

## **The lowland cloud forest of French Guiana – a liverwort hotspot<sup>1</sup>**

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**Abstract** – Tropical lowland cloud forest (TLCF) occurs in moist river valleys in French Guiana, below 400 m, and has never been described. The forest resembles mixed lowland rain forest but differs by the frequent occurrence of fog and the abundance of epiphytes. Species richness of epiphytic liverworts in TLCF of French Guiana is similar to that at 2000 m in the Andes and is three times higher than in Amazonian lowland forest. The high species richness is explained by the favorable air moisture regime in TLCF, which allows these poikilohydric species to thrive in the hot lowland forest. Fog during day times prevents desiccation and allows the plants to reach net photosynthesis in spite of high temperatures. About thirty percent of the liverwort species in TLCF are restricted to the forest canopy and several are obligate epiphylls. Habitat preferences are similar to those in tropical montane cloud forest but taxonomic composition and total abundance are different. Dispersal by asexual reproduction is significantly more common in the forest understory than in the canopy, where dispersibility is less constrained. Canopy species have significantly wider ranges than understory species, presumably due to long range dispersal by spores.

**Tropical lowland cloud forest / French Guiana / liverworts / species richness / epiphytes / epiphylls / forest canopy / long range dispersal**

### **INTRODUCTION**

French Guiana or *Guyane*, an overseas province (*Département d'Outre-Mer*) of France on the Caribbean coast of South America with a total surface of about 80000 km<sup>2</sup>, is renowned for its splendid rain forests. Most of the land is under 500 m and covered by species-rich, mixed lowland rain forest or “forêt haute de basse altitude” (e.g., Oldeman, 1974; Granville, 1986, 2001). Only near the coast, where most of the inhabitants of French Guiana live, the forest is replaced by savannas, secondary forest, or scrubby vegetation. The development of rain forest in the province is enhanced by high precipitation which ranges from about 2000 mm in the south to over 4000 mm in the northeast. The inland region of French Guiana is dissected by rivers and a few mountain ranges reaching to about 900 m in elevation. It is here that the lowland rain forest may give way to cloud forest.

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1. This paper is dedicated to the memory of my dear friend and colleague Dr. Hélène Bischler-Causse, who was one of our foremost experts on the systematics and ecology of liverworts.

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Cloud forest of French Guiana is of two different types. In summit areas tropical (sub)montane cloud forest (TMCF) or “forêt submontagnarde à nuages” (Granville, 2001) occurs, characterized by rather low and stunted growth of trees, high richness of epiphytes, and frequent occurrence of fog. Fog in TMCF develops by uplifting of moist air masses along the mountain slopes and subsequent condensation of the saturated air. TMCF is widespread in the tropics above 500 m (Hamilton *et al.*, 1995) and is very rich in epiphytic bryophytes, especially liverworts (Richards, 1984; Frahm & Gradstein, 1991; Gradstein, 1995a).

A second type of cloud forest, “tropical lowland cloud forest” (TLCF), occurs at much lower elevations, in moist river valleys below 400 m. Patches of TLCF have been observed in the Saül area, in the Inini and Waki valleys, and along larger rivers like the Maroni, Oyapock, Mana, and Approuague (J. J. de Granville, pers. comm.). TLCF resembles tropical lowland rain forest but differs by being frequently enveloped by clouds during night and early morning and by a greater richness of epiphytes, especially liverworts (Gradstein, 2003, in press). Fog in TLCF probably develops by radiation from water-logged soils (this has not yet been studied), not by uplifting of air masses along mountain slopes, and is enhanced by undulating terrain with many small hills and creeks, saturation of air during the night and early mornings, occurrence of heavy rains during the night, and lack of air turbulence. TLCF is known from the Guianas, Colombia, Costa Rica, and Indonesia, and has not yet been described in detail (Gradstein, in press).

The purpose of this paper is to provide a brief description of liverwort diversity in TLCF of French Guiana. Together with my students, I have studied bryophyte diversity of TLCF in the central part of French Guiana, near the village of Saül about 200 km south of the coast (e.g., Montfoort & Ek, 1990; Gradstein *et al.*, 1990; Gradstein, 1995a, 1995b). Other than a zone of minor disturbance surrounding the village, this region is covered by splendid, species-rich moist forest (Oldeman, 1974; Mori & Boom, 1987). The vascular plants and mosses of the region have been treated in detail (Mori *et al.*, 1997, 2002; Buck, 2003) and a liverwort Flora is in preparation (Gradstein & Ilkiu Borges, in prep.). TLCF occurs in valleys where fog develops during the night and early morning and is usually dispersed by noon. Because of the frequent occurrence of fog the hills near Saül are called “Monts la Fumée” (“smoky mountains”).

