

Molecular data challenge traditional subgeneric divisions in the leafy liverwort *Radula*

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Abstract With approximately 200 species, the genus *Radula* is one of the most speciose genera of leafy liverworts. Although the genus is well delimited, its subdivision into subgenera and sections has been controversial. None of the subgeneric subdivisions have been the subject of an explicit test of internal consistency or monophyly based on molecular data and a comprehensive view of evolutionary relationships within the genus is thus still lacking. In the present paper we propose, based on a molecular phylogeny of the genus, a new subgeneric classification for *Radula*, and create three new subgenera. While the reconstructions of ancestral gametophytic characters allow for a morphological description of each of the seven lineages identified in our phylogeny, synapomorphies for these lineages are mostly lacking. Uncertainty of morphological state reconstructions at the deepest nodes of the phylogeny, which point to a rapid morphological diversification of the genus in its early history, do not allow for pinpointing when morphological changes occurred. The classification scheme proposed here is therefore mostly based on molecular features.

Keywords character state reconstruction; morphology; subgeneric classification

Supplementary Material Table S1 is available in the free Electronic Supplement to the online version of this article (<http://ingentaconnect.com/content/iapt/tax>).

■ INTRODUCTION

With approximately 200 species (Yamada, 2003), *Radula* Dumort. is one of the most speciose genera of leafy liverworts, comparable in size with the liverwort genera *Lejeunea* Lib., *Frullania* Raddi, and even *Plagiochila* (Dumort.) Dumort. Like these other large liverwort genera, *Radula* is widely distributed from Arctic to Antarctic regions, with an apparent centre of species diversity in tropical regions. *Radula* is unique among leafy liverworts in having rhizoids produced only from the carinal region of the lobules, branches being predominantly terminal of the *Radula*-type, and underleaves being totally absent (Spruce, 1885; Schuster, 1980a, 1984). These features impart a highly distinctive and unusual morphology to all species within the genus, which has prompted its placement in the widely accepted, monogeneric family Radulaceae (Dumort.) Müll. Frib. Although the genus is well delimited, the exceptional diversity of species coupled with the reduced, somewhat stenotypic morphology has made the subdivision of *Radula* into subgenera and sections that reflect monophyletic groups difficult and controversial (Jones, 1977; Yamada, 1979; Schuster, 1980a).

The first infrageneric classification for *Radula* was published by Stephani (1884), who divided the 92 known species among 12 sections. Stephani (1884) utilized readily accessible characteristics from both morphological and ecological sources to define his sections, and defined each section by a single character. Morphological characters chosen by Stephani included

the possession of acute or acuminate lobe or lobule apices, the possession of densely imbricated or ampliate lobules, or lobules with a strongly inflated carinal region, the presence of amentulose branches, or the dichotomously branching shoot systems (Stephani, 1884). One section, sect. *Epiphyllae* Steph., was created for species which grew on leaves. This sectional classification was highly artificial, and was designed purely to facilitate species identification (Schuster, 1980a).

An alternative infrageneric classification was published almost simultaneously by Spruce (1885), and is likely to have been conceived independently of Stephani's classification. Spruce divided 13 South American species between two subgenera. *Radula* subg. *Cladoradula* Spruce was defined by the subglobose capsule, perianths on short lateral branches, and wide-mouthed perianths, while subg. *Acroradula* Spruce produced perianths terminally on leading axes, had narrow-mouthed perianths and ellipsoidal capsules (Spruce, 1885).

Subsequently, Stephani (1910) modified his earlier treatment of *Radula* and presented seven sections for 220 species. He did not incorporate Spruce's subgenera or the characters associated with the subg. *Cladoradula*–subg. *Acroradula* split. Spruce's subgeneric division was, however, adopted by Castle (1936) in his global study of the genus. Castle (1936) argued that “the characters expressed by the position of the female inflorescence are, without question, the only ones which are entirely trustworthy as a basis for the primary division of the genus into subgeneric groups”. On the basis of this subdivision, Castle

placed 15 species into subg. *Cladoradula*, and 197 species into subg. *Acroradula*. The latter subgenus was divided into 11 sections, most of which were adopted directly from Stephani (1884).

The sectional classification used by Castle was formalized by Grolle (1970), who provided Latin diagnoses and designated a type species for each. This classification was, however, resoundingly criticized by Jones (1977) within the context of a study of African *Radula*. Jones (1977) not only criticized the artificial nature of the classification, but went so far as to state that the sections “lack even the merits of good classificatory units”. This was due to the fact that some characters were neither clear-cut nor mutually exclusive, and in addition were “liable to vary so much that different parts of the same shoot might be placed into different sections” (Jones, 1977). Evidence from a range of morphological characters, including stem anatomy, lobule shape, perianth anatomy, and capsule shape, was presented by Jones to illustrate that Castle’s sections were in some cases positively misleading with regards to relationships. Jones (1977) drew attention to the ability of stem anatomy to identify natural groups of species, and identified five species groups within the African flora primarily on this basis. One of Jones’s species groups corresponded to Spruce’s subg. *Cladoradula*. This group had a highly distinctive stem anatomy, with a medullar layer 2–3 cells deep whose walls were heavily thickened and brown pigmented. While this species group was distinctive, Jones doubted that it was “any more worthy of subgeneric status than the other [species] groups” which he had recognized (Jones, 1977: 462). While Jones advocated complete revision of Castle’s infrageneric classification, and even went as far as identifying his own species groups, and associating defining characteristics with them, he did not formalize his scheme as he believed such a move was premature until a larger sample of species from all geographical areas had been investigated.

The wholesale revision of Castle’s infrageneric classification advocated by Jones has never been undertaken. However, two regional studies published shortly after Jones (1977) did make changes to Castle’s infrageneric classification (Yamada, 1979; Schuster, 1980b). A new subgenus was proposed by Yamada (1979) in his study of Asian species. *Radula* subg. *Odontoradula* Yamada was proposed for species with acute to apiculate or dentate leaf lobes, two to four pairs of dentate female bracts, and spinose perianth mouths. The differences in stem anatomy identified by Jones were also utilized by Yamada to ascribe species to subg. *Cladoradula*, which Yamada was able to divide into two sections, sect. *Chinenses* Yamada for plants with auriculate lobule bases and bipinnate branching, and sect. *Cladoradula* Yamada for plants with non-auriculate lobule bases and pinnate branching. Yamada also recognized nine sections within subg. *Radula* (= subg. *Acroradula* nom. illeg. of Spruce, 1884 and Castle, 1936).

A fourth subgenus was proposed by Schuster (1980a) as a corollary to his studies of North American taxa (Schuster 1980b), which were compared with a small selection of species from other regions. *Radula* subg. *Metaradula* Schust. was proposed for species whose perianths have a basal stem perigynium (Schuster, 1980a, 1984). Like Jones, Schuster (1980a) was critical of Castle’s classificatory scheme, in particular the

use of sect. *Complanatae* Castle as a catch-all for species not immediately attributable to any other section. The subgeneric classification proposed by Schuster followed a historical precedent of segregating a small highly distinctive element from within subg. *Radula* without resolving limits for subg. *Radula* itself. Thus subg. *Radula* remained a catch-all for species that do not fit into the other three subgenera. *Radula* subg. *Radula* contains the greatest numbers of species, which reflects the poor understanding of species relationships within the genus. Further reflecting on this lack of understanding is the fact that within *Radula* subg. *Radula*, species are still arranged according to the sectional classification proposed by Castle (1936) which was inherited directly from Stephani (1884).

