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MITES OF THE GENUS *Ledermuelleria* (PROSTIGMATA : STIGMAEIDAE) ASSOCIATED WITH MOSSES IN CANADA

by

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**Abstract.**

Eleven species of the genus *Ledermuelleria* Oudemans were collected from mosses obtained at many localities in southern Quebec and in eastern Ontario (Canada), and also in the northeastern U.S.A. Altogether 160 moss samples were collected, almost half of which harboured the mites. The mosses comprised 55 species, 38 being *Ledermuelleria*-associated. Habitat records suggest that *L. arctica* Wood, *L. gersoni* Wood and *L. rhodomela* (KocH) mostly occur on mosses colonizing open soils, whereas *L. frigida* Habeeb prefers moss growing in shaded, very humid places. *L. frigida* was studied in the laboratory. It feeds on moss leaves, sucking out cell contents but leaving cell-walls intact. The life cycle lasts about 30 days (at 23 ± 2°C). Reproduction is arrhenotokous, as isolated females have only male descendants. Females, whether confined with males or isolated, laid about 21 eggs. The mites reproduced freely under both long-day (16 hours) and short-day (9 hours) photoperiodic regimes. Transfer experiments showed that *L. frigida* will feed and survive on many moss species. Reproduction, however, occurs only whilst feeding on a few of these. Eggs placed in distilled water hatched and the larvae developed to the adult while thus immersed, but no oviposition took place under water. The species *L. rhodomela, L. clavata* (Canestrini and Fanzago) and *L. schusteri* Summers and Price also fed on various mosses and had similar life cycles.

**Introduction.**

Mites of the genus *Ledermuelleria* Oudemans comprise a group of reddish, globate animals which are related, within the family Stigmaeidae, to the genera *Ledermuelleriopsis* Willmann and *Mulleleria* Wood. The modern taxonomy of *Ledermuelleria* is based on the work of Summers (1957) and Summers and Price (1961), and many additional species were described by Chaudhri (1965) and by Wood (1966).

Isolated specimens of this genus were collected in ground litter, sod, various mulch types and in different soils. Three species — *L. parasitica* Chaudhri, *L. gamma* Chaudhri and *L. gorgast* Chaudhri — were collected from bodies of Phlebotomus sand flies and were presumed by Chaudhri (1965) to be parasitic on these insects. Individual specimens of *L. segnis* (Canestrini and Fanzago) and *L. pectinata* (Ewing) were obtained on tree leaves (Feider, 1954; Summers 1957).
1957), and Wood described *L. corticola* Wood from the bark of various New Zealand trees. Moss is another habitat whence *Ledermuelleria* spp. — often in large numbers — were collected. Thus, Sellnick (1932) found *L. favosa* Sellnick in considerable numbers on tree moss in Liberia; *L. ligulata* Feider was obtained from mosses in Roumania; and Summers and Price (1961) recovered *L. lacuna* Summers from “soil with moss” and *L. schusteri* Summers and Price in “soil and lichen”. Chaudhri (1965) also described some of his species from mites collected in moss, and Wood (1966) described all of his species from similar situations (the allotype of *L. corticola* is from “litter and moss”). Except for these habitat records, next to nothing is known about the ecology and life history of *Ledermuelleria*. However, several other members of the family Stigmaeidae, such as *Agistemus* Summers and *Zetzellia* Oudemans, are known to be predaceous on various microarthropods (Summers 1966).

The repeated allusions to moss as a habitat of *Ledermuelleria* prompted the samplings which initiated the present study and resulted in the discovery that the mites feed and reproduce on mosses.

About a dozen species of *Ledermuelleria* were collected during the sampling phase of this study. Several of them proved to be new to science and were described by Wood (see pages 301-318). One other species, *L. frigida*, was employed for the life-history studies discussed below, as well as for a detailed redescription of all stages, which is to be published elsewhere (Gerson, 1971).

**Moss-Ledermuelleria associations in the field**

Sampling and extraction methods.

The first few moss samples (taken at and around Macdonald College on the western tip of Montreal Island, Province of Quebec, Canada) showed at once that more than one species of *Ledermuelleria* was involved. An extensive moss sampling schedule was then initiated. Moss samples were collected at all sites during the summer and fall of 1968, but several additional samples were taken, at previously visited sites, in the winter and spring of 1969. Samples were obtained from various localities on Montreal Island and nearby, from the Laurentian mountains about 60 miles north of Montreal, from sites on both shores of the Ottawa River, the city of Ottawa being the westernmost point. Other samples were collected from points along the St. Lawrence River from just east of Morrisburg to the mouth of the Saguenay River (all these localities in Canada), and also from various sites in the U.S.A., in Vermont and New York States, the southernmost point being at New Baltimore, near Albany, N.Y. The locations of all sampling points are shown in Figure 1, and data pertinent to these sites, as well as the moss and mite species obtained, are:

Sampling and identification of mosses and *Ledermuelleria* spp.:

1: Jul. 7; St. Hilaire; Soil on rocks; *Atrichum altaeristatum* (Ren. & Card.) Ireland.
2: Jul. 7; St. Hilaire; Rotten log, forest; *Brachythecium plumosum* (Hedw.) B.S.G.
3: Jul. 7; St. Hilaire; Open soil; *Bryum turbinatum* (Hedw.) Turner & *Ceratodon purpureus* (Hedw.) Brid.; *L. rhodomela, L. gersoni.*
4: Jul. 3; Pointe de Cascade; Open soil on rocks; *Ceratodon purpureus; L. gersoni.*
5: Jul. 3; Pointe de Cascade; Open soil on rocks; *Polytrichum piliferum* Hedw. & *Polytrichum juniperinum* Hedw.
6: Jul. 9; Morgan Arboretum nr. Macdonald College; Shady soil; *Brachythecium* sp., *L. schusteri.*
7: Jul. 12; Macdonald College; Open, packed soil; *Ceratodon purpureus, Bryum argenteum* Hedw. & *Fusaria hygrometrica* Hedw.; *L. rhodomela, L. gersoni.*
Aug. 8
Ile Claude; Chateauguay; Gravel, road side; Morgan Arboretum; Shady soil; Brachythecium sp.; Ceratodon purpureus; L. gersoni.

Aug. 14
Macdonald College; Shady arboreal roots; Amblystegium serpens; Brachythecium sp.; L. gersoni.

Aug. 17
Fairview, Pointe Claire; Open playground; Bryum argenteum; Ceratodon purpureus; Barbula unguiculata; L. gersoni.

Aug. 17
Chateauguay; Shady soil; Brachythecium sp.

Aug. 17
Chateauguay; Gravel, road side; Ceratodon purpureus; L. gersoni.

Aug. 17
Beauharnois; Open rocks; Bryum argenteum.

Aug. 17
Beauharnois; Open soil; Barbula unguiculata.

Aug. 18
St. Adolphe d’Orford; Open soil; Diplidiocarpus lineare (Sw.) Lindb.; L. rhodomela.

Aug. 18
Chertsey; Shady soil; Bryum pseudodiplophyllum (Hedw.) Gaertn., Meyer & Scherb.; L. arctica.

Aug. 18
Notre Dame de la Merci; Shady soil; Polystichum piliferum Hedw., L. mircrosegis.

Aug. 18
St. Donat; Open soil; Ceratodon purpureus; Bryum sp., L. rhodomela, L. gersoni.

Aug. 18
St. Théodore; Forest soil; Fissidens cristatus Wils. ex. Mitt.; L. clavata, L. mirosegis.

Aug. 18
Rawdon; Forest soil; Pleurozium schreberi (Brd.) Mitt.; Polytrichum juniperinum.

Aug. 18
Ile Jesus; Gravel, road side; Ceratodon purpureus; L. gersoni.

Aug. 18
St. Agricole; Open field; Polytrichum commune Hedw.

Aug. 18
Ste. Julienne; Shady soil; Polystichum commune; Polytrichum juniperinum; L. mirosegis.

Aug. 20
St. Faustin; Bog; Sphagnum magellanicum Brd.; Sphagnum capillaceum (Weisse) Schrank; Sphagnum recurvum P. Beauv.

Aug. 20
St. Faustin; Bog; Sphagnum recurvum.

Aug. 20
St. Faustin; Rotting log; Hydropnum reptile Michx.; L. frigida.

Aug. 29
Calumet; Hillside rocks; Philonotis fontana (Hedw.) Brid.

Aug. 29
Gatineau; Forest soil; Hyrophyllum haldanianum (Grev.) Kindb.; L. rhodomela.

