E. É. Farkas, R. Lücking & V. Wirth (eds): Scripta Lichenologica – Lichenological Papers Dedicated To Antonín Vězda. Bibl. Lichenol. 58: 27-41; J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin - Stuttgart, 1995

A new isidiate crustose lichen in northwestern North America

IRWIN M. BRODO[1] & AINO HENSSEN[2]

[1] *Canadian Museum of Nature, Research Division, P.O. Box 3443, Station 'D', Ottawa, Ontario K1P 6P4, Canada*
[2] *Fachbereich Biologie der Philipps-Universität Marburg, Karl-von-Frisch Straße, D-35032 Marburg/Lahn, Germany*

Summary: A corticolous crustose lichen having long isidia was found to be common along the west coast of North America from northern California to Alaska, but is apparently undescribed. Fertile specimens with relatively few isidia are also frequently seen. Its developmental anatomy and chemistry have shown it to be distinct from *Loxospora*, which it resembles in many respects. It is therefore classified here as a new genus and species: *Loxosporopsis* HENSSEN and *Loxosporopsis corallifera* BRODO, HENSSEN & IMSHAUG.

Key words: Ascocarp ontogeny, divaricatic acid, gyrophoric acid, *Loxospora*, *Loxosporopsis*, morphology, North America

Introduction

In the coastal and montane forests of the Pacific Northwest, there is a common crustose lichen that produces long isidia and that is most frequently found sterile. It can give the initial impression of being an immature, crustose morphotype of the common fruticose lichen, *Sphaerophorus globosus*, which is often found in the same habitats.

We first encountered this lichen in Oregon and Washington (A. H.) and Vancouver Island (A. H. and I. M. B.). At about the same time, Henry Imshaug noticed it among his Alaskan collections, independently recognizing it as distinct and probably new. It is particularly abundant on the bark of coniferous trees in exposed bogs and swamps and is a conspicuous component of that community on the Queen Charlotte Islands, B. C. The ascomata are sometimes abundant, and these are brown, lecanorine apothecia producing fusiform, septate spores reminiscent of species of the genus *Loxospora*, and it is in that genus that we first attempted to place the lichen. Subsequent studies of its developmental morphology, anatomy

and chemistry, however, revealed that it was apparently a new species, and furthermore, could not be accommodated in the genus *Loxospora*. We are therefore describing it in a new genus, and will discuss its affinities below. In comparison, the apothecial development in *Loxospora* was investigated by us; the results for *L. elatina* (ACH.) A. MASSAL. are presented here.

Material and methods

Material was studied from the following herbaria: CANL, FH, H, M, MIL, MSC, OSC, US; the abbreviations follow Index Herbariorum (HOLMGREN *et al.* 1990); hb. Henssen and hb. Rosentreter refer to the private herbaria of A. Henssen and R. Rosentreter, respectively.

Specimens of *Loxospora elatina* (ACH.) A. MASSAL. studied are as follows: NORWAY. Ad truncos abietinos in monte Bogstadaasen prope Christianiam, 1859, Th. M. Fries (FRIES: *Lich. Scand. Rar. Crit. Exs.* 33; M). — GERMANY. Bayern: Oberbayern, Waldungen im Gebirge bei Reit im Winkel, 1863, Krempelhuber (M). — AUSTRIA. Obersteiermark: im Salzathale zwischen Gr. Reifling und Palfau, an *Pinus silvestris*, 1900, Baumgartner (H). An der Rinde alter Fichten in einem Gebirgstal bei Lofer in Tirol, 1859, Krempelhuber (ARNOLD: *Lich. Exs.* 66; M). — USA. Washington: Snohomish Co., Gold Bar, on *Thuja plicata*, 1994, Tønsberg 21698 (hb. Henssen, BG).

Freezing microtome sections, 18-22 µm thick, were mounted in lactic/glycerine with cotton blue (LB). For studying the iodine reaction, Lugol's solution was added to squash preparations with and without pretreatment of KOH. A Wild M7 dissecting microscope was employed for habit photographs and a Wild M20 compound microscope for micrographs of sections; for both, a Kodak professional film 5–TMX 120, 6 × 6 cm format, was used.

Secondary metabolite chemistry was studied using thin layer chromatography (TLC) using the standardized methods of CULBERSON (1972) with modifications (see MIETZSCH *et al.* 1992).

Results and discussion

1. *Loxosporopsis* HENSSEN gen. nov.

Thallus crustaceus, corticatus. Apothecia sessilia, disco fusco, margine pallido. Asci octospori, paries ascorum amyloideus et apicem versus incrassatus. Ascosporae hyalinae, aciculares, transversaliter septatae, non halonatae. Paraphyses tenues, ramosae, apice non incrassatae. Pycnidia parva, conidia bacillaria.

Typus generis: *Loxosporopsis corallifera* BRODO, HENSSEN & IMSHAUG.

Thallus crustose, corticate. Apothecia adnate with brownish disk and pale margin. Asci 8-spored, wall amyloid, thickened at the apex. Ascospores hyaline, transversely septate, not halonate. Paraphyses thin, branched, tips not thickened. Pycnidia small, conidia rod-shaped.

2. *Loxosporopsis corallifera* BRODO, HENSSEN & IMSHAUG spec. nov.

