

Two new liverworts for Europe in Macaronesia: *Odontoschisma prostratum* (Sw.) Trevis. on the Azores and *Jungermannia callithrix* Lindenb. & Gottsche on the Azores and Madeira.

R. Schumacker

Department of Botany, University of Liège, Department of Botany, Sart-Tilman, B-4000 Liège and Hautes-Fagnes Scientific Station, Mont-Rigi, Robertville, Belgium

J. Vá4a

Department of Botany, Charles University, Benátská 2, CZ-12801 Prague 2, Czech Republic

Abstract. *Odontoschisma prostratum* (Sw.) Trevis. and *Jungermannia callithrix* Lindenb. et Gottsche, two liverworts mainly distributed in the Neotropics, are reported at hand of many collections from Macaronesia. *O. prostratum* occurs on 8 of the 9 Azorean islands, growing on all type of substrates, even epiphyllous, but rarely in bogs. *J. callithrix* is known from 8 Azorean islands and from Madeira, growing epigeic. The phytogeographical interest of the occurrence on the Azores of some 39 liverworts (among 147) belonging to the neotropical and/or paleotropical elements is discussed. Most of the neotropical species may have been easily transported to the Azores by the frequent depressions (or occasionally storms) moving rapidly at relatively low altitude (3,000 m) from the North or Central American eastern coasts or from the Caribbean islands and Bermuda to Western Europe in a few days. Only a few of these species could have been be introduced by human activities, mainly along the coast.

1. Introduction

The small Azorean islands, discovered in 1432, are relatively young in origin: the oldest one is S. Maria (ca. 8 My) and the youngest is Pico (0.37 My). They forms three groups: western (Corvo, 17 km²; Flores, 142 km²), central (Graciosa, 62 km²; Terceira, 402 km²; S. Jorge, 246 km²; Pico, 433 km²; Faial, 172 km²) and eastern (S. Miguel, 757 km²; S. Maria, 97 km²).

Their global area is only 2328 km². The easternmost islands are at ca. 1600 km from Lisbon and and the westernmost islands at 2600 km from the Bermuda and at ca. 3400 km from the Carribbean islands.

Maximal altitudes range from 402 m on Graciosa up to 2351 m on Pico.

The mean annual temperature is ca. 17.5° C at the sea level with low thermal amplitude (13.9 - 22° C) and relative high air humidity (always over 78 %). Temperature gradient is ca. - 0.6° C for 100 m in altitude.

Precipitations vary from 710 mm (S. Miguel) to 1592 mm (Flores) close to sea level, showing an increase of 200 mm for each 43 m in altitude on Flores and ca. 119 m on Faial. Unfortunately the climatic features at high altitude, where the precipitation could reach 10,000 mm or more, are not or scarcely documented (Agostinho, 1947; Borges, 1992; Dias, 1989 and pers.comm. 1999; Sjögren, 1973, 1978).

The geological substrate is relatively homogeneous (Madruga, 1986): mostly trachytic pyroclasts, with some limited intrusions of basalts (bagacina), rarely alkaline basalts, ..

The present Azorean landscape has been very strongly modified by man for more than 550 years. Only few areas remain unchanged today. This is due to historical use for wood cutting, to the fact that 260,000 peoples live there today (111 inhabitants/ km²) and to the recent funding of the E.U. for development of mountain agriculture, covering now more than 70 % of their area, even in the best preserved islands (Dias 1989; Sjögren 1973).

After the early hepaticological investigations of the Azores (Seubert, 1844; Russel, 1862; Mitten, 1865, 1870, 1877; Trelease, 1897; Kindberg, 1898; Sampaio, 1904), substantial progress has been made thanks to intensive field work and publications by Ade & Koppe (1942), Allorge P. & V. (1950), Allorge P. & Persson (1938), Allorge V. & P. (1938a, 1938b, 1942, 1946, 1948, 1950, 1952), Allorge V. & Jovet-Ast (1956), (1931), Bates & Gabriel (1997), Buch & Persson (1941), Crundwell et al. (1994), Gabriel (1994), Gonzáles et al. (1991), v. Hübschman (1973), Losada-Lima & Hernández (1991), Luisier (1938), Persson (1955, 1973), Richard (1936), Sérgio (1974, 1978, 1984, 1985, 1987, 1989, 1994a, 1994b), Sérgio & Dias (1991), Silveira Moniz (1937), Sjögren (1978, 1990, 1993, 1998, 1999a, 1999b), Smokler (1965), as to monographic works or revisions, a.o., by Bisang et al. (1989), Bischler (1970), Bouman & Dirkse

(1994), Grolle (1962, 1966, 1970, 1971, 1972a, 1972b), Grolle & Persson (1966), Grolle & Schumacker (1985), Heinrichs et al. (1997), Jovet-Ast (1986), Kruijt (1988), Sérgio (1974), Sim-Sim (1999), Váña (1974b) and description of species new for science from these islands by Allorge & Jovet-Ast (1950, 1955), Buch & Persson (1941), Grolle (1985), Grolle & Persson (1966), Herzog (1945), Sim-Sim et al. (1995). Important bibliographical sources and distributional data are provided by Sjögren & Hallingbäck (1978), Eggers (1983), Düll (1983), Grolle (1983), Gabriel (1994), Sjögren (1978, 1997, 1999b).

In June 1997 and 1998, the first author spend 9 weeks on Pico, Terceira and Faial islands to investigate their liverworts and hornworts flora and 6 more weeks in 1999 on S. Jorge, S. Miguel, Corvo, Flores as again on Terceira and Pico. Special attention has been given in collecting as much as possible samples of critical genera, including *Odontoschisma* and *Jungermannia*.

As a result of these investigations and revision of many samples collected earlier by V. and P. Allorge (PC), H. Persson (S), G. Schwab and J. Eggers (pers. herb.), C. & H. Sérgio (LISU), R. Gabriel (AZU), E. Sjögren (UPSV) or by the first author, we could identify two new species for the Azores and one for Madeira: *Odontoschisma prostratum* (Sw.) Trevis. (Azores) and *Jungermannia callithrix* Lindenb. et Gottsche (Azores and Madeira), both with a main distribution in Central and/or South America.

