REAPPRAISAL OF *GYMNOCOLEA* AND DESCRIPTION OF A NEW GENUS *RUDOLGAEA* (ANASTROPHYLLACEAE, MARCHANTIOPHYTA)

ALEXEY D. POTEMKIN & ANNA A. VILNET

ALEКSЕЙ Д. ПОТЕМКИН, АННА А. ВИЛЬНЕТ

Abstract

A review of the taxonomic composition of the genus Gymnocolea is provided. Among 15 species attributed to Gymnocolea, only 3 species are recognized within the genus. Their morphological and molecular analyses by rbcl, trnL-F cpDNA and ITS1-2 ndDNA sequences resulted in the transfer of *G. borealis* and *G. fascinifera* to the genus Rudolgaea named after Rudolf M. Schuster and Olga M. Schuster. Thus, Gymnocolea appears to be the monospecific genus with only *G. inflata*.

KEYWORDS: Gymnocolea, hepatics, liverworts, DNA barcoding, systematics

INTRODUCTION

The genus Gymnocolea (Dumort.) Dumort. based on the section Gymnocolea Dumort. of the genus Jungermannia L. was established by Dumortier with brief diagnosis in French “Périchèze nul. Colésule dressée stepetée, retrécie et dentée au sommet” and three species Gymnocolea fluittans (Nees) Dumort., G. inflata (Huds.) Dumort., and G. laxifolia (Hook.) Dumort.

Later Spruce (1882) established the genus Hygrobiella (Hook.) Spruce, based on Jungermannia laxifolia Hook. (= Gymnocolea laxifolia (Hook.) Dumort.) and the section Cladopus Spruce of the genus Cephaloziopsis (Dumort.) Dumort. for Jungermannia fluittans Nees (= Gymnocolea fluittans (Nees) Dumort.) and J. francisci Hook. Afterward, Buch (1927: 89) established the genus Cladopodiella instead of the section Cladopus, which is presently treated as the section Cladopodiella (H. Buch) Gradst. et al. of the genus Odontoschisma (Dumort.) Dumort. (Aranda et al., 2014).

Since the description of Gymnocolea, 15 species were attributed to this genus (https://tropicos.org, accessed 11 Oct 2021). Besides the three species mentioned above, Gymnocolea affinis Dumort., G. arenaria (Nees) Dumort., and G. huebeneriana (Nees) Dumort., proved to be synonyms of Mesoptychia turbinita (Raddi) L. Söd.

erstr. & Váňa, Lophoziosis excisa (Dicks.) Konstant. & Vilnet, and Hygrobiella laxifolia, respectively (Müller, 1954a,b); Gymnocolea acutiloba (Schiffn.) Müll. Frib., G. marginata (Steph.) S. Hatt., G. montana (Horik.) S. Hatt., G. soerensenii Kaal. ex Jorg. are morphologically similar to *G. inflata* and presently treated as its synonyms; G. andina Bucloh, G. cylindroformis (Mitt.) Steere, and G. multiflora (Steph.) R.M. Schust. belong to the genus Gymnocoleopsis (R.M. Schust.) R.M. Schust. Thus, for now only three species of the genus were accepted, that is *G. borealis* (Frisvoll & Moen) R.M. Schust., *G. fascinifera* Potemkin and G. inflata (Bánki et al., 2021b).

The relation of *G. borealis* and *G. inflata* was firstly supported from molecular evidence by Cailliau et al. (2013). In 1994, the first author discussed with R.M. Schuster the taxonomic position of *G. fascinifera* which is characterized by unique origin of rhizoids from the ventral leaf base compared with other Lophozioideae Cavers. R.M. Schuster supposed that *G. fascinifera* could represent a separate genus from Gymnocolea. The question remained open because no data on perianth and sporophyte of this species were available.