Aug. 29
Pointe au Chène; Tree bark; Leskea polycarpa Hedw. Leptodictyum ripariun.

Aug. 29
Papineauville; Forest soil; Brachythecium salebrosum (Web. & Mohr) B. S. G.

Aug. 20
St. Faustin; Rotting log; Heterophyllum haldanianum.
62 : Aug. 20 ; St. Faustin ; Forest soil ; Didymodon scoparium Hedw., Brachythecium sp., L. clavata, L. microsegnis.
63 : Aug. 20 ; St. Faustin ; Forest soil ; Hyphnum reptile.
64 : Aug. 20 ; St. Faustin ; Open soil ; Polytrichum piliferum.
65 : Aug. 20 ; St. Faustin ; Open soil ; Unidentified flowering plant ; L. arctica.
66 : Sep. 4 ; Frelighsburg ; Open soil ; Bryum capillare ; Polytrichum juniperinum ; Ceratodon purpureus ; L. gersoni.
67 : Sep. 4 ; Frelighsburg ; Apple bark ; Amblystegium serpens.
68 : Sep. 4 ; Candiac ; Gravel, road side ; Bryum argenteum ; L. rhodomela.
69 : Aug. 20 ; St. Faustin ; Tree bark ; Brachythecium reflexum (Starke ex Web. & Mohr) B.S.G.
70 : Aug. 20 ; St. Faustin ; Forest soil ; Polytrichum piliferum.
71 : Aug. 20 ; St. Faustin ; Forest soil ; Polytrichum piliferum.
72 : Aug. 20 ; St. Faustin ; Open soil ; Polytrichum piliferum.
73 : Sep. 8 ; Rigaud ; Shady soil ; Brachythecium sp., Hyphnum lindbergii.
74 : Sep. 8 ; Rigaud ; Shady soil ; Mnium cuspidatum.
75 : Sep. 8 ; Rigaud ; Forest soil ; Atrichum alecrisatum.
76 : Sep. 10 ; Rockland (Ont.) ; Open soil ; Brachythecium sp. ; L. pertinax.
77 : Sep. 10 ; Alfred (Ont.) ; Open soil ; Brachythecium salebrosum.
78 : Sep. 10 ; Ottawa (Ont.) ; Broken sidewalk ; Funaria hygrometrica ; Bryum argenteum ; L. rhodomela.
79 : Sep. 10 ; Orleans (Ont.) ; Open soil ; Ceratodon purpureus.
80 : Aug. 20 ; St. Faustin ; Rotting log ; Dicranum scoparium.
81 : Aug. 20 ; St. Faustin ; Shady soil ; Pleurozium schreberi.
82 : Sep. 14 ; Maxville (Ont.) ; Rotting log, forest ; Thuidium delicatulum ; L. frigida, L. microsegnis.
83 : Sep. 14 ; Maxville (Ont.) ; Rotting log, forest ; Plagiochila asplenioides (L.) Dumort. (Hepatic).
84 : Sep. 14 ; Maxville (Ont.) ; Rotting log, forest ; Rhodobryum roseum (Hedw.) Limpr. ; L. arctica.
85 : Sep. 14 ; Maxville (Ont.) ; Rotting log, forest ; Sharpniella turfacens ; Euryhynchium praelongum (Hedw.) B.S.G. ; L. microsegnis, L. frigida.
86 : Aug. 20 ; St. Faustin ; Forest soil ; Heterophyllum kaidanianum ; L. frigida.
87 : Sep. 4 ; Rougemont ; Open soil ; Ceratodon purpureus.
88 : Sep. 4 ; St. Luc ; Gravel, road side ; Ceratodon purpureus.
89 : Sep. 4 ; Bedford ; Shady soil ; Euryhynchium hiatus (Hedw.) Sande Lac. ; Campylium chrysophyllum ; Brachythecium sp. ; L. schusteri, L. rotunda.
90 : Sep. 4 ; Laprairie ; Gravel, road side ; Drepanocladus aduncus (Hedw.) Warnst. ; L. rhodomela.
91 : Sep. 4 ; Cowansville ; Open soil on rocks ; Polytrichum juniperinum ; Polytrichum piliferum ; L. microsegnis.
92 : Sep. 15 ; Finch (Ont.) ; Gravel, road side ; Bryum sp. ; Funaria hygrometrica.
93 : Sep. 14 ; Williamsburg (Ont.) ; Open soil ; Campylium chrysophyllum ; L. clavata, L. microsegnis.
94 : Sep. 14 ; Warina (Ont.) ; Open soil ; Funaria hygrometrica ; Bryum argenteum ; L. arctica.
95 : Sep. 14 ; Upper Canada Village (Ont.) ; Rotten log in forest ; Ceratodon purpureus ; L. microsegnis, L. arctica.
96 : Sep. 14 ; Upper Canada Village (Ont.) ; Forest soil ; Pleurozium schreberi.
97 : Sep. 14 ; Long Sault (Ont.) ; Open soil ; Campylium chrysophyllum ; Hyphnum lindbergii.
98 : Sep. 14 ; Long Sault (Ont.) ; Forest soil ; Brachythecium salebrosum.
99 : Sep. 14 ; Lancaster (Ont.) ; Shady soil ; Campylium chrysophyllum ; L. rhodomela ; L. gersoni ; L. arctica.
100 : Sep. 20 ; Isle Perrot ; Open soil ; Bryum argenteum ; L. gersoni.
101 : Sep. 20 ; Isle Perrot ; Forest soil ; Brachythecium salebrosum.
102 : Sep. 20 ; Isle Perrot ; Forest soil ; Mnium rugicum ; L. clavata.
103 : Sep. 20 ; Isle Perrot ; Forest rocks ; Brachythecium populeum (Hedw.) B.S.G. ; L. microsegnis.
104 : Sep. 20 ; Isle Perrot ; Open soil ; Barbirolla unguiculata ; L. gersoni.
105 : Sep. 20 ; Isle Perrot ; Soil on log ; Ceratodon purpureus ; L. gersoni.
106 : Sep. 24 ; Ste. Helène ; Shady soil ; Atrichum alecrisatum ; L. schusteri.
107 : Sep. 24 ; Quebec City ; Old Town walls. Sterile and unidentifiable.
108 : Sep. 24 ; Ste. Helène ; Shaded rocks ; Brachythecium salebrosum ; L. frigida.
109 : Sep. 24 ; Villeroi ; Open soil ; Sphagnum capillaceum.
110 : Sep. 24 ; Villeroy ; Forest soil ; Funaria hygrometrica ; L. clavata ; L. rhodomela ; L. arctica.
111 : Sep. 25 ; St. Irénée ; Forest soil ; Hyphnum lindbergii.
112 : Sep. 25 ; Cap Santé ; Hillside rock ; Didymodon tophaceus (Bríd.) Lisa ; Cratoneuron filicinum (Hedw.) Spruce.
113 : Sep. 25 ; Lac de Seminaire ; Shady rocky hillside soil ; Pleurozium schreberi ; L. acidophilus.
114 : Sep. 25 ; Ste Anne de Beaupré ; Rotting log ; Leskea polycarpa ; L. frigida.
115 : Sep. 25 ; Baie St. Paul ; Rotting log ; Brachythecium sp.
116 : Sep. 25 ; Baie Ste Catherine ; Hillside rock ; Poikia nutans.
vials, their bottoms covered by plaster-of-paris, served as collecting units. This extractor was plastic bags, and processed in the laboratory through modified Tullgren funnels. Small plastic phyto-mosses, of which such large samples could not be obtained. The samples were placed in a depth of 2-3 cm (except when collecting *Polytrichum* mats, which are thicker). The size of samples (measured dry, after extraction) was usually 300-350 cm² or more, with the exception of epiphytic mosses, of which such large samples could not be obtained. The samples were placed in plastic bags, and processed in the laboratory through modified Tullgren funnels. Small plastic vials, their bottoms covered by plaster-of-paris, served as collecting units. This extractor was...
FIG. 1: Map of sampling area in Canada and U.S.A. Numbers refer to sampling points, detailed in text.
employed because of its simplicity, its speed of action and because the mites are obtained live. Each sample was processed for two days only, as very few additional mites came out after this period. The mites collected were either used for various experiments, preserved in alcohol or mounted. All mosses were identified by Dr. Robert R. Ireland, Curator of Bryophytes at the National Museum of Canada and their names as they appear herein are according to Crum, Steere and Anderson (1965), with the exception of Atrichum alticristatum.

