1977

Oil-Bodies of Selected Leafy Liverworts of East-Central Illinois

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OIL-BODIES OF SELECTED LEAFY LIVERWORTS

OF EAST-CENTRAL ILLINOIS

(TITLE)

BY

Steven Monroe Martin

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY

CHARLESTON, ILLINOIS

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YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING

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OIL-BODIES OF SELECTED LEAFY LIVERWORTS

OF EAST-CENTRAL ILLINOIS

BY

STEVEN MONROE MARTIN

B. S. in Botany, Eastern Illinois University

ABSTRACT OF A THESIS

Submitted in partial fulfillment of the requirements
of the degree of Master of Science in Botany at the Graduate School
of Eastern Illinois University

Charleston, Illinois
1977

Oil-bodies are distinct and varied structures found only in the Hepaticae and with particular frequency in the Jungermanniales. Untill relatively recently the oil-body has been virtually ignored by liverwort morphologists and taxonomists.

This study includes descriptions and photomicrographs of the oil-bodies of 23 species and 14 genera in 9 familes of leafy liverworts of east-central Illinois. Diagnostic characteristics recorded for each species include the number of oil-bodies per cell, size range of the oil-bodies, color, shape, texture and arrangement of the oil-bodies within the cell. It was found that the familes Lepidoziaceae, Calypogeiaceae, Jungermanniaceae, Scapaniaceae, Porellaceae and Frullaniaceae are composed of genera and species that show homogenous oil-body characteristics. The Ptilidaceae contain two species with oil-bodies of different shapes, colors and numbers per cell. In the Harpanthaceae it was found that colors vary among the three species observed along with widely varying textures. Only one species from the Plagiochilaceae was studied.

Because oil-bodies are easy to find in fresh material and contain several distinguishing characteristics, their morphological descriptions can aid taxonomists and phylogeneticists in the systematic arrangements of leafy liverworts and in the construction of keys for their identification. Descriptive and taxonomic works and morphological studies should include detailed oil-body descriptions. Oil-bodies are unique structures that cannot be ignored.

ACKNOWLEDGMENTS

I must express my gratitude to Dr. Charles B. Arzeni for initial inspiration and continuing advice during my graduate research. I am also grateful to Dr. John E. Ebinger and Dr. Wesley C. Whiteside for assisting with this thesis and for their valuable criticism of it. Thanks also goes to Dr. John M. Speer for his advice in photomicrographic techniques and to Mr. J. D. Martin for showing me the darkroom and turning me loose. Special thanks go to Margaret M. Rehagen for all her help and fresh ideas when I had run out.

Last of all I wish to thank my fellow Botany graduate students for their special friendship which has made the entire job a lot easier.

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INTRODUCTION

For the lover of all things natural, no group of organisms in the plant kingdom is more uniquely beautiful and truly pleasing to observe than that group of plants known as the leafy liverworts. If the careful and conservative observer visited any of several wooded areas, moist ravines or sandstone outcroppings of east-central Illinois, he or she could observe with the hand lens the exciting variety in the graceful lines of liverwort growth forms. With the aid of the dissecting scope leaf shapes, leaf margins and branching patterns become more distinct and considerably varied. Smaller structures such as feathery bifid under-lobes, cilia, paracysts, bulging sac-like lobules and perianths come into focus. With further magnification under the compound microscope even deeper secrets are revealed. Among these are variations in aero-lation, cell wall thickenings, trigones, and gemmae.

Within the cell the most outstanding features are the oil-bodies. They vary in size, form, color, markings and texture and hang planet-like in the cytoplasm. Dwarfing the chloroplasts in most cases, the oil-bodies are unique structures that are found nowhere else in the plant kingdom.

Despite the curious beauty and unique characteristics of oil-bodies, they have been repeatedly ignored in many descriptive and illustrative taxonomic works. It is the purpose of this study to observe, describe and photograph the oil-bodies of selected leafy liverworts of east-central Illinois.

Before descriptions and photographs can be adequately appreciated, however, a literature survey must be made and an understanding of general oil-body morphology, origin, development, function, chemistry, distribution and taxonomic significance must be accomplished.

LITERATURE REVIEW

The first written account of oil-bodies was in 1834 by I. W. P. Huebener when he described them in Leptoscyphus taylorii. Later M. Mirbel (1835) published an article in France which described the oil-bodies of Marchantia sp. as white irregular particles in the thallus of the plant. C. M. Gottsche (1943) mentioned the oil-bodies of Haplomitrium hookerii in his anatomical and physiological study of that species and was the first to name them Zellemblaeschem. Perhaps the first classical account of oil-bodies was in 1874 by W. Pfeffer. He was one of the few early investigators to do critical light microscope work with the oil-bodies of liverworts, and he also gave them the name oil-bodies (ölkörper), presently the most commonly used term. Many other papers were produced in the late nineteenth century on this subject or closely related subjects by several authors. Some of them are G. von Holle (1857), J. H. Wakker (1888), G. Hieronymus (1892), and von Kuester (1894).

At the turn of the twentieth century A. J. M. Gargeanne (1903) published "Die Ölkörper der Jungermanniales," the first account of oil-body morphology of the Jungermanniales. During the same year a paper by C. E. J. Lohmann appeared on the chemistry of liverworts with particular emphasis on oil-bodies. These two men were followed by several other investigators such as Mueller (1905), M. F. Rivett (1909), A. Kozlowski (1921), A. Meyer (1920), A. Guillermond (1922), P. Dombray (1926), E. Bergdolt (1926), P. Gavaudan (1927), W. Zwickel (1932), and

C. Zirkle (1932). Following his first article on oil-bodies in 1905, K. Mueller published a more comprehensive article "Untersuchagen Über die Ölkörper der Lebermoose" in 1939. In this study, which is now considered the classical account on oil-bodies, Mueller treated their physiology, function, origin, distribution, taxonomy and chemistry.

More recent researchers include B. Slavik (1950) on specific bodies of hepatics, K. Yamanda (1969, 1970) on the oil-bodies of Metacalypogeia and Frullania, R. Udar (1970, 1971) who described the oil-bodies of Indian liverworts, and C. Suire (1970) who treated their ultrastructure. Perhaps the best recent descriptive and taxonomic studies have been done by R. M. Schuster and S. Hattori. Working together they produced in 1954 a complete, comprehensive and well illustrated study of oil-bodies in the complex family Lejeuneaceae. Earlier in 1951 and 1953 Hattori published two articles on oil-bodies of Japanese hepatics. Another Japanese bryologist who was influenced by Hattori, H. Inoue (1967), wrote a paper on the oil-bodies of Malayan liverworts. This paper contains the only light microscope photographs of oil-bodies publsihed. R. M. Schuster (1966, 1969, 1974) in his three volume work The Hepaticae and Anthocerotae of North America gives the oil-bodies of North American liverworts their most comprehensive taxonomic treatment. His illustrations are unsurpassed in their detail and accuracy.

K. Pihakaski (1966, 1967, 1972) made several studies of the oil-body ultrastructure using electron microscopy to unravel the details of their origin and development. These works include excellent and informative electron photomicrographs of oil-bodies of Bazzania trilobata, Pellia epiphylla and Lophozia ventricosa.

OIL-BODY MORPHOLOGY

The oil-bodies of the Jungermanniales are of very diverse form but are always easily recognizable due to their refractive index, which is different from that of the other intracellular bodies. Oil-bodies are laid down in the cytoplasm of even the youngest cells and are apparently surrounded by and suspended from cytoplasmic strands. Mueller (1951) observed that in young cells stained with diffuse aqueous picric acid and not yet containing chloroplasts, oil-bodies were shown to be already surrounded by and suspended from cytoplasmic strands (Schuster, 1966).