Potemkin (2003), following Kitagawa (1965), suggested the origin of the family Jungermanniaceae from the Lophozoidi ancestor and the position of Gymnocolea

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1. Komarov Botanical Institute, Russian Academy of Sciences, Professor Popov Str., 2, St. Petersburg, 197376 Russia; e-mail: potemkin_alexey@binran.ru; ORCID: 0000-0003-4420-1704
2. Polar-Alpine Botanical Garden, Kola Science Centre, Russian Academy of Sciences, Apatity, Murmansk Province, Russia; e-mail: anya_v@list.ru; ORCID: 0000-0001-7779-2593
in the Jungermanniaceae. The origin of rhizoids from the ventral leaf base in separate species of Jungermanniaceae supposed their relationship with Gymnocolea fascinifera. Subsequent molecular studies have shown a remote position of the genus Gymnocolea from the Jungermanniaceae s.l. (Vilnet el al., 2010). However, no molecular study of G. fascinifera has been made, and Schuster’s question about the taxonomic position of G. fascinifera was unanswered.

The recent find of G. borealis in Russia (Potemkin et al., 2021) initiated us to make a joint morphological and molecular study of available materials of G. fascinifera to compare these two species and clarify their phylogenetic affinity.

**MATERIAL AND METHODS**

**Sampling for morphological studies**

The morphological study was based on the light microscopic investigation of extensive collections of G. fascinifera cited by Potemkin (1993), and other collections, the selected representative being as follow: Gymnocolea borealis. Norway: 1.X.1968 Moen (H); Moen 79510 (H); Russia: Gydansky Peninsula, Troeva G1-138 (LE). Gymnocolea fascinifera. Russia: Republic of Komi, 24.VII.1963 A. Katenin (LE); Bely Island, 27.VII.1984, O.V. Rebristaya 21 (LE); Yamal Peninsula, 19.VII.1978, O.V. Rebristaya 74 (LE); USA: Alaska, 28.VII.1992, Potemkin 92-9701 (LE, holotype).

**DNA extraction, PCR, sequencing**

To test the phylogenetic affinity of G. fascinifera we selected ITS1-2 nrDNA, trnL-F, and rbcL cpDNA sequence data for 46 specimens of liverworts from the suborder Cephalozineae available in GenBank. The ITS1-2, trnL-F and rbcL loci for specimen of G. fascinifera from Alaska, ITS1-2 and trnL-F loci for specimen of G. borealis from the Gydansky Peninsula were sequenced here. Our attempts to obtain nucleotide sequence data for two specimens of G. fascinifera gathered from the Yamal Peninsula in 1978 and 1984 had no success. The list of specimens with voucher details and GenBank accession numbers are shown in Table 1.

DNA was extracted from dried liverwort tissue with DNeasy Plant Mini Kit (Qiagen, Germany). For amplification and sequencing of ITS1-2, trnL-F, and rbcL the primers suggested by White et al. (1990), Taberlet et al. (1991), and Kress & Erickson (2007), respectively, were used. PCR was carried out in 20 μl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C (ITS1-2, trnL-F), 52°C (rbcL), 60 s 72°C), and 2 min of final extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the Cleanup Mini (Evrogen, Russia), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, U.S.A.) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

**Phylogenetic analyses**

The newly obtained nucleotide sequences for G. fascinifera and G. borealis were assembled and then included in the produced datasets in BioEdit 7.0.1 (Hall, 1999). The automatical alignment procedure was done with the option of full multiple alignment with default settings for gaps and extension weights in the ClustalW tool. Then obtained dataset was manually corrected, the part of ITS1-2 at the 5'-end and P8 stem-loop region of trnL-intron were excluded from alignment due to ambiguously aligned positions, absent data at the ends of regions, and absent loci were coded as missing. The preliminary phylogenetic estimation revealed congruence between three studied loci. The ITS1-2 and trnL-F sequence data were cited from single specimen of each species, whereas rbcL from other specimens, thus combination of all three loci in single dataset would be incorrect. Thus, two datasets were produced, ITS1-2+trnL-F and rbcL.