RESULTS AND DISCUSSION.

I. Mosses.

Altogether 162 samples were collected, but 4 are excluded (samples 25, 65, 83 and 107). Mites of the genus Ledermuelleria were found in 78 (49.4%) of the remaining 158 samples.

When in some cases more than one moss species were present in a given sample, although an effort was made to collect only from "pure" moss stands, most of the plants usually belonged to one species, and this species will be termed the dominant moss (dominant in the sample). The other species found will be called secondary. It is reasonable to assume that the mites were mostly associated with the dominant species, but it is deemed best to record all mosses found, though some have been obtained only in combination with others. In sample 66, Bryum capillare is the dominant, and Polytrichum juniperinum and Ceratodon purpureus are secondaries. Both latter species were found to harbour Ledermuelleria spp. when collected alone. Thus the mites recovered from sample 66 may well have been associated only with one or another of these mosses, but it is best at present to assume that in this sample B. capillare was the main host of L. rhodometra. In sample 21, Dicranella rufescens occurred as a secondary, the only time this moss was collected. Thus there is no reason at present to associate it with the mites found in this sample.

The 158 samples included 55 moss species, grouped in 38 genera. Of these 55 species, 38 (69%) were associated with Ledermuelleria spp., and of the remaining 17 species, 15 were collected only once, Pohlia nutans only twice, and Mnium cuspidatum thrice. It is believed that some of these less commonly collected mosses will yet prove to be Ledermuelleria-associated because, of the 32 moss species sampled only once, more than half (17) harboured the mites. More extensive sampling will possibly reveal the occurrence of Ledermuelleria on many additional moss species.

Of the 37 genera here considered (Sphagnum is excluded), 18 were acrocarpous, 19 pleurocarpous. Of the former, 13, and of the latter, 15, genera were associated with Ledermuelleria. Some species of Ledermuelleria were obtained from both types of mosses, and others showed a preference for one or the other type. Mites were recovered from mosses belonging to the orders Dicranales, Eubryales, Fissidentales, Funariales, Hypnobryales, Isobryales, Polytrichales and Pottiales.

The number of Ledermuelleria spp. obtained is large (11) in relation to the 38 associated

1. Mosses may be classified as either acrocarpous or pleurocarpous. The former bear the archegonia, and thus the seta and capsule, at the tip of the stem or branch, whereas the latter bear the archegonia on a short side branch, and not at the tip of the main stem or branch. The acrocarpous species, therefore, grow in an erect manner, while the pleurocarpous mosses grow mostly in a clinging, recumbent manner. Steere (1954) has pointed out the ecological differences associated with each of these growth habits. Acrocarpous genera are more common on soil and rocks, and more frequent in the colder and drier parts of the world. Pleurocarpous genera occur more often on trees, rotten logs and humus, and appear to be better adapted to warmer and more humid regions.

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moss species. When the collection data is reviewed, it becomes evident that a far greater number of moss samples will have to be studied to obtain some understanding of the intricate moss-mite interrelationships. In a few cases, in regard to mosses and mites more commonly sampled, some pattern may be glimpsed. These cases are discussed below. The numbers in parenthesis refer to the sample numbers given. All ecological data concerning the mosses, unless otherwise stated, are from Watson (1968).

*Barbula unguiculata*: In all cases (31, 33, 34, 39, 104) harbouring Ledermuelleria gersoni or *L. rhodomela*. This moss has an extensive range of habitats and is often a soil-patch colonizer, occurring often on calcareous soils (Moul 1952).

*Bryum argenteum*: Associated with Ledermuelleria gersoni or *L. rhodomela* in 9 out of 10 samples. This is a very common colonizing moss, which prefers a slightly basic soil reaction (pH = 8) according to Moul (1952), and it is common on edge of pavements in towns and other roadside situations.

*Ceratodon purpureus*: This was the moss species most commonly collected, occurring (either as a dominant or as a secondary) in 22 samples. *Ledermuelleria* spp. were found in 15 of these; in almost all cases (3, 4, 7, 8, 34, 48, 51, 105, 121, 141, 143, 146) the mites were *Ledermuelleria gersoni* or *L. rhodomela*. This moss is another common pioneering species (Leach 1931), which tolerates a wide range of soil reactions and occurs in many habitats.

*Pleurozium schreberi*: This species is regarded as an indicator plant for acid soil conditions. Mites were obtained in only 2 samples of this moss, and in both cases they were *Ledermuelleria acidophila*.

2. *Ledermuelleria* Species.

Altogether 11 separable species of *Ledermuelleria* were obtained. This number does not include several unmatched males and a female about which no conclusion could be reached. In most samples all stages of individual species were obtained, suggesting that, under field conditions, overlapping of generations occurs.

*Ledermuelleria acidophila* Wood.

*Ledermuelleria acidophila* was equally obtained from acrocarpous and pleurocarpous moss species (the former, 3 species of *Polytrichum*, *Atrichum* and *Dicranum*; whilst the latter, *Pleurozium*, *Heterophyllium*, *Brachythecium* and *Hyphnum*), and from various habitats, such as open soil (119, 156), forest soil (118), rocks or logs in forest (154, 161), or hillside rocks (113, 120). Most of the dominant mosses (*Polytrichum* spp., *Dicranum*, *Pleurozium*) are distinctly acidophilous, only *Hedwigia ciliata* being known to grow on siliceous rocks.

At St. Antoine Abbé, *Ledermuelleria acidophila* was obtained from 2 samples (161, 162) of moss mats formed by pure stands of *Dicranum* and *Hedwigia*, respectively and lying on rocks about 20 yards apart. This case is similar to the Pottersville series (148-150), whence *L. clavata* was recovered from 3 different moss species growing in the same habitat. Hence a habitat preference rather than a moss preference would be indicated. Generally, however, a preference for certain types of moss (acidophilous ones) is more evident in this mite than in other species of *Ledermuelleria*. 
**Ledermuelleria arctica** Wood.

This species was recovered from mosses growing on soil or rotting logs in shaded areas (84, 95, 99, 110) and from open, sandy soil (46, 94). The latter two samples yielded especially large numbers of *L. arctica*. The associated mosses were mostly acrocarpous (*Bryum*, *Ceratodon*, *Funaria*, *Rhodobryum*) one, *Campylium*, being pleurocarpous. All these mosses prefer neutral to basic soil conditions.

Several specimens of *L. arctica* were collected by Mr. Peter G. KEVAN at Hazen Camp, Lake Hazen, Northern Ellesmere Island, North West Territories, (Canada), 81°49'N., 71°18'W., in a marsh characterized by *Eriophorum* sp. and *Pedicularis arctica*, June 12, 1968. Though nothing is known concerning any associated bryophytes in these collections, several of the mosses from which *L. arctica* was recovered in the present study (such as *Bryum argenteum* and *Ceratodon purpureus*) are also known to occur on Northern Ellesmere Island (SCHUSTER et al., 1959), and may serve there as host plants. This record, taken together with the other collection data, suggests that *L. arctica* has a wide, northern distribution and prefers acrocarpous, colonizing mosses.

**Ledermuelleria clavata** (Canestrini & Fanzago).

This species was obtained from an unidentified moss collected from Val David, Quebec, on June 8, 1968, and also in samples 49, 62, 93, 102, 110, 148, 149, 150. It was associated with 7 moss species, 6 of which belong to acrocarpous genera (*Fissidens*, *Dicranum*, *Mnium*, *Philonotis*, *Polytrichum* and *Funaria*). Some of them are calcicolous (*Fissidens cristatus* and the pleurocarpous *Campylium chrysophyllum*); others are acidophilous (*Polytrichum*, *Dicranum*). The mite was obtained from mosses growing in varied habitats: forest soil (49, 62, 102, 110), open road-side (93) and hillside rocks (148-150). In the latter case, samples were taken of 3 moss species growing separately on adjacent rocks. At times this species was found together with *L. microsegnis*.

FRANZ and BEIER (1948) record *L. clavata* from Austria, where they obtained it from dry, as well as very wet, meadows, the pH of the soil being 6.3 in the former sample, 6.1 in the latter. North American records are from Utah, *ex* moss and *ex* poplar humus (SUMMERS, 1957), and from California, *ex* soil litter under oak, laurel and moss (SUMMERS and PRICE, 1961). The species was also collected at the Morgan Arboretum, near Macdonald College (MARSHALL, 1963, MARSHALL and KEVAN, 1964), the pH reaction of the soil at the 2 sites whence it was obtained being 4.2-4.9.