Thallus corticola, cartilagineus, continuus, isidiatus; pagina laevis vel rimosa, non sorediatus; isidia usque ad 1.2 mm longa. Apothecia usque ad 1 mm diam., disco fusco vel nigrescenti, nonpruinoso, margine thallino circumdato, excipulo proprio rudimentali. Ascosporae 3-5-septatae, 35-50(-65) × 5.5-7.5 µm, rectae vel laeviter curvatae et in asco torsivae. Pycnidia plus minusve globosa, in sectione 50-60 µm diam., conidia terminaliter formata, bacillaria, 2.5-3.5 × 0.8-1.2 µm. Acidum divaricatum in thallo et acidum gyrophoricum in apotheciis adest.

Typus: USA. Oregon: Lane Co., Sutton Creek Forest Camp, on the bark of *Pinus contorta*, 28.X.1961, Henssen 13604 a (hb. Henssen – holotype: CANL, FH, GZU, UPS, US – isotypes). — CANADA. British Columbia: Queen Charlotte Islands, Maude Island, in Skidegate Inlet, midway down the south shore, 53°12'N, 132°05'W, on base of *Picea sitchensis*, 12.VII.1967, Brodo 11282 & Shchepanek (CANL, hb. Henssen – paratype).

(Figs 1 A-B, 2 A-C, 3 A-F, 4 A-G)

Thallus clearly visible, thin, 90-120 µm thick, with cortex 23-47 µm thick and a gelatinized epinecral layer up to 12.5 µm thick in old thalli; algal layer 30-35 µm thick. Thallus indefinite, mostly continuous, more or less smooth or rimose, pale, yellowish white or light brown to pale orange, more or less covered with very long, slender, cylindrical isidia, unbranched or branched, 0.5-2.4 mm long, 0.07-0.15 mm in diameter; soredia absent. Prothallus absent. Photobiont *Trebouxia* sp., cells 7-12 µm in diameter.

Apothecia lecanorine, 0.5-0.8(-1) mm in diameter, occurring singly; young apothecia urceolate; disks dark- to pale brown or orange-brown (50-55-56, 71[1]), epruinose. Thalline margin even with disk, rough (radiately fissured), or rarely smooth, even or flexuous, same colour as thallus, but often disk-coloured where contiguous with the disk, 120-144 µm thick, corticate, cortex 24-30 µm, followed proximally by a layer of lichen substances. Proper exciple rudimentary. Apothecia sessile or constricted at the base, flat when mature, smooth, without umbos but sometimes proliferating or regenerating.

Hymenium 110-190 (-215) µm high, hyaline, hymenial jelly non-amyloid; epithecium yellow-brown to dark yellow (87-88), not at all granular, unchanged with KOH or pigment dissolving, C+ pink, the colour usually disappearing quickly; subhymenial tissues 95-215 µm high, up to 300 µm in old, proliferating apothecia with pronounced vertical growth, darkly staining in LB; paraphyses branched and anastomosing, slender (0.8-1.5 µm in diameter), not expanded or pigmented, free in water or KOH. *Asci* club-shaped, 8-spored, wall and tholus uniformly IKI+ light blue,

[1] Numbers refer to colour designations in KELLY (1965).

slightly deeper blue after pretreatment with KOH; tholus with ocular chamber. Ascus dehiscence is by a simple split at the apex, without rostrate extension (COMMON, pers. comm.). *Ascospores* remaining hyaline, at first obscurely 1-3-septate, becoming 3-5-septate when mature, pointed at both ends, straight or slightly curved and twisted in ascus, thin-walled, without a gelatinous epispore, walls evenly thickened, 35-50 (-65) × 5.5-7.5 µm.

Pycnidia very rare, 55-65 × 50-60 µm, conidiophores with 1-3 cells, producing conidia terminally, conidia bacilliariform, 2.5-3.5 × 0.8-1.2 µm.

Chemistry: Thallus cortex PD–, K–, C–, KC–, UV(LW)+ white or blue-white. Thallus medulla PD–, K–, C–, KC–, IKI–. Contains divaricatic acid in the thallus and gyrophoric acid (+ some unidentified compounds) in the apothecia.

Etymology: The species epithet refers to the presence of coralloid isidia.

Habitat: In well-lighted, coastal *Pinus contorta* and *Pseudotsuga menziesii* stands, often in bogs or dune areas, as well as in oroboreal conifer stands such as *Abies procera-Tsuga heterophylla* forests in the Coast Range, sea level up to an elevation of 1,200 m. On branches and trunks of *Pinus contorta, Pseudotsuga menziesii,* and other conifers.

Distribution: A North American endemic, ranging from northern California to southeastern Alaska, along the coast or in the coastal mountains (Fig. 1 A). The distribution of the species on the Queen Charlotte Islands (Fig. 1 B) shows its strong affinity to the northeastern lowland forests (see BRODO 1995).

