea[5]	Neotropics	129	23	82
Chandonanthus/ Tetralophozia/ Plicanthus[6]	World	15	7	53
Chiloscyphus[7]	Australasia	164	38	77
Crossotolejeunea (syn. of *Lejeunea*)[8]	Tropics	45	15	67
Echinolejeunea (syn. of *Lejeunea*)[9]	Neotropics	16	5	69
Fossombronia[10]	East Asia & Oceania (excl. NZ & Aust.)	122	7	94
Frullania[11]	Oceania, Australasia, southern South America	27	11	59
Frullania[12]	Neotropics	19	7	63
Herbertus[13]	Asia	129	12	91
Herbertus[14]	Africa	35	5	86
Isotachis[15]	New Zealand	12	7	42
Lepidozia[16]	New Zealand	29	23	21
Leptoscyphus[17]	southern South America	38	5	87
Lopholejeunea[18]	Asia	137	17	88
Marsupidium[19]	New Zealand	27	7	74
Plagiochila[20]	East and South Asia	42	13	69
Plagiochila[21]	China	266	80	70
Plagiochila sect. *Crispatae* & *Hypnoides*[22]	Neotropics	42	4	90
Pycnolejeunea[23]	World	98	9	91
Saccogynidium[24]	China	9	3	67
Telaranea[25]	World	249	98	61
Tylimanthus[26]	Tropical America, Africa, Macaronesia	16	1	94
Total		**1,872**	**444**	**x 70.8**

[1]Engel & Braggins (1998); [2]Schill & Long (2003); [3]Long (2006); [4]Engel & Smith-Merrill (1997); [5]Dauphin (2003); [6]Schuster (2002); [7]Engel (2010); [8]Reiner-Drehwald & Goda (2000); [9]Ilkiu-Borges (2005); [10]Krayesky, Crandall Stotler & Stotler (2005); [11]von Konrat *et al.* (2006a, 2010b); [12]Uribe (2008); [13]Juslen (2006); [14]Hodgetts (2008); [15]Schuster & Engel (1997); [16]Engel & Schuster (2001), Engel (2004); [17]Hässel (2001); [18]Zhu & Gradstein (2005); [19]Engel & Glenny 2008; [20]So & Grolle (2000); [21]So (2001); [22]Heinrichs & Gradstein (2000); [23]He (1999) He (1999)[24]Gao *et al.* (2001); [25]Engel & Smith-Merrill (1996, 2004); [26]Burghardt & Gradstein (2008).

How many species might there actually be when all synonyms have been accounted for?

In order to arrive at an estimate of global liverwort species numbers, we used the methodology described above, following Scotland & Wortley (2003) and Wortley & Scotland (2004). Essentially, this is a three step method. Firstly, a calculation of synonymy rates is required. This is followed by extrapolation of the mean synonymy rate from a baseline figure of all known names to calculate the total number of possible synonyms. Finally, the total number of species can be derived by subtracting the number of synonyms from the total number of known names. Table 4 provides synonymy estimates for sample liverwort taxa representing over 20 genera. This is derived from a survey of 26 monographs or revisions. There is a total of 19 different first authors indicating that a range of taxa and authors are represented. A summary of the descriptive statistics based on the percentage synonymy of the 26 surveyed monographs and revisions is provided in Table 5. Clearly, synonymy rates for liverworts are highly variable ranging from approximately 21% to as high as 94%, i.e., a range of 73%. The mean synonymy rate is 70.8%.

Using the baseline estimated figure for the number of binomials (25,637), extracted from the ELPT data set, we can begin to make some calculations of the rate of synonymy. This baseline figure does include invalid and illegitimate names, which are often included in synonymy by authors. Assuming an overall rate of synonymy at 70.8% translates to 18,151 potential synonyms and therefore 7,486 would be accepted binomials.

TABLE 5. Descriptive statistics based on the percentage synonymy of the 26 surveyed monographs and revisions.