The genus *Radula* is thus currently divided into four subgenera, three of which (subg. *Cladoradula*, subg. *Metaradula*, subg. *Odontoradula*) segregate distinctive morphological groups, whilst the fourth (subg. *Radula*) contains the remainder. None have been the subject of an explicit test of internal consistency or monophyly based on molecular data and a comprehensive view of the evolutionary relationships within the genus is thus still lacking.

In the present paper, we take advantage of a recent molecular phylogeny of the genus (Devos & al., 2011) to (1) test the monophyly of the four currently accepted subgenera, (2) propose the first molecular-based subgeneric classification that would set the foundation for a complete taxonomic revision of the genus, and (3) establish which characters, if any, employed in traditional classification are capable of circumscribing monophyletic units.

■ MATERIALS AND METHODS

Taxon sampling. — Ninety-three of the approximately 200 known *Radula* species (Yamada, 2003) were sampled, depending on the availability of suitable material for DNA studies. Species from each of the four traditionally recognized subgenera, including the type species, were sampled. *Radula* subg. *Cladoradula* includes the type species, *R. boryana*, together with 11 species (*R. campanigera*, *R. gottscheana*, *R. perrottetii*, *R. aquilegia*, *R. carringtonii*, *R. obtusiloba*, *R. physoloba*, *R. tenera*, *R. tenax*, *R. polyclada*, *R. hastata*). *Radula* subg. *Odontoradula* sensu Yamada (1979) is represented in our phylogeny by six species, i.e., *R. pulchella*, *R. kojana*, *R. apiculata*, *R. acuminata*, *R. dentifolia*, and the nomenclatural type of the subgenus, *R. ocellata*. Within *R.* subg. *Metaradula*, the type species *R. buccinifera* was sampled, along with the five species *R. appressa*, *R. australiana*, *R. flaccida*, *R. stenocalyx*, and *R. tjibodensis*. The remainder of the species belong to subg. *Radula*, including its type species, *R. complanata*. The sampling covers the entire distribution range of the genus with samples from Asia, Australia, New Zealand, Africa, Europe, North and South America as well as various islands and archipelagos such as Reunion, Madagascar, Madeira, Tenerife, Azores, and Canary Islands.

Frullania moniliata, *Jubula pennsylvanica*, and *Porella pinnata* were included in the matrix to serve as outgroups.

These genera have been identified as the closest relatives of *Radula* (Heinrichs & al., 2005; Forrest & al., 2006) and sequences for the six chloroplast genes were downloaded for those outgroups from GenBank.

As detailed in Devos & al. (2011), six chloroplast genes were used for Bayesian inference of phylogenetic relationships within *Radula*. The six chloroplast regions used were *atpB-rbcL*, *psbT-psbH*, *psbA-trnH*, *rps4*, *trnG* and *trnL-F*. Voucher information for the plant material and Genbank accession numbers are given in the Appendix.

Morphological analyses. — Twenty gametophytic morphological characters were scored for each of the species included in the analysis (Table 1; Table S1 in the Electronic Supplement). Those characters were selected because of their previous use for sectional and subgeneric circumscriptions (Stephani, 1884; Spruce, 1885; Castle, 1936; Yamada, 1979; Schuster, 1980a). Characters were scored on the basis of voucher specimens and with reference to Castle's sectional arrangement of species (Castle, 1936, 1950, 1959, 1961, 1962, 1963, 1966, 1967, 1968), as well as Jones (1977), Yamada (1979), Schuster (1980b), and other references. With the exception of capsule shape (Spruce, 1885; Schuster, 1980a), sporophyte characters have not been used to circumscribe sections and subgenera in *Radula*. Sporophyte shape is unknown for cA. 75% of species included in the data matrix, and consequently was not scored.

In our dataset, *Radula retroflexa* was the only species with ligulate lobules (Castle, 1962), while *R. wichurae* was the only species with bordered leaves (Castle, 1959). These characters

Table 1. Morphological gametophytic characters investigated and their character states.

A	Plant colour: (1) brown pigmented when fresh; (0) green
B	Vegetative branching: (1) dichotomous; (0) pinnate or irregular
C	Microphyllous (= "amentulose") branches: (1) present; (0) absent
D	Subepidermis: (1) present; (0) absent
E	Epidermis cell walls: (1) thickened; (0) thin
F	Medulla cell walls: (1) thickened; (0) thin
G	Epidermis cell walls: (1) brown; (0) colourless
H	Leaf lobe: (1) apiculate-acute and toothed; (0) rounded-obtuse and entire
I	Trigones: (1) large; (0) absent or small
J	Lobule insertion: (1) sinuate-oblique to transverse, directed to stem ventral midline; (0) parallel to stem, directed to stem apex
K	Caducous leaves: (1) present; (0) absent
L	Gemmae: (1) present; (0) absent
M	Gynoecea: (1) on short branch; (0) on main axis or long branch
N	Innovations: (1) present; (0) absent
O	Stem perigynium: (1) present; (0) absent
P	Female bracts: (1) 2–4 pairs; (0) 1 pair
Q	Lobule spacing: (1) imbricate; (0) contiguous to remote
R	Lobule proximal margin: (1) ampliate; (0) straight
S	Lobule carinal region: (1) strongly inflated; (0) not inflated
T	Lobule apex: (1) acute to acuminate; (0) rounded to obtuse

were thus autapomorphic in the present species sampling and were not scored. Epiphyllous habit, utilised by Stephani (1884) and Castle (1939), is not a morphological character and was not scored.

In order to identify possible morphological synapomorphies for the clades of interest, morphological ancestral character states were reconstructed onto the phylogenetic trees generated by MrBayes v.3.2 (Ronquist & Huelsenbeck, 2003). Ancestral character state reconstructions were performed after pruning outgroups from the trees. Synapomorphic transitions between states were recorded only when shifts occurred between nodes for which character states were reconstructed with at least 70% probability.

Character state reconstructions were carried out using the 'Multistate' Markov model in BayesTraits v.1.0 (www.evolution.rdg.ac.uk). The probabilities of change on a branch were calculated by estimating the instantaneous forward (q_{01}) and backward (q_{10}) rates among the two states. An MCMC was used to visit, at each iteration, the space of rate parameter values and sample one of the trees generated by the MrBayes analysis. The rate at which parameters were changed ('ratedev') was set at the beginning of each run so that the acceptance rate of the proposed change ranged globally between 20% and 40%. In the absence of information on rates, uniform distributions ranging from 0 to 100 were used as priors. The chain was run for 5,000,000 generations and was sampled for rate parameters and state probabilities at the nodes of interest every 100 generations. In order to circumvent the issue associated with the fact that not all of the trees necessarily contain the internal nodes of interest, reconstructions were performed using a 'most recent common ancestor' approach. This method identifies, for each tree, the node subtending a group of taxa, reconstructs the state at the node, and then combines this information across trees (Pagel & al., 2004).

RESULTS

The ingroup can be divided into seven fully supported lineages (Fig. 1). Four of those lineages (A, C, E, F) include the type species of the currently accepted subgenera *Cladoradula*, *Radula*, *Metaradula*, and *Odontoradula*. The three remaining clades were labeled B, D, and G. Four of the species (*R. campanigera*, *R. boryana*, *R. tenax*, *R. perrottetii*), which have traditionally been included within subg. *Cladoradula* based on their morphology, form with the type species of the subgenus, *R. gottscheana*, a fully supported clade (Fig. 1, clade F) sister to the rest of the genus. Other species included within subg. *Cladoradula* were, by contrast, resolved as members of other lineages. *Radula aquilegia* and *R. carringtonii*, for example, are nested within subg. *Radula* (Fig. 2, clade C), while *R. hastata* is found in clade B (Fig. 2, clade B), and *R. physoloba* is found in clade D (Fig. 2, clade D).