Some life-history data concerning *L. clavata* are presented later.

**Ledermuelleria frigida** Habeeb.

The locations whence this species was collected were indicated above. (p. 321-323). It was associated only with pleurocarpic mosses (*Heterophyllium*, *Hyphnum*, *Leptodictyum*, *Thuidium*, *Sharpieila*, *Brachythecium*, *Leskea*, *Cratoneuron*, *Bryhnia*) growing mostly in shaded, humid areas on rotten logs, arboreal tree roots or rocks. This mite was associated with *Thuidium delicatum*, which grows on slightly acid soils (IKENBERRY 1936) and with mosses growing on neutral to calcareous soils (such as *Campylium chrysophyllum*, which is exclusively calcicoles). Its association with *Cratoneuron filicinum* at Montmorency Falls (sample 123) is of interest, as the hillside whence the sample was obtained was very wet, being always heavily covered by water spray from the adjacent Falls. Also of note is the fact that *L. frigida* was not found to be associated with any of
the common acrocarpous colonizing mosses (Bryum argenteum, Barbula unguiculata, Ceratodon purpureus, Polytrichum spp.). Thus it appears that _L. frigida_ is associated with mosses growing in shaded, humid to very humid habitats, often on logs or roots. This species was initially described from specimens found in water in a small beaver pond (HABEEB, 1958).

**Ledermuelleria gersoni** Wood.

This is the species most often obtained, being taken from a total of 23 samples. In 14 of these it was associated with _Ceratodon purpureus_ (3, 4, 7, 8, 34, 42, 48, 51, 66, 105, 121, 141, 143, 146) and in 5 samples with _Bryum argenteum_ (7, 26, 34, 39, 100). Other acrocarpous moss hosts were _Bryum capillare_, _Barbula unguiculata_, _Bryum turbinatum_ and _Polytrichum juniperinum_ (only once, as a secondary). The pleurocarpous mosses associated with _Ledermuelleria gersoni_ were _Amblystegium serpens_, _Brachythecium sp._, _Brachythecium salebrosum_ and _Campylium chrysophyllum_.

In their soil-reaction preferences, these mosses are neutral (_Amblystegium_), calcicole (_Campylium_, _Barbula_) or tolerant (_Ceratodon_). Most of the mosses associated with this species, such as _Ceratodon_, _Bryum_, _Barbula_ and _Brachythecium_ are colonizing species. The last is a primary colonizer of fallen logs (McCULLOUGH, 1948). These mosses were usually obtained from relatively dry, open soil and fields or in roadside gravel. The emergent pattern is that _Ledermuelleria gersoni_ (like _L. rhodomela_, with which it occurs in four samples - 3, 7, 48, 99) is often associated with mosses that colonize relatively dry and open soil patches. It may thus be regarded as a colonizing element of the moss fauna.

Populations of _L. gersoni_ were recovered in the spring of 1969 at previously-marked sites where former collections were made. These included Macdonald College (22, 23), Ile Perrot (104) and Mont Royal (127). The occurrence of the mites in the mosses at snow thaw, while indicating their winter-long survival, also demonstrates the perennial nature of some _Ledermuelleria_ populations.

**Ledermuelleria microsegnis** Chaudhri.

One of the common species, _L. microsegnis_ occurred with both acrocarpous and pleurocarpous mosses, growing on diverse substrates in different habitats: open soil (91, 93, 122), shaded forest soil (49, 62, 118), mosses growing on rotting logs (82, 95) and on rocks (133, 149). Though mostly associated with acidophilous mosses (_Polytrichum_ spp., _Dicranum scoparium_, _Pleurozium schreberi_), it was also collected from calcicole mosses like _Fissidens cristatus_ and _Campylium chrysophyllum_. Furthermore, _L. microsegnis_ was most often collected together with other _Ledermuelleria_ spp., from the colonizing _gersoni_ to _frigida_, which appears to prefer pleurocarpous mosses in humid habitats. Thus no pattern of habitat preference emerges in regard to _L. microsegnis_.

Different morphological forms within this species ("typical" and "smooth") have been distinguished by Wood (1972: 301-318), and possibly when these are better defined, the moss relationships may also be better understood.

CHAUDHRI (1965) recorded _L. microsegnis_ from Missouri and Nebraska, in moss and leaf litter, respectively.

**Ledermuelleria parviseta** Chaudhri.

CHAUDHRI (1965) noted this species from California, from lichen on rock. In the present study it was obtained only once, from mats of _Cratoneuron filicinum_ growing on a hillside hea-vily wetted by waterfall spray at Montmorency Falls (No. 123).
Ledermuelleria pectinata (Ewing).

This species was obtained only once, in open grassland near Rockland (No. 76), from Brachythecium sp.

North American records include Iowa, from under an old piece of wood (Ewing, 1917); Utah, from oak leaves (Summers, 1957); and California and Nevada, from different soils, often under trees (Summers and Price, 1961).

Ledermuelleria rhodomela (Koch).

This species was obtained from 12 mosses, 9 being acrocarpous, 3 pleurocarpous. The former include Barbula unguiculata (31, 33); Bryum argenteum (7, 31, 33, 68); B. turbinatum (3); Ceratodon purpureus (3, 7, 31, 48); Ditrichum lineare (45); D. pusillum (130); Fissidens adianthoides (19); Funaria hygrometrica (31, 78, 110); and Mniobryum wahlenbergii (21). The pleurocarpous species were Campylium chrysophyllum (99); Drepanocladius aduncus (90) and Hypnum lindbergii (58). Some of these, like Ditrichum spp., are acidophilous (Moul, 1952), others, like Campylium and Bryum, are calcicoles.

Collecting sites give a more constant pattern. This mite was taken in 15 samples, all but 3 (58, 99, 110), being from moss growing in open habitats, often in packed, partly dry soil or on roadside gravel. Of interest is the occurrence of L. rhodomela in samples 31 and 78. The former was collected in sand dumped on the banks of the St. Lawrence River near Coteau du Lac, sand which was being colonized by Bryum argenteum, Funaria hygrometrica and Barbula unguiculata. Sample 78 was from a broken sidewalk in the city of Ottawa, Ontario, colonized by Funaria hygrometrica. It thus seems that L. rhodomela is mostly associated with colonizing mosses in relatively dry habitats, and may therefore be regarded as a colonizing species of Ledermuelleria like L. gersoni. In contrast to L. frigida, it was not found in mosses growing on logs or arboreal tree roots. A habitat preference therefore appears more likely in L. rhodomela also, rather than a specific moss or soil pH preference, although these factors cannot be completely separated.

During January 1969 samples of Ceratodon purpureus and Bryum argenteum were dug out from beneath about 3 feet of snow at a previously-marked site on the Macdonald College campus (site of sample 7). These mosses yielded more than 200 living L. rhodomela (mostly females and deutonymphs), which commenced to oviposit when transferred to suitable moss in the laboratory. The perennial nature of populations of this mite in some moss mats was thus demonstrated. Additional life-history data are presented in a later section.

Other North American records for this species are from Alaska, California, Connecticut and Ontario, in all cases from soil or litter (Summers and Price 1961). Some European workers record L. rhodomela from very humid habitats. Franz and Beier (1948) collected it in very wet soil (pH = 7.7) and in moss meadow, and included L. rhodomela among hygrofile species. Schweizer (1922) records the species (under the name L. patrius) from moss growing on a stream bank and in springs, in Switzerland. The discrepancy between the findings of the European workers and those reported in the present study, regarding the habitat preference of L. rhodomela, suggest that strains or races having different ecological requirements may exist within this species. Alternatively, the name rhodomela, as currently understood, may cover more than one species.

Ledermuelleria rotunda Wood.

This species was recovered only once from a mat comprising Eurhynchium, Campylium and Brachythecium, growing at the forest’s edge (sample 89).
**Ledermuelleria schustert** Summers and Price.

Summers and Price (1961) recorded this species from California, where it was obtained from “soil with moss” and “ex moss and lichen.” In the present study, it was obtained in 7 samples (6, 37, 89, 106, 151, 156, 157) and 6 masses. Of these, 5 belong to pleurocarpous genera (Brachythecium, Campylium, Eurhynchium, Hypnum and Thuidium) and one (Atrichum) is acrocarpous. Apparently, this mite is associated with a limited number of masses, as in 5 out of 6 samples it was found with Brachythecium, Hypnum or Atrichum, either alone or in combination. In all cases *L. schustert* was obtained from mosses growing in shady or partly shady soil, mostly under trees or in groves. The soil preferences of the moss hosts vary from mildly acidic, as with Thuidium delicatulum (Ikenberry 1936), to neutral (Atrichum) or exclusively calcicole (Campylium). Brief life-history notes on this species are given later.

