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NOTES ON THE JUNGERMANNIINEAE OF THE WORLD

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RESUMEN

El suborden Jungermanniineae incluye cinco familias, 47-49 géneros y 570-575 especies. En general, los taxa endémicos tienen una distribución gondwaniana mientras que los de distribución Laurásica son de amplia distribución. La mayoría de las especies son terrícolas o saxícolas. La amenaza principal es la destrucción de su hábitat, pero las especies lignícolas y las epífitas parecen ser más sensibles que las saxícolas y las terrícolas. Con respecto a sus estrategias de vida, la mayoría de las especies amenazadas son las perennes viajeras. En general, los taxa que se reproducen por yemas están menos amenazadas que las que se reproducen sólo sexualmente.

Palabras clave: Hepaticae, Jungermanniineae, conservación, diversidad.

ABSTRACT

The suborder Jungermanniineae includes five families, 47-49 genera and 570-575 species. Generally, endemic taxa have a Gondwanalandic distribution whereas taxa with a Laurasian distribution are usually widely distributed; the majority of species is terricolous or saxicolous. The main threat is habitat destruction, but the lignicolous and epiphytic species seem to be more endangered than the saxicolous and terricolous ones. With regard to their life strategy, the most endangered taxa are the perennial shuttle species. In general, the taxa reproducing by gemmae are less threatened than the taxa reproducing only sexually.

Key words: Hepaticae, Jungermanniineae, conservation, diversity.

The suborder Jungermanniineae is one of the largest suborders of hepatics. In the present concept, it includes five families, namely, Lophoziaceae (25-26 genera in four subfamilies; *ca.* 225 species), Mesoptychiaceae (monotypic), Jungermannia-

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ceae (nine genera in three subfamilies, *ca.* 150 species), Gymnomitriaceae (seven genera in two subfamilies, *ca.* 75-80 species), and Scapaniaceae (five or six genera in four subfamilies, *ca.* 120 species). Thus, the suborder in total comprises 47-49 genera and 570-575 species. In the whole order Jungermanniales with 15 suborders, Schuster (1969) estimates approximately 230 genera (Engel in 1982 mentioned 284 genera) and over 7000 described "species", but the real number of species is estimated by the same author (Schuster, 1984) as 6500-7000 valid species for all hepatics (this number corresponds with data given in various manuals: 6000-10 000 species of hepatics). For an overview of the genera of the Jungermanniineae, with the exact number of species, according to the present status of our knowledge, see Table 1.

Concerning endemism, a relatively high number of endemic taxa is known, at both the specific and generic levels. Generally, endemic taxa have a Gondwanalandic distribution, whereas taxa with a Laurasian distribution are represented mostly by widely distributed taxa. This fact is correlated with sexual conditions and dispersal. Laurasian taxa are generally either monoicous with common production of spores and sometimes also gemmae (especially taxa of the Arctic, *e.g.*, *Lophozia elongata, L. excisa, L. gillmanii, L. rutheana, Anastrophyllum sphenoloboides, Jungermannia confertissima, J. polaris, J. subelliptica, Marsupella bravissima, Prasanthus suecicus, Scapania kaurinii*, and *S. spitzbergensis*) or dioicous commonly with copious gemma produced (*e.g.*, many species of *Lophozia* and *Anastrophyllum*). Taxa with a Gondwanalandic distribution are mostly dioicous and produce gemmae only exceptionally (*e.g., Anastrophyllum stellatum* and *Andrewsianthus jamesonii* produce gemmae copiously).

In the larger genera of mostly holarctic origin (*Lophozia, Tritomaria, Marsupella, Scapania*, and in part *Gymnomitrion* and *Diplophyllum*), the majority of species is widely distributed in North America and Eurasia. A limited number of species is endemic mostly in the Himalayas or in Japan. In the more recent genera *Jungermannia* and *Nardia*, the number of holarctic endemics, mostly Himalayan or Japanese, partly also in the Appalachians, is higher than the number of widely distributed species. The limited number of species of all the mentioned genera known from the tropics represents mostly endemics only or genera that grow in a limited area of distribution. These genera have no species with a pantropical or paleotropical distribution pattern; only some species are distributed in a somewhat wider area in the neotropical mountains (*e.g., Lophozia laxifolia, Jungermannia amoena, J. callithrix, Gymnomitrion andinum*).