Statistic	Number	Statistic	Number
Mean	70.8	Range	73
Standard Error	3.7	Minimum	21
Median	69.5	Maximum	94
Mode	61	Sum	1,841
Standard Deviation	18.8	Count	26
Sample Variance	354.0	Confidence level (95.0%)	7.6

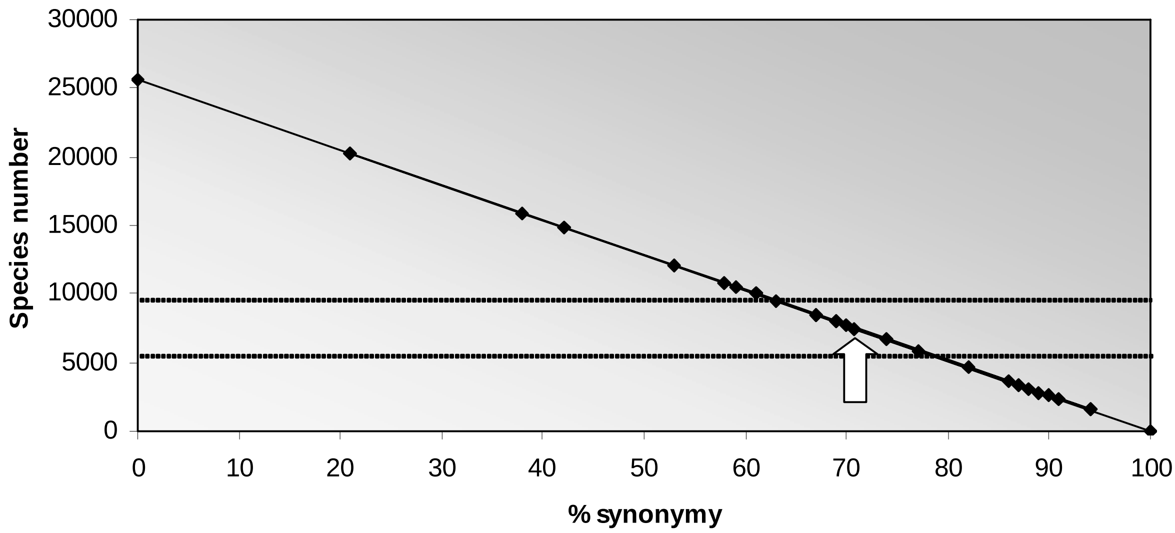

FIGURE 3. The relationship between synonymy rate and number of species. Synonymy rates for individual monographs from Table 4 are displayed as dots. The current best estimate for the number of liverwort species, 7,486, is indicated by the arrow. Upper and lower estimates (the 95% confidence interval) of 5,536 and 9,432, respectively are shown by dashed lines.

The present data set of 26 monographs enables us to calculate the number of species, with 95% confidence, to between 5,536 and 9,432. At the 90% confidence level the number of species ranges from 5,868 to 9,100. Figure 3 shows the relationship between synonymy rate and number of species, based upon a total number of binomials of 25,637. Explained alternatively, if there was 100% synonymy this would translate to no accepted species, whereas if there was zero percent synonymy this would translate to 25,637 species. The current best estimate for the number of liverwort species is 7,486.

Discussion

Current estimates of the number of liverwort species

ELPT DATA SET: The number of published liverwort names and estimated number of species is smaller than seed plants by a factor of 10. However, the same difficulties at arriving at an estimate of seed plants apply to liverworts. The most accurate estimate would be obtained from the direct number of accepted species throughout the world. Hampering this effort in the past was the fact there was no single repository synthesizing information for all published names. In doing so, to some degree we circumnavigate the shortfalls from estimates derived from either a geographical focus or taxonomic focus. At present the ELPT data set has 8,545 binomials that include 6,823 broadly accepted binomials and 1,722 binomials representing conflicting views or a knowledge problem, including some invalid and illegitimate taxa (902 names). The strong utility of the data set is the application of a four-level knowledge ranking system towards each taxon, which is reached through broad community participation. These ranks are defined and outlined by von Konrat *et al.* (2010a). Although it is too early to give much weight to the ranking of our numbers, we are now closer to disentangling accepted species and synonymy than ever before. This system may facilitate refining species estimates using a data-based and evidence-based approach.