Abbreviations: C. Sérgio (CS), H. Sérgio (HS), R. Gabriel (RG), P. & V. Allorge (PVA), H. Persson (HP), R. Schumacker (RS); AZU: herb. University of the Azores, Angra, Terceira, herb. G. Dirkse (GD) (hGD), J. Eggers, (JE)(hJE), G. Schwab (GS) (hGS), A.C. Crundwell (ACC)(hACC) and R.C. Stern RCS (hRCS).

2. *Odontoschisma prostratum* (Sw.) Trevis. (Fig. 1)

The only species of the genus *Odontoschisma* reported by Allorge (1950) as by Sjögren (1978) from the Azores was *O. sphagni*, which was

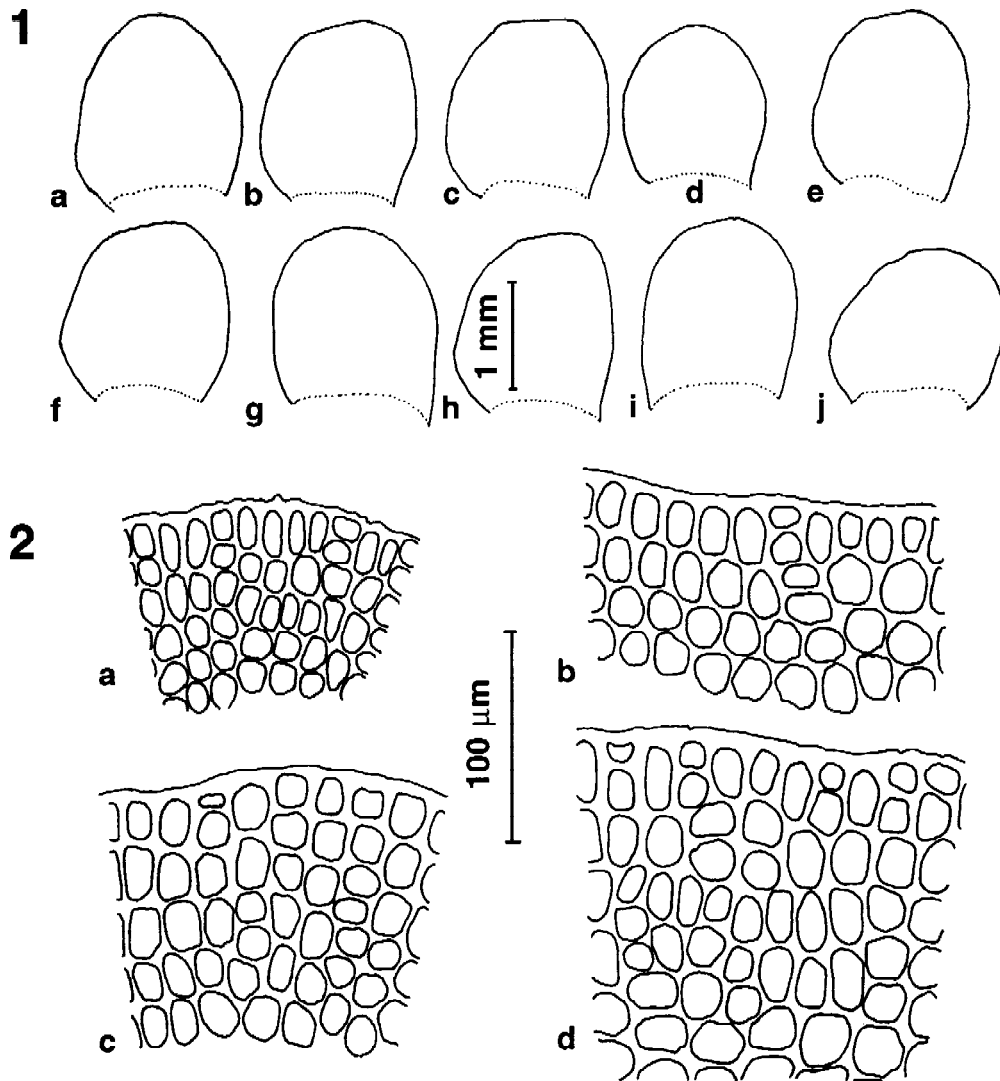


Fig. 1. *Odontoschisma prostratum* (Sw.) Trevis. 1 a-j: leaf shape; 2 a-d: leaf margin (del. R.S.)

apparently growing on a number of substrates: moist soil, humus, peat, trunks, decaying wood, even on fronds of ferns, on cushions of *Leucobryum*, but rarely in bogs. However, according to Eggers (1982) and Gabriel (1994) both, *O. sphagni* and *O. denudatum* (Nees) Dumort., occur on the Azores.

In 1997, 1998 and 1999, the first authors collected numerous samples of *Odontoschisma* on Pico, Faial, Terceira, Flores, S. Jorge and S. Miguel.

It appeared that *O. denudatum* was fairly common, often immediately recognized in the field by its erect, etiolated gemmiferous shoots. It has been observed in many places, growing epigeic, humicolous, epixylic, epiphytic and even epiphyllous on old fronds of ferns (especially on *Elaphoglossum*).

During a visit to the Furnas do Enxofre (Terceira), the attention of the first author was drawn by a very tall (up to 5-6 cm high), erect to prostrate *Odontoschisma*, often tinged with deep

red, growing in dense pure mats on bare soil or humus, close to volcanic fumaroles.

The leaves were mostly longer than wide, flat, except for the somewhat swollen margin and rounded to retuse at their apex. On microscopical examination, they showed a distinct border of 2-4 (5) narrow cells with thickened walls, elongated at right angle to the leaf margin, clearly distinct from the inner cells, these being \pm isodiametric and lacking bulging trigones. These microscopical characters are distinctive for the section *Odontoschisma*.

On fresh material, the leaf cells were filled with 3-5 large (6-7 x 10-12 μ m), ovoid to ellipsoid oil-bodies, coarsely segmented into discrete spherical globules, disappearing rapidly on drying.

Although similar to *O. sphagni*, by the presence of a marginal border but larger, these plants differed in their habit, by the almost constant red colour (except in very shaded habitat), the shape of the leaves and the structure of oil-bodies. The second author identified them readily as *O. prostratum*, a Central and North American species, known from Mexico, Guatemala (S. R. Gradstein in litt.), Honduras, Costa Rica, West Indies (Cuba, Haiti, Jamaica - type, Puerto Rico), Lesser Antilles (Guadeloupe, Martinique), Trinidad and eastern U.S.A., northwards to Maine and Illinois, westwards to Arkansas and Missouri (Schuster, 1974: 862-870; figs. 473-475).