Five of the six sampled species of subg. *Odontoradula* sensu Yamada, namely *R. pulchella*, *R. kojana*, *R. apiculata*, *R. dentifolia*, and the type species, *R. ocellata*, form a fully supported clade (clade E in Figs. 1–2). This clade also

includes four species, *R. plicata*, *R. retroflexa*, *R. tasmanica*, and *R. decora*, that are usually placed in subg. *Radula* based on their morphology. *Radula acuminata*, also included within subg. *Odontoradula*, was instead resolved as a member of the lineage including the type of subg. *Metaradula* (clade A in Figs. 1–2).

Six of the seven sampled species of subg. *Metaradula*, namely *R. australiana*, *R. flaccida*, *R. silvosa*, *R. stenocalyx*, *R. tjobodensis*, and the type species *R. buccinifera*, form a highly supported clade (clade A in Figs. 1–2). The seventh species, *R. appressa*, is resolved in the subg. *Radula* lineage (Fig. 2, clade C). Together with *R. acuminata*, the *Metaradula* lineage also include two species, *R. ratkowskiana* and *R. acutiloba*, that were thought to belong to subg. *Radula* based on their morphology.

The remainder of the species, previously thought to belong to subg. *Radula*, are distributed among four highly supported lineages one of them including the type species of *Radula*, i.e., *R. complanata*. The other three lineages, i.e., B, D, and G, do not correspond to any group previously defined based on morphology (Figs. 1–2).

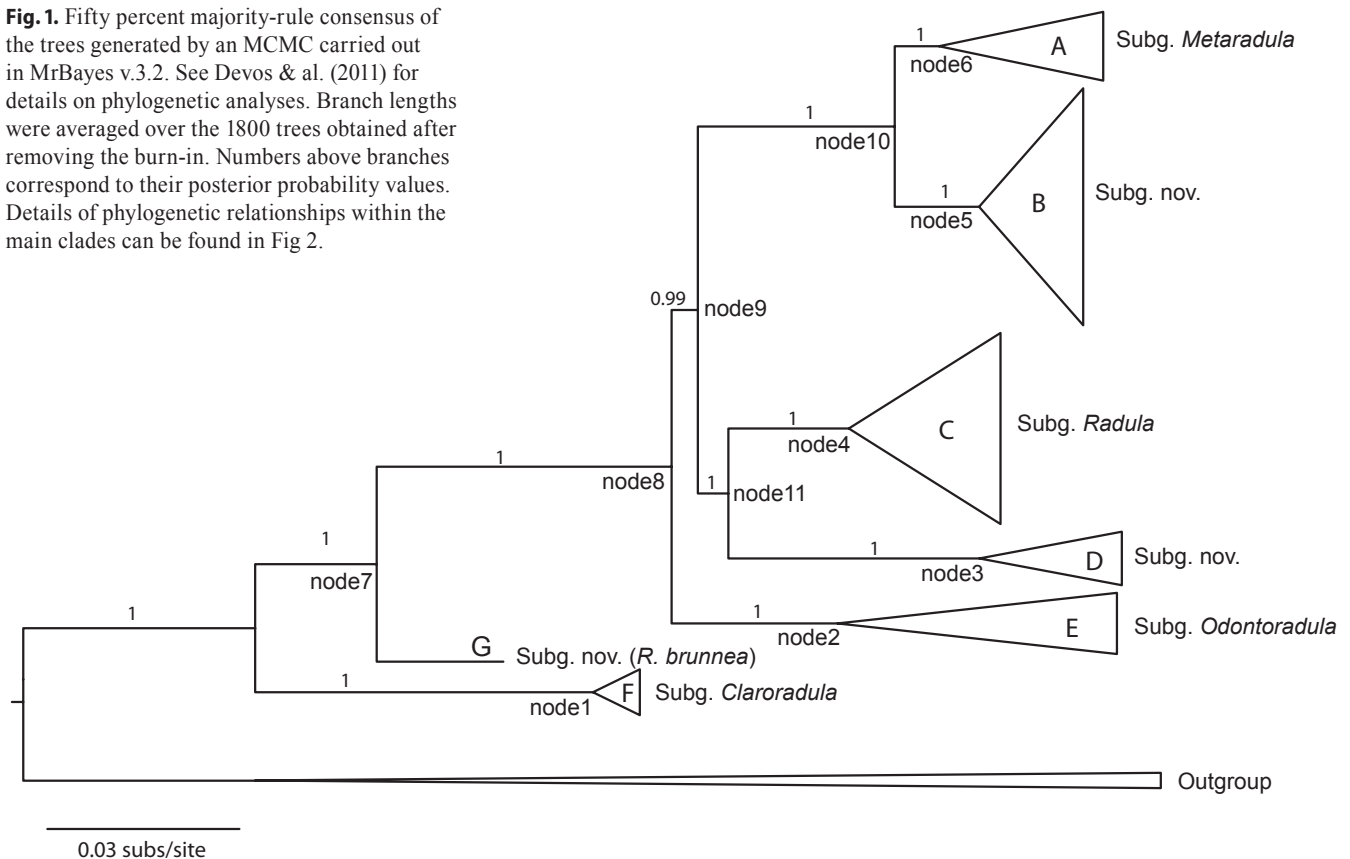
The reconstructions of ancestral morphological character states at the most recent common ancestors (MRCAs) of the seven main clades identified in Fig. 1 are presented in Table 2. All character states at the MRCA of subg. *Cladoradula* (Node 1, Table 2) were reconstructed with posterior probabilities >0.90. Only one synapomorphy, i.e., the loss of a stem perigynium (character O), was identified at the MRCA of clade B, across all characters (node 5, Table 2). The state probabilities

for all other characters at all deep nodes (nodes 7–11), including the root, were, with some exception, generally low and below 0.7 (Table 2).

DISCUSSION

Although fully supported clades including the type species of each of the traditionally defined subgenera of *Radula* (Yamada, 1979; Schuster, 1980b) were resolved in the phylogenetic analysis by Devos & al. (2011), the composition of those clades is largely incongruent with their traditional circumscription. The subg. *Odontoradula* clade identified here is a morphologically heterogeneous group, and the substantial morphological differences between species within this clade are illustrated by the high uncertainty associated with ancestral character state reconstruction at the MRCA of the group. About half of the species share the morphological characters that have been used by Yamada (1979) to describe subg. *Odontoradula*, including acute to apiculate leaf lobes, often marginally toothed at the apex, and gynoecia terminal on long branches or stems and with one to four pairs of bracts. Other species resolved here as members of *Odontoradula* were traditionally included in other subgenera and often exhibit drastically different morphologies. This is the case in *R. retroflexa*, for instance, which shares none of the diagnostic features of subg. *Odontoradula* but rather exhibits a typical morphology for subg. *Radula*, including an obtuse to rounded, entire leaf apex and gynoecia

Fig. 1. Fifty percent majority-rule consensus of the trees generated by an MCMC carried out in MrBayes v.3.2. See Devos & al. (2011) for details on phylogenetic analyses. Branch lengths were averaged over the 1800 trees obtained after removing the burn-in. Numbers above branches correspond to their posterior probability values. Details of phylogenetic relationships within the main clades can be found in Fig 2.