## SPECIES RICHNESS

A preliminary species list of TLCF in the surroundings of Saül includes 129 species of liverworts and one hornwort, *Dendroceros crispus* (included with the liverworts for practical reasons), or about two third of the total liverwort flora of French Guiana (Appendix; Gradstein, 1997a; Gradstein & Ilkiu Borges, in prep.). The majority of the species are Lejeuneaceae (95 spp.; 75%); other families of liverworts have less than ten species each.

More than two thirds of the liverwort species (85 spp.) were recorded on twenty eight mature trees, sampled from the base of the trunk to the outer crown in TLCF along the “crique limonade” near Saül (Montfoort & Ek, 1990). This is the highest number of species ever reported from tropical lowland forest and is similar to that recorded from TMCF at 2000 m in the Andes of Colombia (Wolf,

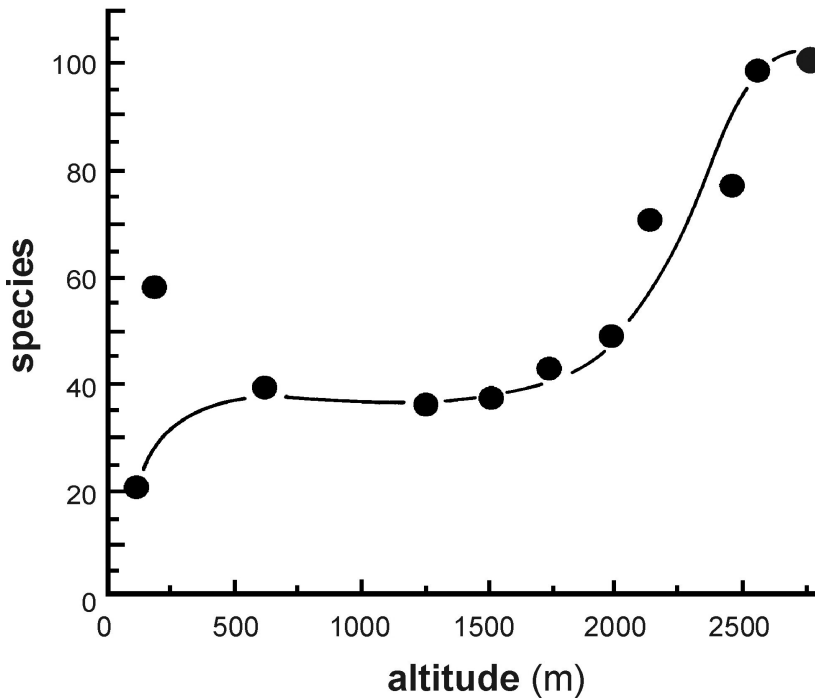


Fig. 1. Species richness of epiphytic liverworts on four trees at different elevations in moist ever-green forest of tropical America. Data below 500 m from Surumoni, Venezuela (low number; Gradstein, unpubl.) and Central French Guiana (high number; Montfoort & Ek, 1990); at 600 m from Bolivia (Acebey *et al.*, 2003); above 1000 m from Colombia (Wolf, 1993). Figure modified after Gradstein (in press).

1993) (Fig. 1). It is one and one-half times higher than in submontane forest of Bolivia and three times higher than in tropical lowland rain forest (TLRF) at Surumoni in Amazonian Venezuela. At Surumoni, four trees had 20 species of liverworts and less than 10 of moss, at Saül about 60 species of liverwort and about 40 of moss (Fig. 1). The large difference in species richness between the lowland forests of Saül and Surumoni is surprising because annual precipitation in the two sites is identical, *ca* 2500 mm (Gradstein, in press). The causes were long unclear but it is now understood that they are due to fog. While fog is frequent near Saül, it is never observed at Surumoni where local topography is relatively flat and distance to the coast much greater (Anhuf & Winkler, 1999).

The relative poverty of tropical lowland forests, such as those of Surumoni, in terms of bryophyte diversity has frequently been noted (*e.g.*, Schuster, 1988) and has been explained by physiological properties of the bryophytes (Richards, 1984; Frahm, 1990; Zotz, 1999) although lack of sampling of the forest canopy also plays a role (Gradstein, 1992, 1995a). Both explanations seem to be right in their own way, yet a third explanation plays a role that has been hitherto overlooked: fog. It now appears that the low species diversity

characteristic of TLRF and the high species diversity of TLCF are due to the absence or presence of fog. In TLRF net photosynthesis during day times is inhibited due to high temperatures and desiccation of the epiphytic bryophytes in the dry air, hampering their survival (Frahm, 2003). Positive carbon budgets require relatively continuous high humidity in the surrounding atmosphere, and frequent wetting. Presence of fog in TLCF prevents desiccation of these poikilohydric plants and allows them to reach net photosynthesis in spite of the high temperature. Since water supply is generally considered the most powerful environmental determinant of epiphyte distribution (Benzing, 1998), I suggest that the more favourable air moisture regime in TLCF allows more bryophyte species to thrive in TLCF than in TLRF. Further studies should be made at other sites to verify these assumptions.