Additional specimens examined: CANADA. British Columbia: Queen Charlotte Islands, Graham Island, Port Clements, 1967, Brodo 9912 A (CANL); Port Lewis, 1967, Brodo 10503 D (CANL); Marie Lake, 1967, Brodo 11677 (CANL); N of Skidegate Mission, 1971, Brodo 17952 (CANL); 13.3 km S of Masset, 1988, Brodo 26615 (CANL); Yakoun Lake, 1988, Brodo 26861 (CANL); Lyell Island, Gogit Point, July 1967, Brodo 11781 (CANL); Maude Island, in Skidegate Inlet, 1967, Brodo 11282 (CANL); Moresby Island, Deena River, 1967, Brodo 10849, 10856 (CANL); Louscoone Inlet, 1967, Brodo 12353 (CANL); between Sandspit and Copper Bay, 1967, Brodo 12883 (CANL); Torrens Island, SE of Skidegate Mission, 1971, Brodo 17317 (CANL); Wathus Island, in Masset Inlet, 1971, Brodo 18272, 18273 (CANL); Vancouver Island, between Sooke and Jordan River, *c.* 10 km W of Victoria, 1962, Henssen 14551 e (hb. Henssen, TRTC); Nanaimo River Valley, near 4th Lake, 1950, Krajina, Spilsbury & Szczawinski 67-267-7 (US); near Sayward, 1950, Krajina & Spilsbury 25-92-1 (US); Bamfield, near Keeha Beach, 1994, Brodo 28818 (CANL); Little Bear Bay, N of Stella Lake, Sayward Prov. Forest, 1980, Inselberg S-063 #13 (MIL); Mayne Island (Gulf Islands), Village Cove, 1980, Dibben (MIL). — USA. Alaska: Tongass National Forest/Chatham area, Douglas Island, 1990, Geiser & Derr L-2394 (CANL); Auk Village, near Juneau, 1963, McCullough 1469 (MIL); Vicinity of Juneau, Mt. Roberts trail, Imshaug 28269B (MSC); Haines Co., NW of Haines, Chilkoot Lake State Rec. Area, 1994, Sharnoff 1393.20 (CANL). California:

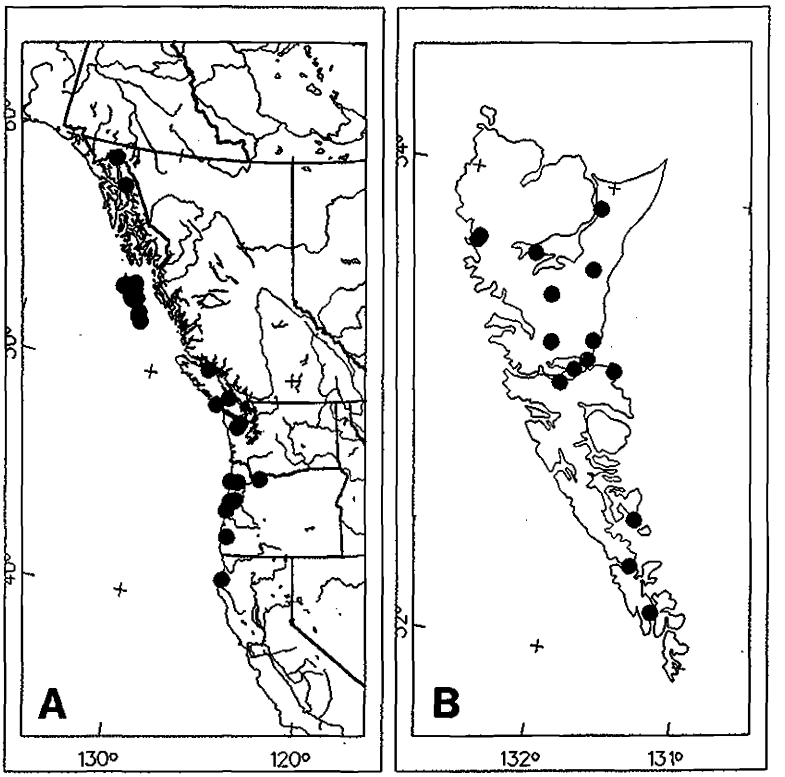


Fig. 1. Distribution of *Loxosporopsis corallifera*. (A) In North America. (B) On the Queen Charlotte Islands, B.C.

Humboldt Co., Lanphere-Christensen Dunes Preserve, 1984, Ahti 42272, with D. H. Norris & P. Wilson (H). Oregon: Benton Co., below Mary's Peak, 1987, McCune 17369 (OSC), 1972, Pike 2891 (OSC); McDonald Forest, N of Corvallis, 1971, Pike 2190 (OSC); Grass Mountain, ACEC, 1992, McCune 20099 (OSC); Coos Co., Elk Creek Campground, Oregon Dunes NRA, 1990, Sharnoff, s. n. (CANL); Lane Co., Sutton Creek Recreation Area, 2 km E of Ocean, 1991, McCune 19393, with DeBolt & Rosentreter (OSC); stabilized dunes near Sutton Creek Campground, *Pinus contorta* – shrub forest, on *Pinus* and *Pseudotsuga menziesii*, 1993, McCune 20237 (OSC, CANL), 1972, Pike 2316 (OSC); Siltcoos River Area, 1994, Rosentreter 9053 & DeBolt (hb. Rosentreter, Henssen); Lincoln Co., Death Ridge, 11 mi. E of Waldport, 1972, Pike 2832 (US, OSC); above Canal Creek, Coast Range, 1993, McCune 20457 (OSC); Multnomah Co., *c.* 19 km NE of Sandy, Lookout Point, 1994, Neitlich 447 (OSC); Tillamook Co., 12 mi. SW of Tillamook, near Camp Meriwether, 1972, Pike 3139 (US, OSC). Washington: Clallam Co., Olympic National Park, Hurricane Ridge, 1961, Henssen 13536 a (hb. Henssen); Jefferson Co., Olympic Peninsula, Hoh River, 1969, Pike 971 (OSC).