Oil-bodies are divided into two basic types according to texture. The first type ranges from smooth to very lightly to roughly papillose or granular (Figure 1-a,b,c). The second type looks very noticeably segmented, made up of from two to many large segments per oil-body (Figure 1-d,e). The latter type has been referred to as the botryoidal or "grape-cluster" type of oil-body (Schuster, 1966). Ocelli (eyespots) also occur on the oil-bodies in some members of the Jungermanniales (Figure 1-b).

Oil-bodies, for the most part, are colorless but sometimes appear brown to reddish and even bright blue as in the case of *Lophocolea echinellus* and *Lejeunea cyanophora* (Schuster, 1966). Bright blueness in the oil-bodies of *Calypogeia trichomanis* have also been observed (Jones, 1965).

Ultrastructure studies of the oil-body have been conducted on a number of occasions beginning with Pfeffer in 1874, who stated that he

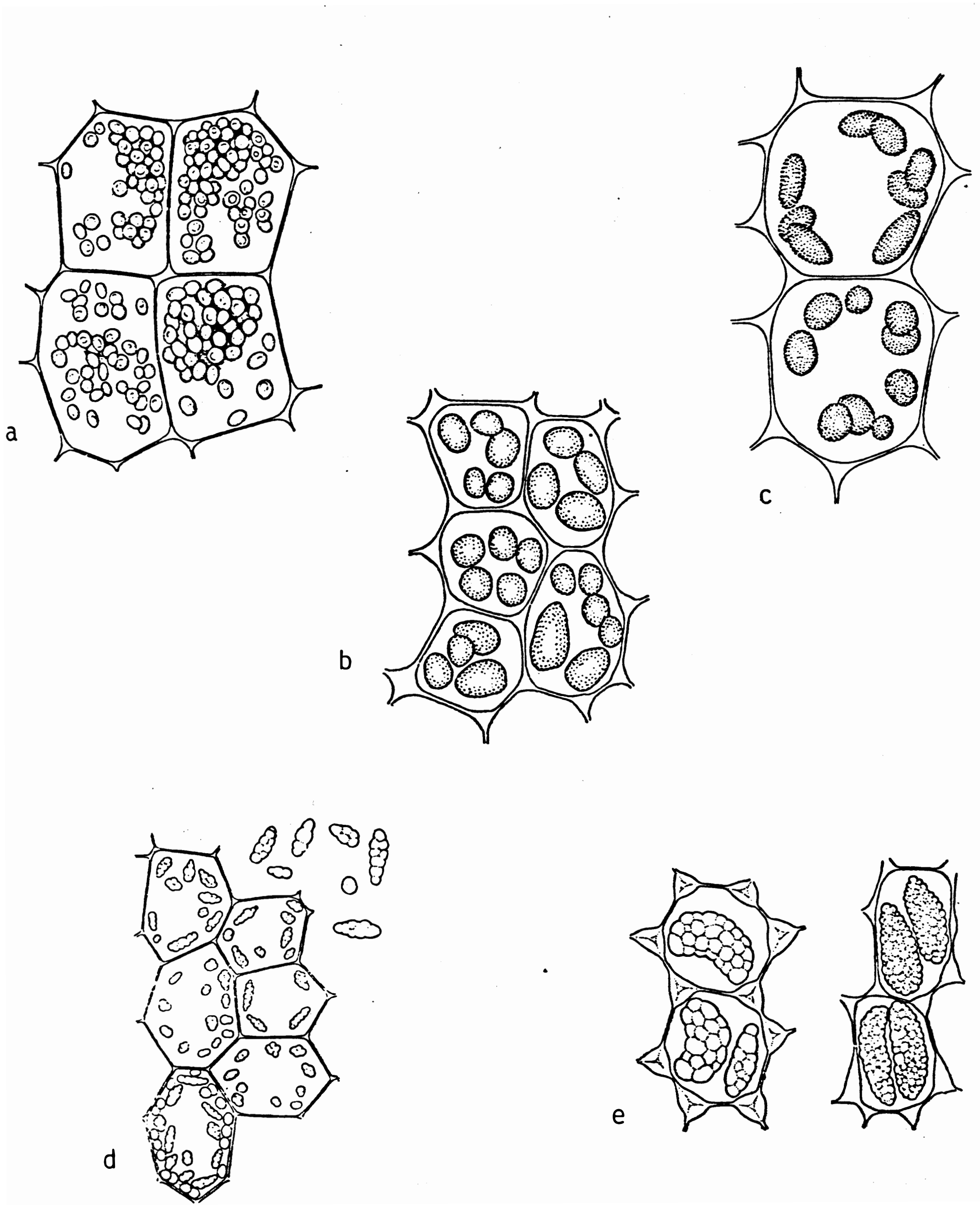

Fig. 1. Oil-body texture types. (a) smooth (with eyespots). (b) lightly papillose. (c) roughly papillose. (d) sparsely segmented. (e) many segmented. (All after Schuster)

observed a complete or incomplete inner membrane dividing the oil-bodies into many parts. Von Holle in 1857 and later Mueller (1905), Schuster (1966) and Smith (1966) considered this membrane genuine, and Garjeanne in 1903 proposed that the structure of the membrane was visible tanninized protein. On the same subject von Kuester (1894) and Lohmann (1903) considered the oil-body membrane as nothing more than an artifact produced by fixatives. These two men also theorized the possibility of the existence of a stroma between the many oil globules that make up one oil-body. Both men proved unsuccessful in fixing the stroma which they believed consisted of protein (Pihakaski, 1967).

These points remained questionable until relatively recently when Kaarina Pihakaski (1966, 1967, 1972) conducted a series of electron microscopic studies of the oil-bodies of Bazzania trilobata, Lophozia ventricosa, and Pellia epiphylla. These studies show that the oil-body is surrounded by a complete outer double membrane, and the oil globule or globules are, in turn, surrounded by a thinner inner membrane. These globules are also surrounded and separated by a proteinaceous stroma (Pihakaski, 1966, 1967, 1972).

The "grape cluster" type of oil-body appears segmented under the light microscope. This appearance is not due to a divided membrane but to many oil globules inside a smooth, nonsegmented membrane surrounded by a stroma. The granular or papillose type consist of many more smaller globules contained within the outer membrane (Figure 2). It should be pointed out that Pihakaski (1966, 1967, 1972) studied only four species, producing some evidence that one of the four, Pellia epiphylla, may not have an inner membrane. This suggests that oil-body morphology and ultrastructure may vary with the species.