## HABITATS

Over 95% of the species of liverworts in TLCF are epiphytes; in this respect TLCF is similar to TLRF (Richards, 1984). The majority of the species grow on bark, the corticolous epiphytes, and a minor portion on living leaves (43 spp.; 35%) (Appendix). A few species inhabit rotten wood (16 spp.; 12%) and only two, *Calypogeia miquelii* and *Riccardia amazonica*, grow on soil. About 60% of the species occur in the canopy of the forest, at 20-45 m above the ground, and about half of these are exclusive to the canopy (40 spp.; 30%). The data clearly indicate that representative sampling of the forest is not possible without inventory of the forest canopy. Many species are missed when collecting is restricted to the forest understory.

Habitat preferences of liverworts in TLCF of French Guiana are very similar to those in TMCF at Monteverde (1500 m), Costa Rica (Nadkarni & Wheelwright, 1999; Gradstein *et al.*, 2001). In both forest types, few species grow on soil or rotten wood, many on living leaves, and one third of the species are restricted to the forest canopy. Taxonomic composition and total abundance of liverworts is different, however. TMCF at Monteverde has fewer Lejeuneaceae (56 spp.; 45%, as compared to 75% [95 spp.] in TLCF) and more Plagiochilaceae (20 spp.; 8 in TLCF) and Lepidoziaceae (12 spp.; 6 in TLCF). Nine families of TMCF (Acrobolbaceae, Adelanthaceae, Herbertaceae, Jungermanniaceae, Monocleaceae, Pallaviciniaceae, Porellaceae, Scapaniaceae, Trichocoleaceae) are lacking in TLCF of French Guiana. Moreover, total biomass of liverworts is higher in TMCF. Thick mats of *Bazzania*, *Plagiochila*, *Herbertus*, *Lepidozia*, *Syzygiella*, and *Tylimanthus*, and of mosses of the genus *Macromitrium*, cover the lower canopy branches at Monteverde and total biomass of the bryophytes is high (Nadkarni, 1984). In TLCF of French Guiana, bryophyte mats on canopy branches are thinner (field observations; biomass not measured) and species of *Lepidozia*, *Syzygiella*, *Tylimanthus*, and *Herbertus* are lacking. The latter genus is abundant in TLCF along the Pacific coast of Colombia, however, where many montane taxa descend to sea level (Gradstein, 1995a).

While corticolous species are most common in the canopy, epiphyllous species in TLCF are more abundant in the forest understory (Montfoort & Ek, 1990). The majority of the epiphylls is not restricted to living leaves, however, and may also grow on bark (Appendix). Species found only on living leaves in TLCF

of French Guiana are *Aphanolejeunea winkleri*, *Cololejeunea apressa*, *C. bekkeri*, *C. linopteroides*, *C. platyneura*, *C. subcardiocarpa*, *C. subscariosa*, *Diplasiolejeunea pellucida*, *Drepanolejeunea polyrhiza*, *Leptolejeunea moniliata*, *Odontolejeunea decemdentata*, and *Radula yanoella*. Of these, only *Drepanolejeunea polyrhiza*, *Leptolejeunea moniliata*, *Radula yanoella*, and the majority of the *Cololejeuneas* have never been reported from substrates other than living leaves and may be "obligate" epiphylls (Richards, 1984). However, as has been pointed out previously, obligate epiphyllism is rare in bryophytes and is difficult to prove (Gradstein, 1997b). I recommend further collecting of the species recorded exclusively from living leaves to verify their status as obligate epiphylls.

### DISPERSAL AND DISTRIBUTION

Because of their limitation to the forest understory and impermanence of their substrates, it has been assumed that dispersibility of species growing in the understory of the forest is constrained and is mainly short-distance dispersal by gemmae and other asexual means of reproduction (Fulford *et al.*, 1970; Richards, 1988). Canopy species, on the other hand, because of their more exposed growth and greater drought-resistance of their spores, would have better chances for long range dispersal and wider ranges (Zanten & Gradstein, 1988; Gradstein, 1992, 1995b).

The data assembled in this study allow for testing of these assumptions. In Table 1 reproductive features, viz. presence of monoicous condition and asexual reproduction, and range size (occurrence of wide tropical ranges) are compared in 72 liverwort species, 36 canopy specialists and 34 understory specialists, of TLCF of French Guiana. The monoicous condition was scored because it is generally believed that spores, essential for long range dispersal, are more freely produced in monoicous species than in dioicous ones (Longton & Schuster, 1983).

The results show that the monoicous condition is more common among canopy species, although not significantly so ( $p = 0,15$ ), while asexual reproduction was significantly more frequent in the understory ( $p = 0,001$ ) than in the canopy. The number of species with asexual reproduction was about seven times higher in understory species than in canopy species; the monoicous condition occurred in 80% of canopy species and in 55% of understory species. Moreover, it appears that wide tropical ranges are significantly more common among canopy specialists than among understory specialists ( $p < 0,05$ ): sixteen canopy species (40%) had wide tropical ranges and occurred also in Africa or elsewhere in the Paleotropics, as compared with only five (13%) understory species (Table 1).