### 3. Natural enemies.

Several species of mite were observed to feed on Ledermuelleria spp., mostly in the small plaster-of-paris containing vials used for collecting arthropods from the funnels. Hence some of the predators may not feed on Ledermuelleria under natural field conditions. However, it is worth recording them here. Only predators actually observed feeding, or those with characteristic red guts (indicating that they had fed on Ledermuelleria) are listed:

Mesostigmata: Asca aphidioides (L.), Cheiroseius nr. tuberculatus (Evans and Hyatt), Diga- masellus angulosus (Willmann), Amblyseius floridanus (Numa), Gamasellus sp.

Prostigmata: Cunaxa sp., Cunaxoides sp.

### Remarks.

The data collected in the course of sampling suggest that most of the commonly collected species of Ledermuelleria tend to be habitat or community specific, rather than host specific. Certain habitats, however, often support quite specific and characteristic moss communities (Watson, 1968), so that there may be indirect host-plant selection. Ledermuelleria gersoni and *L. rhodomela* are associated mostly with acrocarpous, colonizing mosses (Barbula, Brynum, Cerato- don, Funaria) able to grow on “man-made” habitats such as dumped soil (31), broken sidewalks (78) or roadside gravel (39, 42, 51, 68). Other Ledermuelleria species (with the single exception of *L. clavata* and *L. microsegnis* in sample 93) were not obtained from such habitats (although associated with the same mosses in others), but only from “natural” ones. On the other hand, *L. frigida* was collected only from various pleurocarpous mosses growing in shaded, humid habitats, mostly logs or roots. Only in regard to Ledermuelleria acidophila may an acidophilous preference be argued.

The observation that some Ledermuelleria species are associated with colonizing mosses may have other ecological implications. The mites, because of their feeding on the mosses, may be regarded as the primary consumers in this community. Their droppings and dead bodies probably support scavenging species, and they are also preyed upon by predaceous mites. In

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1. Kindly identified by Dr. Evert E. Lindquist, Entomology Research Institute, Canada Department of Agriculture, Ottawa.
this way, *Ledermülleria* plays an important role in the food web developing where mosses serve as the primary producers.

In this study some use has been made of published data concerning moss ecology. Many mosses are rather habitat-specific and their value as "indicator plants" is well known (Watson, 1964). Thus, if a mite (like *Ledermülleria acidophila*) were almost consistently found to be associated with acidophilous mosses, its own acidophilous nature may be assumed. This line of thought should not, however, be followed uncritically. Many of the more common mosses have a wide range of soil type and reaction tolerance, and may therefore be found together with either calcicole, neutral or acidophilous species. Likewise, calcifuge species may sometimes persist in calcicole communities in spite of nutrient deficiencies (Grime, 1963). For these reasons, isolated records must be treated with caution. The above remarks are deemed appropriate as apparently little similar use has formerly been made of established facts concerning moss ecology in the interpretation of data pertaining to arthropod ecology.

**Life history of *Ledermülleria frigida* under laboratory conditions.**

**Methods.** The ability of mosses to undergo severe dessication and then to recover immediately when sufficiently moistened (Watson, 1964), was used to eliminate unwanted arthropods from field collected mosses. The species of bryophyte most cultured was *Heterophyllum haldanianum*, another moss grown was *Amblystegium serpent*. Moss mats were processed through Tullgren funnels for 3-4 days and subsequently placed in distilled water. The recovered moss was then transferred to clean sand in large (diameter 14.5 cm) petri dishes. To stimulate growth, the sand and moss were wetted daily, using distilled water only, and kept in a greenhouse, under long day-length (16 hours) conditions.

High humidity encouraged mould growth which threatened to overrun the cultures, and in an attempt to control the moulds, various Collembola were indiscriminately introduced. Two of these, *Folsomia*¹ sp. and *Sminthurinus*¹ sp., strived under these circumstances and seemingly controlled the moulds to such an extent that mass-production of *Ledermülleria* became possible. Within 2-3 months the moss cultures supported large populations of the mite and were then processed through the funnels. The mites thus obtained were used for the various experiments.

Several other mosses, used in feeding experiments, were also dried and stored until required. The bryophyte most utilized in life-history studies was *Didymodon tophaceus*, obtained from sample 112.

The initial specimens used to establish the culture of *L. frigida* were recovered from *Heterophyllum haldanianum* collected at Baie d’Urfé. The mite was then maintained for many generations in the laboratory moss cultures. All experiments and observations, unless otherwise specified, were conducted under temperature conditions of 23 ± 2°C, the daily photophase being 9-10 hours. While developing, the mites were observed on moss placed in small (9 cm) petri dishes, padded with wet cotton-wool covered by filter paper.

**Development.** The eggs are orange-red, discoidal in form, 120 μ in diameter and 80 μ thick. They are deposited on the moss leaves, usually in the axils. During development (7-15 days) they enlarge in diameter by about 10 %. The hatching larvae initially have the eggs'

¹. Kindly identified by Dr. W. R. Richards, Entomology Research Institute, Canada Department of Agriculture, Ottawa, Canada.
colour, but after 1-2 days, when they begin to feed, their gut contents turn dark green. If prevented from feeding they die within 2 days. Some time after feeding commences the first faecal droplets appear, producing blackish-green shiny spots on the leaves. Feeding by the larvae is usually confined to the base of the leaves. Total larval duration was observed to be 2-5 days.

When preparing to moult the larvae assume a characteristic posture. They lie motionless with their anterior legs spread out in front, their hind legs stretched out behind; their bodies become darker and assume a shiny appearance. This pre-moult period lasts 2-3 days. The emergent protonymph has essentially the same behaviour pattern as the larva, its dark gut contents imparting an almost blackish appearance, despite the basic red pigmentation. The intensity of the dark inner colour is clearly dependant on the moss upon which they feed. Mites feeding on the darker Didymodon were inevitably darker than those feeding on the greener Heterophyllum and Amblystegium. Total protonymphal development lasts 2-8 days. The emerging deutonymph is more mobile than the preceding stages, but otherwise shows little difference in behaviour. Duration of this stage is 3-10 days.

Great variation in the development period of the juvenile stages was observed. This may be attributed to the following factors:

1. *Quality of food-plant.* Development is better on fresh, undamaged moss than on that which has already been attacked. Mosse also differ in their suitability for *L. frigida,* a point elaborated below.

2. *Immersion in water.* The smaller stages — especially larvae — are sometimes caught in drops or films of water on the moss leaves or in the axils. They may survive limited periods of immersion, provided they are able to hold on to some substrate, but immersion without feeding may prolong the duration of the stage concerned.

3. *Sex.* Male juvenile stages, although they undergo the same number of moults, develop faster than do corresponding female stages. No distinction between the sexes of juveniles could be made, so that some of the faster-development rates recorded for nymphs may be attributed to this factor.

For the third moult the deutonymphs seek out the upper (and thus drier) parts of the moss shoots. This moulting stage (teliochrysalis) is rather dark and shiny, like the preceding ones. At about the time female teliochrysalids are found (18-19 days, at least, after the eggs are laid), some males begin to appear. These are rather active, distinguished from similarly-sized nymphs by their very shiny dorsum and pointed opisthosoma. (Both these characteristics also occur in males of other species of *Ladermuelleria*). On finding a teliochrysalis the male palpates and examines it, mounting guard nearby or even on top of it, and always in contact. When disturbed the male will leave the teliochrysalis and wander off, often failing to find it again. Generally, the discrimination of the males does not appear to be very acute, for males were observed to mount guard over deutiochrysalids and male teliochrysalids, even trying to copulate with the emerging deutonymphs and males. Instances were observed in which 2 males guarded the same teliochrysalis. On coming into contact, these males would try to push each other away with their forelegs, but apparently not harming each other.

As the female begins to emerge, the guarding male may grab the cast skin, as if to help the female free itself. The male then mounts the female. The latter may try to repulse the males, even rising on its hind legs to displace it. Copulation itself was not observed, either on account of its briefness or because it occurs in the dark.

Oviposition usually begins 4-15 days after emergence, irrespective of copulation, isolated
virgin females beginning to lay eggs at about the same time as fertilized ones. Total development (egg to egg) thus lasts approximately 30 days, although there is much variation, dependent on the factors discussed above.

