THE LICHEN GENUS NEPHROMA IN NORTH AND MIDDLE AMERICA

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Clifford Major Wetmore

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by

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AN ABSTRACT

Submitted to the College of Science and Arts
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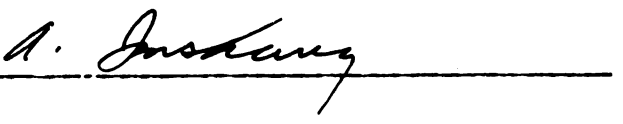
Approved 

ABSTRACT

This revision is based on a morphological, anatomical, and chemical study of 1,918 specimens from twenty-one herbaria, as well as field work in Isle Royale National Park (Michigan), Haiti, and the Dominican Republic.

The morphological and anatomical features are discussed in detail and twenty-nine original figures are included. The protuberances on the lower surface of N. resupinatum (L.) Ach. are corticate and, therefore, not true pseudo-cyphellae as often recorded in the literature. Eight lichen substances have been found in the genus: usnic acid, nephromin, zeorin, nephrin, and four unidentified neutral substances. These substances have taxonomic importance, although other workers in related genera have ignored them.

The genus is placed in the Nephromaceae instead of the Peltigeraceae, where usually classified, because of the differences in ascus structure and development, conidial production and the presence of a lower cortex in Nephroma.

Seven species and two subspecies are recognized and a key for their identification is included along with a diagnosis, nomenclatural notes, and a distribution map for each species.

Gyelnik's four new species and two new infraspecific taxa from North America are reduced to synonymy. Nephroma

tropicum (Müll Arg.) Zahlb. is reduced to a subspecies of N. helveticum Ach. Nephroma bellum (Spreng.) Tuck. is recognized as the correct name for N. laevigatum auct. non Ach. and N. laevigatum Ach. non auct. is recognized as the correct name for what previously has been called N. lusitanicum Schaer.

The need for future work in the chemistry, algal and spore culture, and phylogeny is recognized together with the need for study of the remaining species of Nephroma in the world.

THE LICHEN GENUS *NEPHROMA* IN NORTH AND MIDDLE AMERICA

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A THESIS

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LISTING OF PLATES

I

INTRODUCTION

This is a revisionary treatment of the genus Nephroma, a genus of lichenized Ascomycetes of the Discomycete group, in the Northern Hemisphere of the New World, including Greenland on the east, Alaska on the west, and Panama on the south. In this study I have examined 1,918 specimens from 16 institutional herbaria in the United States and Canada and 5 private herbaria.[1] The herbarium material was supplemented with field studies and collections in Isle Royale National Park (Michigan), and in Haiti and Dominican Republic in the Caribbean. From this field study, I was able to observe the natural variation, habitat, and occurrence, as well as make large collections of material for later study.

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[1]List of herbaria. Abbreviations follow the recommendations of Lanjow and Stafleu (1959). Lichen Herb., Am. Bryol. Soc. (ABSL); Nat. Fungus Colls., Hort. Crops Research Branch (BPI); Nat. Mus. Canada (CAN); Univ. of Col. (COLO); Chicago Nat. Hist. Mus. (F); Farlow Herbarium, Harvard Univ. (FH); Univ. of Mich. (MICH); Missouri Bot. Gard. (MO); Mich. State Univ. (MSC); New York Bot. Gard. (NY); Philadelphia Acad. of Nat. Sci. (PH); Univ. of Toronto (TRTC); Univ. of Calif. (UC); Smithsonian Inst. (US); Wellesley Coll. (WELC); Univ. of Wisc. (WIS). I am grateful to the curators of these herbaria for the loan of this material.

The following personal herbaria were kindly loaned and are without abbreviations. W. L. Culberson (Culberson), C. W. Dodge (Dodge), M. E. Hale (Hale), F. P. Sipe (Sipe) and J. W. Thomson (Thomson).

This is not a monograph because of limitations in scope necessitated by time and facilities. However, I have attempted to examine and re-evaluate as many of the characters that have been reported in the literature as possible, to reaffirm their presence and to evaluate their taxonomic significance.

II

HISTORY

Linnaeus (1753) placed the two species of Nephroma known at his time in his genus Lichen, which included all species which he considered lichens. He recognized L. arcticus and L. resupinatus.

In 1794 Schrader included resupinata in the genus Peltigera for the first time. He only reported P. resupinata and P. sylvatica in this genus in this paper.

In 1803 Acharius placed the recognized species of Nephroma into a separate section of Peltigera (Peltidea ** Opisteria). In 1810 he recognized this section as a separate genus and changed the name to Nephroma. Acharius recognized N. polaris, N. resupinata, N. parilis, and N. helvetica. Acharius used the name Nephroma in the feminine tense in error, for he states that the term came from the Greek word for kidney (in reference to the apothecial shape) which was actually neuter. This error of gender was corrected in 1812 by S. F. Gray to the neuter gender.

In 1860 Nylander described the genus Nephromium for the species of Nephroma with gonimia (blue green algae) and retained Nephroma for those species with goniaia (green algae). However, he apparently considered the blue green algae in the cephalodia of N. expallidum to be of sufficient

importance to place it in his genus Nephromium.

In 1909 Wainio raised Acharius' section Opisteria to generic rank on the idea that the oldest name, regardless of rank, had priority, which is contrary to the present rules of nomenclature (Lanjouw, 1956). Since Nephroma was the first name used for these species in the rank of genus, it has priority over Opisteria.

The next work of importance in the genus was done by Moreau (1927) when he proposed the family Néphromiacées for the genus Nephromium. His argument for the separation from the Peltigeraceae was based on the fact that Nephromium has a lower cortex and Peltigera does not. This separation was later supported by cytological differences in ascogonial development (Moreau, 1928) and differences in the apex of the ascus (Galinou, 1955).

The only monographic attempt of Nephroma was done in the 1930's by Gyelnik (1930, 1931, 1932a, 1932b, 1932c, 1934, 1935, 1936, and 1940) in Budapest. His main species characters were the degree of tomentum, KOH reactions, thallus color, soredia, and tubercles. By using every small variation and combination of these, and a few other characters, he described 28 new species for the Northern Hemisphere, 4 of which were from North America, and 45 infraspecific names, with 2 from North America. Most of these taxa have not been recognized by other lichenologists. Gyelnik also worked in several other groups, but mostly in the Peltigeraceae. Sjödin (1954) states that of the 1,307 new names described by Gyelnik, only a few are accepted today. However, almost all

of his type specimens were destroyed during World War II, which makes a definitive evaluation of his species almost impossible. As a comparison, Du Rietz (1929) recognized only 7 species of Nephroma in the Northern Hemisphere.

III

MORPHOLOGY

A. Methods. Cards containing label data were made out for each specimen and given a consecutive number for this study. Each specimen was then carefully examined under a binocular microscope at 10X magnification for the various morphological characters of isidia, soredia, tomentum, etc. The specimens were also checked for any abnormalities or unusual appearances. Notes were taken on the specimen cards which were later compared with the chemical notes for evaluating the specimen.

Representative specimens were selected for sectioning with a freezing microtome (AO Clinical Microtome, Model 880). A piece of the thallus and an apothecium were allowed to soak in an alcoholic Photo Flo[2] solution (1 pt. Photo Flo : 10 pts. water : 11 pts. 70% EtOH) at least three hours before sectioning. The pieces to be sectioned were frozen in place in a drop of saturated aqueous gum arabic solution to which a crystal of thymol had been added as a preservative. Thallus and apothecial sections were made at 20 u, pycnidial sections at 15 u. Sections were then removed from the blade with a small brush, and placed in a small dish of water where the

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[2]Eastman Kodak Company, Rochester, New York

arabic dissolved leaving the free sections. A few sections were then selected and placed in a drop of lacto-fuchsin stain (0.1% acid fuchsin in lactic acid) on a microscope slide and gently heated to hasten the staining. The cytoplasm of the algae and fungi stained red. Sections were dehydrated through 70%, 80%, 95% EtOH and mounted in Diaphane[3] which gave a permanent slide for anatomical studies.

Much trouble was experienced with the thin apothecial sections which curled as soon as they thawed. The procedure was modified by placing the sections onto a clean microscope slide from the 70% alcohol before they became too stiff to uncurl, as they would become in the 95% alcohol. The sections were straightened out as well as possible and allowed to dry for a minute or two, then carefully rinsed several times in 95% EtOH, and a drop of Diaphane added and then the cover slip. This gave fairly good results with surprisingly few air bubbles.

Clearcol[4], a water soluble mounting medium, was tried, but the lichen substances apparently reacted with the Clearcol to produce bubbles after a few weeks which soon made the slide useless.

Temporary squash mounts were made by soaking apothecia in distilled water overnight, sectioning freehand or by microtome, and mounting in the lacto-fuchsin stain. For

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[3]Will Corporation, Rochester, New York.

[4]H. W. Clark, Melrose, Massachusetts.

spore measurements freehand sections were made and squashed in 25% KOH. Conidial measurements were made in the lacto-fuchsin stain.

All drawings were made with the aid of a camera lucida.

B. Thallus. The thallus of this genus is of the heteromerous type with the algae restricted to a definite layer near the upper surface. In two of the North American species (N. arcticum and N. expallidum), the algal layer is composed of green algae of the genus Coccomyxa, but these species also have blue-green algae of the genus Nostoc (des Abbayes, 1951 and Zahlbruckner, 1926) in restricted areas called cephalodia. Cephalodia are wart-like areas containing blue green algae in a thallus normally containing green algae. In arcticum the cephalodia are on the upper surface (see fig. 1) and are usually larger and broader than in expallidum where they are found on the lower surface (see fig. 2). This is one of the main characters for the identification of these two species.

The fungus of Nephroma, when in combination with the algae, produces a paraplectenchymatous cortex several "cells" thick (see fig. 3). A few fungal hyphae wind around in the algal layer (see fig. 4) and the medulla is a network of loose intertwining hyphae (see fig. 5). The lower cortex is less well organized and is usually only a few "cells" thick, except where it thickens at the edge of an apothecium (see fig. 7).

The composite thallus of the fungus and alga is usually thicker in the specimens from western North America than in those from the east. However, there are specimens from areas in between (e.g., Idaho, Montana and Colorado) which cannot be definitely placed in either group. This difference is sometimes very noticeable when comparing selected specimens from each area; the eastern ones are about 100 - 200 μ mm. thick and the western ones are 200 - 300 μ thick. Thallus thickness variation is due primarily to variation in medulla thickness. In one species, N. helveticum, this difference of thallus thickness is recognized as being worthy of recognition because it is correlated with other characters, but thallus thickness alone is not of very great taxonomic importance in Nephroma.

The size of the thallus varies somewhat between species. Nephroma arcticum is much larger than the other species, its thallus averaging up to 13 cm. (rarely 15 cm.) in diameter[5], while other species avarage about 6 - 8 cm. in diameter. However, I have noticed that the area covered by the thalli of one species on a rock cliff may extend up to a square meter or more in shady, moist situations.

Soredia occur only on N. parile. In this species, the soredia are in maculiform soralia or are marginal on the lobes. The soredia are very granular with a few cortical

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[5]These measurements may, to some extent, reflect the size of the packets the specimens were placed in, as they were made from herbarium material, not in the field.

"cells" covering most of each soredium (see fig. 6). Soredia serve as an asexual means of reproduction and in parile probably constitute the chief form of diaspore. As has been reported by Du Rietz (1924) and Degelius (1954), lichen species with soredia or isidia frequently lack apothecia. This is also true in N. parile where in over 250 specimens I have not found a mature apothecium that could positively be demonstrated to have developed from a sorediate thallus. Two immature apothecia were found, but the rest usually belonged to bellum, which occasionally grows mixed with parile.

Isidia usually occur in N. helveticum and are found occasionally in resupinatum and laevigatum, but never in bellum or parile. The isidia in helveticum ssp. helveticum are flat and small (0.1 - 0.2 mm. wide), but in helveticum ssp. tropicum they are long and rounded (0.2 - 0.5 mm. wide). These round isidia often break open at the tips with age, but cannot be classified as pseudocyphellae. In some of the local races of helveticum ssp. tropicum in Central America the isidia are long and narrow and in one race in the Dominican Republic no isidia have been seen on a mass collection made in 1958 (Wetmore no. 3550).

Various authors have reported pseudocyphellae in N. resupinatum. A pseudocyphella, however, is an opening through the cortex which exposes the medulla and permits it to grow out as a small protuberance, as in Pseudocyphellaria (see fig. 9). Thus, a protuberance (pseudocyphella) in Pseudocyphellaria originates with a break in the cortex followed

by an outgrowth of the medulla. In N. resupinatum, however, the protuberance is produced with the cortex intact (see fig. 8), which is then often accidentally broken to expose the medulla. I, therefore, prefer to follow Gyelnik (1932a) and call these protuberances papillae. Howard (1950) refers to these as "tubercules."

Gyelnik used the character of tomentum to create many species and varieties. His interpretation of tomentum of the thallus was explained in 1932 (Gyelnik, 1932a). He called the surface glabrous if there was no pubescence evident under a hand lens, pubescent if fine short hairs were visible with a hand lens, delicate tomentose if longer hairs were evident with the naked eye, and tomentose if long matted hairs were seen. With these minute separations, he described many variations of hairiness as new taxa. On specimens I have examined, the degree of tomentum of the surfaces is too variable to be used for the separation of species. The lower surface of N. helveticum varies from almost glabrous on rock to quite tomentose on trees in the same locality. The pubescence on bellum is variable from absolutely glabrous to fairly dense, short pubescent on others. Furthermore, the amount and size of the pubescence on the lower surface of Nephroma varies from one lobe to another on the same thallus. This variability has also been reported by Du Rietz (1929). Using the character of pubescence or tomentum on the lower surface of Nephroma in identification has led many taxonomists astray and I consider it, at best a very poor accessory character in most cases of this genus.

Regeneration squamules are common in many species of Nephroma. They occur on the margins or from breaks in the cortex. Experimental studies on regeneration squamules have been done by Thomson (1948) in the genus Peltigera. He found that after cutting or breaking the thallus, new small squamules appeared along the injuries. He came to the conclusion that production of these squamules is not of specific importance. In Nephroma species, bellum rarely has regeneration squamules, but laevigatum, helveticum, arcticum, resupinatum and parile often do. These squamules seem to have little taxonomic value, although there is a tendency for one species not to produce any.