Checking other own collections (RS) and numerous collections made since the last century many other Azorean localities of *O. prostratum* could be traced.

The provisional distribution in the Azores is as follows:

Flores: Rachão do Junco, pentes tourbeuses, leg. PVA (PC); Ribeira Grande, leg. PVA, 1937 (PC); Caldeira Comprida, souches pourrissantes, leg. PVA, 1937 (PC); Caldeira Rasa, tourbières, leg. PVA, 1937 (PC); Caldeir Sêca, leg. HP, 1937 (S) (all sub *O. sphagni*).

Pico: Serra Gorda, en mélange avec *Leucobryum glaucum*, leg. PVA, 1937 (sub *O. sphagni*) (PC); Furna do Pico, leg. HP, 1937 (sub *O.*

sphagni) (S); close to Furna de Frei Matias, small N-exp.rock in pasture, 650 m, leg. JE, AZ 11/12, 6.1981 (sub *O. sphagni*) (hJE); S. Roque de Pico, Cabeco do Redondo, on decaying *Erica* log, soc. *O. denudatum*, 765 m, leg. RS 970607/38 (AZU).

S. Jorge: ravin de Rete do Canario, 700 m, leg. PVA, 1937 (sub *O. sphagni*) (PC); Ribeira Funda, leg. H.P., 1937 (sub *O. sphagni*) (S).

S. Miguel: ravin au-dessus de Lagoa do Furnas, dans les touffes de *Leucobryum glaucum*, leg. PVA 1937 (sub *O. sphagni*), (Bryoth. Azorica n° 28, PC); Lagoa das Furnas, north bank, on soil under *Calluna*, close to fumaroles, 300 m, leg. JE, AZ2/14, 6.1981 (sub *O. sphagni*) (hJE) and leg. GS SN8, 6.1981 (sub *O. sphagni*); idem, on decaying logs of *Cryptomeria*, leg. GS SN28, 6.1981 (sub *O. sphagni*) (hGS); id., on wet shaded bank, leg. RCS, 5.1992 (sub *O. sphagni*) (hRCS); new road from Furnas to Ribeira Quente, damp rock by river, leg. RCS (sub *O. sphagni*), 5.1992 (hRCS); Furnas, hot springs, on dry earth in smoke from the spring, 240 m, leg. GD, n° 9085-9095, 23.9.1998 (hGD).

Terceira: loc. T22, leg. H. Persson, 1937 (sub *O. sphagni*) (S); Lagoa do Negro, on peat and on *Leucobryum juniperoides*, alt. 550 m, leg. ACC n° 954, 4.1980 (sub *O. sphagni*) (hACC); 1 km S of Algar do Carvão, on damp rocks, alt. 525 m, leg. ACC n° 910, 4.1980 (sub *O. sphagni*) (hACC); Furnas do Enxofre, close to fumaroles, 500 m, leg. RCS, 5.1992 (sub *O. sphagni*) (hRCS); idem, leg. CS & RG n° 9308, 07.1994 (LISU, AZU) (sub *Odontoschisma* sp.); idem, leg. RS 970616/18 (AZU, LGHF, PRC); Terra Brava massive, along CF31, E of Pico Alto, moist bank along a path inside the laurel forest, alt. ca. 550 m, leg. RS 970616/26 (AZU, LGHF); N of Algadiços, 600-680 m, on a mat of *Nardia scalaris* in an open wet heath, leg. RS 970617/05 (AZU); idem, in a ravine inside the laurel-juniper forest, on moist rocks, soc. *Bazzania azorica*, leg. RS 970617/24 (AZU); Juncal, ca. 585 m, on moist soil, leg. RS 970622/36 (AZU); Ribeira das Lapas, on fresh bank at the edge of the laurel-juniper forest, 650 m, leg. RS 970623/5 (AZU); Matela, humiferous boulder under old *Erica*, 480 m,

leg. RS 980604/33 and 980604/40 (AZU); NE slope of Pico Rachado, moist vertical cliff of volcanic tuff, 620 m, soc. *Kurzia pauciflora*, leg. RS 980605/19 (AZU); id., on humus under isolated old *Juniperus* in a meadow, 570 m, leg. RS 980605/28 (AZU); id., epiphytic on old *Erica*, leg. RS 980605/34 (AZU); Nariao, N slope at the end of CF3, fresh bank, 572 m, leg. RS 980607/17b (AZU); Misterios Negros, bank along the track to the lava field, ± 620 m, leg. RS 980608/8 (AZU); id., epiphytic on old *Juniperus* in dense *Juniperion* forest, 640 m, leg. RS 980608/33 & RG, 8.06.1998 (AZU); id., at the edge of a 200 years old lava field, between lava boulder, on moist humus, ± 600 m, leg. RS 980610/5 (AZU).

N.B.

1. All collections cited by Ade & Koppe (1942), Allorge (1948,1950) as those cited by Sjögren (1978, 1993, 1996) under *O. sphagni*, from Corvo, Faial, Flores, S. Jorge, S. Maria, S. Miguel, Pico and Terceira belong most probably to *O. prostratum*.
2. *O. prostratum* has also been collected on Madeira by L. Söderström (pers. comm. 1999).

In conclusion, this taxon, collected in many localities on most of the Azores islands - and probably more common - has been observed epigeic (also very close to volcanic fumaroles), humicolous, epilithic, epixylic, epiphytic, epibryophytic (esp. on *Leucobryum*), rarely on *Sphagnum*, and epiphyllous on fronds of ferns, between 500 and 800 m in altitude. Very striking is that the ecology of this taxon is the same as in N. America (Schuster, 1974).

Until now, no collection of typical *O. sphagni* from the Azores could be confirmed.

As discussed at length by Schuster (1974), *O. prostratum*, although different morphologically and ecologically, is obviously closely allied to *O. sphagni*. The taxonomical ranking of this taxon is of the same order than the ranking of *O. denudatum* and *O. elongatum* that have been reduced at the subspecific level by Potemkin (1998). To solve this ranking problem objectively requires further biochemical and genetical

studies, on a large geographical scale.

But, presently, we will adopt the species level as proposed by Schuster (1974).