Phylogeny was estimated by three procedures for each dataset: maximum parsimony (MP) with TNT v. 1.5 (Goloboff & Catalano, 2016), maximum likelihood (ML) with PhyML v. 3.0 (Guindon et al., 2010), and Bayesian reconstruction with MrBayes v. 3.2.1 (Ronquist et al., 2012). The parsimony analysis with TNT involved a New Technology Search for the minimal length tree by five iterations and 1000 bootstrap replicates, default settings were used for other parameters, gaps were treated as missing. The program ModelGenerator (Keane et al., 2006) identified GTR+I+F as the best-fitting evolutionary model for ITS1-2+trnL-F dataset and TN+I+F for the rbcL dataset. According to the stopping frequency criterion for the bootstrap (Pattengale et al., 2010), the ITS1-2 dataset requires 550 replicates to reach convergence with Pearson average n100 = 0.993802 as estimated by RAXML v. 7.2.6 (Stamatakis, 2006), the rbcL dataset – 500 replicates with n100 = 0.992292. The recommended models, number of bootstrap replicates, gamma distribution with four rate categories to estimate among-site rate heterogeneity were used in the maximum likelihood estimation for both datasets.

For the Bayesian analysis, each partition of the combined dataset (ITS1-2, trnL-F) and rbcL dataset was separately assigned the GTR+I+F model that was recommended by the authors of the program; gamma distributions were approximated using four rate categories. Two independent runs of the Metroplis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated, and two starting trees were chosen randomly. Chains were run for five million generations and trees were sampled every 1000th generation. The software tool Tracer (Rambaut & Drummond, 2007) revealed effective sample size (ESS) for ITS1-2+trnL-F as 15323.9952 and auto-correlation time (ACT) as 1174.7589, ESS for rbcL was 14663.5558 and ACT – 1227.6695. As determined by Tracer, the first 500 trees...
| Taxon                                      | Specimen voucher | Accession number |
|-------------------------------------------|------------------|------------------|
| Adelanthus lindenbergianus                | Chile, Holz, 25 (GOET) | GQ899969, GQ900177 |
| Anastrepta orcadensis                    | Russia, Buryatiya Rep., N. Konstantinova, 103–105 (KPABG) | DQ875126, DQ875125 |
| Anastrophyllum assimile                   | USA, N. Konstantinova, A137-18-95 (KPABG) | EU791787, EU791776, EU791778 |
| Barbilophozia barbata                     | Netherlands, N. Konstantinova, 3b-5-59 (KPABG) | EU791779, EU791764, EU791767 |
| Chandonanthus sp.                         | China, Yunnan, D. Long, 34711 (E) | EU791798, EU791798, EU791798 |
| Cylindrocolea recurvifolia               | Japan, T. Yamaguchi (F) | EU791798, EU791798, EU791798 |
| Gymnomitrion commutatum                  | USA, Vermont, B. Shaw, 6970 (DUKE) | EU791798, EU791798, EU791798 |
| Gymnocolea inflata                        | Russia, Sakhalin Prov., Kuril Isl., Iturup I., V. Bakalin, K-58-30-05, 110149 (VBGI) | EU791787, EU791787, EU791787 |
| Hamatostrepta concinna                   | Myanmar, D. Long, 34854 (DUKE) | EU791787, EU791787, EU791787 |
| Hattoria yakushimensis                   | Japan, T. Katagiri, 4281 (NICH) | EU791787, EU791787, EU791787 |
| Isopaches bicrenatus                     | Russia, Yakutia Rep., V. Bakalin, 06-08-1997 (KPABG) | EU791787, EU791787, EU791787 |
| Lophoziopsis excisa                       | Norway, Svalbard, N.A. Konstantinova, K-21-2-05 (KPABG) | DQ875083, DQ875058, DQ875093 |