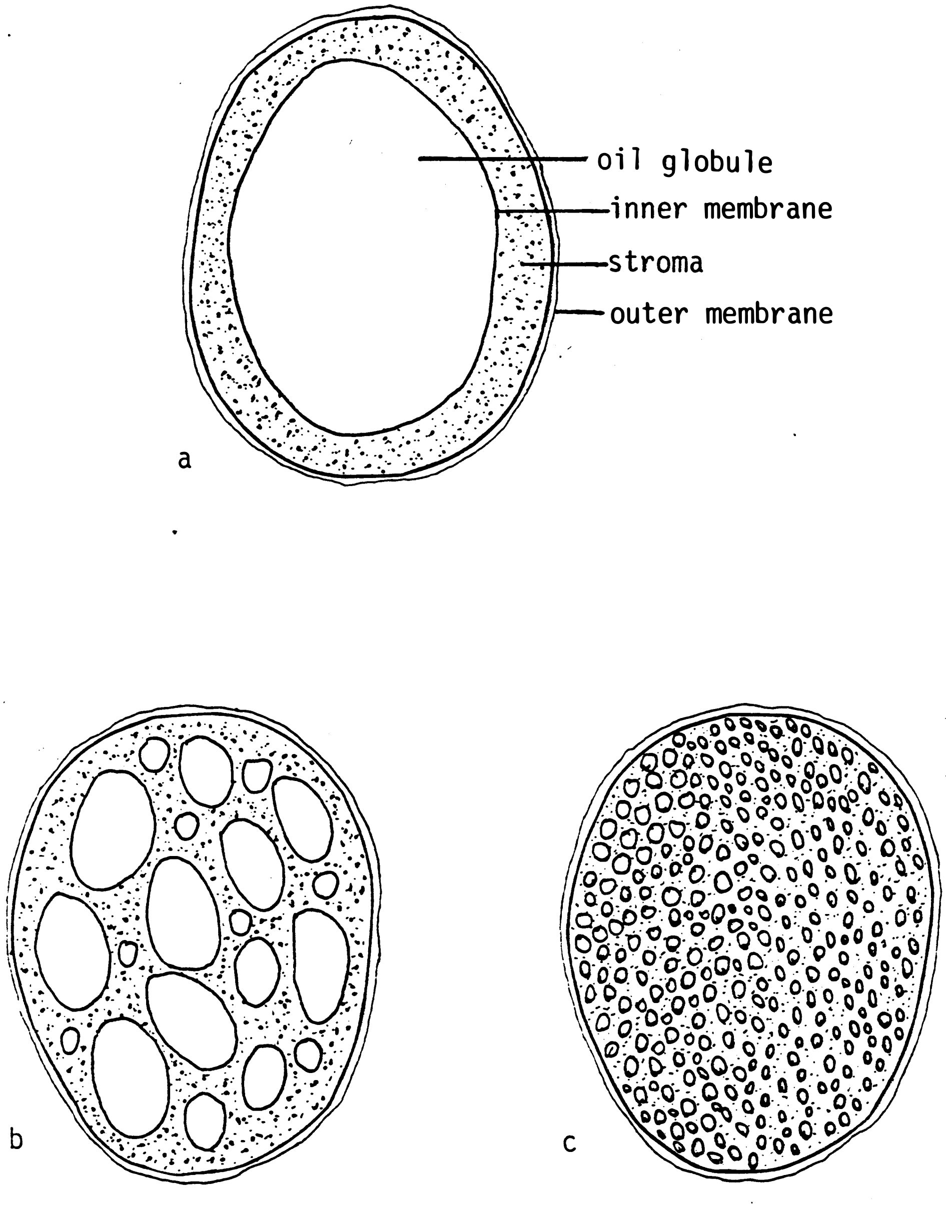

Fig. 2. Diagramatic representation of oil-body ultrastructure. (a) smooth texture type. (b) segmented texture type. (c) papillose texture type. (a and b after Pihakaski)

OIL-BODY ORIGIN AND DEVELOPMENT

As stated earlier oil-bodies are laid down in the cytoplasm of even the youngest cells and apparently are surrounded by and suspended from cytoplasmic strands. They were considered in the early days of research by a number of observers to have a variety of origins. Pfeffer (1874), Garjeanne (1903), Meyer (1920), Dombray (1926), and Zirkle (1932) all held the belief that oil-bodies originated from vacuoles in the cytoplasm. On the other hand, Wakker in 1888 and Kozlowski in 1921 felt that oil-bodies were functionally and structurally altered chloroplasts. Bergdolt in 1926 stated that the oil-bodies originated from special mitochondria he called chondriosomen. In 1950 Slavik presumed their origin to be directly from the cytoplasm (Pihakaski, 1966, 1967).

The discussion of oil-body origin was clarified when Mueller (1939) summarized existing studies and suggested that the "cytoplasmic origin theory" was the most acceptable (Schuster, 1966).

With the aid of the electron microscope Pihakaski (1967) conclusively disproved the "mitochondria and chloroplast origin theories." His reasoning was that, first of all, no intermediate forms between oil-bodies and mitochondria or between oil-bodies and chloroplasts have ever been observed. Secondly, his micrographs revealed that the outer membrane of the oil-body is unlike the double membrane of chloroplasts, mitochondria or nuclei in that oil-body membranes are much thinner. Furthermore, no remnants of granum or stroma membranes or

starch grains have ever been seen in oil-bodies. Pihakaski (1967) also felt that a vacuolar origin was unlikely because of the membrane difference. In fact, the membrane of the oil-body is like no other organelle membrane found in liverworts.

Despite the membrane differences, Pihakaski (1967) felt that from his observations the Golgi apparatus, the endoplasmic reticulum, or the groundplasm may take part in the formation of the membranes of oil-bodies. The actual material that makes up the oil globule is probably secreted by the endoplasmic reticulum and/or the Golgi apparatus at a very early stage. These oil globules may undergo some division by constriction, and the cytoplasm around them may differentiate into the finely granular stroma of the oil-body. At the same time a double membrane forms around the entire complex (Pihakaski, 1966).

Pihakaski pointed out in 1967 in a follow-up electron microscopic study of Bazzania trilobata and Lophozia ventricosa evidence that indicated these two liverworts have different oil-body origins. He states that in Bazzania trilobata the vacuoles found between dense bodies in the young apical leaves play an important role in oil-body development. He observed that light colored spherules are formed within the vacuoles which later coalesce and form larger bodies that are enclosed by a thin membrane. On the other hand, Pihakaski (1967) reported that Lophozia ventricosa has an important stage of oil-body development related to the formation of coherent groups of dark colored lipid spherules. In 1967 Pihakaski restates the differences in the oil-bodies of these two species and makes the suggestion that it is very possible that different conditions may alter the origin and development of the oil-body, whether they be of vacuole, endoplasmic reticulum, or Golgi apparatus origin.

OIL-BODY FUNCTION

The proposed functions of the oil-body are vague and numerous. Stahl (1888) believed that oil-bodies may be a repellent to snails. This seems unlikely since Reboulia is frequently eaten by lepidopterous larvae. On the other hand, most liverworts generally suffer little from insect attacks, and the credit might be given to the oil-bodies. However, this immunity to insect attack is also found among bryophytes which lack oil-bodies; e.g., Anthocerotae and the Musci. Due to the relatively old age of this group of plants it is not difficult to imagine that this could have been the original function of oil-bodies, if not still the function in some species today (Schuster, 1966).

Pfeffer (1874) and von Kuester (1894) observed oil-bodies in the cells of hairs and also in sites where no chloroplasts have ever existed, thus assuming they could not be products of assimilation. Zwickel (1932) also observed oil-bodies in sporophytes and therefore assumed they could not be food reserves (Pihakaski, 1967).