The data support the hypothesis that dispersibility is less constrained in the canopy than in the understory of the forest, and that wide ranges are more common among canopy species than among understory species. The greater importance of spore dispersal among canopy species, as expressed by rareness of asexual reproduction in the canopy, higher number of monoicous species, and the greater drought resistance of their spores (Zanten & Gradstein, 1988), is supportive of the hypothesis that wide ranges of canopy species are due to long range dispersal. A similar situation has been documented for epiphytic versus terrestrial

Table 1. Reproductive features and range size of understory and canopy specialists in the liverwort flora of the lowland cloud forest of French Guiana (species list based on Montfoort & Ek, 1990, with updates). + present, – absent. Species with wide tropical ranges occur in the Neotropics and the Paleotropics, those without are restricted to the Neotropics. Statistical significance based on Chi-square tests.

	<i>Monoicous</i>	<i>Asexual reproduction</i>	<i>Wide tropical range</i>
<b>Understory specialists</b> (n = 36)	19 spp. (55%)	22 spp. (65%)	5 spp. (13%)
<i>Aneura pseudopinguis</i>	–	–	+
<i>Archilejeunea parviflora</i>	+	–	–
<i>Bazzania bidens</i>	–	+	–
<i>B. cuneistipula</i>	–	+	–
<i>Calypogeia miquelii</i>	–	+	–
<i>Ceratolejeunea coarina</i>	+	–	–
<i>C. cubensis</i>	–	–	–
<i>Cyclolejeunea luteola</i>	+	+	+
<i>Cyclolejeunea peruviana</i>	–	+	–
<i>Drepanolejeunea crucianella</i>	–	+	–
<i>D. inchoata</i>	–	+	–
<i>D. orthophylla</i>	–	+	–
<i>D. polyrhiza</i>	+	+	–
<i>Lejeunea asperrima</i>	+	+	–
<i>L. boryana</i>	+	–	–
<i>L. controversa</i>	+	–	–
<i>Leptolejeunea moniliata</i>	+	+	–
<i>Lophocolea bidentata</i>	+	–	+
<i>L. liebmanniana</i>	+	–	–
<i>L. martiana</i>	+	–	+
<i>Microlejeunea crenulifolia</i>	+	–	–
<i>Micropterygium trachyphyllum</i>	+	–	–
<i>Odontolejeunea decemdentata</i>	–	+	–
<i>Pictolejeunea picta</i>	+	+	–
<i>Plagiochila gymnocalcina</i>	–	+	–
<i>P. patentissima</i>	–	+	–
<i>Prionolejeunea aemula</i>	+	+	–
<i>P. denticulata</i>	+	+	–
<i>Radula flaccida</i>	–	+	+
<i>R. kegelii</i>	–	–	–
<i>R. yanoella</i>	–	+	–
<i>Rectolejeunea berteroana</i>	–	+	–
<i>Riccardia amazonica</i>	–	–	+
<i>Stictolejeunea balfourii</i> var. <i>bekkeri</i>	+	–	–
<i>Taxilejeunea isocalycina</i>	+	–	–
<i>Xylolejeunea crenata</i>	+	–	–
<b>Canopy specialists</b> (n = 36)	29 spp. (80%)	3 spp. (8%)	16 spp. (40%)
<i>Acanthocoleus aberrans</i>	+	–	+
<i>Acrolejeunea torulosa</i>	+	+	–
<i>Archilejeunea auberiana</i>	+	–	–
<i>Ceratolejeunea confusa</i>	+	–	–
<i>Cheilolejeunea holostipa</i>	–	–	–
<i>C. trifaria</i>	+	–	+
<i>Colura cylindrica</i>	–	+	+
<i>Cylindrocolea planifolia</i>	+	–	–