3. Apothecial and pycnidial structure and development in *Loxosporopsis*

In habit, *Loxosporopsis corallifera* resembles isidiate species of *Pertusaria*, particularly *P. oculata* (DICKS.) TH. FR., a species having lecanorine apothecia with a broad, dark brown disk (cf. HENSSEN 1976, Plate XIII: C). In *L. corallifera*, however, the isidia are longer, slightly uneven, and the tips do not have a blackish tinge (Fig. 2 C); old apothecia are surrounded by a thin thalline margin and the disk eventually proliferates (Fig. 2 A–B). In *P. oculata*, apothecia and pycnidia originate predominantly in isidia; in *L. corallifera*, they always arise in the thallus.

The cartilaginous thallus of *Loxosporopsis* is limited by an upper cortex. Underneath, the algal cells are ± aggregated into a layer (Fig. 4 C). Ascogonia are formed in groups in a sparsely developed generative tissue between and above the upper algal cells, and frequently at the base of small thallus outgrowths (Fig. 3 A). The hyphae of the generative tissue differentiate into branched paraphyses and a rudimentary exciple, and the first large ascogenous cells are seen (Fig. 3 B). The primordium enlarges and elongates considerably in a vertical direction together with the adjacent thalline tissue (Fig. 3 C).

The young apothecium is sessile. The ascogenous hyphae and ascal initials are irregularly distributed within the hamathecium that is surrounded by a corticate thalline margin including a varying number of algal cells (Figs 3 D, 4 A). Thalline margins without algal cells correspond to the superlecideoid apothecial margin described by FREY (1936) for the genus *Umbilicaria*. The proliferation of the disk in aging apothecia (Figs 2 B, 4 B) also corresponds to species of *Umbilicaria*, in which the growth ceases in sterile sections of the hymenium, and fertile parts continue the vertical elongation (cf. HENSSEN 1970; HENSSEN & JAHNS 1973; HENSSEN *et al.* 1981). The exciple is rudimentary even in mature apothecia.

The tips of paraphyses are richly branched in well developed apothecia (e. g. Brodo 11282 and other Queen Charlotte Island material) forming an epithecium (Fig. 3 E–F). The apothecia are often more or less degenerated, especially in the Oregon specimens, and the ascospores not ejaculated, but lie in the strongly gelatinous hamathecium after disintegration of the ascus wall (Fig. 3 F). The development of the tholus and ocular chamber in the ascus tip is seen in Fig. 4 D–F). The pycnidia are very small, they were observed only in thallus sections (Fig. 4 G). The conidiophore type corresponds to type II of VOBIS (1980).