ESTIMATES DERIVED FROM SYNONYMY RATES: The direct estimate obtained from the EPLT databases, including those binomials where we consider knowledge problems, and the mean estimate obtained from the monographic surveys are very similar with about 7,500 accepted species for the world. Applying the 95% confidence limits, we estimate a lower figure of 5,536 and an upper estimate of 9,432 liverwort species. This simple estimation of a 95% confidence interval illustrates that we can begin testing estimates and application of the data sets. The mean estimate of 7,486 is higher than all previous estimates of the past ten years. Our calculations indicate we can confidently reject the lower estimates of 4,500–5,000 (Forrest *et al.* 2006) and 5000 (Crosby 1980; Gradstein *et al.* 2001; Gradstein & Costa 2003; and Crandall-Stotler *et al.* 2008). However, the slightly higher estimates of 5,000–6,000 (Heinrichs *et al.* 2005; Gradstein & Ilkiu-Borges 2009), 6,000 (Schofield 1985; Groombridge & Jenkins 2002; Heinrichs *et al.* 2007) and 6,500–7,000 (Schuster 1984) fall within the confidence limits on our estimate, as does the slightly higher estimate of 6,000–8,000 presented by Crandall-Stotler & Stotler (2000). The upper boundary on our confidence interval is similar to the Pearson (1995) estimate of 9,000 liverwort species.

The estimate of 7,486 is calculated on the assumption that there are a total of 25,637 binomial names. This total will increase as data compilation proceeds to completion. We contend that this is a conservative estimate of species diversity on a global scale, especially if we consider additional factors as discussed below. This estimate does not include infraspecific names and as a result may underestimate global diversity. The critical issue is how representative is the sample of monographed and revised taxa when calculating overall rates of synonymy (Scotland & Wortley 2003). The size of the sample, and thus the accuracy of the estimated number of liverwort species, can and will be improved by further monographic work and an increased sample size of existing taxonomic and monographic studies that have not yet been included. An increased sample size will likely lead to narrower 95% confidence limits as illustrated by Wortley & Scotland (2004) for seed plants.

In arriving at our estimate, it is critical to assess our knowledge of the current situation and potential problems and pitfalls in arriving at such estimates. Below we consider the following as potential factors that may influence or impact our estimate: 1) the rate of binomial accumulation over time and geographical exploration; 2) the impact of synonymy; 3) the impact of taxonomic inflation, i.e., is the novel discovery of species outpacing new species derived from elevation in rank; 4) are species numbers distorted by large unrevised genera; and 5) the impact of species concepts and cryptic species.

Factors to consider and potential pitfalls associated with current estimates

1) RATE OF BINOMIAL ACCUMULATION: At least 376 species have been described since the year 2000. This represents a significant number considering 1) the relatively few liverwort taxonomists and monographers in the world; and 2) the high number of under-explored areas of the world. It will be interesting to know how the next decade unfolds as additional monographs and revisions are completed, as a greater number of systematic investigations of liverworts include molecular data to resolve species, especially cryptic species, and as collections are made from either unexplored or under-explored areas. If the last two decades are any indication, we predict possibly 350 to 500 new species to be described in the next decade. Species continue to be described and discovered at a significant rate, and the rate of description is unlikely to change in the foreseeable future.

Söderström *et al.* (2008) provided a comprehensive list of liverwort checklists with the starting date of 1900. They concluded that although there were checklists for many areas, substantial portions of the globe either lack lists entirely or lack recent lists. Notable are the lack of lists for the Caribbean Islands, Mexico, most of Central America, and large parts of Melanesia, yet, many of these regions we know to be areas of high species richness (von Konrat *et al.* 2008 a,b). This is significant because checklists are powerful and important tools that can integrate the highly scattered information on nomenclature, systematics, distribution, and even frequency (Söderström *et al.* 2007, 2008).