In 1892 Hieronymus proposed that oil-bodies serve as protection against excessive light. This seems unlikely due to the fact that many liverworts lacking oil-bodies grow in direct and strong sunlight. Others felt that they may have a role in protection against desiccation, but there are examples of xeric liverworts (Riccia, Anthelia) which lack oil-bodies while they are present in some aquatic species. The fact that arctic species may lack oil-bodies also tends to invalidate another theory that oil-bodies serve as some protection from the

cold. If indeed they are functional in protection from low temperatures it would seem that tropical species would either lack oil-bodies or they would have a higher point of solidification. Using this same reasoning, arctic species would be expected to not only have oil-bodies, but they would also have a lower solidifying point. With this in mind, Mueller's (1939) listings of liverworts with reference to their oil-bodies is noteworthy: of forty-three tropical or subtropical species, seventeen lacked oil-bodies and of one hundred and fifteen species from northern climates, only nine lacked oil-bodies. In addition to this is the fact that annual or biennial liverworts such as Anthoceros, Riccia, and Sphaerocarpus in general lack oil-bodies and perennials generally have oil-bodies. This indicates that their presence may have some connection to overwintering (Schuster, 1966).

Mueller (1939) felt that no physiological function could be given to the oil-body, although it may have had one in the past which can no longer be recognized. It seems that oil-bodies are lacking in phylogenetically old genera such as Anthoceros, Sphaerocarpus and Blasia. Mueller's theory remains purely speculative today.

OIL-BODY CHEMISTRY

It has been generally believed for as long as oil-bodies have been observed that they contain neutral fats, fatty acids and ethereal oils. Among the investigators who held this view are Pfeffer (1874), Rivett (1918), Mueller (1905), Guillermond (1922), Lohmann (1903), and Zwickel (1932) (Pihakaski, 1967). Lohmann in 1903 believed that, to a great extent, the volatile, ethereal oil and fat content of the plant was not related to the oil-bodies (Schuster, 1966).

Mueller (1939, 1905) felt strongly that oil-bodies consist of a number of diverse types of ethereal oils. These oils were said to be composed of terpenes and terpene alcohols.

Electron microscopic study has revealed evidence that proteins are present in the oil-bodies of *Pellia epiphylla* and *Bazzania trilobata*. Electron microscopic work shows that proteins are present in the stroma, but not in the globules embedded in the stroma. The globules appear to consist of unsaturated neutral lipids which make up the bulk of stainable lipids in the cell (Pihakaski, 1972). This type of work is useful, but due to the fact that a limited number of liverworts have been examined this way, no general conclusions regarding the specific makeup of other liverworts can be made.

As mentioned earlier Mueller (1939) felt that oil-bodies consist of a great number of diverse types of ethereal oils. He also did considerable work with the optical properties, specific gravity, and

saponification values of these individual oils. It is easy to understand why many today agree with Mueller in his view that different species contain different oils. With this in mind it is also easily postulated that each of these oils has distinctive properties that gives each species a distinctive odor. Mueller (1939) believed that oil-body odors were good classification criteria. Geocalyx has a terpentine odor and Conocephalum has a mushroom smell. Leptolejeuneae smells similar to licorice and Moerckia possesses a uniquely, harsh unpleasant odor. Riella smells of anise, Solenostoma like carrots, Lophozia of cedar oil and Lophocolea has an indistinctive "mossy" smell as do many other species (Schuster, 1966).

DISTRIBUTION AND TAXONOMIC SIGNIFICANCE

Oil-bodies are found only in the Hepaticae and exist no where else in the plant kingdom. They are absent in the Anthocerotales, are found within the Marchantiales but are most common and widespread in the Jungermanniales.

Mueller (1939) describes a vast number of different types of oil-bodies stating that the form, number and size of the oil-bodies are characteristic for each species. Schuster (1966), on the other hand, feels that Mueller has overrated their taxonomic value and names only two types:

> 1) Those occurring throughout the Jungermanniae as small to large bodies, usually two to many per cell (but occasionally only one per cell) and usually not restricted to special cells; such oil-bodies occur in cells that are usually not modified and almost always include chloroplasts.
>
> 2) Those occurring as large spherical bodies formed from numerous minute spherules, one per cell, virtually filling the lumen of the cell, in cells that are usually differentiated in size (often much smaller) from the surrounding cells; furthermore, except in the isolated genus Monoclea, these cells are few and scattered and never bear chloroplasts. This type occurs throughout the Marchantiae.

The group of liverworts described in number one and two above are then again subdivided into many groups by Schuster due to the fact that there is a great deal of variation from one species to another and from one genus to another. This variation occurs in the number per cell, size, form, and apparent segmentation.

In general, the greatest use of oil-bodies is as supplementary criteria for separating series. However, this value varies from one liverwort group to the next. Schuster and Hattori (1954) use oil-bodies for separating species in *Cheilolejeuna* and use them as criteria for postulating a close phylogenetic connection with other liverworts. In other cases oil-body morphology is almost useless taxonomically. Ocelli (eyespots) on the oil-bodies seems to be a valuable tool in the separation of species in the Frullaniaceae (Schuster, 1966).

METHODS

The liverworts used for descriptions and illustrations were collected in east-central Illinois, especially in Coles and Clark Counties. Identifications were accomplished with the help of Dr. Charles B. Arzeni and publications listed in the Literature Cited by Arzeni (1947), Conard (1956), Evans (1897), Schuster (1966, 1969, 1974), Frye and Clark (1937-47), and Watson (1968). Due to the somewhat volatile characteristics of the oil-bodies of leafy liverworts, observations and photographs had to be made as soon as possible before heat and drying out altered their characteristic appearances. It was found that the oil-bodies could be stored without change for reasonable periods of time if the plants were packed loosely and kept lightly moistened at 35-38^{o}F but never below freezing. The collections have since been placed in packets and deposited in the Bryophyte Herbarium of Eastern Illinois University.

Observations were taken only of oil-bodies in the cells of vegetative structures of the gametophyte. Unless otherwise indicated, descriptions and photomicrographs apply only to the oil-bodies of median leaf cells and outer stem cells.

Observations were made of the oil-bodies of fresh non-altered material with the aid of a Nikon compound microscope model S-Ke II with a built-in Loehler illuminating system. Measurements were taken with a calibrated ocular micrometer. Photomicrographs of the oil-bodies

were taken with the Nikon Automatic Microflex Model AFM automatic photomicrographic attachment. Most photomicrographs, unless otherwise indicated, were taken with the oil-immersion lens at a magnification of 1000X. The 1000X image is reduced by the Nikon attachment by passing it through a ½X lens to properly focus the image on the plane of the film. The prints contained in the body of this paper were made from color transparencies, their enlargements appearing with each print. The film used was Kodak High Speed Tungstun Ektachrome ASA-125.

DESCRIPTIONS OF OIL-BODIES

The oil-bodies of 23 species of leafy liverworts representing fourteen genera in eight families are described. Each description includes a measurement and a general description of the cells found in the median section of a typical leaf. This is followed by the description of the oil-bodies contained in these cells.

Six basic characteristics are included in each description of the oil-bodies. First is the range in numbers of oil-bodies per cell; e.g., 6-8 per cell. Secondly is the range in size of the oil-bodies; e.g., 2.5-3 X 4.5-5μ up to 3-4 X 6-8μ. The next two characteristics described are color followed by shape of the oil-bodies. The fifth characteristic deals with textures which are basically smooth, papillose or segmented. Papillose oil-bodies can range from lightly or finely papillose or granular to roughly or coarsely papillose or granular. Segmented oil-bodies may be few to many segmented and may have 1-3 rows of segmentation. The last characteristic is the general arrangement of the oil-bodies within the cell lumen. These six characteristics are then followed by a general comment on the differences of the oil-bodies of the outer cells of the stem as compared to the oil-bodies of the median leaf cells.

Each description is accompanied by at least one enlarged photomicrograph of median leaf cells containing oil-bodies. Unless otherwise indicated, each photomicrograph was taken at 1000X magnification and exhibits an enlargement of 1800X.