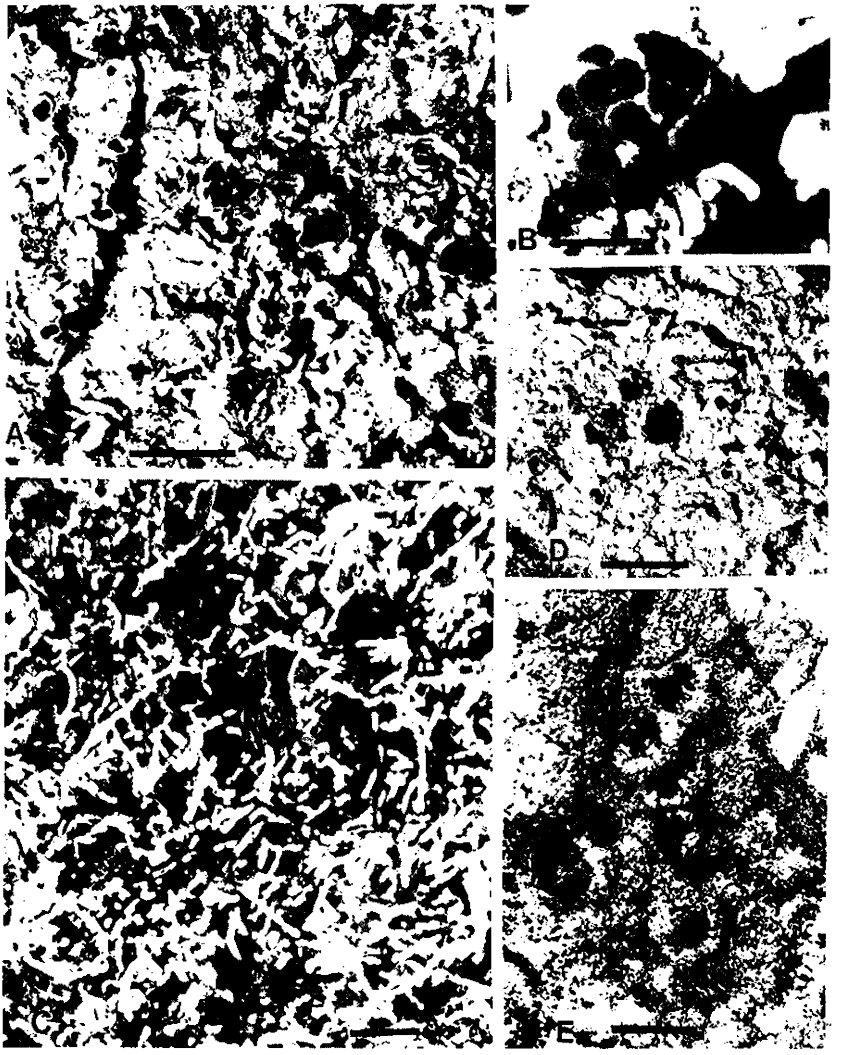
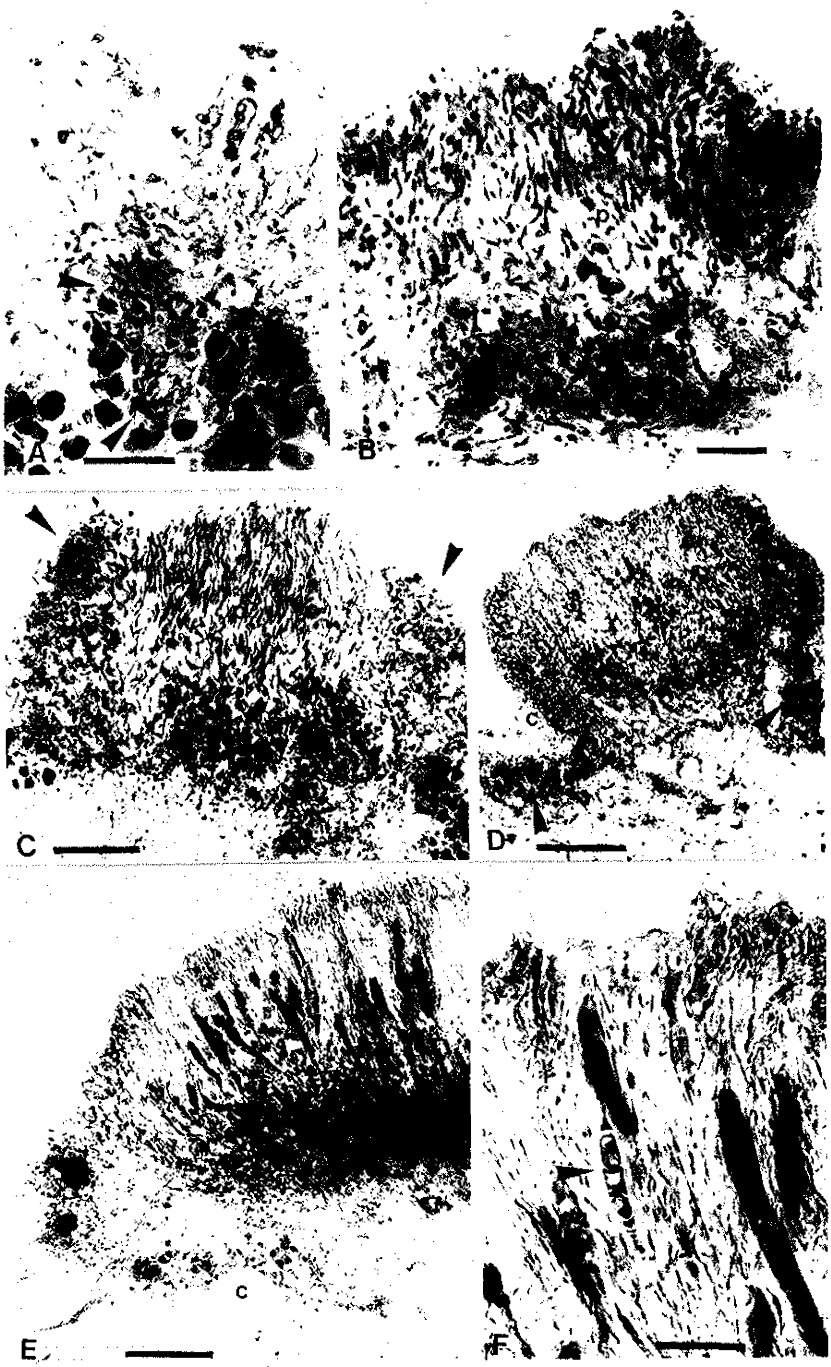


Fig. 2. (A)-(C) Habit of *Loxosporopsis corallifera* (holotype). (A) Fertile thallus. (B) Enlarged proliferating apothecium. (C) Sterile, isidiate thallus. (D)-(E) Habit of *Loxospora elatina*. (D) Crustose thallus with few soralia (Norway, FRIES: *Lich. Scand. Rar. Crit. Exs.* 33). (E) Strongly sorediate thallus (Baumgartner). Scale bar in (A), (D) & E = 2 mm, in (B) = 0.5 mm, in (C) = 1 mm.