3. *Jungermannia callithrix* Lindenb. et Gottsche (Fig.2)

In 1997 and 1998, the first author collected rich materials of a *Jungermannia* remembering the widespread *J. hyalina* Lyell on Pico, Terceira and Faial islands. The second author identified them readily as *J. callithrix* Lindenb. et Gottsche, a species mainly distributed in Central and South America: Chile, Ecuador, Venezuela, Colombia, St.-Vincent, Dominica, Martinique, Dominican Republic, Puerto Rico, Jamaica, Cuba, Guatemala and Mexico (Váña, 1974a).

The differences between *J. hyalina* and *J. callithrix*, both dioecious, are summarized in table 1.

Features of the leaves must be observed at the middle of well developed sterile stems.

Jungermannia hyalina is a very variable species and may sometimes produce modifications with larger cells (*Nardia muelleriana* Schiffn.) or weak shoots with ovate leaves (var. *ovalifolia* Schiffn.). Both taxa, *J. hyalina* and *J. callithrix* belong to a group of closely related taxa including *J. callithrix*, *J. hyalina* Lyell, *J. infusca* (Mitt.) Steph. (East Asia), *J. micrantha* (Mitt.) Steph. (Hawaii, Samoa), *J. polyrhizoides* Grolle (Himalaya), *J. renauldii* Steph. (Madagascar, Reunion) and *J. wattsiana* Steph. (Queensland, New South Wales in Australia). Only *J. hyalina* is widely distributed, partly overlapping the areas of the above mentioned taxa.

All collections from the Azores, kept under *J. hyalina* in PC, S, LISU, AZU, NYBG, herb. J. Eggers, G. Schwab and E. Sjögren belong to *J. callithrix*. Beside many collections of typical *J. hyalina*, 3 collections from Madeira belong to *J. callithrix*. All examined collections from Canary Islands belong to *J. hyalina*.

Specimens examined

AZORES

Table 1

	<i>J. hyalina</i>	<i>J. callithrix</i>
Stem medullary cells	12-30 (-35 µm)	30-45 µm
Leaves orientation	nearly horizontal	± widely spreading
Leaves shape	suborbicular to broadly reniform	ovate to ovate - lingulate
Leaves dorsal insertion	not decurrent, not overcrossing the dorsal merophyte	decurrent, overcrossing the dorsal merophyte
Marginal leaf cells	20-35 µm	(30) 35-40 µm
Mid-leaf cells	25-40 x 25-35 µm	50-60 x 35-40 µm
Basal leaf cells	25-40 (-45) x 25-35 µm	55-80 x 28-35
Cuticle	smooth to faintly verruculose	striolate
Pairs of antheridial bracts	3-8 (-12)	10-16

Corvo: eastern slope of the caldeira, 550 m, moist bank, leg. RS 18.7.1999 (herb.RS), Faial: s.l., leg. HP, 1937 (S); Caldeira, leg. HP, 1937 (S); Cabouco Velho, 500 m, moist bank, leg. RS 980620/11 (AZU); Cabeço das Trintas, 500 m, moist bank, leg. RS 980619/36, c. andr. (AZU); S external slope of the caldeira, along Ribeira de Aguas Claras, 800 m, fresh bank, leg. RS 980622/6 (AZU).

Flores: sous Cavinha, chemin creux, leg. PVA 1.7.1937 (PC); chemin vers Cedras, leg. PVA, 6.7.1937 (PC); vallée de Cedras, leg. PVA, 3.7.1937, c. andr., c. per. (PC); Pedras Altas, leg. PVA, 7.1937 (PC); S. Francisco, vieux murs, leg. PVA 17.7.1937 (PC); grands rochers après S. Francisco, leg. PVA 17.7.1937, c. andr., c. per. (PC); Ribeira da Cruz, leg. PVA, 21.7.1937 (PC); Rachão, leg. PVA, 21.7.1937 (PC); entre Lagès et Lagoa Raga, leg. PVA, 23.7.1937 (PC) [all under *J. hyalina*].

Pico: Prainha, Athalhanha, 625 m, dripping basalts, leg. RS 970612/8 (AZU); ib., ravine in *Junierion*-forest, leg. RS 970612/23 (AZU); between S. Amaro and Terra Alta, 200 m, wet basaltic rock, leg. RS 970606/47, 970606/52 (AZU); W of Piedade, 450 m, moist volcanic scories, leg. RS 970614/

4, c. per. (LGHF); Cabeço do Caveiro, 940 m, dripping tufa, leg. RS 980613/12 (AZU); Misterio da Prainha, along CF11, between Passagem and Cancela, 585 m, fresh bank in a ravine, leg. RS 980615/35 (AZU); ib., close to Atalhanha, 610 m, fresh bank in a ravine, leg. RS 980615/41 (AZU).

S. Jorge: entre Calhetta et Topo, 600 m, ravin, leg. PVA 17.8.1937, c. andr. (PC); Fajã dos Vimes, leg. HS, 7.1997 (LISU), Pico Pinheiro, Parque Florestal, 800-850 m, leg. HS, 8.1997 (LISU); Fajã dos Cabres, leg. HS, 8.1997 (LISU).

S. Maria: Pico Alto, 530 m, on rock at roadside, leg. ACC 692, 29.3.1980 (herb. ACC); Ribeira do Engenho, 225 m, roadside bank, leg. ACC 569, 15.3.1980 (herb. ACC); s.l., 300 m, epigeic, leg. ES n° 18, 12.8.1996 (UPS).

S. Miguel: Lagoa do Congro, 600 m, leg. ?, 4.8.1928 (PC); Pico da Vara, leg. HP, 1937 (S); Furnas, 240 m, leg. HP, 1937 (S); between Pico de Carvao and Sete Cidades, 6-700 m, leg. HP, 16.3.1937 [under ?*Southbya nigrella*] (S); à 2 km de Lagoa do Fogo, on soil and base of *Cryptomeria*, leg. CS 2672 & 2700, 25.5.1980 (LISU); Vista do Rei, Lagoa do Sete Cidades, moist bank,