It is abundantly clear that not all regions have been thoroughly explored and with equal intensity as other regions (Fig. 2). This can be due to the number of active researchers, historical exploration, habitat and climate. For instance, the high number of species described for New Zealand (81) could be indicative of the number of active hepaticologists either residing, or, having active field programs in the region (at least six). It is also a result of the intense research effort going into the production of the New Zealand liverwort and hornwort flora (Engel & Glenny 2008) and reflects the high species diversity and richness of the New Zealand liverwort flora (Schuster 1984; von Konrat *et al.* 2005, 2008 a,b; Engel & Glenny 2008). In contrast, the lower number of species described in western Europe is unsurprising, as it has a rich history of bryological study spanning over 250 years, and the flora is nearly fully documented. However, the lower number is surprising for regions such as Central and South America, and the islands of the South Pacific, which are extremely species rich and are likely to contain a number of undiscovered species. Gradstein & Costa (2003) predict that exploration of the hepatics of the Brazilian part of the Guyana Highland would be highly rewarding and possibly yield species new to science and perhaps even new genera. Regardless of geographic region molecular studies have the potential to aid in the uncovering of cryptic and 'semi-cryptic' diversity, even in accepted well studied species (Heinrichs *et al.* 2009).

2) WILL THE NUMBER OF SPECIES BE REDUCED BY THE HIGH RATE OF SYNONYMY IN MODERN MONOGRAPHS AND REVISIONS?: Obviously, many issues affect the taxonomic history and therefore the extent of synonymy in any given group. This is clearly indicated by the vastly different synonymy rates in Table 4 and the impact extrapolating different synonymy rates in estimating species illustrated in Fig. 3. Taxonomic history is constrained by the geographical range of the taxon, the number of taxonomists that have worked on the group, and the history of collecting and discovery in a particular area, etc. (Scotland & Wortley 2003). Two particularly important issues impinge on the accuracy of the synonymy rate calculated in a taxonomic study of a group. First, the study should be truly monographic in that the complete range of variation of a taxon should be fully considered; otherwise the synonymy rate may be underestimated (Scotland & Wortley 2003). This is possibly a weakness of our survey as very few monographs and revisions are worldwide in scope. That being

said, many studies, even though regional in scope, have considered broader geography and studied type specimens beyond the specific region in which they are focusing. In addition, some of the taxa are known to be geographically restricted. Moreover, the survey sample represents a broad range in 1) 19 different workers (thus different concepts of species, both narrow and broad, and methods); 2) different taxonomic groups; and 3) different spatial scales from local, regional, to global.

Another important factor is the quality of the underlying synonyms themselves as we can not totally reject the potential significance of false synonymy. For instance, *Frullania congesta* Gottsche *et al.* (1845: 451) was accepted by many authors as a synonym of *F. rostrata* (Hooker & Taylor 1845: 87) Gottsche *et al.* (1845: 445), following Hattori (1978). Almost three decades later, von Konrat *et al.* (2006) recognized *F. congesta* as a distinct species, underscoring the important need to examine type material, critically re-examine morphological concepts, and use a broad array of tools at our disposal. This was later reinforced with molecular data (Hentschel *et al.* 2009) that supported its placement, not only as a distinct species, but in an entirely different subgenus. And finally, of course, another important factor to consider in the estimation of global diversity is that many currently accepted taxonomic names have not existed long enough to be evaluated critically and potentially discarded. However, the rate of discarded names with modern tools, is significantly less than a century ago, or even a few decades ago.