Marginal teeth in Nephroma are similar to squamules, but usually are much narrower, and do not arise after injury. They are present only in helveticum. In helveticum ssp. helveticum they are short (0.2 - 0.3 mm. long), flat and broad (0.3 - 0.5 mm.), or lacking entirely, seeming to grade into the narrow indentations of the margin. In helveticum ssp. tropicum the teeth are long (0.3 - 0.5 mm.), roundish, and narrow (0.3 mm.) and always are present. In some Central American races the teeth are narrower than others. This difference in teeth is not considered worthy of specific separation, but, together with other characters, assumes toxonomic value on the infraspecific level.

C. Apothecia. Apothecia of Nephroma are non-emergent and marginal on the lower surface; which distinguishes this genus from all other genera. Some species of Cetraria have

marginal apothecia which originate on the lower surface but are emergent. These are separated into the genus Nephromopsis by some lichenologists. The shinier appearance of the cortices, the presence of rhizoids on the lower surface, lichen substances, and spore differences (Cetraria has hyaline non-septate spores) will also easily separate the two genera.

The apothecial disc is light brown in all species except N. helveticum where it is dark reddish brown. Occasionally the disc is discolored and darkened, becoming blackish, in all species. This probably is due to drying and pressing techniques.

The size of the apothecia varies from species to species. The average maximum size is largest in arcticum (up to 20 mm. diameter, rarely up to 30 mm.) and smallest in helveticum and laevigatum (up to 8 mm.).

The hymenium is quite heavily conglutinated and is 60 - 90 μ thick. Paraphyses are unbranched and four to six cells in length with slightly darkened swollen tips. The apex of the ascus is without the apparatus found in Peltigera and Solorina (see fig. 10. Galinou 1955). Spores are eight per ascus, light brown, and are three-septate. Fink (1935) has reported other septations, but these were probably due to immature or abnormal spores (see fig. 18). Some Southern Hemisphere species, however, have more septa, according to Lamb (1955). The normal spores vary slightly from species to species (see figs. 11 - 17).

An outer wall is visible on all spores, but helveticum ssp. helveticum and laevigatum appear to have an inner wall around each lumen. In arcticum and resupinatum no inner wall is visible under 950X magnification and expallidum, bellum, and helveticum ssp. tropicum are intermediate with the middle lamella visible only between the lumina. The size varies slightly with arcticum and resupinatum being longest and narrowest (23 - 27 μ x 4 - 6 μ, 21 - 24 μ x 4 - 6 μ, respectively) and bellum, expallidum and laevigatum being shortest (17 - 21 μ x 5 - 6 μ). N. helveticum ssp. tropicum is the widest (20 - 23 μ x 6 - 8 μ). The spores of all species were seen to have germinated in the hymenium (see fig. 19) and produced a hypha at one or both ends. The differences in measurements, in most cases, are too slight to be of much importance in routine identification of species in Nephroma.

Below the hymenium is a thin layer of closely packed hyphae called a hypothecium or exciple. When there are two layers the one immediately below the hymenium is the hypothecium and the layer below that is the exciple. When only one tissue is present either term has been used.

D. Pycnidia. Pycnidial characters are often overlooked because of their small size (0.1 - 0.3 mm. diameter) and the small size of the conidia within. In lichens the conidia are thought to be an asexual means of reproduction (des Abbayes, 1951). The largest conidia are in resupinatum, bellum, and laevigatum where they measure 4 - 5 μ x 1 - 2 μ, while in the

rest of the species they measure 3 - 4 μ x 1 - 2 μ. Conidia are borne on any cell of the conidiophore, making it endobasidial (see figs. 20, 21). In Peltigera the conidia are borne only on the terminal cells of the conidiophores, making them exobasidial (des Abbayes, 1951). These conidiophores differences are of major importance on the family level. Zahlbruckner (1926) erroneously reported that both Nephroma and Peltigera are endobasidial.

IV

CHEMISTRY

A. Methods. Chemical characters were evaluated by several techniques: micro-extraction, paper chromatography, solubilities in various organic solvents, and color reactions of the thallus.

Micro-extractions were made of most collections. A small fragment of the thallus was placed on a microscope slide on a warming table set at 65°C. and acetone was added, drop by drop, to extract the substances. The acetone was allowed to evaporate and then the fragment was removed and a drop of G.A.An. (2 pts. glycerine : 2 pts. ethanol : 1 pt. aniline) was added, followed by a cover slip. The slides remained on the warming table until the residue had dissolved. Then they were set aside to cool and crystallize for 20 - 24 hours to assure complete crystallization. G.A.An. was found to crystalize the neutral substances the best of the many reagents generally used by lichenologists, such as, G.E., G.A.oT., G.W.Py., G.A.oAD., G.A.W. For formulas, see Asahina and Shibata (1954) and Evans (1943). The methods used are modifications of those used by these authors.

A word of caution is necessary here concerning the microscope slides and cover slips used in extraction work. These must be thoroughly cleaned in soap and water, then

boiled in acetone before reusing or crystals will carry over from one extraction to the next. Using the acetone last also aids in drying the slides.

Paper chromatography was used to a limited extent in Nephroma, but since the Neutral Substances (Asahina and Shibata, 1954) are not easily detected by most reagents, this method was not very useful. For this work fragments of the thallus were boiled in a test tube of acetone and the solution was applied to the bottom of one-inch wide strips of Whatman No. 1 Chromatography Paper. The strips were suspended in individual test tubes and the solvent was allowed to ascend. In this way replicates could be run in many different solvents and sprays at one time. After about twenty-four hours, the strips were removed, dried, checked for fluorescence with ultraviolet light, and sprayed with the developing reagent (Wachtmeister, 1956).

One of the most useful techniques, used in connection with the microchemical tests for crystals, was a solubility analysis of the substances removed by the hot acetone from the thallus. One great handicap was the lack of sufficient quantities of material to treat by this method. By evaporating the acetone extraction to dryness, then re-dissolving in chloroform or ether, and shaking with 6% sodium carbonate, the neutral substances would remain in the ether or chloroform layer and the acidic substances would be in the sodium carbonate layer. After separating the layers, the sodium carbonate was acidified, precipitating the lichen substance, filtered,

and the substance redissolved in acetone. Further treatments were carried out on the residues to determine which organic solvents would dissolve the various parts of the residue, checking each stage of the procedure with a micro-chemical test of the residue or solution. As the substances became purer, they would crystallize out of the solvents as recognizable crystals, which then could be checked with literature reports and the micro-chemical tests to relate the crystal to the crystals obtained with G.A.An. The fractions were also checked with KOH, $FeCl_3$ and para-phenyldenediamine.

One of the oldest chemical methods used in lichenology is the color reaction of the thallus with various chemicals. Although largely replaced by more accurate methods, sometimes the reactions are reliable enough to still be useful in routine taxonomy. The only one of these tests found valid was the KOH test on the medulla of N. laevigatum to indicate the presence of an anthraquinone. In this test, a small cut was made through the cortex to expose the medulla and a drop of 25% KOH was applied. If the anthraquinone was present the medulla turned pink, red or red-violet. If there was no color change, it was recorded as KOH negative (KOH-).

The KOH reaction was checked on all specimens of Nephroma because some previous workers have made species or varieties from slight KOH reactions due to substances other than anthraquinones.

B. Substances. The lichen substances in the Peltigeraceae were studied by Hesse (1898) and Zopf (1909).

Hesse reported usnic acid and nephrin from N. arcticum[6]. Zopf reported zeorin from arcticum, antarcticum, laevigatum, and parile and nephrin from arcticum, laevigatum, and lusitanicum. Thomson (1950) stated that there were no substances in Peltigera, evidently overlooking the paper by Zopf. Although the identity of the substances reported by the older workers is probably correct, the identity of the species cannot be relied on because of the changes in species concepts.

Bachmann (1887) reported emodin from N. lusitanicum because it acted like the substance emodin in the bark of Rhamnus frangula. Hesse (1898) reported nephromin from lusitanicum. In 1907 Zopf stated that the anthraquinone in lusitanicum was not emodin but different and that Hesse's name nephromin was correct.

The lichen substances in Nephroma belong, mainly, to the neutral group as outlined by Asahina (Asahina and Shibata, 1954). Since little work has been done in this group of substances, a precise determination was not attained.

Nephrin was reported in N. arcticum by Hesse (1898) and later isolated from N. laevigatum and studied by Zopf (1909). According to Zopf, nephrin is $FeCl_3$ negative, is slightly soluble in cold ether, ethanol, acetone or acetic acid and gives spherical crystal clusters when crystallized from acetic acid. He also reported nephrin from N. arcticum and N.

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[6]The names used in this part are as they were used by the author cited, not as used in this paper.

lusitanicum. I have not been successful in isolating sufficient quantities of nephrin to positively verify this substance, but so far as I can tell, the substance which recrystallized out of G.A.An. as hexagonal plates (see fig. 27) seems to be nephrin. It has the same solubilities as nephrin and is $FeCl_3$ negative. Also, in N. arcticum there are only two substances that are $FeCl_3$ negative, one of which is zeorin, so the other can be presumed to be nephrin (and also gives hexagonal plates).

The usnic acid in arcticum is blocked in the microchemical tests by another substances, possibly a carotenoid, but after destroying the carotenoid by prolonged boiling in acetone, I was able to verify the presence of usnic acid. A 5% alcoholic solution of Chloramine-T (CAT) will turn the thallus of N. arcticum light yellow in the presence of usnic acid.

A substance isolated from N. arcticum gives yellowish orange crystals, is $FeCl_3$ + red brown, para-phenylenediamine + red, KOH + yellow, has a yellowish green fluorescence, and is removed from the ether solution by 5% sodium carbonate. The only known lichen substance that is similar to this substance is lichexanthone (Asahina and Shibata, 1954), but this latter substance is $FeCl_3$ + purple and remains in the ether layer on treatment with 5% sodium carbonate. This substance also breaks down on prolonged heating. The crystals obtained from purified substance and on recrystallization from G.A.An. are similar to those in Karrer and Jucker (1950). An ultra violet spectogram would be necessary to prove that this

substance is a carotenoid.

Various clear blades and needles appeared in the G.A.An. slides, some of which were distinctive enough in shape and constancy to be useful in some species. These substances were found to be neutral, but were not further identified. They are designated by letters associated with photographs and descriptions which appear below.

Neutral substances giving clear crystals in G.A.An.:

Substance A. Clear blades, branched, flat, sometimes folded over, acute angles, sometimes feathery appearing due to many short branches. Appearing in G.A.An. slides within one-half hour (see fig. 22). Found in parile 99%, bellum 30%.

Substance B. Clear blades, long, narrower than substance A, branching, flat. Appearing in G.A.An. immediately (sometimes while still on warming table) (see fig. 23). Found in expallidum 100%.

Substance C. Clear needles, long, branching, appearing trapezoidal in cross section. Appearing in G.A.An. slides within one-half an hour (see fig. 24). Found in helveticum 97%.

Substance D. Clear chunks, oblique angle at two corners, acute angle at other two, fairly thick (thicker than substances A, B, or C). Appear in G.A.An. slides within one-half an hour (see fig. 25). Found in bellum 36%.

Zeorin - Clear double pyramid, hexagonal in section, sometimes without tips on pyramids. Appears in G.A.An. within five minutes (see fig. 26). Found in expallidum 100%, bellum 90%, arcticum 59%, parile 51%.

Nephrin - Clear plates of various shapes, square, hexagonal, rhomboidal, and clear quadrangular rods with sloping ends. Appears in G.A.An. within two to three hours (see fig. 27). Found in expallidum 97%, helveticum 78%, arcticum 74%, bellum 36%, parile 5%.

Non-Neutral Substances.

Usnic Acid - Narrow branching, long yellow blades; turns yellow with 5% alcoholic chloramine T solution. Normally this appears in GE, but does not appear in any test of arcticum due to the blocking by the carotenoid. Probably constant in arcticum. Found in arcticum by Hesse (1898).

Nephromin - KOH + red, para-phenylenediamine + red, magnesium acetate + reddish. Does not give conclusive crystals in any reagent. The best tests are with KOH and $Mg(Ac)_2$ in addition to the yellow color of the medulla. Found in varying concentrations in all laevigatum (= lusitanicum) specimens.

Carotenoid - yellow-green boat-like crystals, jointed near the center. Fluoresces greenish yellow under

ultra violet light. Appears in G.A.An. after one-half an hour, para-phenylenediamine + red, KOH + yellow, $FeCl_3$ + red brown. (See fig. 28.) Found in arcticum 100%.

Although the various substances listed have not all been identified to name, they are constant enough in appearance and character to be of value in the identification and classification of the species in this genus. The chemical characters are given value equal to any other morphological or anatomical character.

V

ECOLOGY

Nephroma species are most often found growing in lightly shaded, moist, cool places on moss, rocks, trees, or fallen trees that still have their bark.

In Northern Alaska, according to Dr. John E. Cantlon, who has spent several summers on the Arctic Slope of the Brooks Range, they usually grow in areas protected by late lasting or deep snow cover in the wet meadow areas or between rocks.

As *arcticum* and *expallidum* extend south in the Rocky Mountains, they are found in the moist valleys, not on the ridge tops as do species of the Arctic-Alpine type, according to Dr. Henry A. Imshaug (Imshaug, 1957).

On Isle Royale, my observations indicate that species of *Nephroma* grow on mossy north-facing rock faces or on trees in the valleys. They are not present in dry places or in very dense shade, such as *Thuja* bogs, unless in an opening or at the border.

In Hispaniola *N. helveticum* ssp. *tropicum* was found above 7,500 feet in cool, moist, wooded areas on trees and shrubs, usually in the pine forests. When *Nephroma* is present, the thalli are usually abundant, very small, and highly fertile.

Dodge (1933) reports that Nephroma grows in the high moist areas in Costa Rica.

VI

DISTRIBUTION

The genus has primarily a boreal-oceanic distribution with various modifications. Nephroma laevigatum has a strictly oceanic distribution, resupinatum has basically an oceanic distribution with an extension into the Great Lakes. Nephroma helveticum ssp. tropicum has an oceanic distribution on the west coast of North America and extends into the tropics in oceanic habitats on mountains or islands. Many localities are known from geologically old areas of the United States, such as the Appalachians and in the Ozark Mountains.

The absence of collection records of Nephroma in the Great Plains of the United States and Canada and the coastal regions of the east and south is probably not due to lack of collecting. Since a few collectors have made locally good collections within these regions, it may be assumed that the general environment is not favorable for their growth there.