Blepharostoma trichophyllum (L.) Dum.

Cells of leaf lobes 15-20 X 35-45μ, cylindrical and linear.

Oil-bodies of leaf lobe cells 2-6 per cell (rarely as high as 25), from 1μ spheres up to 3-4 segmented bodies measuring 2-2.5 X 3-3.5μ, colorless, spherical to ovoid, lightly papillose to sometimes 3-4 segmented, very inconspicuous and minute, randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells, in general, larger and fewer per cell, usually 2, 3 or 4 segments per oil-body.

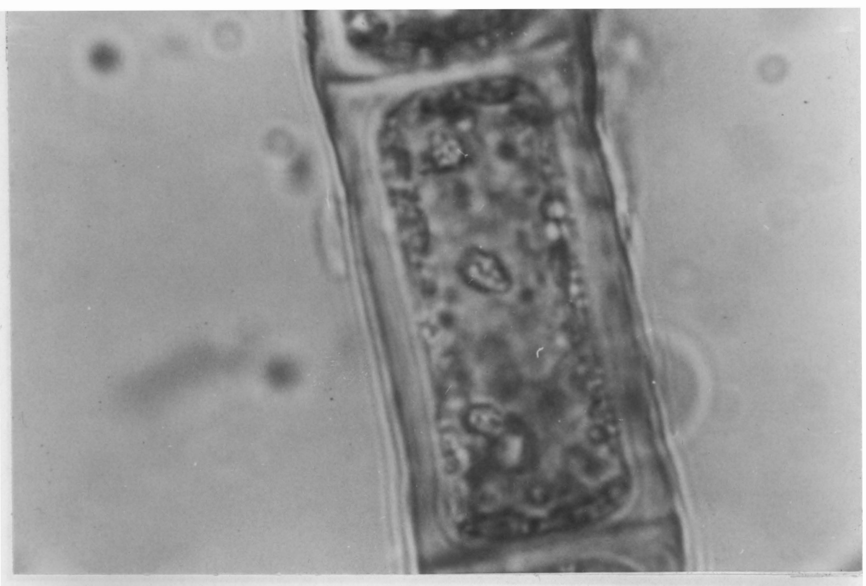

Photo 1. Blepharostoma trichophyllum, oil-bodies of leaf lobe cells at 1800X.

Trichocolea tomentella (Ehrh.) Dum.

Cilia leaf cells ranging from 20-27 X 75-85μ at the base of the cilia and 10 X 50μ at the tips, cylindrical and linear.

Oil-bodies of cilia leaf cells 4-8 per cell (as high as 10), from 2-3 X 2-3μ up to 3-4 X 6μ, shiny, smooth to lightly papillose, spherical to ovoid, very homogenous, tending to be found aggregating at the ends of cells.

Oil-bodies of the outer stem cells and basal leaf cells ovoid to sausage shaped or ellipsoidal, variable in size, 2.5-3 X 4-6.5μ (at times as high as 4-6 X 10μ).

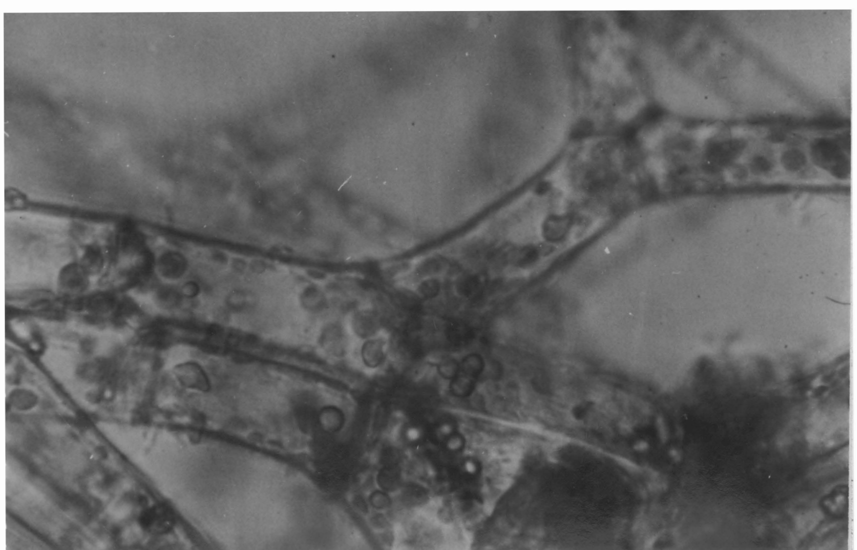

Photo 2. Trichocolea tomentella, oil-bodies of cilia leaf cells at 720X.

Photo 3. Trichocolea tomentella, oil-bodies of cilia leaf cells at 1800X.

Lepidozia reptans (L.) Dum.

Median leaf cells 20-30μ, square to hexagonal, with trigones not always obvious.

Oil-bodies of median leaf cells 10-15 per cell (sometimes as many as 25 or as few as 7), from 3.5-4 X 5μ up to 6-7 X 10-11μ, pale grey to colorless, ranging from globular to egg shaped, smooth to 2-3 unequally segmented or as if with small bulges, largely filling the cell lumen, randomly arranged, sometimes as many as 12-15 different-shaped oil-bodies in a single cell.

Oil-bodies of the outer stem cells rare and usually lacking.

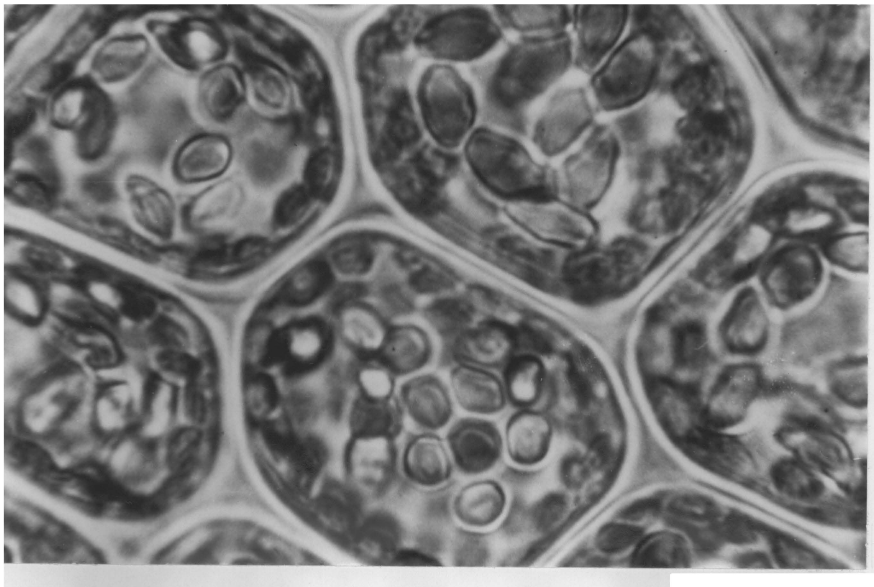

Photo 4. Lepidozia reptans, oil-bodies of median leaf cells at 1800X.

Bazzania trilobata (L.) S. Gray

Median leaf cells from 20-25 X 25-30μ, somewhat irregular in shape and size, with moderately bulging trigones.

Oil-bodies of median leaf cells 3-8 per cell, from 3-4 X 3-4μ up to 4 X 5-6μ, shiny and colorless, spherical to egg shaped, smooth or weakly to distinctly unequally segmented (segments sometimes appearing bud-like), largely filling the cell lumen, randomly arranged.