	<i>Monoicous</i>	<i>Asexual reproduction</i>	<i>Wide tropical range</i>
<i>Diplasiolejeunea cavifolia</i>	+	+	+
<i>D. rudolphiana</i>	+	-	+
<i>Drepanolejeunea fragilis</i>	-	-	-
<i>Frullania apiculata</i>	+	-	+
<i>F. brasileinsis</i>	-	-	-
<i>F. caulisequa</i>	+	-	-
<i>F. gibbosa</i>	+	-	-
<i>F. kunzei</i>	+	-	-
<i>F. nodulosa</i>	+	-	+
<i>F. riojaneirensis</i>	+	-	+
<i>Frullanooides tristis</i>	+	-	+
<i>Harpalejeunea stricta</i>	-	-	-
<i>Lejeunea flava</i>	+	-	+
<i>Leucolejeunea unculoba</i>	+	-	+
<i>Lopholejeunea subfusca</i>	+	-	+
<i>Marchesinia brachiata</i>	+	-	+
<i>Mastigolejeunea auriculata</i>	+	-	+
<i>M. innovans</i>	+	-	-
<i>Metalejeunea cucullata</i>	+	-	+
<i>Microlejeunea epiphylla</i>	-	-	-
<i>Neurolejeunea breutelii</i>	+	-	-
<i>N. seminervis</i>	-	-	-
<i>Pycnolejeunea contigua</i>	+	-	+
<i>P. macroloba</i>	+	-	-
<i>Rectolejeunea flagelliformis</i>	+	+	-
<i>Schiffneriolejeunea amazonica</i>	+	-	-
<i>Taxilejeunea obtusangula</i>	+	-	-
<i>Thysananthus amazonicus</i>	+	-	-
<b>Statistical significance (p): canopy vs. understory</b>	0,15	0,001	0,05

bromeliads in tropical montane forests of Bolivia by Kessler (2002). Epiphytic versus terrestrial pteridophytes, however, did not show significant differences in range sizes (Kessler, 2001), and epiphytic pteridophytes species inhabiting the inner and medium canopy had wider ranges than those growing on the tree trunks and in the outermost canopy (J. Kluge & M. Kessler, pers. comm.). These data indicate that the distribution patterns detected in one group of organisms may not hold for all other groups.

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## REFERENCES

- ACEBEY C., GRADSTEIN S.R. & KRÖMER T., 2003 — Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of tropical ecology* 19: 9-18.
- ANHUF D. & WINKLER H., 1999 — Geographical and ecological settings of the Surumoni-Crane-Project (Upper Orinoco, Estado Amazonas, Venezuela). *Anzeigen der österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 1, 135: 3-23.
- BENZING D., 1998 — Vulnerability of tropical forests to climate change: the significance of resident epiphytes. *Climate change*: 519-540.
- BUCK W.R., 2003 — Guide to the Plants of Central French Guiana: Part 3. Mosses. *Memoirs of the New York botanical garden* 76 (3): 1-167.
- FRAHM J.-P., 1990 — The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova hedwigia* 51: 151-164.
- FRAHM J.-P. & GRADSTEIN S.R., 1991 — An altitudinal zonation of the tropical rain forest using bryophytes. *Journal of biogeography* 18: 669-678.
- FRAHM J.-P., 2003 — Manual of Tropical Bryology, chapter 6: Ecophysiology. *Tropical bryology* 23: 59-68.
- FULFORD M.H., CRANDALL B. & STOTLER R., 1970 — The ecology of an elfin forest in Puerto Rico, 11. The leafy Hepaticae of Pico del Oeste. *Journal of the Arnold arboretum* 51: 56-69.
- GRADSTEIN S. R., MONTFOORT D. & CORNELISSEN J.H.C., 1990 — Species richness and phytogeography of the bryophyte flora of the Guianas, with special reference to the lowland forest. *Tropical bryology* 2: 117-126.
- GRADSTEIN S.R., 1992 — The vanishing Tropical Rain Forest as an environment for bryophytes and lichens. In: Bates J.W. & Farmer A.R. (Eds), *Bryophytes and lichens in a Changing Environment*. Oxford, U.K., Oxford University Press, pp. 232-256.
- GRADSTEIN S.R., 1995a — Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. In: Churchill S.P., Balslev H., Forero E. & Luteyn J.L. (Eds), *Biodiversity and Conservation of neotropical Montane Forests*. New York, New York Botanical Garden Press, pp. 321-334.
- GRADSTEIN S.R., 1995b — Bryophyte diversity of the tropical rainforest. *Archives des sciences, Genève* 48: 91-96.
- GRADSTEIN S.R., 1997a — Hepatophyta, Anthocerotophyta. In: Boggan J., Funk V., Kelloff C., Hoff M., Cremers G. & Feuillet C. (Eds), *Checklist of the Plants of the Guianas (Guyana, Suriname, French Guiana)*. 2nd ed. Washington, Smithsonian Institution, pp. 9-15.
- GRADSTEIN S.R., 1997b — The taxonomic diversity of epiphyllous bryophytes. *Abstracta botanica* 21: 15-19.
- GRADSTEIN S.R., GRIFFIN III D., MORALES M.I. & NADKARNI N.M., 2001 — Diversity and habitat differentiation of mosses and liverworts of the cloud forest of Monteverde, Costa Rica. *Caldasia* 23: 203-212.
- GRADSTEIN S.R., 2003 — Biodiversitätsforschung im tropischen Regenwald. *Kleine Senckenberg Reihe* 45: 95-110.
- GRADSTEIN S.R., in press — The tropical lowland forest — a neglected forest type. In: Bruijnzeel L.E. & Juvik J.O. (Eds), *Mountains in the mist*. Hawaii, Hawaii University Press.
- GRADSTEIN S.R. & ILKIU BORGES A.L., in prep. — Guide to the Plants of Central French Guiana: Part 4. Liverwort and hornworts. *Memoirs of the New York Botanical Garden* 76 (4).
- GRANVILLE J.-J. de, 1986 — *Flore et Végétation*. Cayenne, Saga.
- GRANVILLE J.-J. de, 2001 — Végétation. In: Barret J. (Ed.), *Atlas Illustré de la Guyane*. Centre de la Cartographie de la Guyane, Institut d'Enseignement Supérieur de Guyane, pp. 52-56.