In order to discuss the center of origin of a genus, all species of it must be studied and their distributions compared. However, this has not yet been possible in this study of Nephroma.

VII

TAXONOMY

According to Bessey (1950), all discomycetous lichens belong to the order Lecanorales. Des Abbayes (1951) classified the Nephromaceae along with the Collemataceae, Peltigeraceae and Stictaceae in the order Cyanophilales, which is mainly characterized by blue green algae.

Family. Nephroma species have usually been classified with Solorinella, Solorina, and Peltigera, in the Peltigeraceae because of the non-emergent apothecia, and septate spores. As further research was done, many characters were found by which Nephroma differed from the rest of the family. Moreau (1927) separated Nephroma, because it had a lower cortex, and proposed the new family Néphromiacées, including only Nephromium. This name was not published in Latin and so was not validly published. A year later Mme. Moreau (1928) recognized a difference in ascogonial development between Nephroma and Peltigera. Galinou (1955) described differences in apical structure of the ascus between the two genera. Peltigera was known to have a different type of conidiophore development (exobasidial) than most other genera (des Abbayes, 1951, p. 154) and I have shown Nephroma to have endobasidial development (see above). For these reasons it seems desirable

to separate this genus from the Peltigeraceae and recognize the family Nephromaceae.

NEPHROMA ACH. LICH. UNIV. 521. 1810

Nephromium Nyl. Syn. Lich. 1: 318. 1860. -- Opisteria (Ach.) Wain. Ark. Bot. 8 (4) : 93. 1909. TYPE OF GENUS: N. polaris Ach. (= N. arcticum (L.) Torss.).

Diagnosis: Thallus greenish-yellow or brown, usually quite thin (100 - 300 μ thick); cortices paraplectenchymatous, upper cortex .20 - .40 μ., lower cortex 10 - 30 μ; algal layer 30 - 60 μ thick with loosely interwoven hyphae, algae blue-green (Nostoc) or green (Coccomyxa); medulla of loose hyphae 40 - 260 μ . thick; lower surface of thallus glabrous, pubescent or tomentose with hairs of thicker walls than medullary hyphae (see figs. 29, 30). Apothecia immersed on lower surface at tips of lobes; discs light brown to dark brown; hypothecium hyaline to light brown 20 - 30 μ thick; hymenium 60 - 90 μ thick, paraphyses unbranched, spores three-septate, light brown, eight spores per ascus.[6]

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[6]In the diagnosis of the genus only those characters of North and Middle American species are considered since I have not had an opportunity to study other materials. Synonymy also only applies to names reported or with a direct bearing on names reported from the area in this study.

Key to Species of *Nephroma* in North and Middle America

1. Algal layer with green algae; blue-green algae limited to cephalodia. Section Nephroma ---------- 2
1. Algal layer with blue-green algae; cephalodia absent. Section Nephromium (Nyl.) Stzbgr. ---------- 3
   2. Thallus yellow, cephalodia visible on upper surface, no pubescence on upper surface-- *N. arcticum*
   2. Thallus dull green or brownish, cephalodia internal, visible on lower surface, slight pubescence on upper surface ------- *N. expallidum*
3. Papillae present on lower surface; thallus usually tomentose below ---------- *N. resupinatum*
3. Papillae absent on lower surface; thallus tomentose or etomentose below ---------- 4
   4. Medulla turning pink or red with KOH; medulla usually shades of yellow ---------- *N. laevigatum*
   4. Medulla not turning pink or red with KOH; medulla usually white ---------- 5
5. Thallus with soredia ---------- *N. parile*
5. Thallus without soredia ---------- 6
   6. Thallus with isidia and/or marginal teeth -------- 7
   6. Thallus without isidia or teeth ---------- *N. bellum*
7. Marginal teeth short (0.2 - 0.3 mm.) or lacking; Rocky Mountains and eastward---------- ---------- *N. helveticum* ssp. *helveticum*
7. Marginal teeth long (0.3 - 0.5 mm.); Rocky Mountains & westward & tropics ----- *N. helveticum* ssp. *tropicum*

SECTION NEPHROMA

Section Eunephroma Stizenb. Ber. St. Gall. Naturw. Ges. 1861-1862 : 165. 1862.

Diagnosis: Thallus greenish, algal layer with green algae (Coccomyxa); blue-green algae (Nostoc) present in cephalodia.

Discussion: Stizenberger proposed the name Eunephroma for this section but, according to the present International Code (Lanjouw, 1956), the section containing the type of the genus must bear the generic name unaltered and without author citation.

1. N. ARCTICUM (L.) TORSS.

Lichen arcticus L. Sp. Pl. 1148 . 1753. -- Peltigera arctica (L.) Räuschel, Nomenclat. Bot. ed. 3. 326. 1797. -- Peltidea arctica (L.) Whelbg. Fl. Lappon. 448. 1812. -- Nephroma arcticum (L.) Torss. Enum. Lich. Byssac. Scand. 7. 1843. -- Opisteria arctica (L.) Wain. Ark. Bot. 8 (4): 93. 1909. -- TYPE: Sweden, "Habitat in Suecia boreali, sub Juniperis."

Lichen groenlandicus Oed. Icon. Plant. Daniae 3 (8): 8, tab. 466. 1796. -- Parmelia groenlandica (Oed.) Ach. Meth. Lich. 220 (as sp. dub.). 1803. -- Nephroma arcticum var. groenlandicum (Oed.) Gyel. Ann. Crypt. Exot. 4: 141. 1931.

Lichen polaris Ach. Lich. Suec. Prodr. 163. 1798. -- Nephroma polaris (Ach.) Ach. Lich. Univ. 521. 1810. -- Peltidea polaris (Ach.) Ach. Meth. Lich. 228. 1803. -- Peltigera polaris (Ach.) Spreng. Syst. Veg. 4 (1): 306. 1827. -- Nomen. novum for arcticum plus antarcticum.

Nephroma arcticum f. tuberculimarginatum Gyel. Ann. Crypt. Exot. 4: 128. 1931. TYPE: Alaska, Chilcoot, Coll. Aurel and Arthur Krause.

Nephroma euarctoides Gyel. var. magnilobatum Gyel. Ann. Crypt. Exot. 4: 129. 1931. (= N. euarctoides f. euarctoides). TYPE: Sweden, Harjedalen, Fjällnäs, Coll. Vrang.

Nephroma euarctoides Gyel. var. breutelii Gyel. Ann. Crypt. Exot. 4: 129. 1931. -- Original material: Greenland and Labrador, coll. Breutel No. 204 pp.

Nomenclatural Remarks: Nephroma polaris (Ach.) Ach. was the type species of Nephroma as used by Acharius and he lists Lichen arcticus L. and Lichen antarcticus Jacq. as synonyms. Since these latter species are considered distinct today, N. polaris is treated as a synonym of N. arcticum because arcticum was listed first by Acharius in the original description.

Lichen groenlandicus Oed. was later treated as a synonym of N. polaris by Acharius (1810).

Diagnosis: Thallus 0.19 - 0.32 mm. thick, tomentose below and dark brown to black near the center; lobes broad, crisped or entire; regeneration squamules common. Algal layer

composed of green algae with the blue-green algae restricted to cephalodia near the upper surface of the thallus (see fig. 1). Apothecia large, up to 20 mm. in diameter (rarely 30 mm.), discs light brown; spores sub-fusiform with thin walls (see fig. 11), 23 - 27 μ x 4 - 6 μ. Pycnidia marginal, 0.19 - 0.24 mm. in diameter; conidia cylindrical rods, 3 - 4 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Carotenoid 100%, usnic acid (100%?), nephrin 74%, zeorin 59%. Thallus KOH + very slightly yellow (due to carotenoid). The carotenoid is found in the algal layer and in the medulla as seen by fluorescence under the UV microscope.

Exsiccati examined: Macoun I. 94 (MICH, MSC, UC, WELC); Macoun II. 80 (COLO, FH, MICH, MO, MSC, NY, US, Culberson, Thomson); Tuck. 62 (MICH).

Discussion: This species grows on mossy, wet meadows in protected areas throughout the Arctic and sub-Arctic regions. The southern limit is in southern British Columbia and central New Hampshire. Northern limits of distribution are along the coast of northern Alaska and about 69° N. lat. on Baffin Island (see fig. 31).

2. NEPHROMA EXPALLIDUM (NYL.) NYL.

Nephromium expallidum Nyl. Oefvers. Kgl. Vetensk. - Akad. Förh. 17:295. 1860. -- Nephroma expallidum (Nyl.) Nyl. Flora 48:428. 1865. -- Opisteria expallida (Nyl.) Wain. Ark. Bot. 8 (4): 93 & 94. 1909. TYPE: Norway "In alpe Dovre, Kongsvold, lecta a cel W. P. Schimper."

Diagnosis: Thallus 0.15 - 0.22 mm. thick; lobes often very closely crowded against each other and sometimes regenerate; lower surface darkened toward the center and with variable amounts of tomentum; upper surface glabrous, pruinose or slightly subescent. Algal layer green, giving the thallus a green color; cephalodia internal, near the lower surface (see fig. 2), cephalodial algae blue-green. Apothecia uncommon, up to 10 mm. in diameter with light brown discs; spores with slightly thickened walls (see fig. 12), occasionally very abnormal (see fig. 18), 17 - 21 μ x 5 - 6 μ. Pycnidia marginal, 0.26 - 0.30 mm. in diameter; conidia cylindrical rods, 3 - 4 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Neutral substance B 100%, zeorin 100%, nephrin 97%. Medulla KOH-.

Exsiccati examined: Macoun II. 81 (CAN, FH, MO, NY, US, WELC, Thomson); Macoun II. 83 (CAN, MO, WELC, Culberson); Merrill II. 131 (COLO, F, MICH, MO, NY, WIS).

Discussion: N. expallidum is a fairly distinct species due to its green color, but has been misdetermined in 13% of the collections. It occurs in mossy meadows in very protected areas in the Arctic and in moist valleys in the sub-Arctic. This species has a more temperate distribution than arcticum, but is the least often collected of any Nephroma. It extends from northern Alaska and Baffin Island south to British Columbia and northwestern Ontario (personal correspondence from Mr. Teuvo Ahti, Helsinki, Finland) (see fig. 32). One collection by Macoun from Ottawa, Ontario, is disregarded due to its distance from the normal range of this species, pending further verification by other collections.

SECTION NEPHROMIUM (NYL.) STIZENB.

Nephromium Nyl. Syn. Meth. Lich. 1: 318. 1860 -- Section Nephromium (Nyl.) Stizenb. Ber. St. Gall. Naturw. Ges. 1861-1862: 165. 1862.

3. NEPHROMA RESUPINATUM (L.) ACH.

Lichen resupinatus L. Sp. Pl. 1148. 1753. -- Peltigera resupinata (L.) Schrad. Spicil. Fl. Germ. 1:100. 1794. -- Peltidea resupinata (L.) Ach. Meth. Lich. 289. 1803. -- Nephroma resupinata (L.) Ach. Lich. Univ. 522. 1810 -- Nephromium resupinatum (L.) Arn. Flora 67:231. 1884 -- Opisteria resupinata (L.) Wain. Ark. Bot. 8 (4): 93. 1909.

TYPE: Europe, "Habitat in Europae sylvis."

Peltigera papyracea Hoffm. Deutsch. Fl. 108. 1796. -- Nephroma papyracea (Hoffm.) Röhl. Deutsch. Fl. 3(2):119. 1813. -- Parmelia papyracea (Hoffm.) Wallr. Fl. Crypt. Germ. 3:511. 1831. TYPE: Germany, "In abietum cortice, ramulis dejectus."

Peltigera tomentosa Hoffm. Deutsch. Fl. 108. 1796. -- Parmelia tomentosa (Hoffm.) Wallr. Fl. Crypt. Germ. 3:510. 1831. -- Nephroma tomentosum (Hoffm.) Fw. Jahr. Schles. Gess. für vat. Natur. 2:122. 1850. -- Nephromium tomentosum (Hoffm.) Nyl. Mém. Soc. Sci. Nat. Cherb. 5:101. 1857. TYPE: Germany, "In montosis rupestribus ad terram."

Sticta drummondii Tayl. Lond. Jour. Bot. 6:181. 1847. TYPE: "British North America," Coll. Drummond (FH!).

Nephroma resupinatum f. ramcum Schaer. Enum. Critic. Lic. Eur. 18. tab. 2 f. 3. 1850.

Nephroma resupinatum f. helvum Mass. Sched. Critic. 3:57. 1856. -- Nephromium resupinatum f. helvum (Mass.) Trev. Lich. Venta. No. 155. 1869. -- Nephroma resupinatum var helvum (Mass.) Gyel. Mag. Bot. Lap. 29:23. 1930.

Nephroma resupinatum f. grisescens Gyel. Mag. Bot. Lap. 29:30. 1930. TYPE: Hungary, "Veresko prope Sumjác in comitatu Gömör in Hungaria, Corticola," coll. Lojka.

Nephroma protoresupinatum Gyel. Ann. Crypt. Exot. 4:132. 1931. TYPE: Japan, "Isashiro i Ose," coll. K. Sakuvei No. 94.

Nomenclatural remarks: The type of Peltigera papyracea Hoffm. was seen by Wainio (1888), who identified it as Nephromium tomentosum (Hoffm.). Nyl. (= Nephroma resupinatum (L.) Ach.) For further discussion see Hasselrot (1953).

Nephroma protoresupinatum Gyel. was the name by Gyelnik for N. resupinatum without isidia. The presence or absence of isidia is too variable for the recognition of separate species.

Diagnosis: Grayish-brown thallus, 7 cm. in diameter (rarely up to 9 cm.), 0.17 - 0.19 mm. thick with varying degrees of pubescence on the upper surface; regeneration squamules on the margins of the lobes or from cracks in the thallus; lower surface always tomentose but tomentum occasionally short; papillae always present (sometimes scarce) on lower surface (see fig. 8). Algal layer with blue-green algae; the apothecia 11 mm. in diameter (rarely 15 mm.), discs light brown; spores subfusiform with thin walls (see fig. 13), 21 - 24 μ x 4 - 6 μ. Pycnidia marginal 0.15 - 0.20 mm. in diameter; conidia rod shaped 4 - 5 μ x 1 - 2 μ.

Lichen substances and chemical reactions: None.