| Neoorthocaulis attenuatus                | Poland, Strebel, 226 (GOET) | EU791787, EU791787, EU791787 |
| Neoorthocaulis floerkei                  | Canada, British Columbia, B. Shaw, 6992 (DUKE) | EU791787, EU791787, EU791787 |
| Nowellia curvifolia                      | Russia, Caucasus, N. Konstantinova, K-123-2-09 (KPABG) | EU791787, EU791787, EU791787 |
| Odontoschisma fluitans                   | Russia, Murmansk Prov., V. Bakalin, 1, D. Long, 226 (DUKE) | EU791787, EU791787, EU791787 |
| Plicanthus birmensis                      | Russia, Primorskiy Kray, V. Bakalin, P-76-5-05 (KPABG) | EU791787, EU791787, EU791787 |
| Plicanthus hirtellus                     | China, Yunnan, D. Long, 34407 (E) | EU791787, EU791787, EU791787 |
| Pseudolophozia sudetica                  | Czech Republic, 2 (DUKE) | EU791787, EU791787, EU791787 |
| Rudolgaea borealis                       | Russia, Gydansky Peninsula, E.I. Troeva, G1-138 (LE), 1 | EU791787, EU791787, EU791787 |
| Rudolgaea fascinifera                    | USA: Alaska, A. Potemkin, 92-9701 (LE) | EU791787, EU791787, EU791787 |
| Scapania undulata                        | Italy, Schaefer-V erwimp and V erwimp, 27551 (GOET) | EU791787, EU791787, EU791787 |
| Schizophyllopsis sphenoloboides          | Norway, Svalbard, N. Konstantinova, K-58-30-05, 110149 (VBGI) | EU791787, EU791787, EU791787 |
| Schljakovianthus quadrilobus             | USA: Alaska, B. Shaw, F982b/8 (DUKE) | EU791787, EU791787, EU791787 |
| Sphenolobus minutus                      | Norway, Svalbard, N. Konstantinova, K-58-30-05, 110149 (VBGI) | EU791787, EU791787, EU791787 |
| Sphenolobus saxicola                     | Czech Republic, N. Bohemia, B. Buryova, 26.9.1995 (DUKE) | EU791787, EU791787, EU791787 |
| Syzygiella autumnalis                    | Russia, Buryatiya Rep., N. Konstantinova, 103–105 (KPABG) | DQ875083, DQ875058, DQ875093 |
| Tetralophozia filiformis                 | China, Yunnan, B. Shaw, 5790 (DUKE) | EU791787, EU791787, EU791787 |
| Vietnamiella epiphytica                  | Vietnam, Lao Cai Prov., V. Bakalin, V-9-7-17 (VBGI), 1 | EU791787, EU791787, EU791787 |
in each run were discarded as burnin, thereafter 9000 trees were sampled from both runs for each dataset. The average standard deviation of split frequencies between two runs for ITS1-2+trnL-F was 0.004813, for \( rbcL \) 0.003465. Bayesian posterior probabilities were calculated from trees sampled after burn-in.

The infrageneric variability of ITS1-2, \( trnL-F \), and \( rbcL \) for the family Anastrophyllaceae were calculated as the average pairwise \( p \)-distances in Mega 5.1 (Tamura et al., 2011) using the pairwise deletion option for counting gaps.

RESULTS

Molecular results

For Gymnomitron fascinifera ITS1-2, \( trnL-F \), and \( rbcL \) nucleotide sequences were newly obtained, for \( G. \) borealis ITS1-2 and \( trnL-F \) (Table 1). The combined ITS1-2+\( trnL-F \) alignment for 27 specimens consists of 1373 sites, among them, 977 sites belong to ITS1-2 and 396 sites to \( trnL-F \). The number of conservative positions in ITS1-2 and \( trnL-F \) is 461 (47.18\%) and 235 (59.34\%), respectively, the number of variable positions is 352 (36.03\%) and 132 (33.33\%), and the number of parsimony-informative positions is 192 (19.65\%) and 67 (16.91\%). In the \( rbcL \) alignment of 26 specimens with 1120 positions, there are 828 (73.93\%) conservative sites, 262 (23.39\%) variable sites, and 142 (12.67\%) parsimony informative positions.