The large genera of Gondwanalandic origin, *Anastrophyllum, Andrewsianthus, Jamesoniella*, and *Syzygiella* have widely distributed taxa in the holarctic regions, as well (*e.g., Anastrophyllum michauxii, A. minutum, Jamesoniella autumnalis*), and rarely also in the tropics (*Anastrophyllum auritum, A. piligerum* - pantropical; some taxa are widely distributed in SE Asia or in the Neotropics). There are also widely distributed taxa in the subantarctic area such as *Jamesoniella colorata.*

Endemism of the small genera is of more significance. There are some Laurasian

Table 1. Number of species (biodiversity) in the genera of Jungermanniineae

LOPHOZIACEAE	(25-26 genera)	*ca.* 225
Lophozioideae	(16-17 genera)	*ca* .175
Lophozia	(incl. *Barbilophozia, Lophonardia*)	*ca.* 80
Anastrophyllum	(incl. *Sphenolobus*)	35-40
Andrewsianthus	(incl. *Cephalobus*)	*ca.* 30
Tritomaria		8
Chandonanthus		4
Tetralophozia		3
Roivainenia		2
Gymnocoleopsis		1-2
Anastrepta		1
Eremonotus		1
Gerhildiella		1
Gymnocolea		1
Hattoria		1
Pseudocephaloziella		1
Sphenolobopsis		1
Vanaea		1
?Rhodoplagiochila		1
Jamesonielloideae (7 genera)		45
Syzygiella		21
Jamesoniella		14
Cryptochila		6
Anomacaulis		1
Denotarisia		1
Pisanoa		1
Protosyzygiella		1
Gottschelioideae (1 genus)		2
Gottschelia		2
Nothostreptoideae (1 genus)		2
Nothostrepta		2
MESOPTYCHIACEAE (1 genus)		1
Mesoptychia		1
JUNGERMANNIACEAE (9 gener)		*ca.* 150
Jungermannioideae (7 genera)		*ca.* 145
Jungermannia (incl. *Phragmatocolea*)		120-125
Nardia		15-16
Horikawaella		2
Cryptocolea		1
Cryptocoleopsis		1
Diplocolea 1		

Table 1. *continued*

Scaphophyllum	1
Mylioideae (1 genus)	4
Mylia	4
Notoscyphoideae (1 genus)	1
Notoscyphus	1
GYMNOMITRIACEAE (7 genera)	77-78
Gymnomitrioideae (5 genera)	72
Marsupella (incl. *Poeltia*)	40
Gymnomitrion	20
Herzogobryum	7
Acrolophozia	3
Prasanthus	2
Stephanielloideae (2 genera)	5-6
Stephaniella	4-5
Stephaniellidium	1
SCAPANIACEAE (5-6 genera)	114-128
Scapanioideae (2-3 genera)	107-121
Scapania	90-100
Diplophyllum (incl. *Macrodiplophyllum*)	16-20
(*Krunodiplophyllum*)	1
Blepharidophylloideae (1 genus)	5
Blepharidophyllum	5
Delavayelloideae (1 genus)	1
Delavayella	1
Douinioideae (1 genus)	1
Douinia	1

as well as Gondwanalandic generic endemics (see Table 2). Evolutionary centres are summarized in Table 3. A great part of the genera, including thre three largest ones (*Jungermannia, Scapania*, and *Lophozia*), as well as some smaller ones such as *Marsupella, Diplophyllum, Nardia, Tritomaria*, and *Mylia*, are Laurasian in origin with the majority of species distributed in holarctic regions. Some species penetrate to the tropical high mountains. However, there are also some genera of Gondwanalandic origin with recent distribution in the subantarctic regions, for example, *Herzogobryum, Cryptochila*, and *Blepharidophyllum* or mainly in the tropics -*Anastrophyllum, Andrewsianthus, Syzygiella, Jamesoniella, Stephaniella*, and *Chandonanthus.*

As far as the habitat requirements, the majority of species is terricolous or saxicolous. Many genera (nearly all genera of Jungermanniaceae except *Jungermannia* and *Mylia, Mesoptychia*, all genera of Gymnomitriaceae, nearly all genera of Sca-