Exsiccati examined: Cummings I. 354 (ABSL, CAN, MO, NY, US, Culberson); Cummings II. 276 (F, MICH. MO, NY, PH); Macoun I. 33 (MICH, MSC, NY, TRTC, UC, US, WELC, WIS); Macoun I. 126 (US); Macoun II. 82 (CAN, COLO, MICH, MSC, MO, NY, US,

WELC, Culberson, Thomson); Merrill I. 218 (MICH, NY, US, Culberson). Rel. Farl. 477 (WIS); Tuck. 13 (MICH).

Discussion: Sometimes the white tips of the papillae are hidden in the long tomentum or may be found only on certain parts of the lower surface instead of being uniformly distributed. This species grows on rocks and trees in cool, moist, shady places, such as valleys or rocky cliffs. Its distribution is primarily oceanic with a disjunct area in the Great Lakes. The most northern collections are from near Yakutat, Alaska, the southernmost from southern Oregon and Massachusetts (see fig. 33).

4. NEPHROMA BELLUM (SPRENG.) TUCK.

Peltigera bella Spreng. Syst. Veg. ed 16. 4(1):306. 1827. -- Nephroma bella (Spreng.) Tuck. Boston Jour. Nat. Hist. 3:293. 1840. TYPE: "America borealis," coll. Torrey. (FH!).

Nephromium laevigatum (Ach.) Nyl. var. subtomentellum Nyl. Notiser ur Sällsk. Faun. Fl. Fenn. II. 5:116. 1866. -- Nephroma laevigatum Ach. var. geniunum Korb. f. subtomentellum (Nyl.) Blombg. et Forss. Enum. Pl. Scand. 106. 1880. -- Nephroma subtomentellum (Nyl.) Gyel. Meg. Bot. Lap. 29:25. 1930. -- Nephromium subtomentellum (Nyl.) Gyel. Hedw. 72:2. 1932.

Nephroma filarskyanum Gyel. f. envulgare Gyel. Ann.

Crypt. Exot. 4: 148. 1931. TYPE: Switzerland, "In silvis alpine's ad arbores et saxa," coll. Schaer. Lich. Helv. No. 259. (= N. filarskyanum f. filarskyanum Gyel.).

Nephroma filarskyanum f. castaneum Gyel. Ann. Crypt. Exot. 4:148. 1931. TYPE: Hungary, "Hercynia super. ad arbor."

Nomenclatural Remarks: Nephroma bellum (Spreng.) Tuck. is the oldest name for the species that has been called N. laevigatum Auct. non Ach. and N. subtomentellum (Nyl.) Gyel. Gyelnik (1935) has shown that the medulla of the type specimen of N. laevigatum Ach. is KOH + red which would mean that the KOH- specimens need a different name. Hasselrot (1953) chose N. bellum, but Lamb (1954) chose N. subtomentellum because he had not seen the type of Peltigera bella. I have seen what is probably the isotype of bellum and concur with Hasselrot.

N. filarskyanum Gyel. f. envulgare Gyel. and N. filarskyanum f. castaneum Gyel. are based on minor differences in KOH reactions and thallus color differences which are hardly worthy of taxonomic recognition.

Diagnosis: Thallus brown, 6 cm. in diameter (rarely up to 8), is 0.18 - 0.29 mm. thick; upper surface glabrous or very slightly pubescent; margins entire or with small lobules, rarely with regeneration squamules; lower surface usually rugulose to some extent; isidia and soredia absent.

Algal layer of blue-green algae. Apothecia 10 mm. (rarely up to 15 mm.) in diameter; discs light brown; spores ellipsoidal with thickened walls, 17 - 21 μ x 5 - 6 μ (see fig. 14). Pycnidia marginal, 0.09 - 0.15 mm. in diameter; conidia rod-shaped, 4 - 5 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Zeorin 90%, nephrin 36%, Neutral Substance D 36%, Neutral Substance A 30%, Medulla KOH + light yellow or KOH-.

Exsiccati examined: Cummings I. 116 (MSC, MO, NY, US, WELC, WIS, Culberson); Macoun I. 32 (CAN, FH, NY, US, WELC); Macoun I. 129 (US); Macoun II. 83 (COLO, MICH. Dodge, Thomson); Rel. Farl. 477 (BPI, FH, MICH, NY, UC); Rel. Tuck. 118 (F, FH, MICH, UC, US, WELC, WIS, Culberson, Thomson).

Discussion: N. bellum has been misdetermined 16% of the time due probably to the variability of the pubescence on the lower surface which may vary from none at all to quite pubescent on the same thallus. This species occurs on mossy rocks and on trees in moist shady places. It sometimes covers areas of a square meter or more on rocks, but the average thallus size rarely exceeds 6 cm. The distribution is from western Alaska south to middle California and Greenland south to Virginia (see fig. 34).

5. NEPHROMA HELVETICUM ACH.

Nephroma helvetica Ach. Lich. Univ. 532. 1810. -- Lichen scutatus * Nephroma helvetica (Ach.) Lam. Encyc. Meth. Bot., Suppl. 3:422. 1813. -- Peltigera helvetica (Ach.) Spreng. Syst. Veg. 4(1):305. 1827. -- Nephromium helveticum (Ach.) Nyl. Lich. Nov. Zeland 43. 1888. TYPE: Switzerland, "Habitat in montibus Helvetiae," coll. Schleicher.

5a. NEPHROMA HELVETICUM ACH. SSP. HELVETICUM COMB. NOV.

Nephroma aspera Tuck. Bost. Jour. Nat. Hist. 3:293. 1841. Original material: New England USA, "Ragland in Brookline, Manchester Woods, Medford Hills, Lexington. Also Chelmsford.", coll. Russell (FH !).

Nephroma massachusettsianum Gyel. Ann. Crypt. Exot. 4:136. 1931. TYPE: Massachusetts: "N[ew] B[edford], No. 162." (MO !).

Nephroma plittii Gyel. Ann. Crypt. Exot. 4:137. 1931. TYPE: Maryland, Baltimore Co., "On a small fallen tree trunk, ravine beyond the Caves." coll. Plitt No. 60c. (BPI !, WELC !).

Nomenclatural Remarks: Nephroma aspera Tuck. was described before Tuckerman saw Acharius' helveticum. He later (Tuckerman, 1845) made it a synonym of helveticum.

Nephroma massachusettsianum Gyel. was based on a

difference in pubescence on the upper surface, which I do not consider of specific importance.

Nephroma plittii Gyel. was described as different from N. sublaevigatum (Nyl.) Zahlb. because of an isidiate margin. These "isidia" are actually small, flat regeneration squamules which often appear on this species.

Diagnosis: Thallus brown, about 8 cm. in diameter, 0.10 - 0.16 mm. thick, algae blue-green; upper surface of the thallus with varying amounts of pubescence and small, flat isidia (0.1 - 0.2 mm. wide); margins with indentations, broad lobules or small teeth 0.2 - 0.3 mm. long; lower surface tomentose or pubescent; regeneration squamules common, sometimes covering the whole thallus. Algae blue-green. Apothecia common, about 8 mm. in diameter; discs dark brown, often fringed by the margin of the lobes; spores ellipsoidal with thickened walls which appear to be double (see fig. 15), 20 - 23 μ x 6 - 7 μ. Pycnidia marginal, 0.09 - 0.15 mm. in diameter; conidia rod-like, 3 - 4 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Neutral Substance C 97%, nephrin 78%, medulla KOH-.

Exsiccati examined: Hale 21 (CAN, COLO, MSC, UC, Culberson, Thomson); Macoun I. 32 (MO, MSC, WIS); Macoun I. 33.(MO); Macoun I. 75 (MO, MSC, WIS, NY, UC, US, WELC); Macoun I. 127 (US); Macoun II. 83 (FH, MSC, NY, US); Macoun II. 86

(CAN, COLO, MO, NY, US, WELC, Thomson); Thoms. 54 (F, MICH, MO, WELC, WIS, Thomson); Tuck. 14 (MICH, NY).

Discussion: The tomentum on the lower surface is extremely variable depending on the substratum. If the thallus is in close contact with the rock, there will be practically no tomentum visible, while parts of the same thallus that are raised from the rock will have fairly long tomentum. When on trees, the tomentum varies similarly, but not so drastically. This subspecies grows on mossy rocks and trees in moist, cool places and sometimes covers a square meter or more on a rocky surface in moderate shade. This is the most common and most widespread Nephroma. It is found from Hudson's Bay south to Texas. In the west it gradually grades into helveticum ssp. tropicum, (Idaho, Montana, and Colorado, see fig. 35).

5b. NEPHROMA HELVETICUM ACH. SSP. TROPICUM (MÜLL. ARG.) COMB. NOV.

Nephromium tropicum Müll. Arg. Flora 66:21. 1883. -- Opisteria tropica (Müll. Arg.) Wain. Ark. Bot. 8(4):93. 1909. -- Nephroma tropicum (Müll. Arg.) Zahlb. Cat. Lich. Univ. 3:442. 1925. LECTO TYPE: Hawaiian Islands, coll. Mann.

Nephromium sublaevigatum Nyl. Syn. Lich. 1:321. 1860. -- Opisteria sublaevigata (Nyl.) Wain. Ark. Bot. 8(4):93. 1909. -- Nephroma sublaevigatum (Nyl.) Zahlb. Cat. Lich. Univ. 3:442. 1925. TYPE: Mexico, Pico de Orizaba, coll. Galeotti No. 6960. (CHE, Dodge !).

Nephromium saxicolum B. de Lesd. Lich. Mexique 9. 1914.

-- Nephroma saxicolum (B. de Lesd.) Zahlb. Cat. Lich. Univ. 3:422. 1925. TYPE: Mexico, State of Michoacan, Morelia, coll. Cerro Azul No. 3761.

Opisteria denticulata Wain. Dansk. Bot. Ark. 4(11):14. 1926. -- Nephroma denticulata (Wain.) Gyel. Mag. Bot. Lap. 29:25. 1930. TYPE: Mexico, "Pico, de Orizaba, ad corticem arbores 10000 - 12000 sm."

Nephroma sipeanum Gyel. Ann. Crypt. Exot. 4:147. 1931. TYPE: Oregon, "On oak, Eagle Point, Jackson Co." coll. Gooding (Sipe No. 501) (Sipe !, BPI !, MSC !).

Opisteria endomiltodes Wain. Dansk. Bot. Ark. 4(11):14. 1926. -- Nephroma endomiltodes (Wain.) Zahlb. Cat. Lich. Univ. 8:316. 1932. TYPE: Mexico, "Ad rupem in Pico de Orizaba, 10000 - 12000 sm.".

Nephromium canadense Räs. Ann. Missouri Bot. Gard. 20:17. 1933. -- Nephroma topicum var. canadense (Räs.) Zahlb. Cat. Lich. Univ. 10:286. 1939. TYPE: Canada, British Columbia, on branches of Picea in forest, Aleza Lake.

Nomenclatural Remarks: Nephromium tropicum Müll Arg. was chosen as the type of this subspecies because of the abundance of Hawaiian material collected by Mann to serve as a type collection as opposed to the small scrap representing Nephromium sublaevigatum Nyl. Nephroma tropicum has also been the name most often used for the tropical material. The original material of N. tropicum also includes material from Australia, Celon and Réunion Island. No name has previously been used on the subspecies level in N. helveticum so tropicum

is acceptable, but if it is desired to recognize this group as a species, the correct name would be Nephroma sublaevigatum (Nyl.) Zahlb.

Diagnosis: Thallus brown, about 7 cm. in diameter, 0.25 - 0.29 mm. thick; soredia absent; upper surface more or less pubescent; large, round isidia present usually (0.5 mm. long x 0.2 - 0.5 mm. wide); marginal teeth long and round (0.3 - 0.5 mm. long x 0.3 wide); lower surface of the thallus evenly tomentose. Algae blue-green. Apothecia very common, up to about 10 mm. in diameter with dark brown discs; spores ellipsoidal, walls thickened, 20 -23 μ x 6 - 8 μ (see fig. 16). Pycnidia marginal, 0.10 - 0.18 mm. in diameter; conidia rod-shaped, 3 - 4 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Neutral Substance C 97%, nephrin 78%. Medulla KOH-.

Exsiccati examined: Cummings II. 276 (WELC).

Discussion: This subspecies is separated from ssp. helveticum because of the thicker thallus of ssp. tropicum, longer, rounded isidia and teeth, and by the tendency for longer, more constant tomentum. Subspecies tropicum, thus outlined, has a strictly oceanic-type of distribution. This subspecies grows on trees in cool, shady, moist places along the western coast of North America from northern Alaska

to middle California and appears again in the high mountains in Central America and on Hispaniola (see fig. 35).

6. NEPHROMA LAEVIGATUM ACH. NON AUCT.

Nephroma laevigatum (Ach. Syn. Lich. 242. 1814. -- Peltidea laevigata (Ach.) Somrft. Suppl. Fl. Lapp. 125. 1826. -- Peltigera laevigata (Ach.) Duby, Bot. Gallic. 2:597. 1830. -- Nephromium laevigatum (Ach.) Nyl. Mém. Soc. Sci. Nat. Cherb. 5:101. 1857. -- Opisteria laevigata (Ach.) Wain. Ark. Bot. 8(4):93. 1909. TYPE: Sweden "Habitat in Suecia ad terram locis montosis."

Nephroma lusitanicum Schaer. Enum. Crit. Lich. Europe 323. 1850. -- Nephromium lusitanicum (Schaer.) Nyl. Flora 53:38. 1870. -- Opisteria lusitanica (Schaer.) Wain. Ark. Bot. 8(4):93. 1909. TYPE: Portugal, "Ad arborum truncos in Lusitania."

Nephromium lusitanicum var. hibernicum Nyl. in Leight. Lich. Fl. Gt. Brit. ed. 3. 100. 1879. -- Nephroma lusitanicum var. hibernicum (Nyl. in Leight.) Zahlb. Cat. Lich. Univ. 3:434. 1925. -- Nephroma hibernicum (Nyl. in Leight.) Gyel. Ann. Crypt. Exot. 4:140. 1931. TYPE: Ireland, Doughruagh Mt., coll. Larbalestier.

Nephroma washingtoniense Gyel. Ann. Crypt. Exot. 4:134. 1931. TYPE: Washington, "On limbs of spruces, Pacific Beach." coll. A. S. Foster. Merrill Lich. Exs. No. 181. (CAN!, MICH!, NY!, US!).

Nomenclatural Remarks: Nephroma laevigatum Ach. non auct. -- see under N. bellum.