The MP analysis with TNT yielded 5 equally parsimonious trees with a length of 1715 steps, with CI = 0.617857 and RI = 0.436842 for the ITS1-2+\( trnL-F \)
The MP calculations for \( rbcL \) resulted in 7 equally parsimonious trees with a length of 567 steps, with CI = 0.557407 and RI = 0.449309. The ML criterion recovered a tree with a Log likelihood -7221.21 for ITS1-2+\( trnL-F \) and -4422.13 for \( rbcL \). Arithmetic means of Log likelihoods in Bayesian analysis for each sampling run were -6968.49 and -6969.90 for ITS1-2+\( trnL-F \) and -4181.88 and -4182.04 for the \( rbcL \) dataset. The tree topologies achieved in all estimations from both datasets became highly congruent with each other.

The tree topology from ML analysis of ITS1-2+\( trnL-F \) is presented with ML and MP bootstrap support values (BS) and Bayesian posterior probabilities (PP) for each node. In Fig. 2 the ML tree for the \( rbcL \) dataset with BS from MP and ML calculations and PP from BA was provided. The backbone affinity within family Anastrophyllaceae is poorly supported in both calculations but similar with relations published in Bakalin et al. (2020). Gymnocolea fascinifera and G. borealis composed a clade in both trees: with 0.86 PP in ITS1-2+\( trnL \) and 0.96 PP in \( rbcL \). In other estimation relation of both species has not got bootstrap support. The closest relatives to them appear to be recently described Vietnamiella epiphytica from Sino-Himalaya and Hattoria yakushimensis from Japan. The two specimens from remote localities of the type species of the genus Gymnocolea – G. inflata – are placed in a clade separated from G. fascinifera + G. borealis by several phyla with other genera.

The infraspecific \( p \)-distances calculation was provided for species G. borealis based on \( rbcL \) and G. inflata for ITS1-2, \( trnL-F \) and \( rbcL \). The variability of \( rbcL \) between two samples of G. borealis from Sweden and the Gydansky Peninsula is 0.6%, the variability among specimens of G. inflata from Svalbard and the Nizhny Novgorod Region is 2.1% in ITS1-2 and 0.9% in \( trnL-F \), between specimens from Svalbard and the United Kingdom is 0.4% by \( rbcL \) (data not shown). The multiplied samples of G. borealis and G. inflata were grouped and \( p \)-distances were calculated for the family Anastrophyllaceae (Tables 2a, b). The specimens of G. fascinifera and G. borealis are distinct from each other in the same range (5.3% in ITS1-2, 5.5% in \( trnL-F \), 3.1% in \( rbcL \) or 5.3/5.5/3.1) as they both differ from G. inflata (4.4-5.2/6.6-7.8/3.5-4.4%). Taking into account position on phy-
Table 2. The value of \( p \)-distances between genera of family Anastrophyllaceae: a) based on ITS1-2 and trnL-F, b) based on rbcL.