4. Apothecial and ascal structure and development in *Loxospora*

Loxospora elatina varies considerably in habit (TØNSBERG 1992): the thallus might be a cartilaginous crust bearing a few soralia (Fig. 2 D) or


A
B
C
D
c
E
c
F

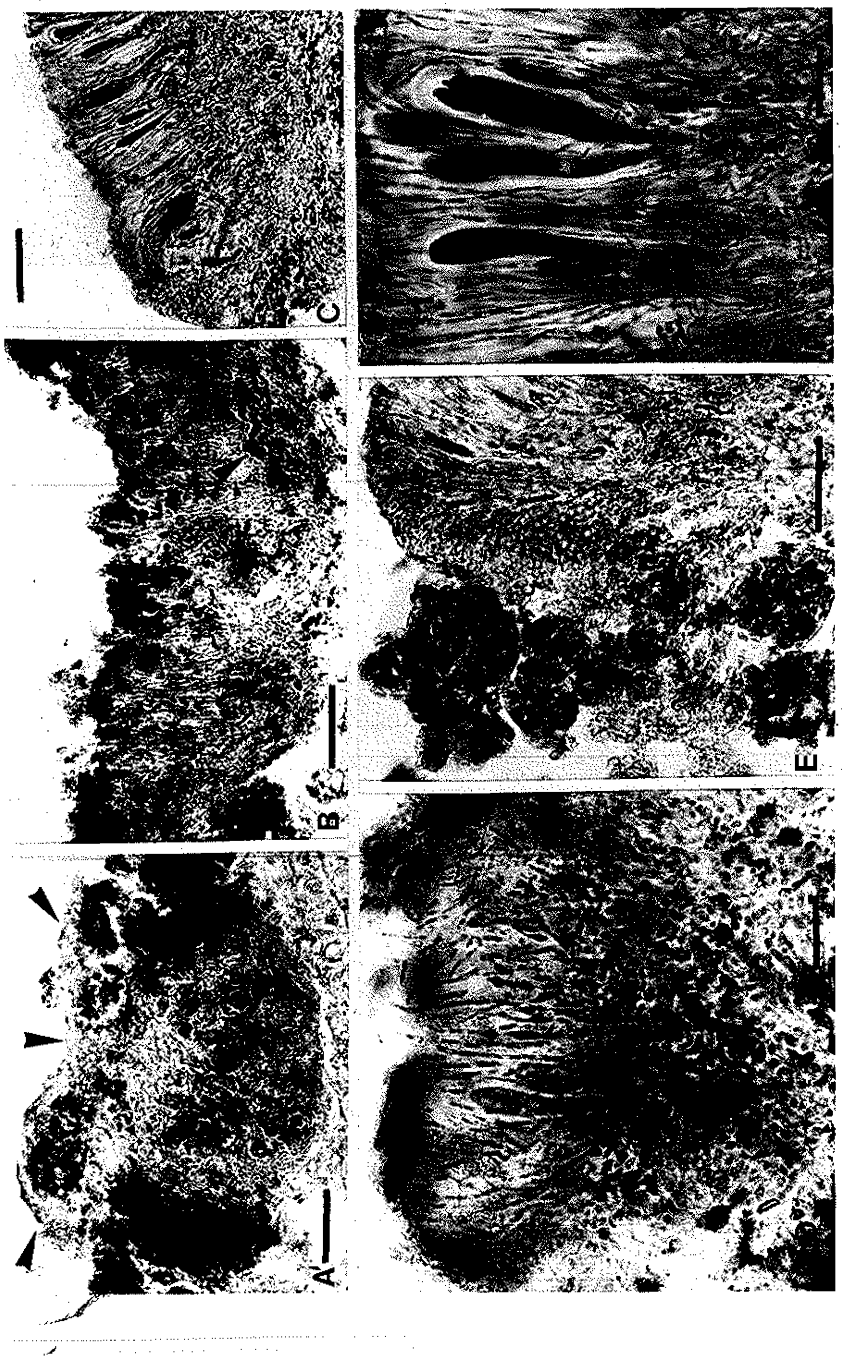
more or less completely dissolved into soredia (Fig. 2 E). The development of apothecia is hemiangiocarpic. In a specimen with a well developed, crustose thallus (Norway, FRIES: *Lich. Scand. Rar. Crit. Exs.* 33), small primordia covered by thalline tissue were observed (Fig. 5 A). The globose hyphal web of generative tissue encloses remnants of ascogonia and groups of ascogenous hyphae, in part, large-celled. The primordium opens by subsequent horizontal growth, the hamathecium then being composed of densely aggregated paraphyses, and the first ascus initials are seen (Fig. 5 B).

In thalli dissolved into soredia, the youngest stages observed were apothecia with well developed paraphyses and asci containing young spores (Fig. 5 D). In mature apothecia, the exciple is mainly restricted to the lateral part. The thalline margin corresponds to that in *Loxosporopsis corallifera* in being corticate and including varying numbers of algal cells (Fig. 5 C, E). The paraphyses are mainly unbranched. Septate, acicular ascospores are slightly twisted in the ascus (Fig. 5 F). The ascus wall with an adjacent gelatinous sheath stains intensely blue in IKI, and an amyloid cap was observed in the tholus above the ocular chamber. Ascus dehiscence is by a simple split at the apex, without rostrate extension (COMMON, pers. comm.). The hemiangiocarpy of the apothecial ontogeny is more pronounced in other species of *Loxospora*, e. g., *L. cismonica* and *L. ochrophaea* (HENSSEN, in prep.).