Nephroma washingtoniense Gyel. was described because it had a white medulla instead of yellow, but was still KOH + red. This description fits the description of Nephromium lusitanicum var. hibernicum Nyl. in Leight, but apparently Gyelnik did not think the description of hibernicum was complete enough to be able to identify his specimen with it. He described washingtoniense on page 134 and raised hibernicum to a species on page 140. Since the medulla color varies from white to yellow, these names are synonyms of N. laevigatum.

Diagnosis: Thallus yellow-brown or brown, about 9 cm. in diameter (rarely up to 12 cm.), 0.07 - 0.14 mm. thick; upper surface glabrous, sometimes with isidia; regeneration squamules usually present; medulla white to dark yellow, lower surface with little pubescence. Algae blue-green. Apothecia frequent, about 8 mm. in diameter, discs light brown and sometimes discolored; spores ellipsoidal, with thickened walls, often appearing double; 17 - 20 μ x 5 - 7 μ (see fig. 17). Pycnidia marginal 0.16 - 0.23 mm. in diameter; conidia rod-shaped, 4 - 5 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Nephromin 100%. Medulla KOH+ pink to deep red violet.

Exsiccati examined: Cummings I. 219 (CAN, MO, MSC, NY, US, WELC, WIS, Culberson); Cummings II. 149 (F, MICH, NY, PH, US, WELC); Macoun I. 32 (UC); Macoun I. 128 (US); Macoun I. 159 (MICH, MO, MSC, NY, TRTC, UC, US, WELC, WIS); Macoun II. 85 (CAN, COLO, MO, NY, US, WELC, Thomson); Merrill I. 143 (CAN, MICH, NY, US); Merrill I. 181 (CAN, MICH, NY, US).

Discussion: This species was misdetermined 18% of the time. The yellow medulla color is not diagnostic because with varying amounts of nephromin the color of one thallus will be white when little nephromin is present, but dark yellow when more nephromin is found in the medulla. A more sensitive test for the anthraquinone nephromin is KOH which turns pink to deep red violet.

This species is found on trees and rocks in oceanic areas in North America. It has a similar habitat in Europe (Degelius, 1935; Fagerstrom, 1954). This is by far the most oceanic species of Nephroma in North and Central America. It occurs from British Columbia to California and from Labrador to Massachusetts (see fig. 36). There is one collection of Macoun's from Brighton, Ontario, but since this is the only collection away from the oceans and since Macoun's labels were often mixed up, this collection is being ignored. If, however, more collections are found from the Brighton area, Macoun's collection will have to be considered.

7. NEPHROMA PARILE (ACH.) ACH.

Lichen parilis Ach. Lich. Suec. Prod. 164. 1798. -- Peltidea parilis (Ach.) Ach. Meth. Lich. 289 (as sp. dub.). 1803. -- Nephroma parilis (Ach.) Ach. Lich. Univ. 522. 1810. -- Lichen scutatus * Nephroma parilis (Ach.) Lam. Encycl. Meth. Bot. Suppl. 3:422. 1813. -- Peltigera parilis (Ach.) Spreng. Syst. Veg. 4(1):305. 1827. -- Nephromium laevigatum (Ach.) Nyl. var. parile (Ach.) Nyl. Syn. Lich. 1:320. 1860. -- Nephroma laevigatum (Ach.) Ach. f. parile (Ach.) Mudd, Manual British Lich. 81. 1861. -- Nephromium parile (Ach.) Nyl. Flora 68:47. 1855. -- Nephromium laevigatum (Ach.) Nyl. var. laevigatum (Ach.) Boist. subvar. parile (Ach.) Boist. Nouv. Fl. Lich. 2:82. 1903. -- Opisteria parilis (Ach.) Wain. Ark. Bot. 8(4):93. 1909. TYPE: Sweden; "Habitat ad latera montium."

Nephroma parile f. hybridum Gyel. Ann. Crypt. Exot. 4:142. 1931. TYPE: Hungary, Magas Tatra, coll. Timkó No. 2717.

Nephroma subparile Gyel. Mag. Bot. Lap. 29:24. 1930. -- Nephromium subparile (Gyel.) Räs. Ann. Missouri Bot. Gard. 20:16. 1933. TYPE: Japan, Sagalien, coll. Abbe Faurie No. 378.

Nomenclatural Remarks: Nephroma parile (Ach.) Ach. f. hybridum Gyel. was described by Gyelnik because it had isidia-like soredia. The soredia in N. parile are granular and sometimes look like isidia, but are not different enough for

taxonomic recognition.

Nephroma subparile Gyel. is glabrous instead of pubescent, a difference which falls within the normal variability of the species N. parile.

Diagnosis: Thallus brown, about 8 cm. in diameter (rarely up to 14 cm.), 0.12 - 0.19 mm. thick; granular soredia present in bluish-gray maculiform patches on the upper surface or on the margins; lower surface variably pubescent, rugulose; regeneration squamules sometimes present. Algae blue-green. Mature apothecia not known. Pycnidia marginal, rare, 0.18 - 0.32 mm. in diameter; conidia rod-shaped, 4 - 5 μ x 1 - 2 μ.

Lichen substances and chemical reactions: Neutral Substance A 99%, zeorin 51%, nephrin 5%. Medulla KOH + yellow or KOH-.

Exsiccati examined: Macoun I. 32 (MICH); Macoun I. 76 (MO, MSC, NY, UC, US, WELC, WIS); Macoun II. 84 (CAN, NY, US, WELC, Thomson).

Discussion: This species is easily distinguished by its soredia and was only misdetermined 6% of the time. It may at times be confused with Parmelia subargentifera, but the Parmelia has green algae, more powdery soredia, medulla is C + red, and there are minute hairs near the tips of the

lobes on the upper surface which give the thallus a dusty appearance. N. parile is found commonly on rocks, or on trees, often associated with Leptogium in moist, shaded valleys. Its distribution is from southern Alaska to Washington and Idaho, in New Mexico and Colorado, and from Greenland to Tennessee (see fig. 37).

VIII

FURTHER STUDY

A. Lichen substances. Because of the limiting factors of time and large quantities of material, exact identification of the lichen substances in Nephroma have not been attempted in this treatment of the genus. Further work along the lines already begun, in order to identify these substances with known types or describe new ones, seems to be highly desirable. Ultraviolet absorption spectra of the purified substances is an additional tool that should be used in substance characterization. More reagents should be tried to bring out the neutral substances in the chromatographic analyses.

B. Algal and spore culture. This area has not been touched in this study or in the studies of other authors. The alga from each species should be brought into uni-algal culture and identified. The spores from each species should also be germinated and the germination patterns studied.

C. Southern Hemisphere species. There are indications that there are more species of Nephroma in the Southern Hemisphere than in the Northern Hemisphere. A continuation of the study of this genus would logically lead next to an inclusion of the rest of the species. Herbarium

specimens should be borrowed and field work is almost a necessity since many of the species are known from only two or three collections.

D. Phylogeny of Nephroma. In this study no attempt has been made to set up a phylogenetic sequence because it would not be wise to further section the genus or propose the phylogeny without knowledge of the Southern Hemisphere species. At present, I see no clear-cut sequence of development within the genus nor do I see the true relationship of this genus to closely related families. These answers should be forthcoming after further study of the world's Nephroma.

IX

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X

APPENDIX

Index to Exsiccati

Cummings I. 116 (MO, MSC, NY, US, WELC, WIS, Culberson) = *N. bellum*.

Cummings I. 219 (CAN, MO, MSC, NY, US, WELC, WIS, Culberson) = *N. laevigatum*.

Cummings I. 354 (ABSI, CAN, MO, NY, US, Culberson) = *N. resupinatum*.

Cummings II. 149 (F, MICH, NY, PH, US, WELC) = *N. laevigatum*.

Cummings II. 276 (F, MICH, MO, NY, PH) = *N. resupinatum*.

Cummings II. 276 (WELC) = *N. helveticum* ssp. *tropicum*.

Hale 21 (CAN, COLO, MSC, UC, Culberson, Dodge, Thomson) = *N. helveticum* ssp. *helveticum*.

Macoun I. 32 (CAN, PH, NY, US, WELC) = *N. bellum*.

Macoun I. 32 (MO, MSC, WIS) = *N. helveticum* ssp. *helveticum*.

Macoun I. 32 (UC) = *N. laevigatum*.

Macoun I. 32 (MICH) = *N. parile*.

Macoun I. 33 (MSC, NY, TRTC, UC, US, WELC, WIS) = *N. resupinatum*

Macoun I. 33 (MO) = *N. helveticum* ssp. *helveticum*.

Macoun I. 75 (MO, MSC, NY, UC, US, WELC, WIS) = *N. helveticum* ssp. *helveticum*.

Macoun I. 76 (MO, MSC, NY, UC, US, WELC, WIS) = *N. parile*.

Macoun I. 94 (MICH, MSC, UC, WELC) = *N. arcticum*.

Macoun I. 126 (US) = *N. resupinatum*

Macoun I. 128 (US) = N. laevigatum.

Macoun I. 129 (US) = N. bellum.

Macoun I. 159 (MICH, MO, MSC, NY, TRTC, UC, US, WELC, WIS) = N. laevigatum.

Macoun II. 80 (COLO, FH, MICH, MO, MSC, NY, US, Thomson) = N. arcticum.

Macoun II. 81 (CAN, FH, MO, NY, US, WELC, Thomson) = N. expallidum.

Macoun II. 82 (CAN, COLO, MICH, MO, MSC, NY, US, WELC, Culberson, Thomson) = N. resupinatum.

Macoun II. 83 (CAN, MO, WELC, Culberson) = N. expallidum.

Macoun II. 83 (COLO, MICH, Dodge, Thomson) = N. bellum.

Macoun II. 83 (FH, MSC, NY, US) = N. helveticum ssp. helveticum.

Macoun II. 84 (CAN, NY, US, WELC, Thomson) = N. parile.

Macoun II. 85 (CAN, COLO, MO, NY, US, WELC, Thomson) = N. laevigatum

Merrill I. 143 (CAN, MICH, NY, US) = N. laevigatum.

Merrill I. 181 (CAN, MICH, NY, US) = N. laevigatum.

Merrill I. 218 (MICH, NY, US, Culberson) = N. resupinatum

Merrill II. 131 (COLO, F, MICH, MO, NY, WIS) = N. expallidum.

Rel. Farl. 477 (WIS) = N. resupinatum.

Rel. Farl. 477 (BPI, FH, MICH, NY, UC) = N. bellum.

Rel. Tuck. 118 (F, FH, MICH, UC, US, WELC, WIS, Culberson, Thomson) = N. bellum.

Thomson 54 (F, MICH, MO, WELC, WIS, Thomson) = N. helveticum ssp. helveticum.

Tuck. 13 (MICH) = N. resupinatum.

Tuck. 14 (MICH, NY) = N. helveticum ssp. helveticum.

Tuck. 62 (MICH) = N. arcticum.

PLATE I

Fig. 1. Cephalodium of N. arcticum (L.). Torss. (Imshaug no. 6816). CA: cephalodial algae (Nostoc), H: densely branched hyphae of cephalodium, B: area of dense hyphae around cephalodium, UC: upper cortex, TA: thallus algae (Coccomyxa), M: medulla, LC: lower cortex, T: short, matted tomentum.

Fig. 2. Cephalodium of N. expallidum (Nyl.) Nyl. (Thomson no. 3367). UC: upper cortex, TA: thallus algae (Coccomyxa), M: medulla, LC: lower cortex, B: area of dense hyphae around cephalodium, CA: cephalodial algae (Nostoc), H: densely branched hyphae and some dead algal cells of cephalodium.

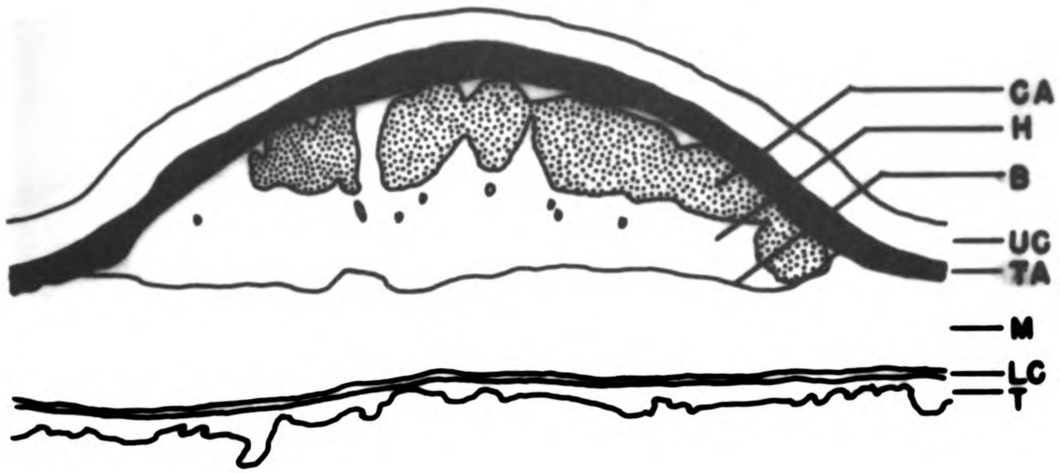
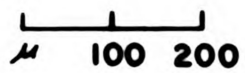


Fig. 1



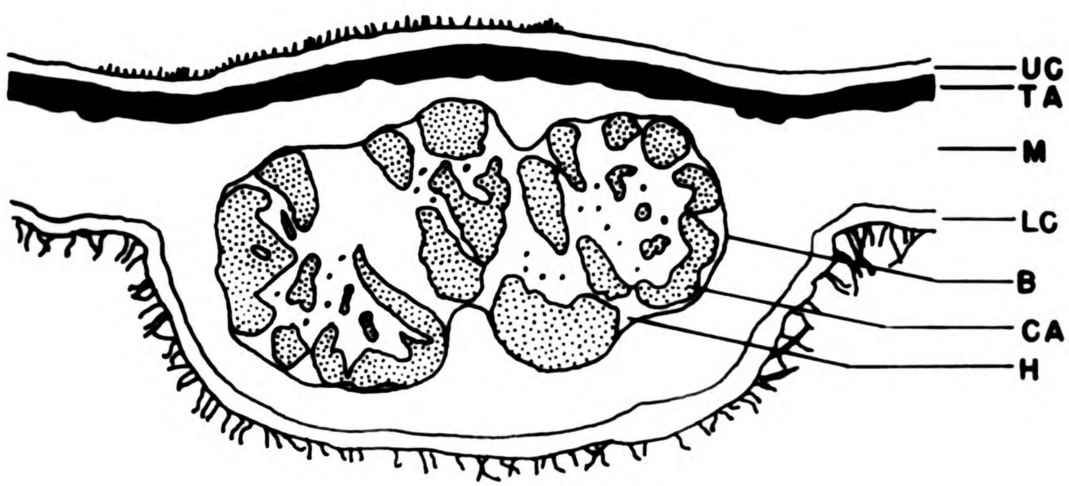


Fig. 2

PLATE II

Detail of tissues in thallus sections of *Nephroma* as in *N. expallidum* (Nyl.) Nyl. (Thomson no. 3367).