No discussion on liverwort synonymy can bypass the impact of Stephani and his major publication, Species Hepaticarum, a worldwide treatment of the species of Hepaticae and Anthocerotae. Stephani described over 5,200 species. Gradstein (2006) provided a biographic account of Stephani and an assessment of the scientific significance of his publications. Modern bryologists have developed misgivings regarding Stephani's contribution to bryology due to the typological concept he seems to have applied to species. A frank assessment was presented recently by Gradstein (2006) who stated that Stephani's major work, Species Hepaticarum, "holds the reputation of being one of the most notorious publications in bryology and a century after its appearance, taxonomists are still busy clearing the mess." After nearly a century of taxonomic investigation only about 1,000 species described by Stephani remain accepted—according to our ELPT data set. An unknown proportion of these have been independently revisited and accepted in monographs and revisions since the time of Stephani. Thus the impact of Stephani's names remains significant.

3) TAXONOMIC INFLATION: On the basis of data from primates Isaac *et al.* (2004) argued that species numbers were increasing primarily due to taxonomic inflation, i.e., the majority of new species resulted from elevation in rank rather than new discoveries. This was also supported by Mace (2004). Taxonomic inflation may confound our attempts to measure species loss, and hence meet global targets such as the Convention on Biological Diversity (Isaac *et al.* 2004). Based on ELPT data, at least for the last three decades, we could only find 40 records where an infraspecific taxon had been elevated to the rank of species. Taxonomic inflation does not appear to be a major confounding factor in our estimate of liverwort diversity.

Another potential factor of estimating diversity is the number of invalid and illegitimate names. It is worth noting that at least some of the invalid or illegitimate names are and have been strongly considered as real biological entities and readily recognised. A good example is *Fossombronia maritima* Scott & Pike (1987: 378) that was invalid because multiple gatherings were cited as the type. Six additional *Fossombronia* Raddi (1818: 29) taxa, published at the time, were also invalid for that reason. Later, Cargill attempted to correct them in McCarthy (2003). It was successful for the other six but it failed for *Fossombronia maritima* G.A.M.Scott & D.C.Pike because in the meantime *Fossombronia maritima* (Paton 1973: 244) Paton (1994: 367) was published so we still have *Fossombronia maritima* G.A.M.Scott et D.C.Pike ex Cargill as nom. illeg. although generally accepted as a good taxon.

4) ARE ESTIMATES OF GLOBAL SPECIES NUMBERS DISTORTED BY SPECIES-RICH UNREVISED GENERA?: Any estimate of global diversity must consider the impact and implications of large, purportedly species-rich, unrevised genera. In liverworts, there are several large genera or families that remain unrevised on a global scale, including *Frullania* Raddi (1818: 9), *Plagiochila* Dumortier (1835: 14), and a number of genera in Lejeuneaceae. For example, *Frullania* with just over 2,000 published names, is widely accepted to have an estimated 300-375 accepted species (e.g., Schuster 1992, Gradstein *et al.* 2001), yet no data has been provided

to support this supposition. On the contrary, growing data and evidence may suggest the estimated "300-375" is a minimum estimate at best. Consider: 1) novel *Frullania* species continue to be discovered and described (e.g., Zhu & So 1997; Sim-Sim *et al.* 2000; von Konrat & Braggins 2005; von Konrat *et al.* 2010b), even almost outpacing new synonyms in some areas, and notwithstanding the fact discoveries have been made in well botanized areas let alone those that have not been botanized at all; 2) at least 90 morphologically easily discernable species were supported by molecular data (Hentschel *et al.* 2009), yet this was represented by only a partial sample; 3) molecular data is unveiling many cryptic and semi-cryptic *Frullania* species (Heinrichs *et al.* 2010); 4) the impact of false synonymy as discussed above; and 5) preliminary ELPT data indicates 668 accepted binomials excluding 124 of dubious or uncertain status. It is impossible to provide an authoritative estimate of the number of species, but together, available data and information indicates that 300-375 species is almost certainly an under-estimate. Equally, the ELPT data of over 660 accepted species will most likely be an over-estimate, and somewhere in the middle would seem a strong possibility.