- HAMILTON L. S., JUVIK J.O. & SCATENA F.N., 1995 — *Tropical Montane Cloud Forests*. New York, Springer.
- KESSLER M., 2001 — Pteridophyte species richness in Andean forests in Bolivia. *Biodiversity and conservation* 10: 1473-1495.
- KESSLER M., 2002 — Environmental patterns and ecological correlates of range-size among bromeliad communities of Andean forests in Bolivia. *The botanical review* 68: 100-127.
- LONGTON R. & SCHUSTER R.M., 1983 — Reproductive biology of bryophytes. In: Schuster R.M. (Ed.), *New Manual of Bryology*. Vol. 1. Nichinan, Hattori Botanical Laboratory, pp. 386-462.
- MONTFOORT D. & EK R., 1990 — *Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guiana*. Utrecht, Institute of Systematic Botany (MSc thesis).
- MORI S.A. & BOOM B.M., 1987 — The Forest. In: Mori S.A. and collaborators, *The Lecythidaceae of a Lowland Neotropical Forest: La Fumée Mountain, French Guiana*. *Memoirs of the New York botanical garden* 44: 9-29.
- MORI S.A., CREMERS G., GRACIE C.A., de GRANVILLE J.-J., HOFF M. & MITCHELL J.D., 1997 — Guide to the vascular plants of central French Guiana: Part 1. Pteridophytes, gymnosperms, and monocotyledons. *Memoirs of the New York botanical garden* 76 (1): 1-442.
- MORI S.A., CREMERS G., GRACIE C.A., de GRANVILLE J.-J., HEALD S.V., HOFF M. & MITCHELL J.D., 2002 — Guide to the vascular plants of central French Guiana: Part 2. Dicotyledons. *Memoirs of the New York botanical garden* 76 (2): 1-776.
- NADKARNI N.M., 1984 — The biomass and nutrient capital of epiphytes in a neotropical elfin forest. *Biotropica* 16: 249-256.
- NADKARNI N.M. & WHEELWRIGHT N.T., 1999 — *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. New York, Oxford University Press.
- OLDEMAN R.A.A., 1974 — L'architecture de la forêt Guyanaise. *Mémoires O.R.S.T.O.M.* 73: 1-204.
- RICHARDS P.W., 1984 — The ecology of tropical forest bryophytes. In: Schuster R.M. (Ed.), *New Manual of Bryology*. Vol. 2. Nichinan, Hattori Botanical Laboratory, pp. 1233-1270.
- RICHARDS P.W., 1988 — Tropical forest bryophytes: synusiae and strategies. *Journal of the Hattori botanical laboratory* 64: 1-4.
- SCHUSTER R.M., 1988 — Ecology, reproductive biology and dispersal of the Hepaticae in the Tropics. *Journal of the Hattori botanical laboratory* 64: 237-269.
- WOLF J., 1993 — Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri botanical garden* 80: 928-960.
- ZANTEN B.O. VAN & GRADSTEIN S.R., 1988 — Experimental dispersal geography of neotropical liverworts. *Beihefte zur Nova hedwigia* 89: 41-94.
- ZOTZ G., 1999 — Altitudinal changes in diversity and abundance of non-vascular epiphytes in the tropics – an ecological explanation. *Selbyana* 20: 256-260.

### Appendix

Liverworts and hornworts recorded from tropical lowland cloud forest of Central French Guiana (Saül region). The list is based on study of over one thousand collections of liverworts in GOET, NY, and U, made in the surroundings of Saül in recent years by various collectors (Gradstein & Ilkiu Borges, in prep.). b = bark, e = living leaves, s = soil, w = rotten wood; I = understory, II = canopy.