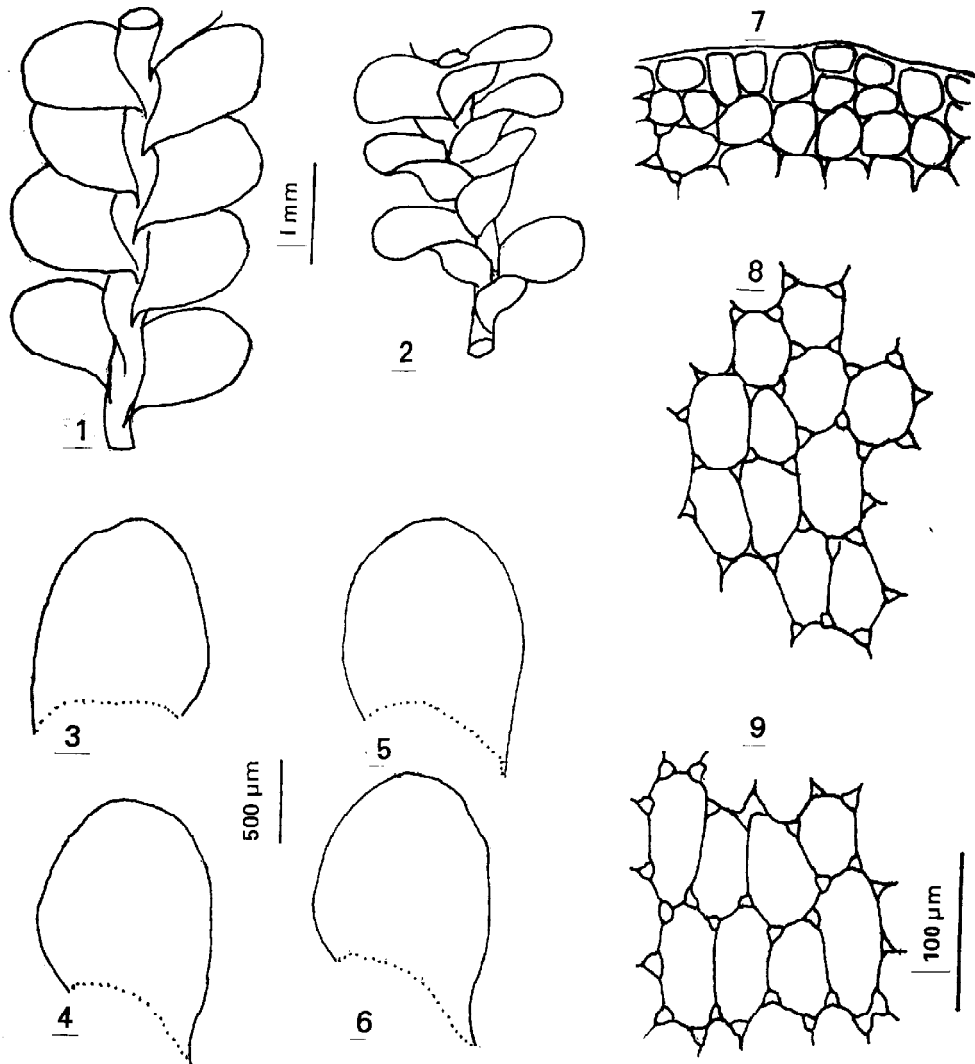


Fig. 2 *Jungermannia callithrix* Lindenb. et Gottsche. 1: part of a sterile stem; 2: part of an androecia; 3-6: leaves; 7: leaf marginal cells; 8: leaf median cells; 9: leaf basal cells. (del. R. S.)

leg. CS 2646, 25.5.1980 (LISU); Pico da Cruz, leg. Ade, 23.5.1935, [under *Mylia taylorii*] (Stuttgart).

Terceira: Caldeira do Guilherme Moniz, Cabrita, 450 m, roadside bank, leg. ACC, 5.4.1980 (herb. ACC); east end of Serra do Noriã, 400 m, roadside bank, leg. ACC, 5.4.1980 (herb. ACC); Serrata, 150-200 m, fresh shaded bank, leg. RS 970619/7 (AZU);

Nariã, 500-575 m, bank of small brook, leg. RS 970622/4, c. andr. (AZU); Ribeira das Lapas, 650 m, on humus in a ravine, leg. RS 970623/51 (AZU); Matela, 450m, on shaded boulder, leg. RS 980604/30 (AZU); Pico Rachado, NE slope, 540 m, bank of small brook, leg. RS 980605/46; Doze Ribeiras, 615 m, fresh shaded bank, leg. RS 980607/17 (AZU).

N.B.

1. The indication of *J. hyalina* on Corvo (Sjögren, pers. comm., 1999) should be referred to *J. callithrix*.
2. In herbarium Mitten (NYBG) we have found the oldest known collection of *J. callithrix* (c. per.) from the Azores, made by Godman in 1866 (Mitten 1870).

MADEIRA

Ribeira Frio, Porto da Suna, 900 m, along levada, Leg. Nobrega & HP, 9.3.1952 (S); Mt. dos Peicegeiros, leg. HP, 26.7.1952 (S); Fanal, Chão do Caminho Velho (above Seixal), 1000-1200 m, leg. Nobrega, 28.7.1952 (S).

4. Discussion

The occurrence *Odontoschisma prostratum* and *Jungermannia callithrix* on the Azores still increase the number of aAorean hepatics having their main distribution, or closely allied species, in warm temperate and tropical montane regions of America (19 sp.) and /or - but at a lesser degree - in Africa or Africa and America (resp. 3 and 7 sp.), beside other 7 pantropical species. Only 3 endemic species have closely allied species in Eastern Asia or in Australia.

This represents more 25 % of the hepatics (147) recorded with certitude from the Azores (after critical revision of many doubtful indications by the first author) (Sjögren, coll. Schumacker, 1999b).

In Table 2, these species are listed with their presently known distribution, their sex distribution and their dispersal possibilities by spores, gemmae or fragments.

More than the half belong to the neotropical element.

Among the Azorean hepatic flora, 16 genera on 64 (25 %) have their main bulk of species in the Tropics, with a limited number of species in W-Europe and Macaronesia. These high percentages are rather surprising, if one consider the relatively young age of the Azorean islands: 0.37 - 8.12 My.

On the Azores, most of the species listed in Table 2 are growing in the cloud forest zone (*Juniperion brevifoliae*) between (400-) 600-1000 (-

1500) m or in deep-shaded wooded ravines at lower altitude. Then, they could only be successful, only after establishment of the main species of the *Juniperus-Laurus* forest and good development of this forest on the lava fields, once cooled. The time-span for this is fully unknown in absence of paleo-palynological investigations in bogs and in marine sediments of these islands.