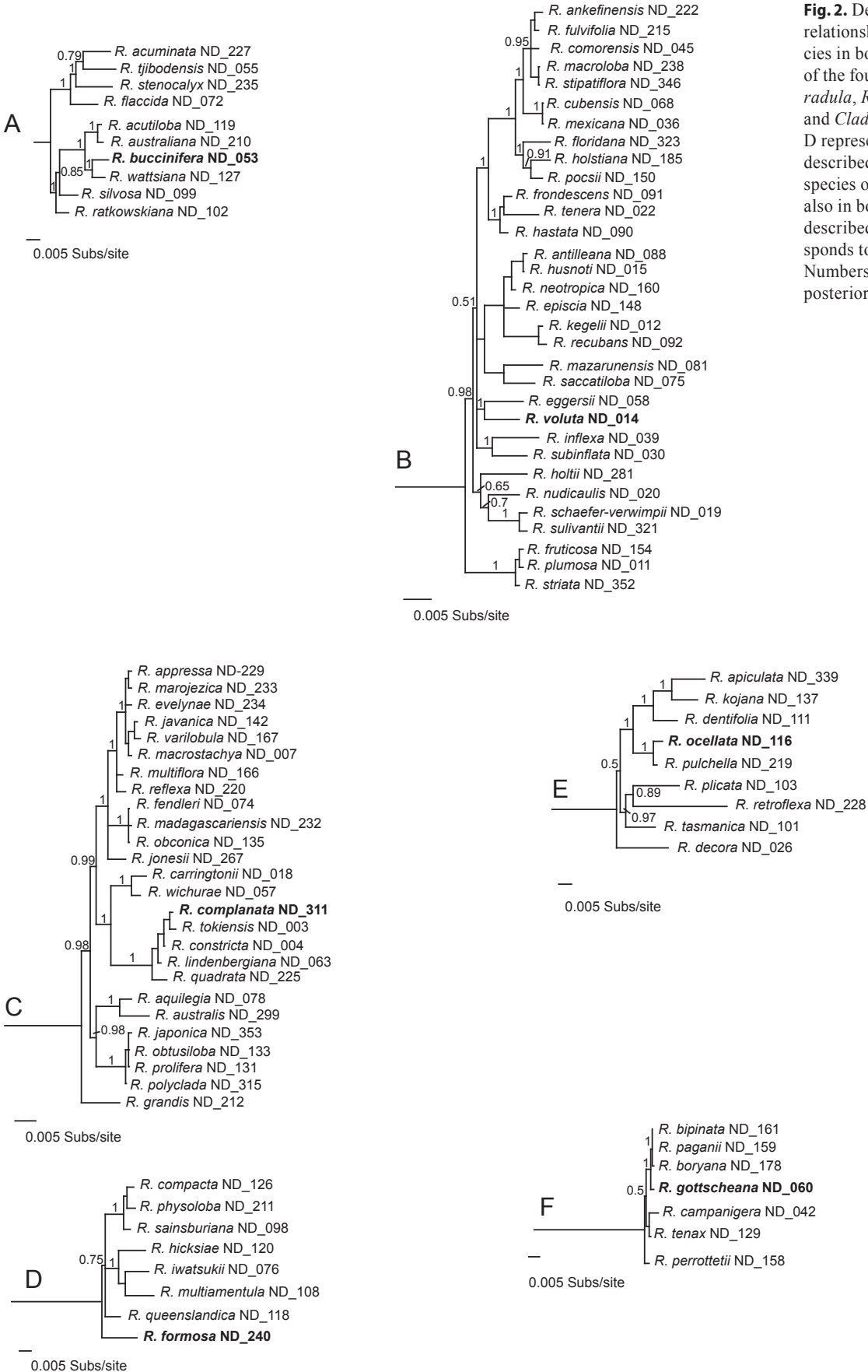


Fig. 2. Details of phylogenetic relationships within clades. Species in bold are the type species of the four subgenera, *Metaradula*, *Radula*, *Odontoradula*, and *Cladoradula*. Clades B and D represent two of the newly described subgenera. The type species of those subgenera are also in bold. The third subgenus described in this paper corresponds to clade G (see Fig. 1). Numbers above branches are posterior probabilities.

Table 2. Probabilities of ancestral character states for the 20 morphological characters investigated in *Radula*. See Table 1 for the list and description of the characters and their states. P(0) is the average posterior probability of state 0 and is given for all the characters at all the nodes in our phylogeny (nodes 1–11). Nodes are numbered as in Fig. 1. The Standard Deviation (SD) around the average posterior probability of state 0 is also given. Posterior probabilities P(0) < 0.3 and > 0.7 are considered significant and indicated in bold.

Character		P(0) at											
		Root	Node 11	Node 10	Node 9	Node 8	Node 7	Node 6	Node 5	Node 4	Node 3	Node 2	Node 1
A	Average	0.44	0.53	0.71	0.53	0.53	0.39	0.84	0.87	0.72	0.51	0.64	0.01
	SD	0.04	0.03	0.07	0.04	0.04	0.06	0.06	0.07	0.11	0.12	0.08	0.04
B		0.54	0.58	0.75	0.57	0.58	0.57	0.87	0.90	0.90	0.88	0.79	0.99
		0.05	0.06	0.08	0.07	0.08	0.05	0.06	0.06	0.05	0.06	0.08	0.02
C		0.61	0.49	0.84	0.55	0.61	0.64	0.93	0.95	0.95	0.03	0.89	1.00
		0.10	0.08	0.09	0.09	0.11	0.10	0.06	0.04	0.05	0.05	0.09	0.01
D		0.32	0.61	0.79	0.61	0.63	0.27	0.90	0.94	0.87	0.87	0.83	0.00
		0.10	0.10	0.10	0.11	0.12	0.09	0.07	0.05	0.10	0.09	0.10	0.00
E		0.45	0.44	0.40	0.45	0.51	0.42	0.55	0.05	0.30	0.10	0.82	0.01
		0.05	0.06	0.11	0.07	0.05	0.06	0.14	0.04	0.13	0.07	0.10	0.01
F		0.43	0.36	0.75	0.44	0.51	0.39	0.71	0.94	0.05	0.07	0.79	0.08
		0.06	0.09	0.14	0.05	0.06	0.07	0.17	0.06	0.05	0.06	0.12	0.12
G		0.48	0.48	0.47	0.49	0.51	0.45	0.62	0.08	0.36	0.50	0.72	0.01
		0.03	0.03	0.08	0.03	0.02	0.04	0.10	0.05	0.12	0.12	0.10	0.01
H		0.71	0.73	0.91	0.76	0.64	0.73	0.96	0.98	0.97	0.63	0.38	1.00
		0.17	0.17	0.09	0.17	0.25	0.16	0.05	0.03	0.04	0.29	0.31	0.00
I		0.44	0.53	0.72	0.53	0.52	0.40	0.86	0.84	0.84	0.17	0.41	0.01
		0.05	0.03	0.09	0.04	0.04	0.06	0.07	0.10	0.08	0.10	0.10	0.03
J		0.18	0.65	0.83	0.65	0.67	0.15	0.92	0.96	0.94	0.92	0.87	0.00
		0.12	0.10	0.10	0.12	0.13	0.09	0.06	0.03	0.05	0.06	0.10	0.01
K		0.52	0.52	0.61	0.52	0.53	0.54	0.83	0.44	0.67	0.73	0.71	0.99
		0.02	0.03	0.09	0.02	0.03	0.03	0.05	0.20	0.13	0.08	0.06	0.01
L		0.58	0.31	0.56	0.36	0.45	0.61	0.38	0.96	0.11	0.93	0.88	0.99
		0.08	0.13	0.17	0.15	0.15	0.08	0.17	0.03	0.13	0.06	0.09	0.01
M		0.52	0.45	0.73	0.48	0.51	0.56	0.86	0.92	0.33	0.81	0.77	0.00
		0.02	0.08	0.07	0.07	0.07	0.04	0.06	0.04	0.18	0.08	0.08	0.00
N		0.48	0.53	0.28	0.51	0.48	0.45	0.15	0.08	0.59	0.19	0.24	0.99
		0.02	0.07	0.06	0.06	0.05	0.03	0.05	0.04	0.20	0.08	0.07	0.04
O		0.69	0.77	0.22	0.60	0.56	0.71	0.02	0.99	0.98	0.98	0.45	1.00
		0.13	0.11	0.14	0.15	0.21	0.12	0.04	0.02	0.02	0.03	0.24	0.00
P		0.74	0.79	0.92	0.81	0.64	0.75	0.97	0.98	0.98	0.97	0.37	1.00
		0.17	0.15	0.08	0.15	0.28	0.16	0.04	0.02	0.03	0.04	0.33	0.00
Q		0.55	0.48	0.76	0.51	0.54	0.57	0.87	0.91	0.40	0.88	0.79	0.99
		0.06	0.08	0.08	0.08	0.08	0.06	0.06	0.05	0.17	0.06	0.09	0.01
R		0.51	0.53	0.65	0.52	0.52	0.54	0.80	0.70	0.75	0.82	0.70	0.05
		0.01	0.02	0.05	0.01	0.01	0.02	0.05	0.14	0.09	0.05	0.05	0.08
S		0.52	0.55	0.48	0.53	0.49	0.55	0.41	0.65	0.89	0.58	0.27	0.99
		0.02	0.03	0.11	0.03	0.03	0.03	0.11	0.20	0.05	0.11	0.10	0.01
T		0.54	0.57	0.73	0.57	0.58	0.57	0.80	0.93	0.90	0.82	0.78	0.99
		0.05	0.06	0.08	0.07	0.08	0.06	0.08	0.04	0.05	0.09	0.09	0.01