#### **Aneuraceae**

*Aneura pseudopinguis* Herz. – b, w; I

*Riccardia amazonica* (Spruce) Schiffn. – s, w; I

#### **Calypogeiaceae**

*Calypogeia miquelii* Mont. – s; I

#### **Cephaloziellaceae**

*Cylindrocolea planifolia* (Steph.) R. M. Schust. – b; II

#### **Dendrocerotaceae**

*Dendroceros crispus* (Sw.) Nees – b; I

#### **Geocalyceae**

*Leptoscyphus porphyrius* (Nees) Grolle – b, w; I, II

*Lophocolea bidentata* (L.) Dumort. – b; I

*Lophocolea liebmanniana* Gottsche – b; I

*Lophocolea martiana* Nees – b, w; I

#### **Frullaniaceae**

*Frullania apiculata* (Reinwardt *et al.*) Dumort. – b; II

*Frullania brasiliensis* (Sw.) Nees – b; II

*Frullania caulisequa* Nees – b; II

*Frullania gibbosa* Nees – b; II

*Frullania kunzei* (Lehm. & Lindenb.) Lehm. & Lindenb. – b; II

*Frullania nodulosa* (Reinwardt *et al.*) Nees – b; II

*Frullania riojaneirensis* (Raddi) Aongstr. – b; II

#### **Lejeuneaceae**

*Acanthocoleus aberrans* (Lindenb. & Gottsche) Kruijt – b; II

*Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. – b; II

*Aphanolejeunea angustissima* (Steph.) Pócs – b, e; I

*Aphanolejeunea clavatopapillata* Steph. – b; I

*Aphanolejeunea contractiloba* A. Evans – b, e; I

*Aphanolejeunea sicaefolia* (Gott. ex Steph.) A. Evans – b, e; I

*Aphanolejeunea winkleri* Morales & A. Lücking – e; I

*Archilejeunea auberiana* (Mont.) A. Evans – b; II

*Archilejeunea fuscescens* (Hampe ex Lehm.) Fulford – b; I, II

*Archilejeunea parviflora* (Nees) Schiffn. – b; I

*Bryopteris filicina* (Sw.) Nees – b; I, II

*Ceratolejeunea coarina* (Gottsche) Steph. – b, e; I

*Ceratolejeunea confusa* R. M. Schust. – b; II

*Ceratolejeunea cornuta* (Lindenb.) Schiffn. – b, e; I, II

*Ceratolejeunea cubensis* (Mont.) Schiffn. – b; I

*Ceratolejeunea guianensis* (Nees & Mont.) Steph. – b; I, II

*Cheilolejeunea adnata* (Kunze) Grolle – b, e, w; I, II

*Cheilolejeunea clausa* (Nees & Mont.) R. M. Schust. – b; I, II

*Cheilolejeunea holostipa* (Spruce) Grolle & Zhu – b; II

*Cheilolejeunea rigidula* (Mont. & Nees) R. M. Schust. – b; I, II

*Cheilolejeunea trifaria* (Reinwardt *et al.*) Mizut. – b; II

- Cheilolejeunea* sp. nov. – b, e; I  
*Cololejeunea apressa* (A. Evans) Benedix – e; I  
*Cololejeunea bekkeri* Tixier – e; I  
*Cololejeunea cardiocarpa* Mont. – b, e; I, II  
*Cololejeunea linopteroides* H. Rob. – e; I  
*Cololejeunea obliqua* (Nees & Mont.) Schiffn. – b, e; I, II  
*Cololejeunea platyneura* (Spruce) S. Arn. – e; I  
*Cololejeunea subcardiocarpa* Tixier – e; I  
*Cololejeunea subscariosa* (Spruce) Steph. – e; I  
*Colura cylindrica* Herzog – b, e; II  
*Colura sagittistipula* (Spruce) Steph. – b; II  
*Colura tortifolia* (Nees & Mont.) Trevis. – b, e; I, II  
*Cyclolejeunea chitonia* (Tayl.) A. Evans – b, e; I, II  
*Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A. Evans – b, e; I, II  
*Cyclolejeunea luteola* (Spruce) Grolle – b, w; I  
*Cyclolejeunea peruviana* (Lehm. & Lindenb.) A. Evans – b, e; I  
*Diplasiolejeunea brunnea* Steph. – b, e; I  
*Diplasiolejeunea cavifolia* Steph. – b, e; II  
*Diplasiolejeunea pellucida* (Meissn. ex Spreng.) Schiffn. – e; I, II  
*Diplasiolejeunea rudolphiana* Steph. – b; II  
*Drepanolejeunea bidens* Steph. – b, e; I  
*Drepanolejeunea crucianella* (Taylor) A. Evans – b, w; I  
*Drepanolejeunea fragilis* Bischler – b, e; II  
*Drepanolejeunea inchoata* (Meissner) Steph. – b, e; I  
*Drepanolejeunea orthophylla* (Nees & Mont.) Bischler – e; I  
*Drepanolejeunea polyrhiza* (Nees) Grolle & Zhu – e; I  
*Frullanoides tristis* (Steph.) van Slageren – b; II  
*Harpalejeunea oxyphylla* (Nees & Mont.) Steph. – b, e; I, II  
*Harpalejeunea stricta* (Lindenb. & Gottsche) Steph. – b; II  
*Harpalejeunea tridens* Bescherelle & Spruce – b; II  
*Lejeunea asperrima* Spruce – b, e; I  
*Lejeunea boryana* Mont. – b; I  
*Lejeunea caespitosa* Lindenb. – b; I, II  
*Lejeunea controversa* Gottsche – b; I  
*Lejeunea flava* (Sw.) Nees – b; II  
*Lejeunea laetevirens* Mont. & Nees – b, e; I, II  
*Lejeunea phyllobola* Nees & Mont. – b; I, II  
*Lejeunea recurvistipula* (Lehm. & Lindenb.) Gottsche – b; I, II  
*Lejeunea* sp. A – b, e; I, II  
*Lepidolejeunea involuta* (Gottsche) Grolle – b; I, II  
*Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn. – b, e; I, II  
*Leptolejeunea exocella* (Spruce) A. Evans – e; I, II  
*Leptolejeunea moniliata* Steph. – e; I  
*Leucolejeunea unciloba* (Lindenb.) A. Evans – b; II  
*Lopholejeunea nigricans* (Lindenb.) Schiffn. – b, r; I  
*Lopholejeunea subfusca* (Nees) Schiffn. – b; II  
*Marchesinia brachiata* (Sw.) Schiffn. – b; II  
*Mastigolejeunea auriculata* (Wils.) Schiffn. – b; II  
*Mastigolejeunea innovans* (Spruce) Schiffn. – b; II  
*Mastigolejeunea plicatiflora* (Spruce) Schiffn. – b; II  
*Metalejeunea cucullata* (Reinwardt *et al.*) Grolle – b; II  
*Microlejeunea acutifolia* Steph. – b, e; I, II