How could these species reach the Azores?

Most probably by the simplest way, as already demonstrated by van Zanten & Gradstein (1988)! Most of the species listed in Table 2, being mostly limited to mature, or going-to-mature *Juniperion* forests, have good dispersal possibilities although predominantly dioecious. We may guess that they could arrive naturally on the Azores, transported by the frequent winds of the low altitude depressions moving from then eastern American atlantic coasts to the W or SW. The distance between the Carribean Islands and the westernmost island (Flores) being only ca. 3400 km.

Also dustfalls, frequently observed in Europe (originating mostly from Sahara), may bring particles of sand varying from 2.2 to 12 µm in diameter, much more heavier than any spore, gemmae or small fragment of bryophytes (Ozer et al., 1998) may take part to this dispersion process.

This means that with a mean wind speed of 100 km/h, diaspores from the Carribea islands could reach the Azores within 40 hours and by 200 km/h within less than a day: a very short time; from the Bermuda this time span would be shorter.

This allows to the diaspores to survive without problems during their transport (van Zanten & Gradstein, 1988; Erpicum M. (Liège), pers. comm. 1999).

Later, once the oldest islands have been colonized, these species could easily spread on the youngest islands in the same way that the diaspores of the main species of the *Juniperion* forest have obviously easily done, as attested by their occurrence on most of the islands.

Exceptions are: *Cheilolejeunea cederkreutzii* (4

AF: Africa, AM: America, AS: Asia, OC: Oceania, AU; Australia incl. New Zealand; WE: Western Europe (+p.p. mediterranean); AZ: Azores. D: dioecious, M: monoecious, SPO: spores, GEM: gemmae, FRA: fragments; *: present, +: possible. ** Azorean endemic; *** Macaronesian endemic.

- (1) unpublished data from A. Bernecker and T. Pócs
- (2) unpublished data from J. Heinrichs
- (3) unpublished data from J.W. Bates, D. Rycroft and J. Heinrichs

of 9 islands), *Acanthocoleus aberrans* (2 of 9 isl.), *L. cuneifolius* (3 of 9 isl.), *Pallavicinia lyellii* (3 of 9 isl.), *Radula nudicaulis* (4 of 9 isl.), *Jamesoniella rubricaulis* (2 of 9 islands), all these species being mostly sterile, not producing gemmae today and, consequently, only able to spread by dispersal of fragments.

Very striking, a.o. is the strictly limited occurrence of *Jamesoniella rubricaulis* on Pico - the youngest-borne island - in only 3 places, between 1200-1500 in altitude, and on S. Miguel (1 loc., leg. R.S., 1999) attesting of a very recent transport of this S. American species on the Azores.

Among the species listed in table 2, *Anthoceros caucasicus* (a weedy species on banks along road- and tracksides as other Anthocerotales) and perhaps *Exomorthea pustulosa* (growing mostly at low altitude along the coasts) are most probably introduced (intense maritime traffic and acclimatation of exotic decorative plants, since the 15th century).

Acknowledgements

The authors are greatly indebted to the herbarium keepers of AZU, LISU, NYBG, PC and S, to A.C. Crundwell, G. Dirkse, J. Eggers, G. Schwab, E. Sjögren and R.C. Stern for the loan of their collections, to A. Bernecker, R. Grolle and T. Pócs who provide unpublished phytogeographical data, to R. Gabriel for her friendly help and collaboration in the field and to N. Hodgetts for improving the English of the manuscript.

The research of the first author on the Azores between 1997 and 1999 has been generously supported financially by the National Foundation for Scientific Research, the Ministry of Education and Research and the University of Liège.

References

- Ade, A. & Koppe, F. 1942.** Beitrag zur Kenntnis der Moosflora der atlantischen Inseln und der pyrenäischen Halbinsel. *Hedwigia* 81: 1-36.
- Armitage, E. 1931.** Some bryophytes of the Azores. *Journal of Botany* 69: 75-76.
- Agostinho, J. 1947.** Clima e Vegetação. Açoreana 4: 149-181.
- Allorge P. & V. 1950.** Hépatiques récoltées par P. et V. Allorge aux îles Açores en 1937. *Revue bryologique et lichénologique* 19: 90-118.
- Allorge, P. & Persson, H. 1938.** Contribution à la flore hépatologique des îles Açores. *Annales Bryologici* 11: 6-14.
- Allorge, V. & P. 1938a.** Sur la présence d'hépatiques épiphyllées aux îles Açores. *Comptes Rendus hebdomadaires de l'Académie des Sciences* 206: 1323-1325.
- Allorge, V. & P. 1938b.** Sur la répartition et l'écologie des hépatiques épiphyllées aux Açores. *Boletim da Sociedade Broteriana, Ser. 2, 13:* 211-236.
- Allorge, V. & P. 1942.** Bryophyta Azorica. Paris [Exsiccatae].
- Allorge, V. & P., 1946.** Les étages de la végétation muscinale aux îles Açores et leurs éléments. *Mémoires de la Société de Biogéographie* 8: 369-386.
- Allorge, V. & P. 1948.** Végétation bryologique de l'île de Flores (Açores). *Revue bryologique et lichénologique* 17: 126-164.
- Allorge, V. & Jovet-Ast, S. 1950.** *Aphanolejeunea teotonii* nov. sp., hépatique des Açores. *Revue bryologique et lichénologique* 19: 19-24.
- Allorge, V. & Jovet-Ast, S. 1955.** *Cololejeunea azorica* V.A. et S. J.-A., Lejeunéacée nouvelle de l'île San Miguel. *Mitteilungen der Thüringischen Botanischen Gesellschaft* 1 (2/3): 17-22.
- Allorge V. & Jovet-Ast, S. 1956.** *Targionia loorberiana* K.M. dans la péninsule Ibérique, aux Açores et aux Canaries. *Revue bryologique et lichénologique* 25: 134-135.
- Bates, J.W. & Gabriel, R. 1997.** *Sphagnum cuspidatum* and *S. imbricatum* ssp. *affine* new to Macaronesia, and other new island records for Terceira, Azores. *Journal of Bryology* 19: 645-648.
- Bisang, I. Schumacker, R., Sérgio, C. & Grolle, R. 1989.** Clé d'identification des espèces du genre *Frullania* Raddi (Hepaticae) en Europe et en Macaronésie. *Giornale Botanico Italiano* 122: 255-266.
- Bischler, H. 1970.** Les espèces du genre *Calypogea* sur le continent africain et les îles africaines. *Revue bryologique et lichénologique* 37: 63-134.
- Borges, P.A.V. 1992.** Biogeography of the Azorean *Coleoptera*. *Boletim do Museo Municipal do Funchal* 44: 5-76.
- Bouman, A.C. & Dirkse, G. 1990.** The genus *Radula* in Macaronesia. *Lindbergia* 16: 119-127.
- Buch, H. & Persson, H. 1941.** Bryophyten von den Azoren und Madeira. *Societas Scientiarum*