with only one pair of bracts. Although extensive data on sporophytic traits are missing for many species, the morphological heterogeneity in gametophytic traits examined here seems to be further paralleled by the wide range of variation of the generative features displayed by the species of subg. *Odontoradula*. For example, *R. dentifolia* is unique in its massive perianths which have multistratose walls above the point of fusion with the calyptra, capsules with 2-phase development, linear thickenings, and spiral dehiscence (Renner & Braggins, 2005).

Within subg. *Cladoradula*, a subgenus traditionally including species with the female inflorescence restricted to the tips of short reduced lateral branches (Yamada, 1979), the reconstructions of ancestral state at the MRCA exhibited high posterior probabilities, >0.90 for all of the investigated characters, suggesting morphological homogeneity within the clade with no or few reversals. Yet, despite their typical *Cladoradula*-type morphology, *R. aquilegia*, *R. carringtonii*, and *R. hastata* were resolved in the present analysis as part of different lineages.

Finally, although all the species of subg. *Metaradula* sampled here except *R. appressa* were resolved as monophyletic, the clade also includes species usually placed in different subgenera. For example, although it shares with other members of subg. *Metaradula* an *Isotachis*-type stem perigynium, *R. ratkowskiana* differs from other species in this subgenus in stem anatomy, capsule shape, capsule wall anatomy (2-phase, not 1-phase), and spore ornamentation (Renner & Braggins, 2005).

In liverworts, many traditional taxonomic concepts have been confirmed by recent molecular phylogenetic evidence, e.g., in Lejeuneaceae Cas.-Gil (Wilson & al., 2007), *Leptoscyphus* Mitt. (Vanderpoorten & al., 2010) and *Frullania* (Hentschel & al., 2009). Major discrepancies between traditional and molecular systematics, such as association of *Treubia* Goebel with *Haplomitrium* Nees as the first diverging lineage of extant liverworts (e.g., Crandall-Stotler & al., 2005), the inclusion of the leafy Pleuroziaceae (Schiffner) K. Müller within simple thalloids (Crandall-Stotler & al., 2005) and the re-interpretation of the apparently thalloid *Mizutania* Furuki & Z. Iwats. (*Mizutaniaceae* Furuki & Z. Iwats.) as a highly specialized member of the leafy genus *Calypogeia* Raddi (Masuzaki & al., 2010; Pressel & al., 2011), were due to an over-emphasis on growth morphology and actually allowed for a finer circumscription of the major liverwort lineages based on more robust, albeit less obvious morphological features such as the ultrastructure of the blepharoplast, the shape of the apical cell or the morphology of the sexual branches (Crandall-Stotler & al., 2008, 2009).

In *Radula*, only one synapomorphy, namely the loss of stem perigynium, was identified at the MRCA of clade B, across all characters. Although the probabilities of ancestral state reconstructions at the MRCAs of the main lineages identified here were mostly high, allowing each individual lineage to be described morphologically, the average probabilities associated with the ancestral state reconstructions at deeper nodes were low, making it impossible to define where shifts in character state occurred. In binary characters, evidence for phylogenetic signal in the data is found anytime the probabilities of ancestral states differ from 0.5 and signal intensity is proportional to departure of ancestral state probabilities from 0.5 (Vanderpoorten

& Goffinet, 2006). Thus, the low probabilities associated with state reconstructions towards the deepest node of the phylogeny indicate that phylogenetic signal in morphological evolution has eroded towards the root in *Radula*, making it impossible to define morphological synapomorphies at this taxonomic level.

We propose a new infrageneric classification scheme for *Radula* and create three new subgenera to accommodate the species included in clades B, D, and G resolved here. While the reconstructions of ancestral gametophytic traits allow for a fairly thorough description of the character states that are characteristic for the MRCAs of each of those seven lineages, actual synapomorphies are mostly lacking. At present, the classification scheme is therefore based almost only on molecular features. A survey of morphological characters in Australasian species by Renner & Braggins (2004, 2005) revealed, however, considerable structural diversity in the sporophytic generation, which appeared to be more variable than anticipated on the basis of observed levels of character variation in the gametophyte. Although their character analysis was not translated into a classificatory scheme, their data suggest that more morphologically tractable phylogenetic groups may exist within the genus *Radula* than are reflected in the current subgeneric classification, which is based primarily on gametophytic characters. Sporophytic characters could provide clade-defining synapomorphies, as has been demonstrated in other groups of leafy liverworts such as Lejeuneaceae (Gradstein & al., 2003; Wilson & al., 2007) and Plagiochilaceae (Heinrichs, 2002). Since sporophytes are known for only a small subset of the taxa included within this phylogeny, future studies should focus on the sporophyte generation in a wider range of species.

■ TAXONOMIC IMPLICATIONS

The following is a synopsis of a new subgeneric classification of *Radula* based on the results of this study. Character states listed for each subgenus are those that were reconstructed at the MRCA with an average posterior probability of >0.7 (see text for details).

- [clade A] *Radula* subg. *Metaradula* R.M. Schust. in *Phytologia* 56: 69. 1984 – Type: *Radula buccinifera* (Hook. f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees
Plants green when fresh, with pinnate or irregular vegetative branching; microphyllous branches absent. *Stem* subepidermis lacking; medullary cell walls thin. *Leaves* with rounded-obtuse and entire lobes; cells punctate to clearly papillose; trigones lacking or small; lobule insertion parallel to stem, directed to stem apex; caducous leaves and gemmae absent. *Gynoecea* on main axis or long branch, with innovations; perigynium present.
- [clade B] *Radula* subg. *Volutoradula* Devos, M.A.M. Renner, Gradst., A.J. Shaw & Vanderp., **subg. nov.** – Type: *Radula voluta* Taylor ex Gottsche, Lindenb. & Nees
Plantae vivae viride, cum ramificatione vegetativa pinnata vel irregulari; rami microphylli desunt. Parietes cellularum epidermidis brunnei, crassi; parietes cellularum medullae tenues.