Similarly, *Plagiochila*, with almost 2,800 published names has been reported to have an estimated number of 400-450 species worldwide (Gradstein *et al.* 2001; Heinrichs 2002; So & Grolle 2000). It has been argued, quite correctly, that many early bryologists tried to cope with the bewildering diversity in *Plagiochila* by creating numerous binomials, often based on single collections from limited geographic areas (Heinrichs *et al.* 2004). In recent revisions (e.g., Heinrichs 2002), acceptance of broader morphological variation has often lead to range extensions of assumed endemics. The estimate of 400–450 species, seemingly has been argued on the basis of personal experience with a geographical focus. Yet, different areas have different histories of taxonomic investigation, which potentially influences perspective, and its extrapolation into a global context. For instance, Gradstein & Costa (2003) noting their significantly lower estimate of liverworts for Brazil (approximately 600 compared to previously published reports of 1,161), reflected the large amount of synonymy of the hepatic flora in the Neotropics. Hence, contemporary investigators encounter synonyms more frequently than they encounter new species. But, contrast this with New Zealand, or Great Britain, where an ongoing legacy of comprehensive taxonomic investigation (e.g., Schuster & Engel 1985—*Schistochila* Dumortier (1835); Inoue and Schuster (1971); Engel (unpublished data)—*Plagiochila*) has purged these geographic areas of a greater part of their synonymy burden, and in these instances it is misleading to extrapolate regional estimates to a global context. Similar factors can also be considered for *Radula* Dumortier (1822), Lejeuneaceae, and other taxa.

In summary, these large species rich units which remain to be revised globally is indeed an important factor, but we contend the ELPT figures, albeit preliminary, may in fact not be wildly distorted considering that new species continue to be discovered coupled with the vast areas yet to be explored. Consider also Lejeuneaceae; preliminary ELPT data has in the order of 1,683 accepted taxa in addition to 570 accepted taxa of a lower confidence. It is widely contended that the family has in the order of 1,000 accepted species (Wilson *et al.* 2007; Groth-Malonek *et al.* 2004; Gradstein *et al.* 2001). Again, this is based on regional experience, largely in the Neotropics where significant reduction of names to synonymy is evidently warranted, yet there remain large regions that 1) have not been explored at all (Gradstein & Costa 2003); 2) floras that remain to be revised; 3) and discovery of new species (Glenny 1996; Renner *et al.* 2009).

5) SPECIES CONCEPTS: Interestingly, recent papers discussing global estimates of seed plants omit any discussion of species concepts. Although it is not the purpose of this paper to discuss species concepts - there is a plethora of papers on the subject (e.g., see references in Shaw 2008; Mayden 1997; Hey 2001; Vanderpoorten & Shaw 2010). Although the determination of species is regarded as one of the most important activities of the taxonomist, the majority of biologists, including botanists, undertaking monographs and revisions do not discuss the concepts or the criteria to delimit species (McDade 1995; Padial & De la Riva 2006). While no empirical data exists, a similar statement can undoubtedly be applied to liverwort systematics (von Konrat *et al.* 2006b) and bryophyte systematics and taxonomy in general (Shaw 2008). We assume, for this paper, that most contemporary species concepts resemble, at some level, "units of evolution" and that the most commonly applied approach to delimiting species of bryophytes is morphological (Shaw 2008). However, over the last decade, biological and phylogenetic concepts have become increasingly employed in

recent liverwort systematic papers (e.g., Heinrichs *et al.* 2005; Heinrichs *et al.* 2009). Because it is impossible to discern, in the vast majority of cases, which concept has been employed, we accept diversity estimates to be broadly reflecting a mixture of concepts. Although a mixture of species concepts is unsatisfactory for testing many hypotheses (Isaac *et al.* 2004), to help alleviate this problem, in part, we advocate and promote that there is great utility in future workers proffering concepts they employ to arrive at their taxonomic conclusions.