Oil-bodies of the outer stem cells more or less the same as the oil-bodies of the median leaf cells in size, shape, color, texture, and number per cell.

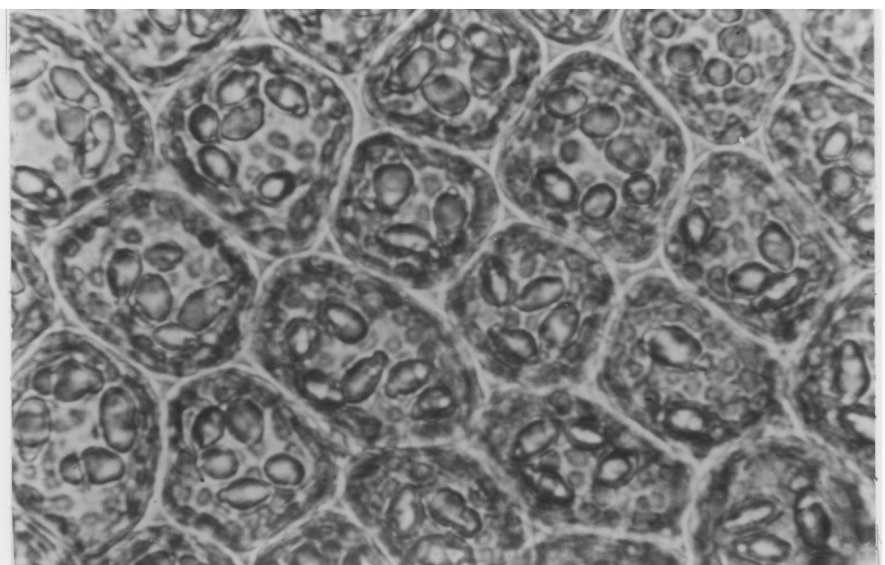

Photo 5. Bazzania trilobata, oil-bodies of median leaf cells at 720X.

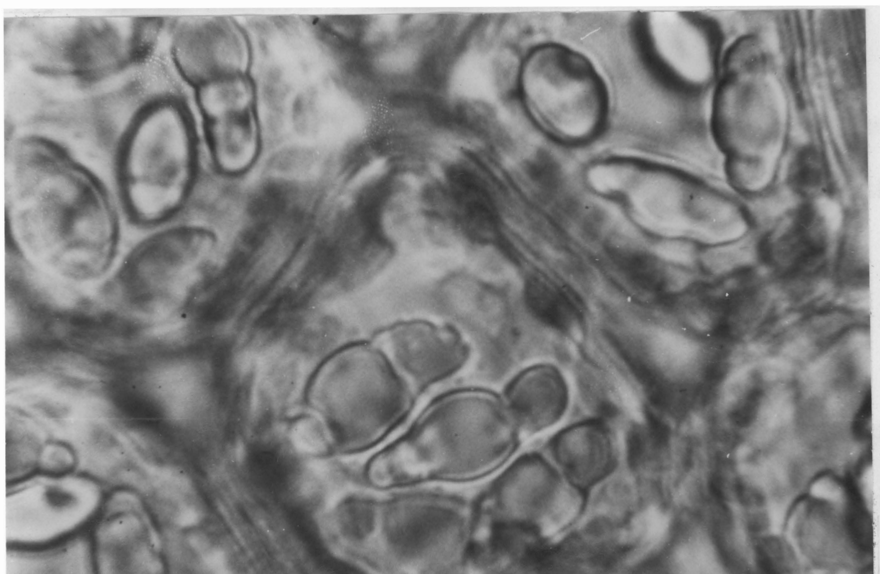

Photo 6. Bazzania trilobata, oil-bodies of median leaf cells at 1800X.

Calypogeia muelleriana (Schiffn.) K. Müll.

Median leaf cells more or less isodiametric, 35-40µ, trigones lacking.

Oil-bodies of median leaf cells 6-13 per cell, from 2.5-3 X 5µ up to 2-5 X 11µ, colorless, very obviously segmented in most cases, sometimes appearing slightly papillose to smooth, 3-5 segments per oil-body in the smaller ones, as high as 8-15 in the larger ones, each segment 1.5-2.5µ in diameter, randomly arranged within the cell lumen, somewhat tending to group close to the cell wall.

Oil-bodies of the outer stem cells fewer in number, 1-3 per cell, but the same as the oil-bodies of median leaf cells in size, shape, color and texture.

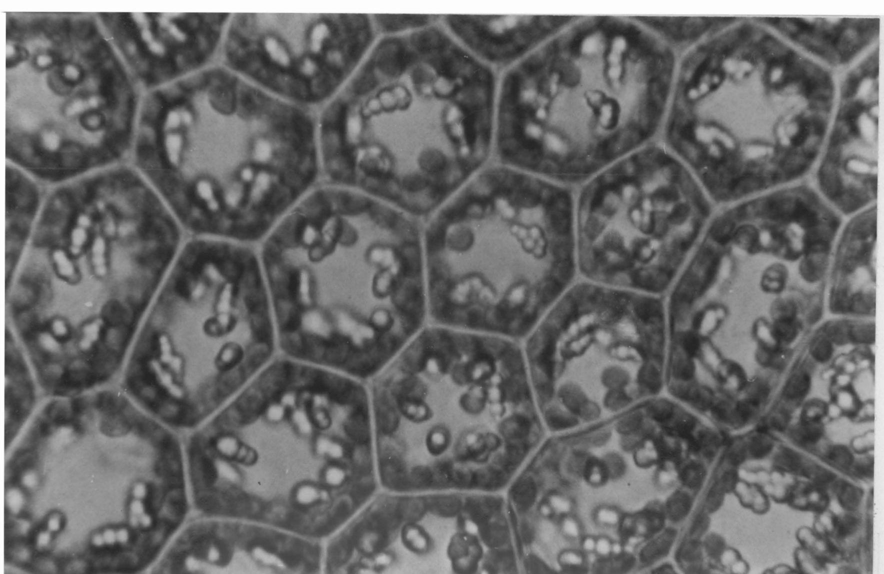

Photo 7. *Calypogeia muelleriana*, oil-bodies of median leaf cells at 720X.

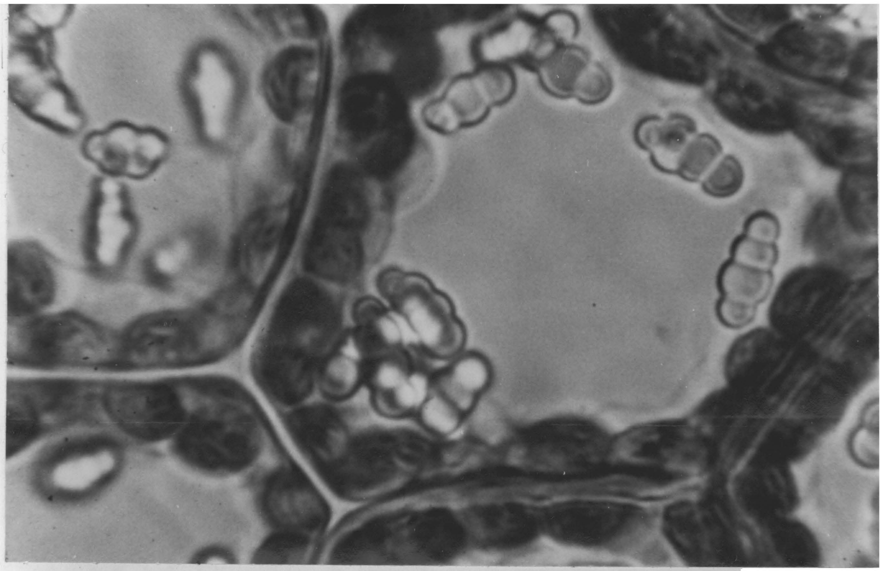

Photo 8. Calypogeia muelleriana, oil-bodies of median leaf cells at 1800X.