### a)

| Species | \( p \)-distances ITS1-2/trnL-F, % |
|---------|---------------------------------|
|         | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| 1 Rudolgaea (Gymnocolea) fascinifera | 5.3/5.5 |
| 2 Rudolgaea (Gymnocolea) borealis | -/3.6 |
| 3 Hattoria yakushimensis | 7.7/5.8 |
| 4 Vietnamiella epiphytica | 5.3/5.6 |
| 5 Tetralophozia filiformis | 6.2/5.3 |
| 6 Plicanthus bimensis | -/5.0 |
| 7 Chandonophora sp. | 4.4/7.8 |
| 8 Neoorthocaulis attenuatus | 5.0/6.7 |
| 9 Gymnocolea inflata | 4.4/7.5 |
| 10 Schljakovia kunzeana | 4.1/6.4 |
| 11 Anastrophyllum assimile | 6.2/6.7 |
| 12 Schizophylophia sphenoboides | 5.0/7.5 |
| 13 Schljakovianthus quadrilobus | 5.9/7.5 |
| 14 Sphenolobus minutus | 5.0/6.1 |
| 15 Anastrepta orcadensis | 4.1/6.9 |
| 16 Croxocalyx hellerianus | 6.9/7.6 |
| 17 Barbilophozia barbata | 6.5/5.3 |
| 18 Isopaches bicrenatus | 5.8/5.6 |

### b)

| Species | \( p \)-distances rbcL, % |
|---------|----------------------------|
|         | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 Rudolgaea (Gymnocolea) fascinifera | 3.1 |
| 2 Rudolgaea (Gymnocolea) borealis | 3.4 |
| 3 Hattoria yakushimensis | 3.6 |
| 4 Vietnamiella epiphytica | 3.6 |
| 5 Tetralophozia filiformis | 3.6 |
| 6 Plicanthus hirtellus | 4.1 |
| 7 Neoorthocaulis attenuatus | 3.8 |
| 8 Gymnocolea inflata | 4.4 |
| 9 Schljakovianthus quadrilobus | 3.1 |
| 10 Sphenolobus saxicola | 3.4 |
| 11 Anastrepta orcadensis | 3.8 |
| 12 Hamatostrepta concinna | 4.1 |
| 13 Barbilophozia barbata | 4.3 |
| 14 Isopaches bicrenatus | 4.1 |
logenetic trees with supported relation to *Hattoria* and *Vietnamiella* only in BA estimation of rbcL data, level of molecular differentiation from *Gymnocolea, Hattoria* and *Vietnamiella* and morphological features clearly distinguished them from three cited genera, we suggested *G. fascinifera* and *G. borealis* as well-defined species that should be transferred from the genus *Gymnocolea* to a new genus described here.

**Rudolgaea** Potemkin & Vilnet, gen. nov. Figs. 3–6

*Diagnosis*: Being morphologically distinct in habit, leaf shape and areolation from the related *Hattoria* and *Vietnamiella* it resembles *Gymnocolea inflata* and *Odontoschisma fluitans*. It differs from *Gymnocolea inflata* in the occurrence of some rhizoids or their fascicles from ventral leaf bases, lack of caducous perianths, outer cortical cells of larger shoots mostly ± smaller than inner stem cells, often tangentially orientated and occasionally thick-walled. It is distinct from *Odontoschisma fluitans* in the origin of some rhizoids or their fascicles from ventral leaf bases, distinctly striolate-papillose leaf and stem surface, and terminal furcate branching.

**Type**: *Rudolgaea fascinifera* (Potemkin) Potemkin & Vilnet (≡ *Gymnocolea fascinifera* Potemkin).

*Etymology*. The genus bears the name of Prof. Rudolf Mathias Schuster (Rudy) and his wife, Olga Marguerite Schuster, his permanent companion and assistant for over 60 years, from their marriage in 1943 to her death in 2005.

**Rudolgaea fascinifera** (Potemkin) Potemkin & Vilnet, comb. nov. Figs. 3–5

*Basionym*: *Gymnocolea fascinifera* Potemkin, 1993, *Arctoa* 2: 76.

*Description*: Potemkin, 1993.

*Illustrations*: Potemkin, 1993: Figs 5, 6; this article: Figs. 3–5.