- Fennica. *Commentationes Biologicae* 8(7): 1-15.
- Crundwell, A.C., Greven, H. & Stern, R.C. 1994.** Some additions to the bryophyte flora of the Azores. *Journal of Bryology* 18: 329-337.
- Dias, E.O. 1989.** Flora e vegetação endémica na Ilha Terceira. Trabalho de síntese para as provas de aptidão pedagógica e capacidade científica. Angra do Heroísmo, Universidade dos Açores, Departamento de Ciências Agrárias.
- Düll, R. 1983.** Distribution of European and Macaronesian Liverworts (Hepaticophytina). *Bryologische Beiträge* 2: 1-115.
- Eggers, J. 1982.** Artenliste der Moose Makaronesiens. *Cryptogamie, Bryologie, Lichénologie* 3: 283-335.
- Ferreira, D.B. 1980.** Contribution à l'étude des vents et de l'humidité dans les îles centrales de l'archipel des Açores. Centro de Estudos Geográficos. INIC, Rel. 9, 2 Vol., Lisboa.
- Frahm, J.-P. 1995.** Correlations between European, tropical Africa and tropical America moss flora. *Fragmenta Floristica Geobotanica* 40: 235-250.
- Gabriel, R. 1994.** Briófitos da Ilha Terceira (Açores). Ecologia, distribuição e vulnerabilidade de espécies seleccionadas. Universidad dos Açores, Departamento de Ciências Agrárias, Angra, 211 p. + ann.
- González-Mancebo, J.M., Losada-Lima, A., Hernández, C.D. & Durrant, H.J. 1991.** Bryophyte Flora of volcanic caves in the Azores and the Canary Islands. *Lindbergia* 17: 37-46.
- Gradstein, S.R., Pócs, T. & Vána J. 1993.** Disjunct Hepaticae in tropical America and Africa. *Acta Botanica Hungarica* 29: 127-171.
- Grolle, R. 1962.** Monographie der Lebermoosgattung *Leptoscyphus* Mitt. *Nova Acta Leopoldina*, Neue Folge 25: 1-143.
- Grolle, R. 1966.** *Dicranolejeunea* auf den atlantischen Inseln. Translations of the British Bryological Society 5: 95-99.
- Grolle, R. 1970.** Zur Kenntnis der Frullanien in Europa und Makaronesien. *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, Mathematisch-Naturwissenschaftliche Reihe* 19: 307-319.
- Grolle, R. 1971.** *Jamesoniella* und Verwandte. *Feddes Repertorium* 82: 1-99.
- Grolle, R. 1972 a.** Zur Kenntnis von *Adelanthus* Mitt. *Journal of the Hattori Botanical Laboratory* 35: 325-370.
- Grolle, R. 1972b.** *Bazzania* in Europa und Makaronesien. *Lindbergia* 1: 193-204.
- Grolle, R. 1983.** Hepatics of Europe including the Azores; an annotated list of species, with synonyms from the recent literature. *Journal of Bryology* 12: 403-459.
- Grolle, R. & Persson, H. 1966.** Die Gattung *Tylimanthus* auf den atlantischen Inseln. *Svensk Botanisk Tidskrift* 60: 164-174.
- Grolle, R. & Schumacker, R. 1982.** Zur Synonymie und Verbreitung von *Plagiochila spinulosa* (Dicks.) Dum. und *P. killarniensis* Pears. *Journal of Bryology* 12: 215-225.
- Heinrichs, J., Grolle, R. & Drehwald, U. 1998.** The conspecificity of *Plagiochila killarniensis* Pearson and *P. bifaria* (Sw.) Lindenb. (Hepaticae). *Journal of Bryology* 20: 495-497.
- Herzog, T. 1945.** Eine neue *Plagiochila* Art auf den Azoren. *Revue bryologique et lichénologique* 14 [1944]: 161-162.
- Hübschman, A. (von) 1974.** Bryosoziologische Studien auf der Azoreninsel São Miguel. *Revista da Faculdade de Ciências de Lisboa, Ser. 2, C 17: 627-702.*
- Jovet-Ast, S. 1986.** Les *Riccia* de la région méditerranéenne. *Cryptogamie, Bryologie, Lichénologie* 7, suppl.: 287-431.
- Kindberg, N.C. 1898.** Contributions à la flore du Portugal et des Açores. *Revue bryologique* 6: 90-91.
- Kruijt, R.C. 1988.** A monograph of the genera *Dicranolejeunea* and *Acanthocoleus*. *Bryophytorum Bibliotheca* 36.
- Losada-Lima, A. & Hernández-García C.D. 1991.** A contribution to the floristic knowledge of caves on the Azores. *Mémoires de Biospéléologie* 18: 219-220.
- Luisier, A. 1938.** Hepáticas dos Açores. *Brotéria, Ser. Ciências Naturales* 7: 187-189.
- Madruça, J. da 1986.** Andossolos dos Açores. Contributo para o seu estudo. Angra do Heroísmo. Universidade dos Açores.
- Mitten, W. 1865.** Contributions to the cryptogamic flora of the Atlantic Islands. *Journal of the Linnean Society, Botany* 8: 1-10.
- Mitten, W. 1870.** Hepaticae. In Godman, F. 1870. *Natural History of the Azores or Western Islands*: 316-328.
- Mitten, W. 1877.** Musci and Hepaticae collected by N. Mosely, naturalist to H.M.S. Challenger. *Journal and Proceedings of the Linnean Society, Botany* 15: 59-73.
- Ozer, P., Erpicum, M., Cortemiglia, G.C. & Luchetti, G. 1998.** A dustfall event in November 1996 in Genoa, Italy. *Weather* 53: 140-145.