Table 2. Endemism of the Jungermanniineae

1. Endemism in Laurasia
   (a) Endemics of Arctic and Subarctic Regions
      Cryptocolea (1 sp.) - circumarctic
      Mesoptychia (1 sp.) - circumarctic + Baikal Lake, Altai Mts.
      Prasanthus (2 spp.) - circumarctic + Alps
      Eremonotus (1 sp.) - Arctic + Scotland, Alps, Tatra Mts.
      Douinia (1 sp.) - subarctic (Pacific coast from Alaska to British Columbia, Atlantic Europe, Japan)
   (b) Endemics of East Asia
      Cryptocoleopsis (1 sp.) - Japan
      Hattoria (1 sp.) - Japan
      Scaphophyllum (1 sp.) - Bhutan + Taiwan
   (c) Endemics of Himalaya
      Delavayella (1 sp.)
      Diplocolea (1 sp.)
      Gerhildiella (1 sp.)
      Horikawaella (2 spp.)
2. Endemism in Gondwana
   (a) Endemics of Antarctic and Subantarctic Regions
      Blepharidophyllum (5 spp.) -circumsubantarctic
      Herzogobryum (7 spp.) -circumsubantarctic
      Acrolophozia (3 spp.) - New Zealand + Patagonian region
      Roivainenia (2 spp.) - Tasmania + Patagonian region
      Nothostrepta (2 spp.) - Patagonian region
      Krunodiplophyllum (1 sp.) -Patagonian region
      Pisanoa (1 sp.) - Patagonian region
      Protosyzygiella (1 sp.) - Patagonian region
   (b) Endemics of the Andes
      Pseudocephaloziella (1 sp.) -Venezuela
      ? *Rhodoplagiochila* (1 sp.) -Venezuela
      Stephaniellidium (1 sp.) - Colombia, Argentina
      Vanaea (1 sp.) - Guyana
      Marsupella subg. *Nanomarsupella* (1 sp.) - Venezuela
   (c) Endemics of Southeast Asia
      Anomacaulis (1 sp.)
      Denotarisia (1 sp.)

paniaceae except *Scapania* and *Douinia*, part of the Lophoziaceae) have all known species of this ecology only. The lignicolous species, growing on rotten wood or epiphytic on the bark of trees, belong mostly to the family Lophoziaceae, especially Jamesoniellοideae and partly also Lophozioideae. This type of substrate is

Table 3. Areas of high diversity (?evolutionary centres) of the Jungermanniineae

1. Laurasia
   (a) Laurasia only
      Mylia (4 spp.)
      Gymnocolea (1 sp.)
      Anastrepta (1 sp.) - disjunct
   (b) Laurasia + penetration to Gondwanalandic mountains
      Nardia (15-16 spp.) - to Africa, South and Central America
      Tritomaria (8 spp.) - to Africa, partly Central America and Australasia
      Tetralophozia (3 spp.) - to Africa
      Sphenolobopsis (1 sp.) - to Australasia (disjunct)
   (c) Laurasia + penetration to Gondwanalandic mountains + subantarctic regions
      Scapania (90-100 spp.) - 1 species bipolar
      Lophozia (*ca.* 80 spp.) - 1-2 species bipolar
      Marsupella (40 spp.) - 2 species bipolar
      Gymnomitrion (20 spp.) - 1 species bipolar
      Diplophyllum (16-20 spp.) - ? 1 species bipolar
   (d) Laurasia + penetration to Gondwanalandic mountains and lowland + subantarctic regions
      Jungermannia (120-125 spp.) - no species bipolar

2. Gondwana
   (a) Pantropical + penetration to subantarctic regions + Laurasia
      Anastrophyllum (35-40 spp.) - mostly S America + Australasia
      Jamesoniella (14 spp.) - mostly Australasia
   (b) Subantarctic + penetration to tropics
      Andrewsianthus (*ca.* 30 sp.) - to tropical mountains + lowland
      Cryptochila (6 spp.) - to tropical mountains
   (c) Paleotropical
      Chandonanthus (4 spp.)
      Gottschelia (2 spp.)
      Notoscyphus (1 sp.) - penetrating to Hawaii + S Japan
   (d) Neotropical
      Syzygiella (21 spp.) - penetrating to Africa, Australasia and Hawaii
      Stephaniella (4-5 spp.) - penetrating to Africa
      Gymnocoleopsis (1-2 spp.) -penetrating to Africa + subantarctic region

exceptional in the Jungermanniaceae (*Jungermannia leiantha, J. subulata*, problematic species *J. lignicola*, and *Mylia* species) and Scapaniaceae (*Scapania apiculata, S. umbrosa, S. massalongoi, S. carinthiaca*, and *Douinia ovata*).