Fig. 3. Paraplectenchymatous cortex with nearly isodiametric "cells".

Fig. 4. Algal layer of thallus (*Coccomyxa*).

Fig. 5. Loose hyphae of medulla.

Fig. 3

Fig. 4

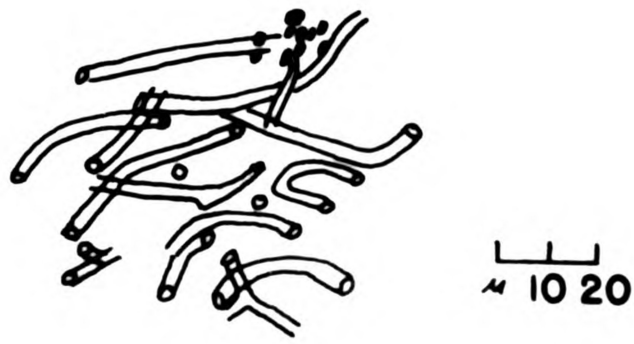


Fig. 5

PLATE III

Fig. 6. Soredia of N. parile (Ach.) Ach. (Lepage no. 6184). S: slightly corticate soredia, UC: upper cortex, A: algal layer (Nostoc), M: medulla, LC: lower cortex, P: pubescence on lower surface.

Fig. 7. Margin of apothecium of Nephroma showing thickening of lower cortex at edge of hymenium. UC: upper cortex, A: algal layer (Coccomyxa), M: medulla, LC: lower cortex, HT: hypothecium, HM: hymenium. Drawing from N. expallidum (Nyl.) Nyl. (Thomson no. 3367).

Fig. 6

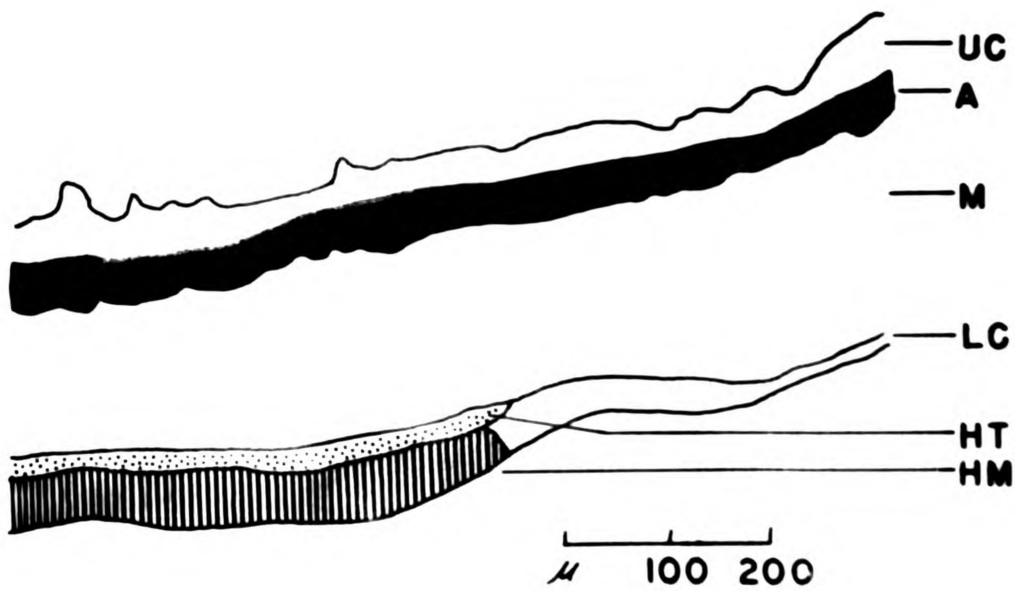


Fig. 7

PLATE IV

Fig. 8. A median section of papilla of N. resupinatum (L.) Ach. showing continuous lower cortex. UC: upper cortex, A: algal layer (Nostoc), M: medulla, LC: lower cortex, PA: papilla.

Fig. 9. A median section of a pseudocyphella of Pseudocyphellaria showing discontinuous lower cortex and the medulla growing out through the break. UC: upper cortex, A: algal layer, M: medulla, LC, T: lower cortex and matted tomentum.

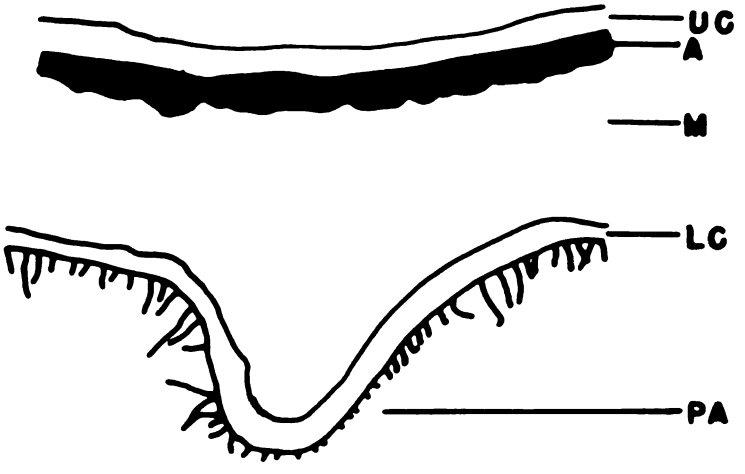


Fig. 8

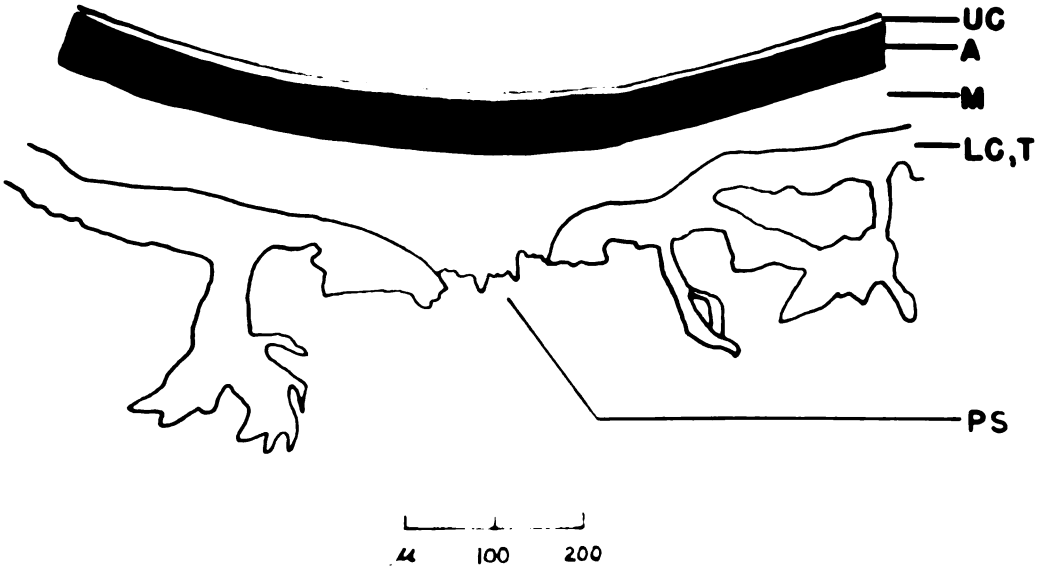


Fig. 9

PLATE V

Fig. 10. Ascus tips showing lack of apparatus on N. resupinatum (from Gelinou 1955).

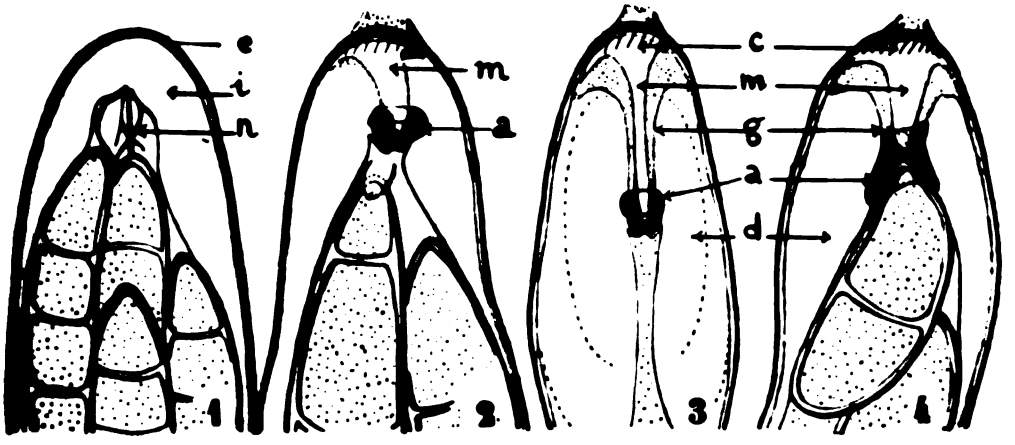


Fig. 1 à 4 : Système apical de *Nephroma resupinatum* (1), de ***Peltigera scutata*** (2), de ***P. venosa*** (3), **et de *Solorina crocea*** (4). (*e*, **tunique externe**; *i*, **tunique interne**; *n*, **nasse apicale**; *c*, **coussinet**; *m*, **manubrium**; *g*, **gaine amyloïde du manubrium**; *a*, **anneau**; *d*, **partie latérale du dôme apical**.)

Fig. 10

PLATE VI

Fig. 11. Spores of N. arcticum (L.) Torss. (Macoun, Aug. 1904).

Fig. 12. Spores of N. expallidum (Nyl.) Nyl. (Macoun, July 1902).

Fig. 13. Spores of N. resupinatum (L.) Ach. (Macoun, Can. Lich. #82).

Fig. 14. Spores of N. bellum (Spreng.) Tuck. (Setchell, July 1899).

Fig. 15. Spores of N. helveticum Ach. ssp. helveticum (Macoun, July 1902).

Fig. 16. Spores of N. helveticum Ach. ssp. tropicum (Müll. Arg.) Wetm. (Spruce, Lich. Amaz. et Andini no. 416).

Fig. 17. Spores of N. laevigatum Ach. (Herre, May 1932 & July 1949).

Fig. 18. Abnormal spores of N. expallidum (Nyl.) Nyl. (Macoun, Can. Lich. #81).

Fig. 19. Germinating spores of N. helveticum Ach. ssp. helveticum (Macoun, July 1902).

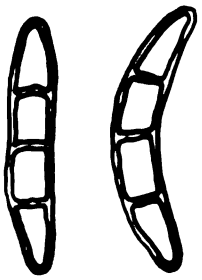


Fig. 11

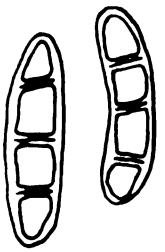


Fig. 12

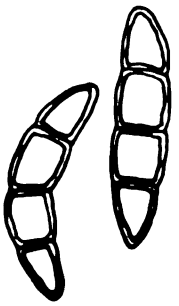


Fig. 13

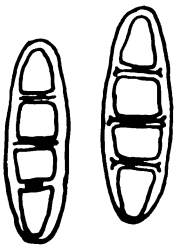


Fig. 14

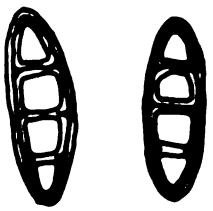


Fig. 15

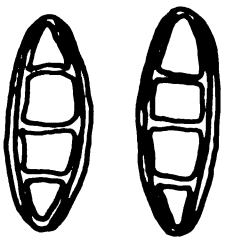


Fig. 16

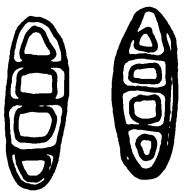
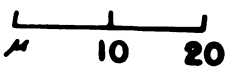


Fig. 17



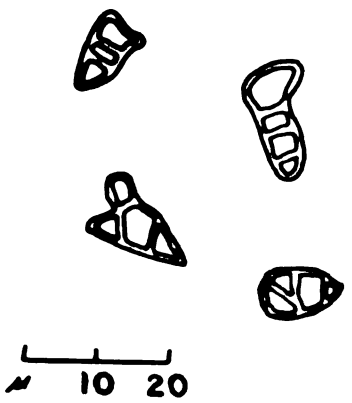


Fig. 18

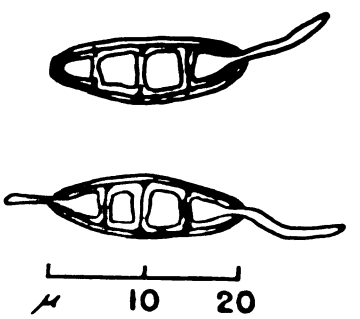


Fig. 19

PLATE VII

Fig. 20. Endobasidal conidiophore (N. helveticum Ach. ssp. tropicum (Müll. Arg.) Wetm. - Cantlon and Gillis no. 57-2130).

Fig. 21. Endobasidial conidiophores (N. helveticum Ach. ssp. tropicum (Müll. Arg.) Wetm. - Dodge no. 7785).

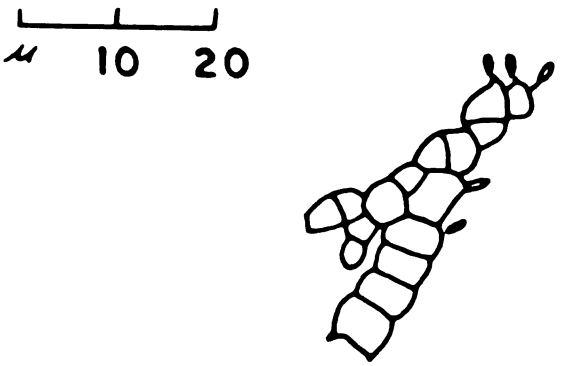


Fig. 20

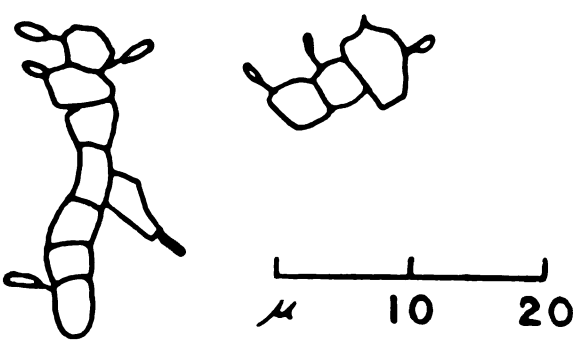


Fig. 21

PLATE VIII

Fig. 22. Neutral Substance A recrystallized in G.A.An. (*N. parile* (Ach.) Ach.).