- Persson, H. 1973.** The Azorean Bryophytes collected by P. Dansereau et A.R. Pinto da Silva in 1964. *Agronomia Lusitana* 35: 5-19.
- Persson, H. 1955.** Remarks on the *Porella pinnata* group. *Annales Societatis Zoologicae et Botanicae "Vanamo"* 9 (suppl.): 225-231.
- Potemkin, A.D. 1998.** On *Odontoschisma sphagni* (Dicks.) Dum. (Hepaticae, Cephaloziaceae) in Russia, with a key and consideration of differentiation of the Russian species of *Odontoschisma*. *Arctoa* 7: 197-202.
- Richards, P.W. 1936.** A collection of Bryophytes from the Azores. *Annales Bryologici*. 9: 131-138.
- Russel, J.L. 1862.** Some notes on the cryptogamic vegetation of Faial. *Proceeding of the Essex Institute* 2: 134-137.
- Sampaio, A.S. 1904.** Memoria sobre a Ilha Terceira. Angra do Heroísmo.
- Schuster, R.M. 1974.** The Hepaticae and Anthocerotae of North America. 3. New York, Columbia University Press, 880 p.
- Sérgio, C. 1974.** Le genre *Fossombronia* au Portugal, à Madère et aux Açores. *Bulletin de la Société Botanique de France* 121: 319-326.
- Sérgio, C. 1978.** *Lejeunea eckloniana* Lindenb. (hépatique) dans la Macaronésie. *Boletim da Sociedade Portuguesa de Ciências Naturais* 18: 39-41.
- Sérgio, C. 1984.** The distribution and origin of Macaronesian bryophyte flora. *Journal of the Hattori Botanical Laboratory* 56: 7-13.
- Sérgio, C. 1985.** Notulae Bryoflorae Macaronesicae. I. 1 - Considerações sobre a presença de *Frullania muscicola* Steph. e *Frullania ericoides* (Nees) Mont. nos Açores e Madeira. *Portuguesa Acta Biológica, Serie B* 14: 161-168.
- Sérgio, C. 1987.** Contribuição para estudo taxonómico e fitogeográfico de *Anthoceros caucasicus* Steph. na Península Ibérica e Macaronesia. *Actos do VI. Simpósio Nacional de Botânica Criptógâmica*: 605-614.
- Sérgio, C. 1989.** Notulae Bryoflorae Macaronesicae II. 3 - *Sphaerocarpos texanus* Austin nova hepática para a flora da Macaronésia. *Portuguesa Acta Biológica, Série B* 15: 419.
- Sérgio, C. 1994a.** Duas novas espécies de *Fossombronia* para a brioflora dos Açores. *Revista de Biologia* 15: 183.
- Sérgio, C. 1994b.** *Petalophyllum ralfsii* (Wils.) Nees & Gott. ex Lehm., espécie nova para os Açores e para Macaronesia. *Revista de Biologia* 15: 184.
- Sérgio, C. & Dias, E. 1991.** Notulae Bryoflorae Macaronesicae. II. 4 - Algumas Ricciaceae e Anthocerotaceae novas para a ilha Terceira. *Portuguesa Acta Biológica, Série B* 15: 421-423.
- Seubert, M. 1844.** *Flora Azorica* quam ex Collectionibus Schedidque Hochstetteri Patris et Filii. Bona.
- Silveira Moniz (da), T. 1937.** *Flora briológica. Espécies novas para os Açores.* *Boletim da Sociedade Portuguesa de Ciências Naturais* 1: 240-247.
- Sjögren, E. 1973.** Recent changes in the vascular flora and vegetation of the Azores Islands. *Memórias da Sociedade Broteriana* 22: 1-453.
- Sjögren, E. 1978.** Bryophyte vegetation in the Azores Islands. *Memórias da Sociedade Broteriana* 22: 1-273.
- Sjögren, E. 1990.** Bryophyte flora and vegetation on the island of Graciosa (Azores), with remarks on floristic diversity of the Azorean islands. *Arquipélago, Life and Earth Sciences* 8: 63-96.
- Sjögren, E. 1993.** Bryophyte flora and vegetation of the island of Corvo (Azores). *Arquipélago, Ciências Biológicas e Marinhas* 11 A: 1-18.
- Sjögren, E. 1997.** Epiphyllous bryophytes in the Azorean islands. *Arquipélago, Life and Marine Sciences* 15A: 1-49.
- Sjögren, E. 1999.** Azorean bryophytes communities - a revision of differential species. *Arquipélago, Life and Marine Sciences* (in press).
- Sjögren, E (coll. Schumacker, R.) 1999.** Distribution of bryophytes in the Azores Islands, with information on their presence on Madeira, in the Canary Islands and in the World. *Arquipélago, Life and Marine Sciences* (in press).
- Sjögren, E. & Hallingckäck, T. 1978.** A bryological bibliography of the Macaronesian island groups of the Azores, Madeira, Canaries and Cape Verde. *Memórias da Sociedade Broteriana* 26: 274-283.
- Sim-Sim, M. 1999.** The genus *Frullania* in Portugal and Madeira. *Cryptogamie, Bryologie* 20: 83-144.
- Sim-Sim, M., Sérgio, C., Mues, R. & Kraut, L., 1995.** A new *Frullania* species (Trachycolea) from Portugal and Macaronesia: *Frullania azorica* sp. nov. *Journal of Bryology* 16: 111-123.
- Smookler, M.M. 1965.** Bryophyte report (S. Jorge). *Chelsea College Azores Expedition, July-October 1965*: 48-63.
- Trelease, W. 1897.** Botanical observations on the

Azores. Annual Report of the Missouri Botanical Garden 8: 77-220.

Váña, J. 1974a. Studien über die Jungermannioideae (Hepaticae). 4. *Jungermannia* Subg. *Plectocolea* und Subg. *Solenostoma*: Allgemeines, süd- und mittelamerikanische Arten. Folia Geobotanica Phytotaxonomica 9: 179-208.

Váña, J. 1974b. Studien über die Jungermannioideae (Hepaticae). 5. *Jungermannia* Subg. *Plectocolea* und Subg. *Solenostoma*: Afrikanische Arten. Folia Geobotanica Phytotaxonomica 9: 277-312.

Zanten, B.O. (van) & Gradstein, S.R. 1988. Experimental dispersal geography of neotropical liverworts. Beiheft zur Nova Hedwigia 90: 41-94.