The ovipositing female straddles on the underside of the leaf, holding the latter by its first and third pairs of legs. The fourth pair of legs and the posterior part of the opisthosoma are thus placed beyond the leaf’s margins. After the egg is produced, it is pushed by means of the fourth pair of legs on to the leaf, often into its axil. The female keeps touching the egg for some time, possibly transferring to it some finishing substances from the genital orifice, or checking it for hardening, or both. Eggs from which the ovipositing females were removed immediately after deposition collapsed and failed to hatch. The apical ends of fresh moss shoots are usually preferred for initial deposition, other eggs then being laid on the lower leaves. Only one egg per leaf is deposited. They are neither inserted into the leaf tissue nor glued thereon, and a mild water stream will wash them away, suggesting one mode of dispersal under field conditions.

To obtain data on total egg production, daily oviposition rates and hatching percentage, isolated females were placed in individual dishes when in the teliochrysalis stage. Males were introduced into one series of dishes containing the females, whereas females in another series were kept in isolation. The lower parts of the dishes were covered with filter paper partitioned with “Tanglefoot” into 4 quarters. Fresh Didymodon shoots were placed in each section of the filter paper. Every ovipositing female was observed daily and, after each 2-day period, transferred from one quarter of the dish to the next. After 2 days in the fourth quarter the females were transferred to a new dish. Thus, several petri dishes were often utilized to obtain the total egg complement of a single female. Care was taken to maintain males with the appropriate females at least for the first week following female emergence. The average weekly egg production of 10 mated females of L. frigida, compared with that of 10 unmated females, is presented in Figure 2. As only males developed from eggs deposited by unmated females (arrhenotokous reproduction), the presence of females among the descendants of a given female was taken as proof of the latter having mated.

The average number of eggs laid by mated females was 21.0, the comparative figure for unmated females being 21.9. As may be seen in Figure 2, egg production was similar in both groups, although oviposition by unmated females was somewhat delayed. Unmated females also lived longer, the 3 longest life spans recorded for this group being 61, 63 and 64 days, compared with 46, 53 and 53 for mated females. The daily egg production did not exceed 3, and the record number of eggs deposited was 40, by a mated female. Of the 210 eggs laid by the 10 mated females, 18.1 % failed to hatch. The comparative percentage for the 219 eggs laid by the 10 unmated females was 19.6.

A characteristic of L. frigida is its uneven pattern of oviposition after the first group of eggs has been laid. Several females deposited 10-15 eggs each during the second week of adult life, oviposition then tapering off. A pause of 8-15 days sometimes occurred before the next eggs were produced. No correlation was found between female life span and number of eggs laid. Some of the irregular oviposition may be due to nutritional factors, as females transferred onto fresh moss usually laid some eggs after an initial 2-3 days of feeding. However, as care was taken in these oviposition experiments always to supply the females with undamaged moss, other factors seem to be involved.

Some eggs were deposited even in the last week of life, shortly before death. Most of these late eggs were abandoned by the females on the outside of the leaf. Some failed to hatch, so that this mode of egg deposition may be a senility symptom of the females. When unmated females
were brought in contact with their male offspring, they readily mated, as attested by the resultant female progeny.

The females, except when seeking new feeding and oviposition sites, do not move around much. They may remain immobile on moss shoots for long periods and, when touched, tend to curl up, as if lifeless. But when their posterior setae are touched by a fine needle or brush, they will move their forelegs. Dead females remain at the site of feeding, their bodies turning brownish and slowly disintegrating.

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Feeding and survival. *Ledermuelleria frigida* feeds on the leaves and stems of the gametophytes of various mosses. A feeding mite can be observed, under high power magnification, to have the underside of its gnathosoma appressed to the leaf surface. Some inner movement is evident in the body, possibly associated with the body compression needed in the protraction of the chelicerae (Snodgrass, 1948).

When attacked leaves are examined, various randomly-distributed cells are seen to be without their usual green contents (Plate 1, Nos. 2 and 4, and for comparative undamaged leaves, Nos. 1 and 3). The cell walls appear to be undamaged. The interpretation is that the mites wound the thin outer cuticle (or, when this is not present, the outer cell walls) with their chelicerae and then, appressing their mouths to the wound, suck out the green cell contents. It is these cell contents that impart the dark colour to the mites' guts. Young moss shoots upon which
mites have been feeding lose their green colour, attaining a silver-grey hue with many dark specks. (faecal drops). Some shoots, under laboratory conditions, even shrivelled.

Preliminary observations had suggested that *L. frigida* does not feed indiscriminately on mosses. Therefore, to obtain more data on this aspect, a series of feeding experiments was conducted. Most of the mosses used were obtained from the samplings (Table 1) and kept dry till needed. *Pogonatum urnigerum* (Hedw.) P. Beauv., however, was collected by Dr. Dorothy E. Swales at Mont Tremblant Park, Quebec, September 11, 1968, and kindly made available to the author.

Moss shoots were placed on wet filter paper in petri dishes and at least 15 *L. frigida* females (previously starved for 24 hours) introduced per dish. Cases in which the mites left the mosses within 2-3 days, laid no eggs and wandered off, were regarded as "No Survival". When the mites remained on the moss and lived there for at least 15 days, evidently feeding and defaecating but not producing eggs, the result was noted as "Survival but no Oviposition". On other mosses oviposition began 3-4 days after feeding commenced. The results of these experiments are presented in Table 1.

Among the mosses suitable for oviposition were several from which *L. frigida* was collected in field samples, as well as others which were not known to harbour these mites under field conditions. Particularly good oviposition occurred while feeding on *Didymodon tophaceus*, and for that reason, this bryophyte was used in other experiments. None of the mosses in the other two groups upon which no oviposition occurred were associated with *L. bryophaga* in the field.

Among the 5 moss species which did not support survival of *L. frigida*, 4 belong to the family Polytrichaceae (*Atrichum*, *Pogonatum* and *Polytrichum* spp.). These mosses have lamellae (longitudinal thin sheets or plates of tissue) on the upper side of their leaves and often thickened cell walls on their lower surfaces (Parihar, 1965). Therefore inability to feed (and hence lack of survival) on these mosses could be related to the inability of the mites to penetrate the lamellae or cell walls of the plant hosts. Penetration is effected by the stylets (the movable digits of the chelicerae) and an indication of their strength could be obtained by measuring parameters relating to their size and thickness. Such measurements, along with comparative one pertaining to other *Ledermuelleria* species found in *Polytrichum* mosses, are presented in Table 2. The ratio between the length of the total chelicerae and the length of the cheliceral stylets (abbrevia-
ted to t/s in the last column of Table 3) is believed to give an indication of the anchorage site of the stylets. In L. frigida the t/s ratio is high because the stylets are anchored near the apices of the fixed cheliceral digits (GERSON, 1971) besides being very short. In L. microsegnis, the stylets, though not much longer than those of L. frigida, are attached near the middle of the fixed digits. Presumably the latter points of attachment would give the stylets more leverage.

It may be seen from Table 2 that L. frigida has the weakest mouth parts of all 5 species.

**TABLE 1:** Survival and oviposition of Ledermulleria frigida on various moss species. (+: Presence of L. frigida in field collections).

<table>
<thead>
<tr>
<th>Survival and Oviposition</th>
<th>Survival but no Oviposition</th>
<th>No Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblystegium serpens</td>
<td>Bryum argenteum</td>
<td>Atrichum altemcristanum</td>
</tr>
<tr>
<td>Barbula suguiuculata</td>
<td>Bryum pseudotriquetrum</td>
<td>Leucobryum glaucum</td>
</tr>
<tr>
<td>Brachythecium salesbrosun (+)</td>
<td>Dicranum scoparum</td>
<td>Pogonatum urnigerum</td>
</tr>
<tr>
<td>Brachythecium sp.</td>
<td>Ditrichium pusillum</td>
<td>Polytrichum commune</td>
</tr>
<tr>
<td>Ceratodon purpureus</td>
<td>Fissidens tazifolis</td>
<td>Polytrichum piliferum</td>
</tr>
<tr>
<td>Didymodon tophaceous</td>
<td>Funaria hygrometrica</td>
<td></td>
</tr>
<tr>
<td>Drepanocladus aduncus</td>
<td>Haultia ciliata</td>
<td></td>
</tr>
<tr>
<td>Heterophyllum holdavaniaum (+)</td>
<td>Mnium wahlenbergii</td>
<td></td>
</tr>
<tr>
<td>Hypnum lindbergii (+)</td>
<td>Mnium cuspidatum</td>
<td></td>
</tr>
<tr>
<td>Hypnum reptile (+)</td>
<td>Mnium rugicium</td>
<td></td>
</tr>
<tr>
<td>Lepidodictyum riparium (+)</td>
<td>Pleuroziurn schreberi</td>
<td></td>
</tr>
<tr>
<td>Thuidium delicatulum (+)</td>
<td>Rhaconitrium heterostichum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rhodobryum roseum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sphagnum magellanicum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sphagnum recurvum</td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 2:** Mean length and thickness (in microns) of the stylets of the several Ledermulleria spp. females obtained in Polytrichum mats and of L. frigida.