6) IMPACT OF CRYPTIC SPECIES: The vast majority of bryophyte species are described based on the assumption of a congruence between speciation processes and accumulation of morphological disparity between sister species (Heinrichs *et al.* 2009). However, since the 1990's, a growing number of studies based on isozyme or molecular data have illustrated support for cryptic or nearly cryptic species, i.e., genetic subdivision has occurred within some morphologically uniform or almost uniform species (e.g., Odrzykoski & Szweykowski 1991; Boisselier-Dubayle *et al.* 1998; Shaw 2000; Shaw & Allen 2000; Feldberg *et al.* 2004; Hedenäs & Eldenäs 2007; Heinrichs *et al.* 2010). Although most studies employing molecular markers have focused on deeper relationships among genera and families, genetic data have increasingly been applied to species-level problems as well (Shaw 2008; Vanderpoorten & Shaw 2010). Yet, there remains a limited number of molecular studies at the level of species, hampering our efforts to quantify the contribution of cryptic species to the global biodiversity of liverworts, but existing studies clearly suggest a significant part of bryophyte biodiversity is undetected with traditional morphological concepts alone (Heinrichs *et al.* 2009). On the other hand, it is also critical that taxonomists apply the most appropriate molecular tools. Vanderpoorten & Shaw (2010), this issue, encourage bryophyte systematists working at the species level to supplement sequence data with information from other kinds of markers that are better suited to recently diverged taxa, suggesting that DNA fingerprinting methods including RFLPs, ISSRs, and microsatellites, are especially useful for many species-level systematic problems.

A synthesis: Towards a working estimate of the number of liverwort species

We contend that the strongest estimate is based on integrative evidence based on quantitative data. To do otherwise is an exercise in stating belief. If we consider the following: 1) the number of published species has not reached a plateau and new species continue to be discovered; 2) not all regions have been thoroughly explored and with equal intensity as other regions; 3) novel discovery of species outpaces new species derived from elevation in rank or new combinations; 4) synonymy rates are not uniform across taxonomic groups; and 5) species numbers are not necessarily distorted by large unrevised genera. With these several factors combined, we contend there is strong evidence to support a mean estimate in the order of 7,500 species. Calculating using 95% confidence levels, a lower limit is around 5,500 and an upper limit of 9,500. In the course of time it might be feasible to consider an upper limit in the order of 10,000, especially with increased tools, technology, continuing monographs and revisions, and continued field work.

Future prospects?

First, unless an inventory is more or less complete (e.g. 90% complete for birds), extrapolations based on existing data are associated with very large margins of error. This, in addition to issues relating to synonymy, partly explains current levels of uncertainty about species numbers even for relatively well-known taxa such as vascular plants (Scotland & Wortley 2003; Wortley & Scotland 2004). Second, any extrapolation from existing data is sensitive to the dynamics of the discovery process over time, as well as to the proportion of known species used in the extrapolation. Increasing the number of monographs and revisions surveyed will almost certainly lead to estimates with greater confidence levels.

The current speed of taxonomic research is slow and, without dramatic improvements of the working methods, will likely miss the discovery of many species before their extinction (Godfray 2002). DNA taxonomy and web-based approaches are currently favored by some as major steps forward to achieve a faster rate and more accessible classifications (Pons *et al.* 2006; Godfray *et al.* 2007). However, monographic and revisional work based on detailed morphological investigation will remain fundamental.

It is too early to say how ongoing advances in taxonomic understanding will impact liverwort diversity estimates. However, in some groups of liverworts, many taxa are in the process of being reduced to one or a few species while in other groups cryptic species are uncovered. The challenge of recognizing synonyms and sibling species is clearly enormous, and it emphasizes the profound need for additional funding of primary taxonomic research of monographs and revisions. Working towards the development of a standardized global, but amenable list, providing a platform and forum for debate, discussion, and verification, will contribute to these endeavours.

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