Foliares lobi rotundato-obtusi integerrimique; cellulae laeves, trigonis carentibus vel parvis; lobuli insertio ad caulem parallela, ad caulis apicem directa; gemmae desunt. Gynoecia secus axin principalem vel ramum longum, cum innovationibus; perigynium deest.

Plants green when fresh, with pinnate or irregular vegetative branching; microphyllous branches absent. *Stem* epidermis cell walls brown, thickened; medullary cell walls thin. *Leaves* with rounded-obtuse and entire lobes; cells smooth; trigones lacking or small; lobule insertion parallel to stem, directed to stem apex; caducous leaves and gemmae absent. *Gynoecia* on main axis or long branch, with innovations; perigynium absent.

3. [clade C] *Radula* subg. *Radula* – Type: *Radula complanata* (L.) Dumort.

Plants green when fresh, with pinnate or irregular vegetative branching; microphyllous branches absent. *Stem* subepidermis lacking; medullary cell walls thickened. *Leaves* with rounded-obtuse and entire lobes; cells smooth; trigones absent or small; lobule insertion parallel to stem, directed to stem apex; caducous leaves and gemmae present or absent. *Gynoecia* on main axis or long branches, with innovations; perigynium absent.

4. [clade D] *Radula* subg. *Amentuloradula* Devos, M.A.M. Renner, Gradst., A.J. Shaw & Vanderp., **subg. nov.** – Type: *Radula formosa* (C.F.W. Meissn. ex Spreng.) Nees

Plantae cum ramificatione vegetativa pinnata vel irregulari; ramis microphyllis munitae. Caulina subepidermis deest; parietes cellularum epidermidis medullaeque crassi. Cellulae foliares laeves; trigonis magnis auctae; lobuli insertio ad caulem parallela, ad caulis apicem directa; folia caduca et gemmae desunt. Gynoecia secus axim principalem vel longum ramum, cum innovationibus; perigynium deest.

Plants yellow green, orange green, mid green, brown green, bronze green, or black green when fresh, with pinnate or irregular vegetative branching; microphyllous branches present. *Stem* subepidermis lacking; epidermis and medullary cell walls thickened. *Leaves* rounded, entire or dentate; cells smooth, with large trigones; lobule insertion parallel to stem, directed to stem apex; caducous leaves and gemmae absent. *Gynoecia* on main axis or long branch, with innovations; perigynium absent.

5. [clade E] *Radula* subg. *Odontoradula* K. Yamada in J. Hattori Bot. Lab. 45: 201. 1979 – Type: *Radula ocellata* K. Yamada

Plants mid green to lime green when fresh, with pinnate or irregular vegetative branching; microphyllous branches absent. *Stem* subepidermis lacking; epidermis cell walls thin, colourless; medullary cell walls thin. *Leaves* rounded to apiculate or acuminate, entire or variously dentate or serrate; cells smooth or bearing a single low dome-shaped papilla, particularly over cells of keel; lobule insertion parallel to stem, directed to stem apex; caducous leaves and gemmae absent. *Gynoecia* on main axis or long branches, with innovations; perigynium absent.

6. [clade F] *Radula* subg. *Cladoradula* Spruce in Trans. Proc. Bot. Soc. Edinburgh 15: 315. 1885 – Type: *Radula gottscheana* Taylor

Plants brown when fresh, with pinnate or irregular vegetative branching; microphyllous branches absent. *Stems* with a subepidermis; epidermis cell walls thickened, brown; medullary cell walls thickened. *Leaves* with apiculate-acute and toothed lobes; cells smooth and with large trigones; lobule insertion sinuate-oblique to transverse, directed to stem ventral midline; caducous leaves present, gemmae absent; *Gynoecia* on short branches without innovations; perigynium absent.

7. [clade G] *Radula* subg. *Dactyloradula* Devos, M.A.M. Renner, Gradst., A.J. Shaw & Vanderp., **subg. nov.** – Type: *Radula brunnea* Steph.

Plantae vivae virides, cum ramificatione vegetativa pinnata vel irregulari; rami microphylli desunt. Caulina subepidermis praesens; parietes cellularum epidermidis crassi, brunnei; medullae cellularum parietes crassi. Foliares lobi rotundato-obtusi, intergri; cellulae laeves, trigonis magnis auctae; lobuli insertio sinuato-obliqua ad transversa, ad caulis ventralem lineam directa; folia caduca et gemmae desunt. Gynoecia secus axin principalem vel ramum longum; perigynium deest.

Plants green when fresh, with vegetative branching pinnate or irregular; microphyllous branches absent. *Stem* subepidermis present; epidermis cell walls thickened, brown; medullary cell walls thickened. *Leaves* with rounded-obtuse, entire lobes; cells smooth, with large trigones; lobule insertion sinuate-oblique to transverse, directed to stem ventral midline; caducous leaves and gemmae absent. *Gynoecia* on main axis or long branch, with innovations; perigynium absent.

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Appendix. Voucher specimens: species, collector and collection number followed by herbarium, DNA accession number, GenBank accession numbers (*trnG*, *psbA-trnH*, *trnL-trnF*, *rps4*, *atpB-rbcL*, *psbT-psbH*).

R. acuminata Steph., *T. Pocs 02102/AA* EGR, ND_227, HM992384, HM992127, HM992463, HM992295, HM992034, HM992208; *R. acutiloba* Steph., *J.A. Curnow 5635* CBG, ND_119, HM992356, HM992098, HM992442, HM992267, HM992005, HM992183; *R. ankefinensis* Gottsche ex Stephani, *S. & T. Pocs 04011/G* EGR, ND_222, HM992382, HM992125, HM992461, HM992293, HM992032, HM992207; *R. antileana* Castle, *S.R. Gradstein 9448* GOET, ND_088, HM992343, HM992085, HM992429, HM992254, HM991992, HM992175; *R. apiculata* Sande Lac. ex Stephani, *T. Yamaguchi 1731* BR, ND_339, –, HM992143, HM992478, HM992311, HM992050, –, *R. appressa* Mitt., *T. Pocs 90113/AH* EGR, ND_229, HM992386, HM992129, HM992465, HM992297, HM992036, HM992209; *R. aquilegia* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, *A. Schäfer-Verwimp & Verwimp 26039* Herb. Schäfer-Verwimp, ND_078, HM992341, HM992083, HM992427, HM992252, HM991990, HM992173; *R. australiana* Yamada, *D. Glenny CHR559976* CHR, ND_210, HM992377, HM992119, HM992456, HM992287, HM992026, HM992202; *R. australis* Austin, *B. Shaw 6089* DUKE, ND_299, HM992399, HM992142, HM992477, HM992310, HM992049, HM992231, *R. bipinnata* Mitt., *T. Pocs NY8016* NY, ND_161, HM992372, HM992114, –, HM992282, HM992021, HM992197; *R. boryana* (F. Weber) Nees, *T. Pocs 88110/AR* E, ND_178, HM992375, HM992117, –, HM992285, HM992024, HM992200; *R. brunnea* Steph., *N. Ohnishi H3196644* H, ND_001, HM992315, HM992054, HM992403, –, HM991961, HM992147; *R. buccinifera* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, *A. Schäfer-Verwimp & Verwimp 14336* Herb. Schäfer-Verwimp, ND_053, HM992332, HM992072, HM992417, HM992241, HM991979, HM992162; *R. campanigera* Mont., *N. Ohnishi HIRO225* GOET, ND_042, HM992330, HM992070, –, HM992239, HM991977, HM992160; *R. carringtonii* J.B. Jack, *A. Schäfer-Verwimp & Verwimp 25734* Herb. Schäfer-Verwimp, ND_018, HM992323, HM992062, HM992409, HM992231, HM991969, HM992153; *R. comorensis* Steph., *A. Schäfer-Verwimp & Verwimp 23835* Herb. Schäfer-Verwimp, ND_045, HM992331, HM992071, HM992416, HM992240, HM991978, HM992161; *R. compacta* Castle, *J.A. Curnow 4525* CBG, ND_126, HM992358, HM992100, –, HM992269, HM992007, –, *R. complanata* (L.) Dumort., *B. Shaw F915* DUKE, ND_311, HM992393, HM992136, –, HM992304, HM992043, –, *R. constricta* Steph., *T. Koponen H3187494* H, ND_004, HM992317, HM992056, –, HM992225,

Appendix. Continued.