Fig. 23. Neutral Substance B recrystallized in G.A.An. (*N. expallidum* (Nyl.) Nyl.)

Fig. 24. Neutral Substance C recrystallized in G.A.An. (*N. helveticum* Ach.)

Fig. 25. Neutral Substance D recrystallized in G.A.An. (*N. bellum* (Sprong.) Tuck.)

Fig. 22 100μ

Fig. 23 100μ

Fig. 24 100μ

Fig. 25 10μ

PLATE IX

Fig. 26. Zeorin recrystallized in G.A.An. (N. expallidum (Nyl.) Nyl.)

Fig. 27. Nephrin recrystallized in G.A.An. (N. expallidum (Nyl.) Nyl.)

Fig. 28. Carotenoid recrystallized in G.A.An. (N. arcticum (L.) Torss.)

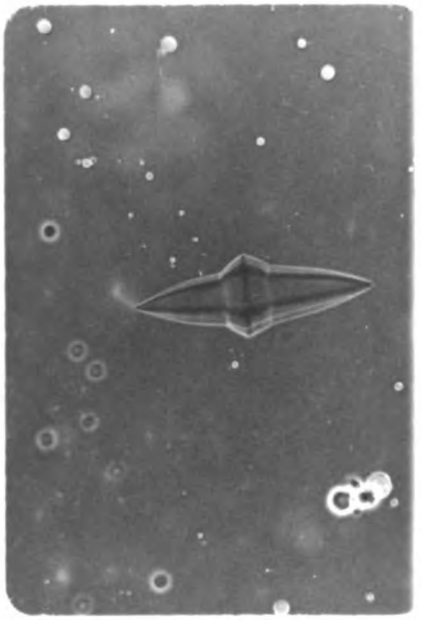


Fig. 26

100μ

Fig. 27

Fig. 28

100μ

PLATE X

Fig. 29. Tomentum on lower surface of N. resupinatum (L.) Ach. (Wetmore no. 1700) showing thick walls.

Fig. 30. Medullary hyphae with thin walls and septa. (N. exoallidum (Nyl.) Nyl. - Thomson no. 3367).

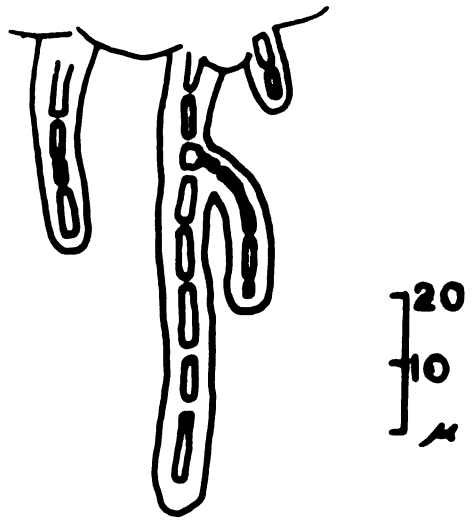


Fig. 29

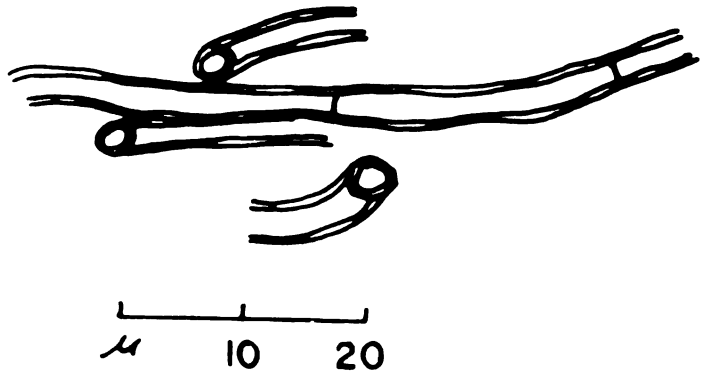


Fig. 30

PLATE XI

Fig. 31. Distribution map of N. arcticum (L.) Torss. in North and Middle America. Open circles represent records of unseen specimens (Ahti personal correspondence, Dahl et al, 1937; Dahl, 1950; Lynge, 1932 and 1937).

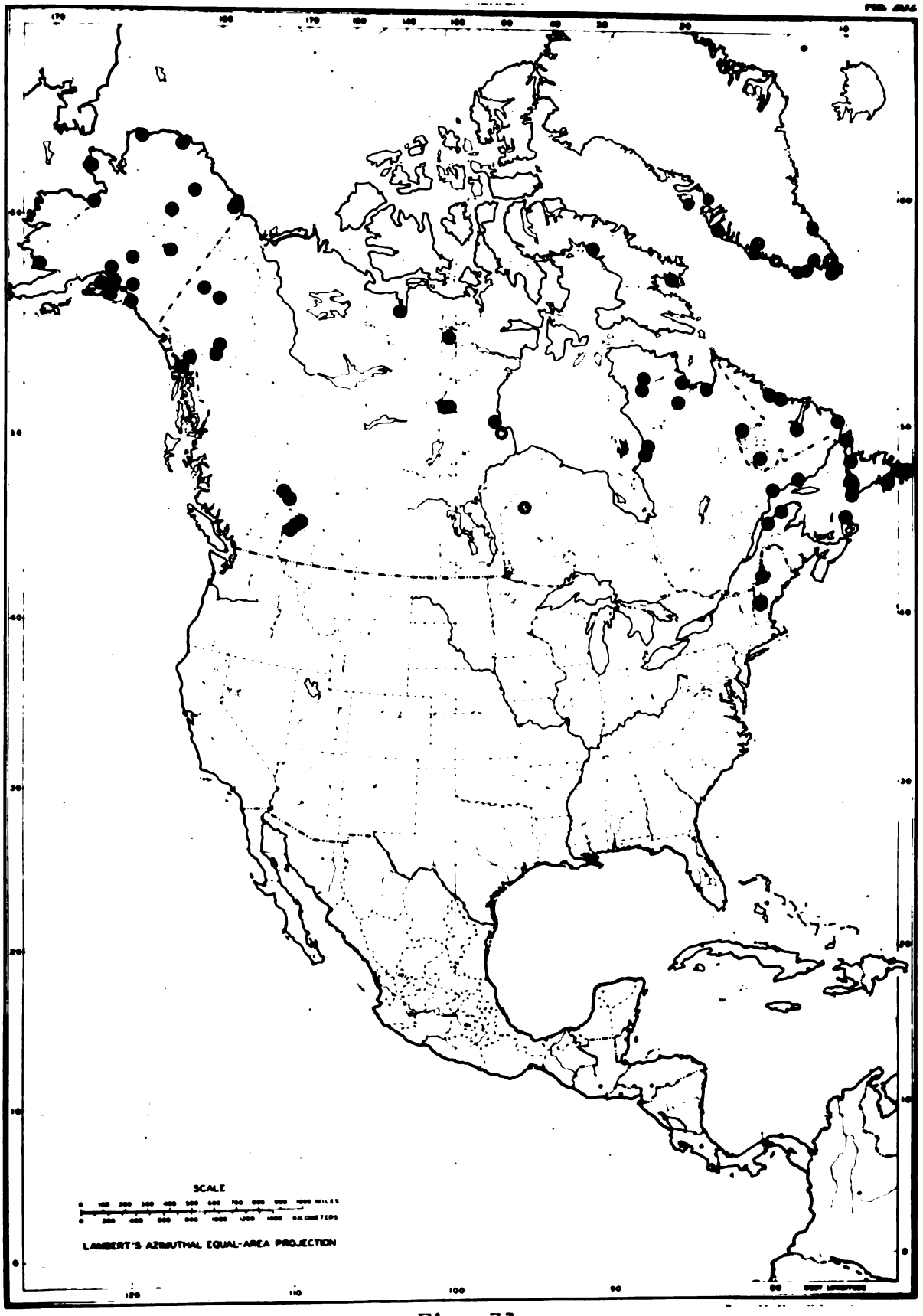


Fig. 31

PLATE XII

Fig. 32. Distribution map of N. expallidum (Nyl.) Nyl. in North and Middle America. Open circles represent records of unseen specimens (Dahl, 1950; Lynge 1937).

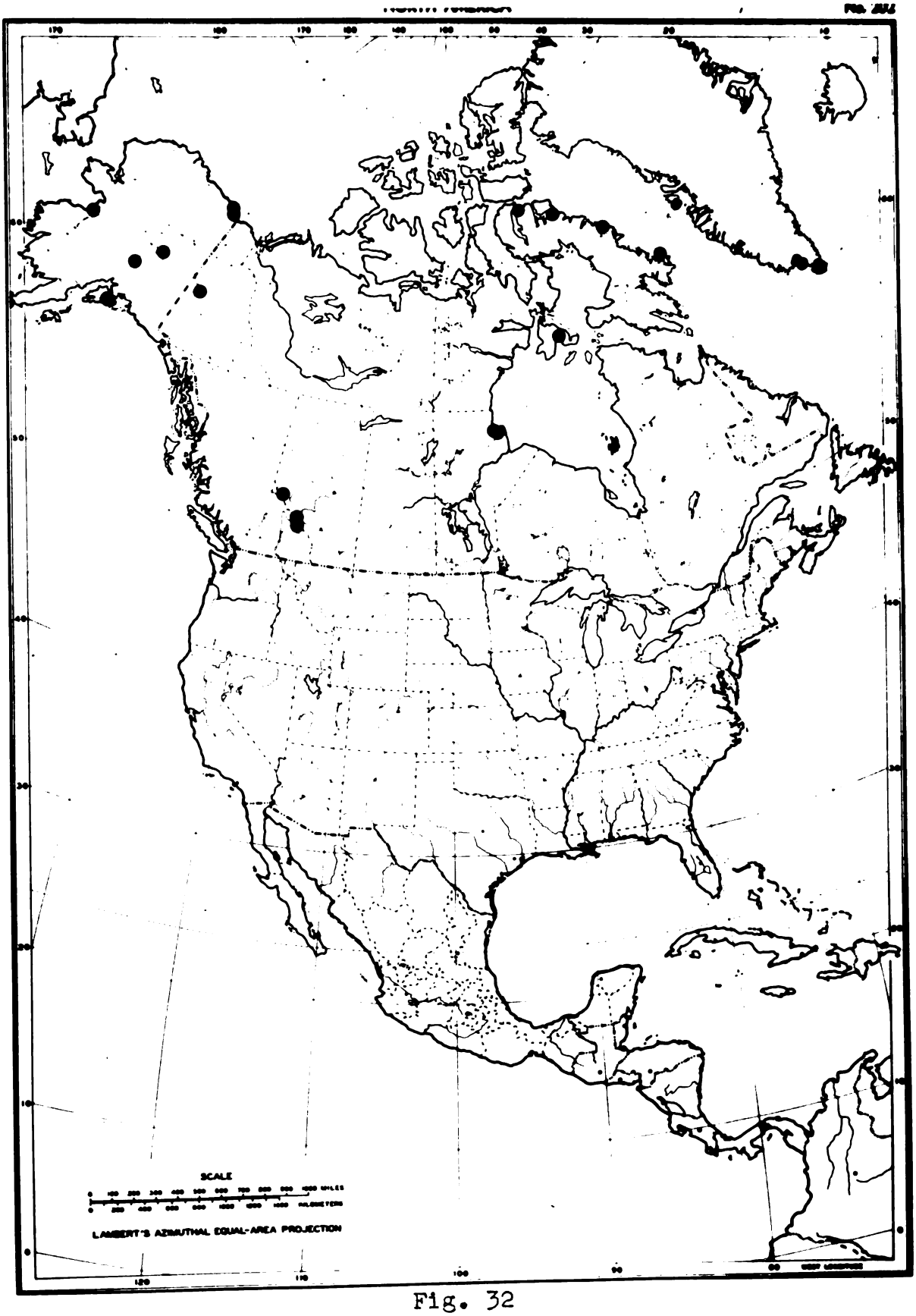


Fig. 32

PLATE XIII

Fig. 33. Distribution map of N. resupinatum (L.) Ach. in North and Middle America. Open circles represent records of unseen specimens (Dahl, 1950).

PLATE XIV

Fig. 34. Distribution map of N. bellum (Spreng.) Tuck. (= N. laevigatum auct non Ach.) in North and Middle America. Open circles represent records of unseen specimens (Dahl et al, 1937; Dahl, 1950).