In the tropics, there is a correlation between altitude and substrate type. Terricolous and saxicolous species of the Jungermanniineae occur in higher altitudes

Table 4. Present knowledge of the Jungermanniineae

Jungermannia (120-125 spp.) - some papers of Amakawa (1959, 1960, 1963, 1966, 1967, 1968, 1969, 1970, 1972) and Vana (1972a, b, 1973a-d, 1974a-d, 1975a-d, 1976).
Scapania (90-100 spp.) - Müller (1905): regional, recent monograph lacking.
Lophozia (*ca* .80 spp.) - only regional, recent monograph lacking.
Marsupella (40 spp.) - only regional, recent monograph lacking (Vana, in prep.).
Anastrophyllum (35-40 spp.) - only regional, recent monograph lacking (Vana, in prep.).
Andrewsianthus (*ca.* 30 spp.) - only regional, recent monograph lacking.
Syzygiella (21 spp.) - Inoue (1966).
Gymnomitrion (20 spp.) - only regional, recent monograph lacking (Vana, in prep.).
Diplophyllum (16-20 spp.) - only regional, recent monograph lacking.
Nardia (15-16 spp.) - Vana (1976).
Jamesoniella (14 spp.) - Grolle (1971).
Tritomaria (8 spp.) - Schuster (1966).
Herzogobryum (7 spp.) - Grolle (1966).
Cryptochila (6 spp.) - Grolle (1971).
Blepharidophyllum (5 spp.) - Grolle (1965).
Stephaniella (4-5 spp.) - Schmitt & Winkler (1968).
Mylia (4 spp.) - Potemkin & Kazanovskij (1993).
Chandonanthus (4 spp.) - no monograph.
Tetralophozia (3 spp.) - no monograph.
Acrolophozia (3 spp.) - no monograph.

(alpine areas, and the páramos), whereas lignicolous/corticolous taxa occur in the tropical forest regions.

The main threat for taxa of this later group is habitat destruction. Lignicolous and epiphytic species seem to be more endangered than saxicolous and terricolous ones. Forest practices (the cutting of old trees, rotten tree trunks, etc.) cause drastic reduction of the habitat substrate for lignicolous species in the holarctic region. In the tropical area we should add the disappearing tropical rain forests (tropical deforestation) as the main threat. Furthemore, some other types of habitat loss could be considered such as the destruction of peat meadows and mires, the habitat for *Jamesoniella undulifolia*. Five species of the Jungermanniineae (*Diplocolea sikkimensis, Hattoria yakushimensis, Jamesoniella undulifolia, Marsupella profunda,* and *Nardia huerlimannii*) are included in the World Red List as Bryophyte representatives.

Concerning life strategy, the most endangered taxa are the perennial shuttle species (During, 1979) with the "gametophytic survival as a strategy" (Schuster, 1983); these species have no gemmae and lack sexual reproduction as far as known. The occurrence of such species is now interpreted as marginal or caused by suboptimal conditions inhibiting the gametangia production. Generally, taxa

reproducing by gemmae ("gametophytic reproduction and dispersal") are less threatened than the taxa reproducing only sexually ("sporophytic reproduction and dispersal").

The Jungermanniineae, as a whole group, is still insufficiently known. Taxonomically, about half of the group is well known or recently monographed (mostly smaller genera up to 20 species, *e.g., Blepharidophyllumn, Herzogobryum, Jamesoniella, Nardia,* and *Syzygiella*). The largest and the most difficult genus *Jungermannia,* has been recently studied by Amakawa (1959-60, 1963, 1966-69,1970, 1972) and by the author of this article (Váňa, 1972, 1973, 1973a,b,c; 1974, 1974a,b,c; 1975, 1975a,b,c; 1976; 1978). The monograph of *Scapania* by Müller (1905) is out of date. Some genera are under the scope of recent taxonomical studies and monographs are in preparation for *Anastrophyllumn, Gymnomitrion,* and *Marsupella.* Other species, mostly the "extra-European" and "extra-North American" ones from the genera *Lophozia* and *Scapania,* as well as of the genus *Andrewsianthus* and some others, need taxonomic clarification. A summary of our knowledge of the Jungermanniineae is given in Table 4.

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