*Distribution*. Indefinite yet, probably undercollected and overlooked; recorded from the Yamal Peninsula, West Siberian Arctic and the Seward Peninsula, Alaska (Potemkin, 1993), Komi Republic (Potemkin, 2008), Chelyabinsk Region (Ivchenko & Potemkin, 2015), and probably from subarctic Yakutia (Sofronova et al., 2015).
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Rudolgaea borealis (Frisvoll & Moen) Potemkin & Vilnet, comb. nov.                                               Fig. 6

Basionym: Lophozia borealis Frisvoll & Moen, 1980, Lindbergia 6: 138. f. 1–3.
Descriptions: Frisvoll & Moen, 1980; Damsholt, 2002, 2013.
Illustrations: Schuster, 1969: Fig. 251: 14–18 as Gymnocoela inflata (illustrated specimen RMS 45791 attributed to G. borealis by Schuster, 1986: 6); Frisvoll & Moen, 1980: Figs. 1–4; Damsholt, 2002: Plate 53, reprinted in Damsholt, 2013: Plate 46; Potemkin et al. (2021): Fig. 1.

Distribution. Arctic and subarctic, probably circum-polar, indefinite yet because of specific habitats.

Fig. 4. Rudolgaea fascinifera (Potemkin 92-9701, LE, holotype).
A–D: leaves; E: dorsal cortical cells; F: basal leaf cells with striolate papillose surface; G: ventral leaf base with rhizoids. Scales: A, B: 160 μm, C, D: 125 μm, E, F: 25 μm, G: 100 μm.

Rudolgaea borealis (Frisvoll & Moen) Potemkin & Vilnet, comb. nov.

KEY TO SPECIES OF RUDOLGAEA AND GYMNOCOELA

1. Pigmented plants blackish brown, sometimes with traces of purple, not lustrous when wet; rhizoids never originate from leaf bases; cortical cells of larger shoots subequal to inner stem cells and orientated largely radially; perianths common, frequently caducous; on acid soil, rocks, in oligotrophic mires, and wet habitats .................................. Gymnocoela inflata s.l.
— Pigmented plants yellow and golden brown, when wet lustrous, or scorched brown and not lustrous; some rhizoids or their fascicles, when present, originate from ventral leaf bases; cortical cells of larger shoots mostly ± smaller than inner stem cells and
often orientated tangentially in larger stem cross-sections; perianth rare, not caducous; in acid to subneutral wet habitats .............................................. 2

2. Pigmented plants yellow and golden brown, when wet lustrous; rhizoids absent, few or ± abundant in some shoot sectors, single rhizoids sometimes originate from leaf bases; leaf and stem surfaces remarkably striolate papillose; leaf cells with 1–6(–8) oil bodies; cortical cells 12–20(–25) μm wide; stem (7–)9–11 cells high; in subneutral wet habitats with dense vegetation, in moderately to extremely rich fen vegetation, in carpets to lawns, where the groundwater level in summer lies well below the surface, never in intermediate fens and on hummocks in Scandinavia; in wet hollows of cotton-grass-sedge bog between flat mounds in the Gydansky Peninsula ..........................................

.................................................. Rudolgaea borealis

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Pigmented plants scorched brown, never lustrous; rhizoids very few or sparse, in more or less distinct fascicles from the ventral leaf base and adjacent part of the stem (leaves detach with rhizoids); leaf and stem surface faintly striolate papillose or smooth; leaf cells with (2–)5–12(–16) oil bodies; cortical cells broader, (20–)23–28(–30) μm wide or when subisodiametric (28–)30–34(–38) μm wide; stem (5–)6–8(–11) cells high; in acid wet habitats, including troughs of polygonal tundras, in Sphagnum tussock bog and bogs with flowing water, in herb-willow, grass-cotton grass and sedge-lichen-moss tundras, often among Drepanoclados s.l. and Sphagnum, with Scapania paludicola var. rotundiloba, Ptilidium ciliare, Pseudolepicolea freyi, Barbilophozia kunzeana, B. binsteadii, Gymnocolea inflata, Odontoschisma elongatum, Blepharostoma, etc. (Potemkin, 1993) ........ Rudolgaea fascinifera
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