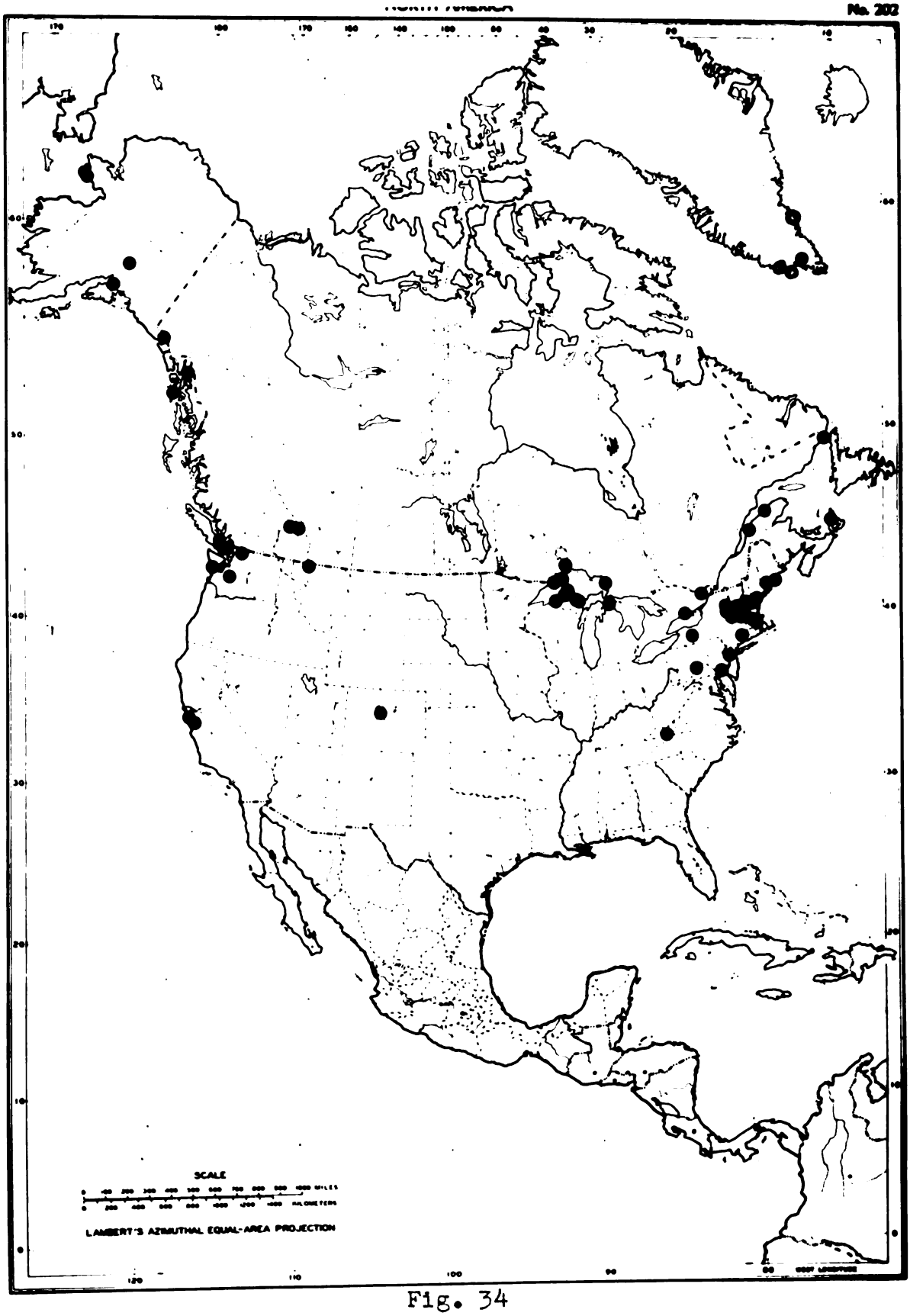


Fig. 34

PLATE XV

Fig. 35. Distribution map of N. helveticum Ach. in North and Middle America. Open circles represent ssp. tropicum (Müll. Arg.) Wetm.

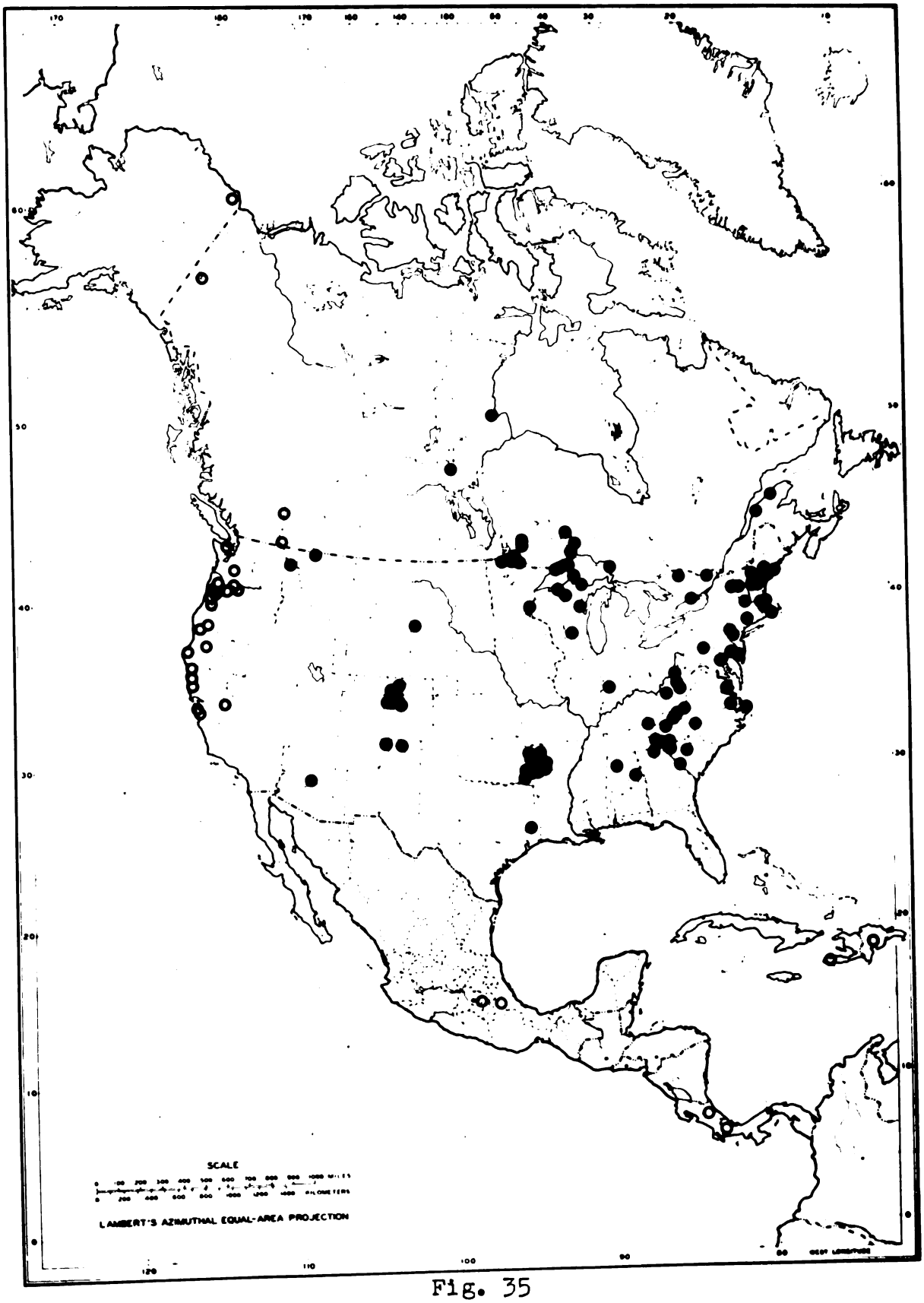


Fig. 35

PLATE XVI

Fig. 36. Distribution map of N. laevigatum Ach. non auct. in North and Middle America.

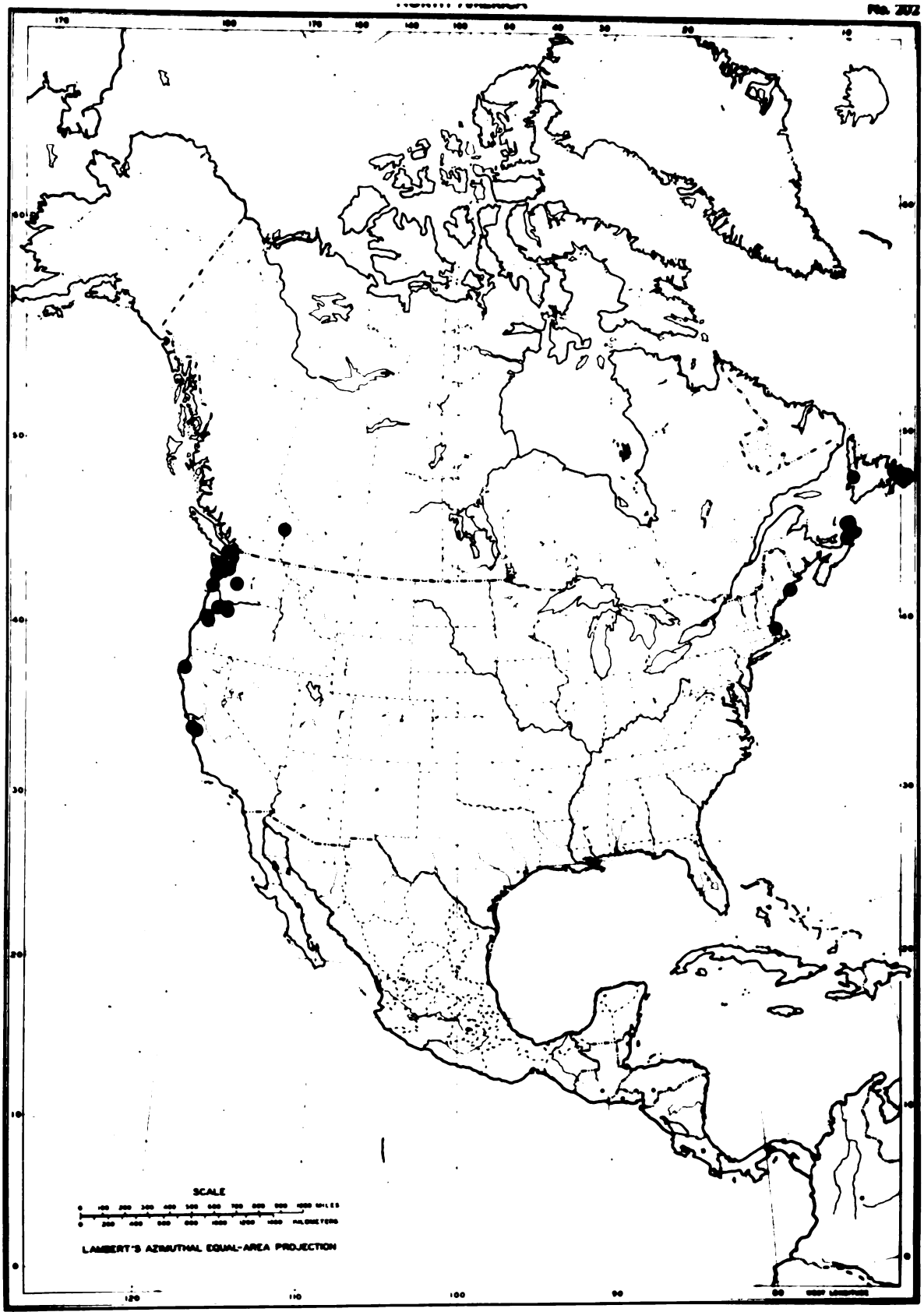


Fig. 36

PLATE XVII

Fig. 37. Distribution map of N. perile (Ach.) Ach. in North and Middle America. Open circles represent records of unseen specimens (Dahl et al, 1937; Dahl, 1950).

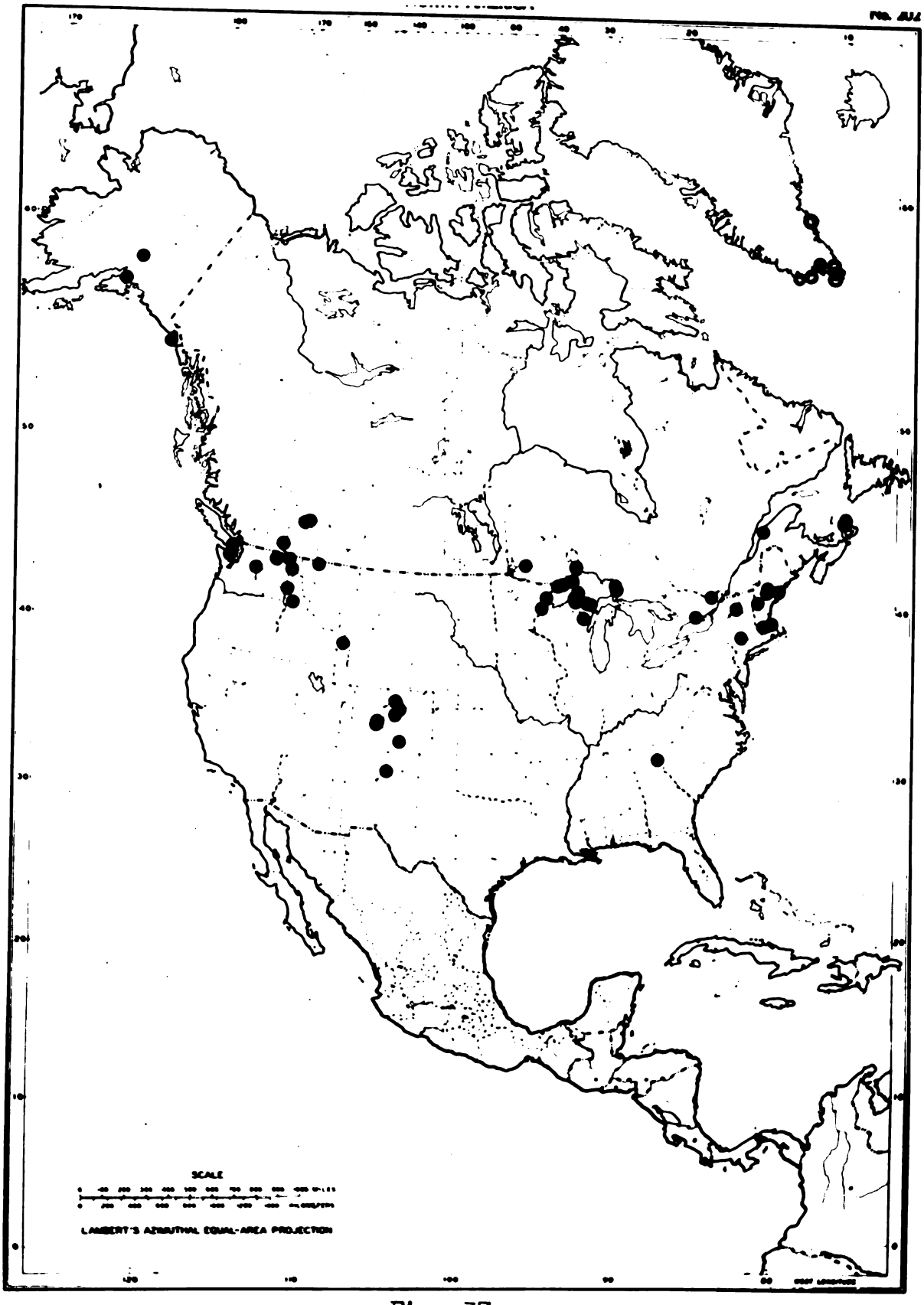


Fig. 37