5. Apothecia vs. isidia

There is a consistently inverse relationship between the abundance of isidia and of apothecia in the populations we have seen. This phenomenon is not unusual in lichens and has been noted before, especially with regard to sorediate species. TØNSBERG (1992: 86) has a good discussion of this. RAMBOLD *et al.* (1990) observed a similar relationship between isidiate and fertile morphs of *Koerberiella wimmeriana* (KÖRB.) STEIN, although they regarded the relationship as based on stages of development.

Fig. 3. (A)-(F) Apothecial development in *Loxosporopsis corallifera* (microtome sections in LB. A: McCune 20237; B-F: Brodo 11282. c = cortex; e = exciple; p = paraphyses). (A) Primordium with group of ascogonia (arrow). (B) Primordium with differentiating paraphyses and ascogenous hyphae, ascal initials indicated by arrows. (C) Subsequent stage with developing thalline margin (arrows). (D) Young apothecium: hamathecium with groups of ascogenous hyphae and ascal initials; algal cells indicated by arrows. (E) Marginal part of mature apothecium. (F) Part of hymenium with 5 septate, non-ejaculated ascospore (arrow). Scale bar in (A), (B) & (F) = 20 µm, in (C) & (E) = 50 µm, in (D) = 100 µm.


C
B
A
E

The systematic position of the genera *Loxospora* and *Loxosporopsis* is still unclear. Primordia with large-celled ascogenous hyphae occurring in groups from which ascus initials arise, are also known, for example, in *Pertusaria oculata*, but in *Pertusaria*, a cupular proper exciple is formed at an early stage (HENSSEN 1976). Another similarity with *Pertusaria* is the restriction of the amyloid reaction to the ascus wall, with a negative reaction in the hymenial jelly. We also noted that the apical structure of young asci, e.g., having a very narrow ocular chamber, corresponds in *L. corallifera* and *P. oculata*. The similarity in habit of the two species has been mentioned above.

The secondary chemistry does not suggest any fundamental relationships. Divaricatic acid does not occur in *Pertusaria* (ARCHER 1993) or *Ochrolechia* (which, however, also has species producing gyrophoric acid in the hymenium), nor in other possible relatives, with the exception of *Ophioparma* as mentioned above. The substance occurs most characteristically in species of *Anzia* and *Pannoparmelia* (YOSHIMURA 1987) with scattered occurrences among other species in the Lecanorales, as well as in *Fuscidea*, a genus in the Fuscideaceae, with vastly different asci and paraphyses (see OBERHOLLENZER & WIRTH 1985; TØNSBERG 1992). The Fuscideaceae is now regarded, at least tentatively, to be best classified within the Teloschistales (HAFELLNER 1984; ERIKSSON & HAWKSWORTH 1993).

Possible relationships of *Loxosporopsis* with the Haematommaceae and Ophioparmaceae (within the Lecanorales) still need to be explored. The asci of *Haematomma* s. str. are of the *Lecanora*-type (HAFELLNER 1984), having a axial body within the thickened, amyloid tholus, something lacking in *Loxosporopsis*. The asci of *Loxosporopsis, Loxospora, Ochrolechia* and *Pertusaria* (the latter two genera in the Pertusariaceae) all are similar in having one or more amyloid ascus wall layers (more strongly amyloid in *Ochrolechia* and *Loxospora* than in *Pertusaria* and *Loxosporopsis*), a slightly thickened apex, containing an ocular chamber but no axial body, and opening by a non-rostrate split (often conspicuously bivalved in *Pertusaria*) (COMMON, pers. comm.; HONEGGER 1982; SCHMITZ *et*

Fig. 5. Structure and development of apothecia in *Loxospora elatina* (microtome sections in LB; A, C & F: Norway, FRIES: *Lich. Scand. Rar. Crit. Exs.* 33; D, E: Baumgartner. c = cortex, e = exciple). (A)-(C) Primordium with ascogenous hyphae and covering thallus layer (arrows). (B) Subsequent stage with open disk, densely aggregated paraphyses; ascal initials indicated by arrows. (C) Marginal section of mature apothecium. (D) Young apothecium. (E) Marginal section of mature apothecium with adjacent soredia. (F) Part of hymenium; ascus with young ascospores indicated by an arrow. Scale bar in (A)-(C) & (E) = 50 µm, in (D) & (F) = 20 µm.

al. 1994). The asci of *Loxospora* and *Ophioparma* are quite similar, both having an amyloid thickening at the apex. Details of this relationship will be provided in a forthcoming paper (HENSSEN, in prep.). The hymenial jelly is non-amyloid in all of the above genera except *Ochrolechia* (SCHMITZ *et al.* 1994; HONEGGER 1982). The conidial formation is Vobis Type V in *Haematomma* (ROGERS & HAFELLNER 1988) and Type II in *Loxosporopsis*, but the conidia are very similar. The branching of the paraphyses is also similar. The ontogeny of the ascomata, however, still remains to be clarified in all the Haematommaceous taxa. In sum, based mainly on anatomical and developmental characters, it is reasonable to hypothesize at present, that *Loxosporopsis* and *Loxospora* might be most closely related to the Pertusariales.