Calypogeia fissa (L.) Raddi

Median leaf cells 30-40 X 50-60μ, isodiametric with small trigones.

Oil-bodies of median leaf cells 4-8 per cell, from 2.5-3 X 4μ up to 3-4 X 7-9μ, colorless, segmentations not well defined, segments of oil-bodies 4-12, 2.5-3μ in diameter and sometimes arranged in two rows, randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells very similar to the oil-bodies of the median leaf cells in size, color, shape, texture and number per cell.

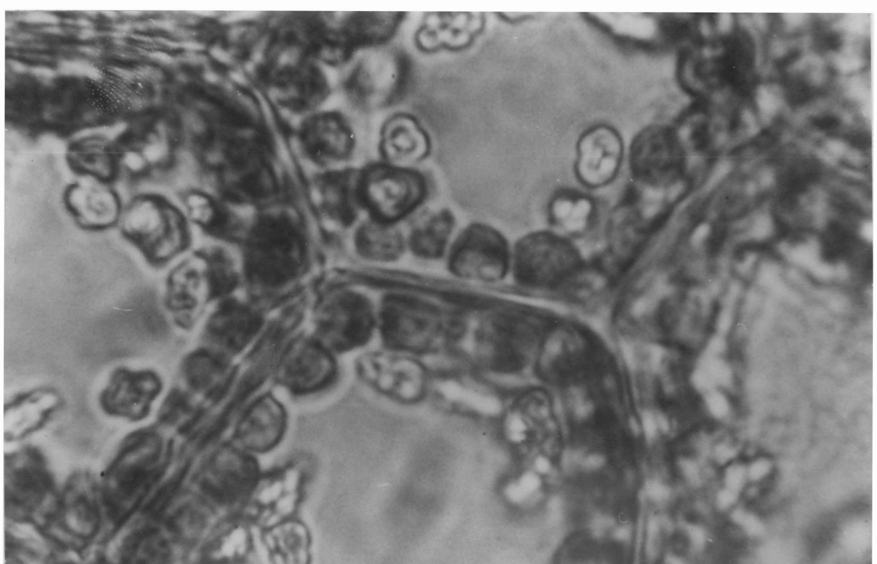

Photo 9. *Calypogeia fissa*, oil-bodies of median leaf cells at 1800X.

Lophocolea heterophylla (Schrad.) Dum.

Median leaf cells 15-20 X 15-30μ, somewhat isodiametric with small, inconspicuous trigones.

Oil-bodies of median leaf cells 4-7 per cell, from 2.5-3 X 2.5-3μ up to 3.5-4 X 7-8μ, colorless, ovoid to sausage shaped to irregularly shaped, strongly papillose or granular, randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells similar to the oil-bodies of median leaf cells in size, color, shape, and texture but fewer per cell (3-4).

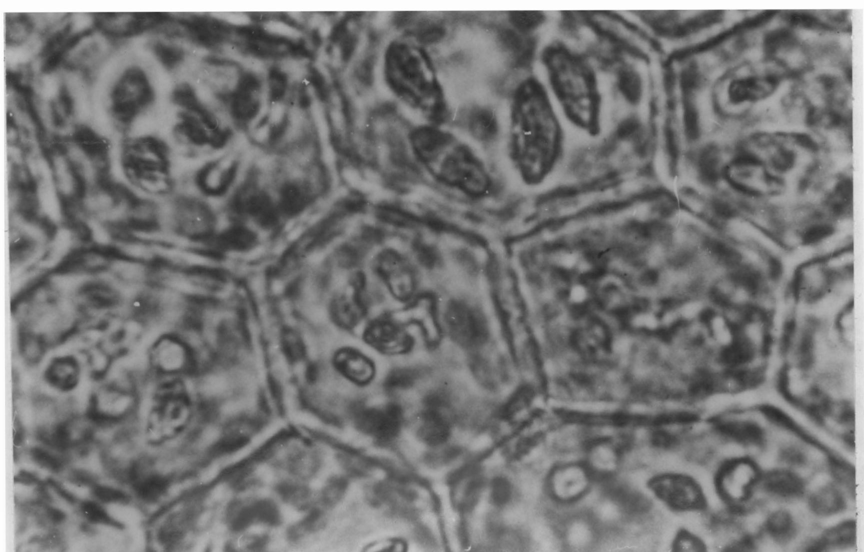

Photo 10. Lophocolea heterophylla, oil-bodies of median leaf cells at 1800X.

Lophocolea minor Nees

Median leaf cells 25-30µ, somewhat irregularly shaped with small trigones.

Oil-bodies of median leaf cells 6-10 per cell (as high as 14-17 in some cases), from 3-4 X 4µ up to 3-4 X 8µ, red-brown, spherical to ovoid, smooth to finely papillose or granular, largely filling the cell lumen, grouping close to the cell wall.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, color, texture and number per cell.

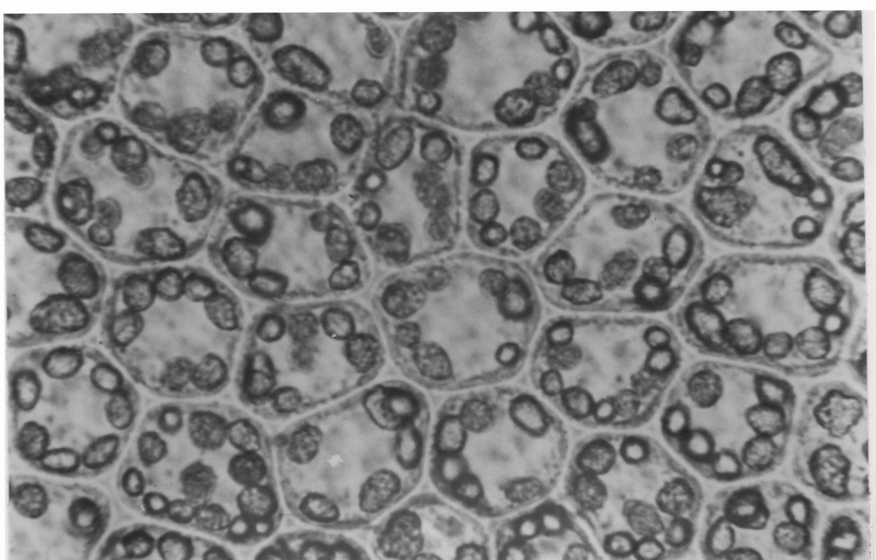

Photo 11. Lophocolea minor, oil-bodies of median leaf cells at 720X.