HM991963, –; **R. cubensis** Yamada, *A. Schäfer-Verwimp & M. Preussing 23532* Herb. Schäfer-Verwimp, ND_068, HM992337, HM992078, HM992422, HM992247, HM991985, HM992168; **R. decora** Gottsche ex Stephani, *I. Holz & Franzaring CH0060* GOET, ND_026, HM992327, HM992066, HM992413, HM992235, HM991973, –; **R. dentifolia** Grolle, *M.A.M. Renner AK280588* AK, ND_111, HM992353, HM992095, HM992439, HM992264, HM992002, –; **R. eppersii** Yamada, *A. Schäfer-Verwimp & M. Preussing 23330/A* Herb. Schäfer-Verwimp, ND_058, HM992334, HM992075, HM992420, HM992244, HM991982, HM992165; **R. episcia** Spruce, *S. Churchill, M. Serrano & al. MO23708* MO, ND_148, HM992366, HM992108, HM992449, HM992277, HM992015, HM992191; **R. evelynae** Yamada, *T. Pocs, R.E. Magill & A. Rupf 9288/R* EGR, ND_234, HM992389, HM992132, HM992468, HM992300, HM992039, HM992212; **R. fendleri** Gottsche ex Stephani, *A. Schäfer-Verwimp & M. Preussing 23250/A* Herb. Schäfer-Verwimp, ND_074, HM992339, HM992080, HM992424, HM992249, HM991987, HM992170; **R. flaccida** Lindenb. & Gottsche, *A. Schäfer-Verwimp, J. Heinrichs, R.A. Wilson & S.O. Yandun 24422* GOET, ND_072, HM992338, HM992079, HM992423, HM992248, HM991986, HM992169; **R. floridana** Castle, *B. Shaw 6209* DUKE, ND_323, HM992396, HM992139, HM992474, HM992307, HM992046, HM992218; **R. formosa** (Meissn. ex Spreng.) Nees, *T. Pocs s.n.* EGR, ND_240, HM992392, HM992135, HM992471, HM992303, HM992242, HM992215; **R. frondescens** Steph., *I. Holz CR000493* GOET, ND_091, HM992345, HM992087, HM992431, HM992256, HM991994, HM992177; **R. fruticosa** Steph., *U. Drehwald NY970175* NY, ND_154, HM992368, HM992110, HM992451, HM992278, HM992017, HM992193; **R. fulvifolia** (Hook. & Tayl.) Gottsche, *T. Pocs s.n.* EGR, ND_215, HM992379, HM992122, HM992458, HM992290, HM992029, HM992204; **R. gottscheana** Taylor, *S. Ingram & K. Ferrell-Ingram Ingram 1765*, ND_060, HM992335, HM992076, –; HM992245, HM991983, HM992166; **R. grandis** Steph., *D. Glenny CHR571846* CHR, ND_212, –; HM992121, HM992457, HM992289, HM992028, HM992203; **R. hastata** Steph., *S.R. Gradstein 9443* GOET, ND_090, HM992344, HM992086, HM992430, HM992255, HM991993, HM992176; **R. hicksiae** Yamada, *J.A. Curnow & H. Streimann 3689* CBG, ND_120, HM992357, HM992099, HM992443, HM992268, HM992006, HM992184; **R. holstiana** Steph., *Hodgetts M2668a* E, ND_185, HM992376, HM992118, HM992455, HM992286, HM992025, HM992201; **R.holtii** Spruce, *N. Devos & A. Vanderpoorten DV003* DUKE, ND_281, HM992398, HM992141, HM992476, HM992309, HM992048, HM992219; **R. husnotii** Castle, *M.J. Lyon DB12895* MO, ND_015, HM992322, HM992061, HM992408, HM992345, HM991968, HM992230; **R. inflexa** Gottsche ex Stephani, *A. Schäfer-Verwimp & Verwimp 17830* Herb. Schäfer-Verwimp, ND_039, –; HM992069, –; HM992238, HM991976, HM992159; **R. iwatsukii** Yamada, *A. Schäfer-Verwimp & Verwimp 18757/A* Herb. Schäfer-Verwimp, ND_076, –; HM992082, HM992426, HM992251, HM991989, HM992172; **R. japonica** Gottsche ex Stephani, *M. Higuchi 1198* BR, ND_353, HM992402, HM992146, HM992481, HM992314, HM992053, HM992223; **R. javanica** Gottsche, *S. Churchill, M. Decker & F. Morgo MO22187* MO, ND_142, HM992365, HM992107, HM992448, HM992276, HM992014, HM992190; **R. jonesii** Bouman, Dirkse & K. Yamada, *N. Devos s.n.* DUKE, ND_267, HM992397, HM992140, HM992475, HM992308, HM992047, –; **R. kegelii** Gottsche ex Stephani, *N. Salazar DB3609* GOET, ND_012, HM992320, HM992059, HM992406, HM992228, HM991966, HM992150; **R. kojana** Steph., *M. Mizutani 14255* DUKE, ND_137, HM992364, HM992106, HM992447, HM992275, HM992013, –; **R. lindenbergiana** Gottsche ex Hartm., *A. Schäfer-Verwimp & Verwimp 25732/A* Herb. Schäfer-Verwimp, ND_063, HM992336, HM992077, HM992421, HM992246, HM991984, HM992167; **R. macroloba** Steph., *T. Pocs s.n.* EGR, ND_238, HM992391, HM992134, HM992470, HM992302, HM992041, HM992214; **R. macrostachya** Lindenb. & Gottsche, *S.R. Gradstein & G. Dauphin DB12894* GOET, ND_007, HM992318, HM992057, HM992404, HM992226, HM991964, HM992148; **R. madagascariensis** Gottsche, *A. Szabo 9614/DV* EGR, ND_232, HM992387, HM992130, HM992466, HM992298, HM992037, HM992210; **R. marojezica** Jones, *T. Pocs 90103/AE* EGR, ND_233, HM992388, HM992131, HM992467, HM992299, HM992038, HM992211; **R. mazarunensis** Yamada, *A. Schäfer-Verwimp & Verwimp 17767* Herb. Schäfer-Verwimp, ND_081, HM992342, HM992084, HM992428, HM992253, HM991991, HM992174; **R. mexicana** Lindenb. & Gottsche ex Gottsche, *A. Schäfer-Verwimp & M. Preussing 23204* Herb. Schäfer-Verwimp, ND_036, HM992329, HM992068, HM992415, HM992237, HM991975, HM992158; **R. multiamentula** Hodgs, *M.A.M. Renner AK280299* AK, ND_108, HM992352, HM992094, HM992438, HM992263, HM992001, HM992182; **R. multiflora** Gottsche ex Schiffner, *K.R. Wood NY9604* NY, ND_166, HM992373, HM992115, HM992453, HM992283, HM992022, HM992198; **R. neotropica** Castle, *B. Allen NY11935* NY, ND_160, HM992371, HM992113, HM992452, HM992281, HM992020, HM992196; **R. nudicaulis** Steph., *A. Schäfer-Verwimp & M. Preussing 23447* Herb. Schäfer-Verwimp, ND_020, HM992325, HM992064, HM992411, HM992233, HM991971, HM992155; **R. obconica** Sull., *B. Shaw 4874* DUKE, ND_135, HM992363, HM992105, HM992446, HM992274, HM992012, HM992189; **R. obtusiloba** Steph., *W.B. Schofield 115550* DUKE, ND_133, HM992362, HM992104, –; HM992273, HM992011, HM992188; **R. ocellata** Yamada, *J.A. Curnow 3664* CBG, ND_116, HM992354, HM992096, HM992440, HM992265, HM992003, –; **R. paganii** Castle, *B.M. Thiers NY5297* NY, ND_159, HM992370, HM992112, –; HM992280, HM992019, HM992195; **R. perrottetii** Gottsche ex Stephani, *M. Mizutani NY15272* NY, ND_158, HM992369, HM992111, –; HM992279, HM992018, HM992194; **R. physoloba** Mitt., *M.A.M. Renner CHR555962* CHR, ND_211, HM992378, HM992120, –; HM992288, HM992027, –; **R. plicata** Mitt. ex Hook. f., *M.A.M. Renner AK280391* AK, ND_103, HM992351, HM992093, HM992437, HM992262, HM992000, –; **R. plumosa** Mitt. ex Stephani, *J. Hyvönen DB3600* GOET, ND_011, HM992319, HM992058, HM992405, HM992227, HM991965, HM992149; **R. pocsii** Yamada, *S. Churchill, M. Serrano & al. MO23444* MO, ND_150, HM992367, HM992109, HM992450, –; HM992016, HM992192; **R. polyclada** Evans, *B. Shaw F956* DUKE, ND_315, HM992394, HM992137, HM992472, HM992305, HM992044, HM992216; **R. prolifera** Arnell, *W.B. Schofield 115792* DUKE, ND_131, HM992361, HM992103, HM992445, HM992272, HM992010, HM992187; **R. pulchella** Mitt. ex Steph., *H. Streimann 63817* EGR, ND_219, HM992380, HM992123, HM992459, HM992291, HM992030, HM992205; **R. quadrata** Gottsche, *T. Pocs, E.M. Kungu & A. Szabo 9230/S* EGR, ND_225, HM992383, HM992126, HM992462, HM992294, HM992033, –; **R. queenslandica** Yamada, *J.A. Curnow 3846* CBG, ND_118, HM992355, HM992097, HM992441, HM992266, HM992004, –; **R. ratkowskiana** Yamada, *M.A.M. Renner AK280205* AK, ND_102, HM992350, HM992092, HM992436, HM992261, HM991999, HM992181; **R. recubans** Taylor, *M. Burghardt DB21422* GOET, ND_092, HM992346, HM992088, HM992432, HM992257, HM991995, HM992178; **R. reflexa** Nees & Mont., *T. Pocs s.n.* EGR, ND_220, HM992381, HM992124, HM992460, HM992292, HM992031, HM992206; **R. retroflexa** Taylor, *S. & T. Pocs 03281/C* EGR, ND_228, HM992385, HM992128, HM992464, HM992296, HM992035, –; **R. saccatiloba** Steph., *A. Schäfer-Verwimp & Verwimp 18053* Herb. Schäfer-Verwimp, ND_075, HM992340, HM992081, HM992425, HM992250, HM991988, HM992171; **R. sainsburiana** Hodgs & Allison, *M.A.M. Renner AK282969* AK, ND_098, HM992347, HM992089, HM992433, HM992258, HM991996, HM992179; **R. schaefer-verwimpii** Yamada, *A. Schäfer-Verwimp & M. Preussing 23443/A* Herb. Schäfer-Verwimp, ND_019, HM992324, HM992063, HM992410, HM992232, HM991970, HM992154; **R. silvosa** Hodgs & Allison, *M.A.M. Renner AK280392* AK, ND_099, HM992348, HM992090, HM992434, HM992259, HM991997, HM992180; **R. stenocalyx** Mont., *T. Pocs s.n.* EGR, ND_235, HM992390, HM992133, HM992469, HM992301, HM992040, HM992213; **R. stipatiflora** Steph., *T. Arts REU52/24* BR, ND_346, HM992400, HM992144, HM992479, HM992312, HM992051, HM992221; **R. striata** Mitt. ex Stephani, *U. Drehwald 970175* BR, ND_352, HM992401, HM992145, HM992480, HM992313, HM992052, HM992222; **R. subinflata** Lindenb. & Gottsche, *I. Holz & Schäfer-Verwimp DB13093* GOET, ND_030, HM992328, HM992067, HM992414, HM992236, HM991974, HM992157; **R. sullivantii** Austin, *B. Shaw 6189* DUKE, ND_321, HM992395, HM992138, HM992473, HM992306, HM992045, HM992217; **R. tasmanica** Steph., *M.A.M. Renner AK280184* AK, ND_101, HM992349, HM992091, HM992435, HM992260, HM991998, –; **R. tenax** Lindb., *P.G. Davison & M.L. Hicks 2946* DUKE, ND_129, HM992360, HM992102, –; HM992271, HM992009, HM992186; **R. tenera** Mitt. ex Stephani, *A. Schäfer-Verwimp, J. Heinrichs, R.A. Wilson & S.O. Yandun 24230* Herb. Schäfer-Verwimp, ND_022, HM992326, HM992065, HM992412, HM992234, HM991972, HM992156; **R. tjiobodensis** Goebel, *A.L. Ilkiu-Borges, S.R. Gradstein, K.T. Yong & M. Ponniah DB16663* GOET, ND_055, –; HM992073, HM992418, HM992242, HM991980, HM992163; **R. tokiensis** Steph., *T. Koponen H3187760* H, ND_003, HM992316, HM992055, –; HM992224, HM991962, –; **R. varilobula** Castle, *S.R. Hill NY21274* NY, ND_167, HM992374, HM992116, HM992454, HM992284, HM992023, HM992199; **R. voluta** Taylor, *A. Vanderpoorten AVW857* LG, ND_014, HM992321, HM992060, HM992407, HM992229, HM991967, HM992151; **R. watsiana** Steph., *H. Streimann 54341* CBG, ND_127, HM992359, HM992101, HM992444, HM992270, HM992008, HM992185; **R. wicheruae** Steph., *A. Schäfer-Verwimp & Verwimp 26018* Herb. Schäfer-Verwimp, ND_057, HM992333, HM992074, HM992419, HM992243, HM991981, HM992164; **OUTGROUP: Frullania moniliata** (Reinw., Blume & Nees) Mont., *Mizutani s.n.* ABSH, –; AY507484, HM167700, –; HM167631, –; **Jubula pennsylvanica** (Stephani) Evans, *Risk 11005* DUKE, AY608179, AY607954, AY608131, AY608075, AY607906, AY608011; **Porrella pinnata** L., *Goffinet 4744* DUKE, GQ368627, AY312915, AY312945, AY608101, AY607914, AY608020