<table>
<thead>
<tr>
<th>Ledermulleria</th>
<th>No.</th>
<th>Stylet length</th>
<th>Stylet thickness</th>
<th>t/s</th>
</tr>
</thead>
<tbody>
<tr>
<td>acidophila</td>
<td>10</td>
<td>53.7</td>
<td>2-3</td>
<td>2.3</td>
</tr>
<tr>
<td>clavata</td>
<td>10</td>
<td>40.3</td>
<td>3-4</td>
<td>2.7</td>
</tr>
<tr>
<td>frigida</td>
<td>10</td>
<td>23.0</td>
<td>1</td>
<td>4.2</td>
</tr>
<tr>
<td>microsegnis</td>
<td>10</td>
<td>32.2</td>
<td>3-4</td>
<td>2.2</td>
</tr>
<tr>
<td>rotunda</td>
<td>1</td>
<td>58.0</td>
<td>2</td>
<td>1.9</td>
</tr>
</tbody>
</table>

The leaves of most mosses have only a single cell layer, and some even lack an outer cuticle (WATSON, 1964). Therefore feeding on mosses of the first two groups in Table 1 could occur. The failure to oviposit while feeding on mosses of the second group may be related to nutritional deficiencies. The fact that other Ledermulleria species could associate with Polytrichum suggests that the failure of L. frigida to survive on this moss was largely due to the mechanical factors discussed. The failure to live on Leucobryum glaucum may likewise be related to leaf structure of the moss. Leaves of Leucobryum consist of 2 layers of hyaline cells, between which the green cells are located (WATSON, 1964). Possibly the short stylets of L. frigida failed to reach the inner green cells.
Many masses have only a reduced rhizoid system, utilized mainly for anchoring the plants. In *Polytrichum*, however, there is a complicated, coiled rhizoidal system which forms a dense underground mass (Watson, 1968; Parihar, 1965). Presumably the mites may feed on these plant parts and *L. clavata* was, in fact, seen to feed on moss rhizoids (see below). Another species, *L. parviseta*, was found on lichens (Chaudhri, 1965), and Summers and Price (1961) record *L. schusteri* from "moss and hepatica" and "moss and lichens". For these reasons it is believed that these mites may also feed on other moss parts, as well as on other cryptogams, although this study mostly stressed feeding on leaves. *Ledermaulleria* is the first member of the family Stigmaeidae shown to be phytophagous.

Starvation tests on *L. frigida* were made in small closed plastic vials, the bottoms of which were coated with a mixture of plaster-of-paris and charcoal (10:1). The vials were kept at close to 100% relative humidity and at 23 ± 2°C. Ten females (of undetermined age) were placed in each of 4 such vials, no food whatever being added. The mortality of the mites was daily observed and recorded. Mortality of 50% occurred after 12 days, 75% after 15, and the last survivor died on the 25th day. No cannibalism was observed, cadavers and their occasional moulds being ignored by the immobile mites. The starving females did not oviposit.

Many of the masses from which *L. frigida* was collected grow near springs, streams and ponds. In these situations the mites may sometimes be submerged for shorter or longer periods, and it seemed pertinent to find out whether they would survive such immersion. The mites (40 females of undetermined age, as before) were placed in petri dishes the bottoms of which were covered by a disc of filter paper on which a thin layer of clean, washed sand was spread. The sand was then covered by about 1 cm of distilled water, which caused the mites to become totally immersed. The water was periodically replenished. After 2 days some females were floating, obviously dead, while the others were moving slowly through the sand grains, gradually selecting resting sites. Subsequently it was seen that mites which lost their hold on the substratum (be it filter paper or sand) floated away and died within 1-2 days, their bodies becoming a lusterless brownish-red. The living mites slowly lost their darker inner colour and became uniformly red. They did not move on to the glass sides of the dishes.

Over 60% of the mites were still alive after 15 days, and on that day 10 females were taken out and placed on fresh *Heterophyllum* shoots. Settling soon took place and feeding began, viable eggs being produced after 7-8 days. On the 21st day another group of 5 mites was likewise removed from the water and placed on the moss, and oviposition commenced after a similar interval.

The remaining live mites tended to settle and nestle between and under sand grains, and to re-seek this micro-habitat on removal therefrom. This reaction as well as their withdrawal movement when touched were used as viability criteria. As the mites died they lost their grip on the substratum and floated away. The last female died 45 days after immersion. No eggs were deposited under water.

These results demonstrate the tolerance of *L. frigida* to starvation both in and out of water, and also to total immersion. The results also suggest some adaptations of this mite to living in occasionally-flooded habitats.

Development under water. Observations have already shown that eggs of *L. frigida* hatch while submerged in water droplets. Therefore the larval (and other) stages could be studied under water right from the moment of hatching.

Small moss shoots (*Heterophyllum* or *Amblystegium*) were placed in watch-glasses partially filled with distilled water, care being taken that no part of them emerged. The watch-glasses
themselves were kept in petri dishes partially filled with water. Groups of 10 freshly laid eggs were introduced into each of the watch-glasses and observed daily. Hatching occurred as usual, although the larvae had greater difficulty in freeing themselves from the empty eggshells. They soon settled down and began to feed, as evidenced by their darkening guts. They then moulted, and development proceeded to the adult stage at the usual rate, all the while being submerged.

The gut contents of the immersed mites appeared darker than those of mites developing in air. Movement was more sluggish and the mites, after each moult, had difficulties in freeing themselves of the discarded skins. They would struggle with the skins and occasionally lose hold of the moss, floating away. Failure to regain a foothold on the plants inevitably lead to death. The faeces had a mycelium-like aspect which sometimes entangled the legs of the mites and thus endangered their lives. Frequent transfers on to fresh mosses, as well as use of clean water proved useful in this context. Behaviour of the males — easily recognizable by their shiny dorsum — was different than when living outside water. They were as sluggish as the females and did not search for them. Both adult stages, except for changes in their feeding positions, did not move around. No eggs were deposited by females while immersed.

Some females, after failing to lay eggs for 15 days, were taken out of the water and transferred onto fresh moss together with a few males. Oviposition commenced after 2 days, the eggs being viable and the emergent larvae developing to normal adults at the usual rate. Both males and females were produced, so obviously copulation was effected, indicating that both sperm and ovum development were normal in the immersed mites. Another 2 females, taken out of water after 60 days at this stage, laid only 1 dead egg between them. The longest living of the submerged females survived for a total of 115 days (at 23 ± 2°C), of which about 80 were as an adult.

Very little information is available as to the responses of phytophagous mites to total immersion in water, HERNE (1968) being a recent exception. This worker submerged all stages of the European red mite, Panonychus ulmi (Koch) in distilled water for periods up to 48 hours. Mortality of eggs was negligible, that of active stages low but appreciable, and no feeding, egg hatching, moulting or oviposition occurred. Though in general the life-history pattern of Ledermuelleria, as herein detailed, is similar to that of many spider-mites, the responses to immersion were quite different. Perhaps the most significant difference is the ability of L. frigida to feed under water.

Survival in water may confront Ledermuelleria, a terrestrial arthropod, with problems in its water and electrolyte balances. EDNEY (1957) has suggested that the problem of excess water in the environment may be met by the impermeability of the cuticle or by the excretion of a hypotonic urine, whilst retaining the electrolytes. Salt uptake, according to EDNEY (op. cit.) is accomplished by feeding or by uptake, together with water, through permeable regions of the integument. Ledermuelleria frigida possibly utilizes several of these mechanisms, and the large and deep dorsal dimples (for their description, see GERSON, 1971), which greatly enlarge the surface area of the mite, may partake in this. Whatever the variety of mechanisms involved, the usual occurrence of L. frigida in terrestrial (though humid) habitats, taken together with its prolonged survival in water, suggest that this mite may have an unusual water-balance mechanism.