*Microlejeunea crenulifolia* (Gottsche) Steph. – b; I  
*Microlejeunea epiphylla* Bischler – b, e; II  
*Neurolejeunea breutelii* (Gottsche) A. Evans – b; II  
*Neurolejeunea seminervis* (Spruce) Schiffn. – b; II  
*Odontolejeunea decemdentata* (Spruce) Steph. – e; I  
*Odontolejeunea lunulata* (Weber) Schiffn. – b, e; I, II  
*Odontolejeunea rhomalea* (Spruce) Steph. – b, e; I, II  
*Pictolejeunea picta* (Gottsche ex Steph.) Grolle – b, w; I  
*Prionolejeunea aemula* (Gottsche) A. Evans – b, w; I  
*Prionolejeunea denticulata* (Weber) Schiffn. – b, e, w; I  
*Pycnolejeunea contigua* (Nees) Grolle – b; II  
*Pycnolejeunea macroloba* (Nees & Mont.) Schiffn. – b; II  
*Rectolejeunea berteriana* (Gottsche) A. Evans – b, e, w; I  
*Rectolejeunea flagelliformis* A. Evans – b; II  
*Schiffneriolejeunea amazonica* Gradst. – b; II  
*Stictolejeunea balfourii* (Mitt.) Jones var. *bekkeri* Gradst. – b; I  
*Stictolejeunea squamata* (Willdenow) Schiffn. – b, e, w; I, II  
*Symbiezidium barbiflorum* (Lehm. & Lindenb.) A. Evans – b, e; I, II  
*Taxilejeunea isocalycina* (Lehm. & Lindenb.) Steph. – b, e; I  
*Taxilejeunea obtusangula* A. Evans – b; II  
*Thysananthus amazonicus* (Spruce) Schiffn. – b; II  
*Xylolejeunea crenata* (Nees & Mont.) He & Grolle – b, w; I

#### **Lepidoziaceae**

*Arachniopsis diacantha* (Mont.) Howe – b, w; I  
*Bazzania bidens* (Nees) Trevis.  
*Bazzania cuneistipula* Spruce – b; I  
*Bazzania diversicuspis* Spruce – b; I, II  
*Bazzania hookeri* (Lindenb.) Trevis. – b; I, II  
*Micropterygium* Lindenb.  
*Micropterygium trachyphyllum* Reimers – w; I

#### **Metzgeriaceae**

*Metzgeria decipiens* Schiffn. – b, e; II

#### **Plagiochilaceae**

*Plagiochila disticha* (Lehm. & Lindenb.) Lindenb. – b; I, II  
*Plagiochila gymnocalycina* (Lehm. & Lindenb.) Lindenb. – b; I  
*Plagiochila montagnei* Nees – b; I, II  
*Plagiochila patentissima* Lindenb. – b; I  
*Plagiochila raddiana* Lindenb. – b; I, II  
*Plagiochila rutilans* Lindenb. – b; I, II  
*Plagiochila simplex* (Sw.) Lindenb. – b, w; I, II  
*Plagiochila subplana* Lindenb. – b; I, II

#### **Radulaceae**

*Radula flaccida* Lindenb. & Gottsche – b, e; I  
*Radula javanica* Gottsche – b, e; I, II  
*Radula kegelii* Gottsche ex Steph. – b; I  
*Radula yanoella* R. M. Schust. – e; I