Acknowledgements

This paper is dedicated to Prof Antonín Vězda for his extraordinary contributions to our knowledge of the taxonomy and morphology of so many crustose lichen groups. The studies of A. H. were financially supported by the Deutsche Forschungsgemeinschaft. Work on *Loxosporopsis* was part of a larger study of the lichens of the Queen Charlotte Islands, a project supported by grants from the Canadian Museum of Nature. We thank Dr J. A. Elix for identifying the divaricatic acid in our material, Dr B. McCune and Dr R. Rosentreter for providing us with freshly collected material of *Loxosporopsis corallifera*, Dr Tor Tønsberg for fresh, fertile specimens of *Loxospora elatina*, Dr Klaus Kalb for stimulating discussions, Ms H. Brandtner for technical assistance, Ms Laurie Consaul for preparation of the distribution maps, and the curators of the herbaria for the loan of material in their care. We are especially grateful to Ralph Common for permitting us to present his unpublished observations on ascus structure. We also thank Dr Fenja Brodo for useful comments on the manuscript.

References

ARCHER, A. W. (1993): A chemical and morphological arrangement of the lichen genus *Pertusaria*. – *Bibl. Lichenol.* 53: 1-17.

BRODO, I. M. (1995): Lichens and lichenicolous fungi of the Queen Charlotte Islands, British Columbia, Canada. 1. Introduction and new records for B. C., Canada and North America. – *Mycotaxon* (in press).

CULBERSON, C. F. (1972): Improved conditions and new data for the identification of lichen products by a standardized thin-layer chromatographic method. – *J. Chromatogr.* 72: 113-125.

CULBERSON, C. F., CULBERSON, W. L. & JOHNSON, A. (1986): Two new lichen products, elatinic acid and methyl barbatate, from the genus *Haematomma* (Ascomycotina, Haematommataceae). – *Mycologia* 78: 888-891.

ERIKSSON, O. E. & HAWKSWORTH, D. L. (1993): Outline of the Ascomycetes – 1993. – *Syst. Ascomycetum* 12: 51-257.

Frey, E. (1936): Vorarbeiten zu einer Monographie der Umbilicariaceen. – *Ber. Schweiz. Bot. Ges.* **45**: 198-230.

Hafellner, J. (1984): Studien in Richtung einer natürlicheren Gliederung der Sammelfamilien Lecanoraceae und Lecideaceae. – *Beih. Nova Hedwigia* **79**: 241-371.

Henssen, A. (1970): Die Apothecienentwicklung bei *Umbilicaria* Hoffm. emend. Frey. – *Deutsch. Bot. Ges. Neue Folge Nr.* **4**: 103-126.

Henssen, A. (1976): Studies in the developmental morphology of lichenized ascomycetes. – *In*: Brown, D. H., Hawksworth, D. L. & Bailey, R. H. (eds): *Lichenology: Progress and Problems*. Systematics Association Special Volume No. 8. Academic Press, London, New York, San Francisco. 107-138 + 20 plates.

Henssen, A. & Jahns, H. M. (1973; »1974«): *Lichenes, eine Einführung in die Flechtenkunde, mit einem Beitrag von Johan Santesson.* Thieme Verlag, Stuttgart. I-XII, 465 pp.

Henssen, A., in cooperation with Keuck, G., Renner, B. & Vobis, G. (1981): The Lecanoralean Centrum. – *In*: Reynolds, D. R. (ed.): *Ascomycete Systematics: The Luttrelian Concept.* Springer Verlag, New York. 138-234.

Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. (1990): *Index Herbariorum. Part I: The Herbaria of the World, 8. edition.* International Association for Plant Taxonomy & New York Botanical Garden, Bronx, N. Y, 693 pp.

Honegger, R. (1982): The ascus apex in lichenized fungi III. The *Pertusaria*-type. – *Lichenologist* **14**: 205-217.

Kelly, K. L. (1965): *ISCC–NBS Color Name Charts Illustrated with Centroid Colors.* Suppl. National Bureau of Standards Circ. 553. Washington, D. C.

Mietzsch, E., Lumbsch, H. T. & Elix, J. A. (1992): *Wintabolites (Mactabolites for Windows). Users Manual.* University of Essen, Essen, 54 pp.

Oberhollenzer, H. & Wirth, V. (1984): Beiträge zur Revision der Flechtengattung *Fuscidea*. – *Beih. Nova Hedwigia* **79**: 537-595.

Rambold, G., Hertel, H. & Triebel, D. (1990): *Koerberiella wimmeriana* (Lecanorales, Porpidiaceae) and its lichenicolous fungi. – *Lichenologist* **22**: 225-240.

Rogers, R. W. & Hafellner, J. (1988): *Haematomma* and *Ophioparma*: two superficially similar genera of lichenized fungi. – *Lichenologist* **20**: 167-174.

Schmitz, K. E., Lumbsch, H. T. & Feige, G. B. (1994): Systematic studies in the Pertusariales II. The generic concept in the Pertusariaceae (lichenized Ascomycotina). – *Acta Bot. Fenn.* **150**: 153-160.

Tønsberg, T. (1992): The sorediate and isidiate, corticolous, crustose lichens in Norway. – *Sommerfeltia* **14**: 1-331.

Vobis, A. (1980): Bau und Entwicklung der Flechten Pycnidien und ihrer Conidien. – *Bibl. Lichenol.* **14**: 1-141 + 215 Abbildungen.

Yoshimura, I. (1987): Taxonomy and speciation of *Anzia* and *Pannoparmelia*. – *Bibl. Lichenol.* **25**: 185-195.