Another problem to be overcome while submerged is oxygen uptake. Feeding mites may obtain oxygen from the green mosses. How the nonfeeding mites get it is not known, but retention of air films or bubbles in or around the dorsal dimples may occur.
Effect of light. Various plant-feeding mites are known to undergo diapause. The inducing factor is often change in photoperiod, which may be modified by different temperatures; exhaustion of the food supply can also cause diapause when otherwise the photoperiod would not (Boudreaux, 1963). Many observations during the current study have shown that as L. frigida females begin to exhaust their food plant, oviposition greatly diminishes and then ceases. The mites may survive for some time on the shrivelling plants, and, when transferred to fresh moss, oviposition would resume within 3-4 days. Food exhaustion, by itself, thus does not appear to induce diapause.

The possible effect of various photoperiods on L. frigida was studied by keeping the mites under 3 different photophase regimes.

1. Long-day (16 hours). Light intensity at moss level 300-500 foot-candles (ft-c.) during day, 280 ft-c. during evening. Artificial light source fluorescent bulbs. Ambient temperature 24 ± 3°C.
2. Short day (8-9 hours). Light intensity at moss level, 25 ft-c. Light source as before. Temperature 23 ± 2°C.
3. Total darkness. Light intensity less than 1 ft-c. Cultures kept in a dark box within a closed drawer. Temperatures 23 ± 2°C.

Eggs of undetermined age were collected from the stock culture and put, with fresh moss shoots, into padded petri dishes, the latter then being placed in the various environments. The dishes were observed twice weekly, special care being taken with the cultures kept in the dark. These were removed from the drawer only after the room was darkened, examination being conducted in diffuse light. Altogether these mites were exposed to less than 5 minutes of rather weak light (10 ft-c.) per week. The mosses were periodically and uniformly changed.

Development was normal in all cultures. After attaining adulthood and depositing eggs under all 3 light regimes, the mites were left therein for the duration of another generation. Eggs were deposited by second generation females which developed under long- and short-day photophases, but not by those held in total darkness. This result suggests that L. frigida may need a certain amount of light to produce eggs, and that this light may be received while at the prelarval stage (as apparently occurred with the first-generation mites). Neither the long nor the short photophases brought about any cessation of development.

Assuming that a winter diapause occurs under natural conditions, it would most probably be manifested by the autumnal females, which are subjected to shortening days and low temperatures. Therefore some L. frigida were obtained in the fall and settled in the laboratory on appropriate mosses. The sample was collected at the end of November, 1968, after the first snowfall and about 3 weeks of freezing temperatures, from Baie d’Urfé, Quebec (site of sample 10). Many mites were recovered from this sample, and they soon began to oviposit viable eggs. In conclusion, there seems to be no indication that L. frigida has a diapause.

Life history notes on other Ledermuelleria species.

Ledermuelleria rhodomela: This species developed better on Ceratodon and Heterophyllium than on Didymodon. Development time, at 23 ± 2°C, was about 30 days. The eggs are round, reddish, 110-120 μ in diameter. They hatch in water and the larvae feed there for a while, but they do not moult and die in the water. Females placed without moss in water behaved like L. frigida females, 35% being alive after 21 days, 10% after 30 days. No eggs were deposited on removal from water after either of these periods. Mites collected after the initial snowfall
in November, from below snow in January, and as the snow thawed in March, always laid viable eggs from which both males and females developed.

Ledermuelleria clavata: Feeding on the rhizoids of Mnium rugicum under laboratory conditions was observed in this species. Development time was variable, periods of 24 to 38 days being recorded. The eggs are round, reddish, 115-125 μ in diameter, their development in water was as described for L. rhodomela. When placed in distilled water, 55% of the females were alive after 27 days, 35% after 28 days, but no eggs were oviposited on removal from water.

Ledermuelleria schusteri: Reared on Hypnum lindbergii (the plant-host in sample 151). Development of eggs was as in preceding species. An impression was gained that L. schusteri deposited a far larger number of eggs than the other species observed, but no counts were made. Moss shoots on which this mite oviposited were sometimes almost red, due to the many eggs thereon, 3-4 being often deposited on a single leaf.

Three species of Ledermuelleria were collected on the bodies of Phlebotomus sand-flies obtained in Panama (CHAUDHRI, 1965). These are L. parasitica, from P. gomesi Nitzulescu and L. gamma and L. gorgasi, found on P. pini Fairchild and Hertig. These mites were presumed by CHAUDHRI (op. cit.) to be ectoparasitic on the insects.

There is nothing in the present study to preclude the possibility that some Ledermuelleria species have parasitic habits. However, the wide-spread association of Ledermuelleria with mosses and the established feeding of several species on these plants cast some doubts on this possibility. The doubts are deepened when the habits of Phlebotomus are considered. These insects are usually associated with microhabitats that are humid (and thus likely to promote moss growth), where larvae live and adults rest (ADLER and THEODOR, 1957; HANSON, 1961). In Panama, whence the above mites came, mosses are very common in the forests, especially at higher elevations where P. pini occurs. Both adults and larvae would frequently come into contact with mosses, the former stages possibly resting there for considerable periods (Graham B. FAIRCHILD, personal communication, 1969). Because of these considerations it is postulated that the relationship between Phlebotomus and Ledermuelleria is only a fortuitous phoretic association.

This argument is further strengthened by a recent report (MACFARLANE, CHALDI and DANCESCO, 1969) on the phoresy of the tenuipalpid Brevipalpus phoenicis Geijskes, a well-known phytophagous mite, on some phlebotomine flies in Tunis.

**DISCUSSION.**

The data presented suggest that L. frigida has evolved some special adaptations to living on mosses. As the prominent ecological feature of mosses is their restriction to humid habitats, the adaptations of L. frigida to these were mostly studied.

The egg is deposited on the leaf, neither glued thereon nor inserted therein. It may be washed away by water and may hatch either in or out of water. The larvae and other stages feed both in and out of water. They survive immersion for long periods, even without feeding, and females oviposit on being removed from the water. All these attributes will greatly assist the mite, not only in its survival, but also in its dispersal in streams and ponds. Another possible mode of dissemination is in association with various moss parts, which may be broken off by wind or water and drift away — see PARIHAR (1965) for a discussion of moss dispersal mechanisms. Prolonged longevity and egg-laying are also advantageous in dispersal. Should a single unfer-
tilized female reach a suitable moss, it would only deposit male eggs. The female could, however, live long enough to mate with its progeny and then produce female eggs. In this way a new mite colony could be initiated by a single female. The ability of *L. frigida* to obtain the nutrients required for oviposition from many moss species is also of survival value.

Most of the attributes discussed above pertain to survival and dispersal under almost aquatic conditions. In this context the moss hosts of *L. frigida* and their habitats should be recalled. Many of these mosses were found in shaded, humid localities, and are known to prefer the proximity of water. The inference is that this mite has evolved adaptations to living on these pleurocarpous mosses.

When the scant life-history data available for *L. rhodomela* are compared with those concerning *L. frigida*, it is evident that the former species is somewhat less adapted to a semi-aquatic existence. This is in agreement with habitat data obtained in the samplings, which showed *L. rhodomela* to be associated with colonizing mosses often growing in open (and thus drier) soil.

Species of *Ledermuelleria* show various degrees of adaptation to survival both in and out of water, just as the mosses themselves do, being adapted to intermittent water supply (Watson 1964). It is evident, however, that the mites — even *L. frigida* — are less adapted to aquatic conditions than the plants upon which they feed as the mites would not reproduce while immersed. One would thus speculate that *Ledermuelleria* is an arthropod of terrestrial origin which has evolved adaptations to a semi-aquatic habitat. The terrestrial habits of the stigmaeid mites lend support to this hypothesis. Life-history studies on related genera, especially *Mullederia* and *Ledermuelleriopsis*, with special emphasis on feeding habits, may help to resolve problems concerned with development of phytophagy and bryophagy in this group of mites.

In the course of this study 11 species of *Ledermuelleria* were collected from mosses growing in varied habitats. Several similar records are available from different parts of both the Old and the New worlds. Taken together, these sets of observations suggest that corresponding moss-*Ledermuelleria* associations probably occur almost wherever these mites are found, although feeding on other cryptogams cannot be excluded. It would thus appear that the association is far from being a recent one. When the antiquity of the plant-hosts is also considered, it can be seen that a fuller understanding of the moss-*Ledermuelleria* relationship may be of more than restricted acarological interest.

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