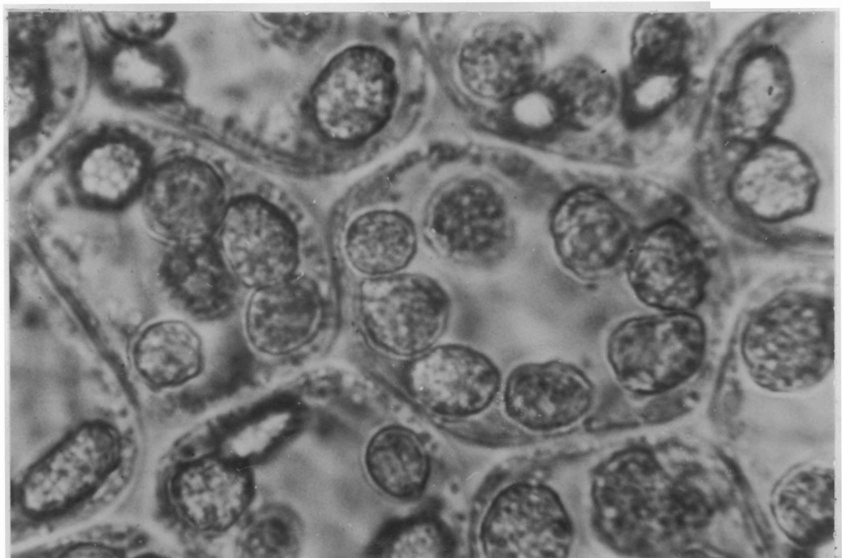

Photo 12. Lophocolea minor, oil-bodies of median leaf cells at 1800X.

Lophocolea bidentata (L.) Dum

Median leaf cells 12-17 X 30-37μ, somewhat hexagonal to irregularly shaped with small trigones.

Oil-bodies of median leaf cells 10-18 per cell (rarely as few as four very large, sausage shaped oil-bodies per cell), from 3-3.5μ spheres up to 4.5-5 X 10μ, brown, spherical to ovoid to sausage shaped, papillose or granular, largely filling the cell lumen, randomly arranged, sometimes tending to group close to the cell wall.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, color and texture, but usually fewer per cell.

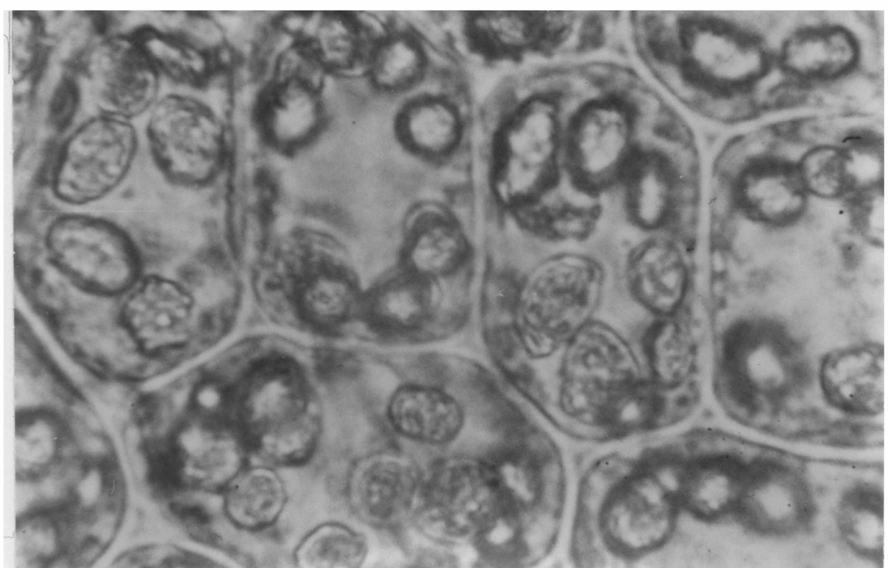

Photo 13. Lophocolea bidentata, oil-bodies of median leaf cells at 1800X.

Jungermannia lanceolata L.

Median leaf cells 25-30 X 30-35µ, irregularly shaped, many-sided to round, trigones distinct.

Oil-bodies of median leaf cells 5-10 per cell (as high as 15), from 5.5-6 X 5.5-6µ up to 5.5-6 X 10-11µ, light brown, spherical to ovoid, granular or papillose, closely grouping to the cell wall.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, color, texture and number per cell.

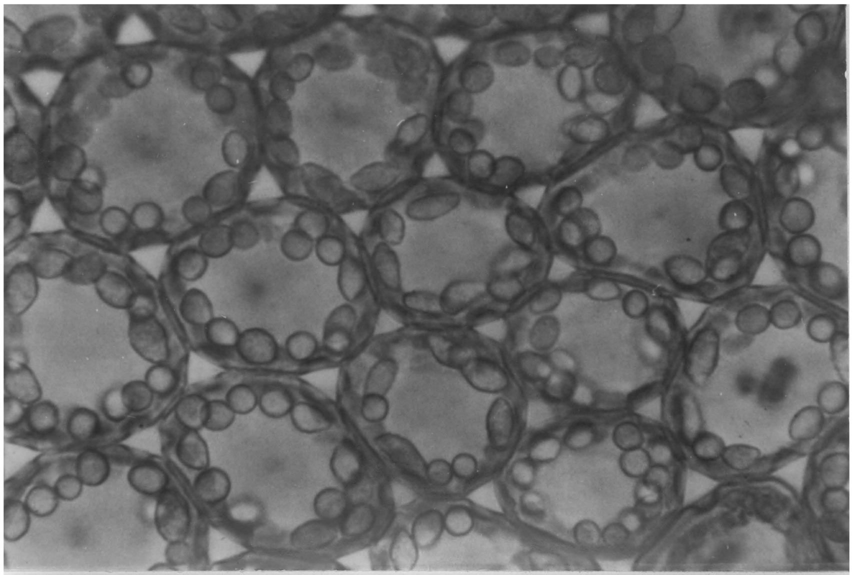

Photo 14. Jungermannia lanceolata, oil-bodies of median leaf cells at 720X.

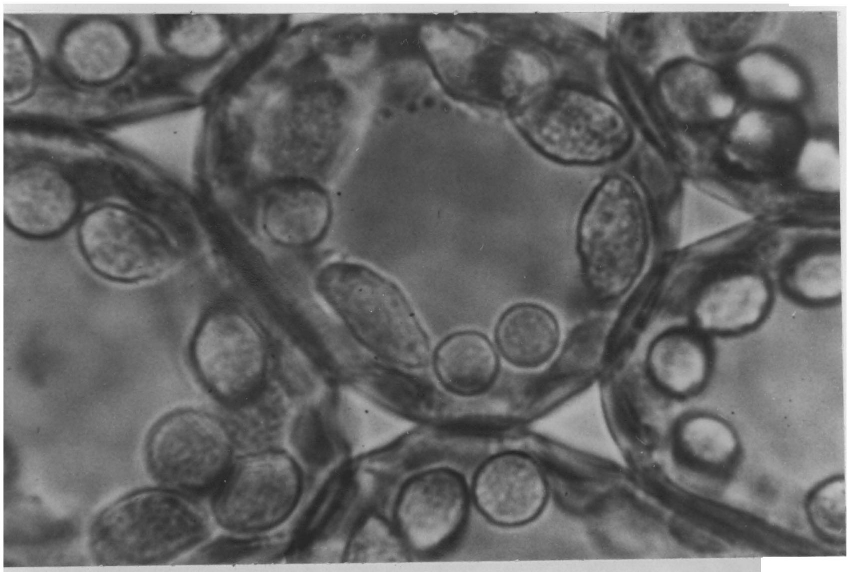

Photo 15. Jungermannia lanceolata, oil-bodies of median leaf cells at 1800X.

Jamesoniella autumnalis (DC.) Steph.

Median leaf cells 25-30 X 35-40μ, somewhat irregularly shaped with small trigones.

Oil-bodies of median leaf cells 8-18 per cell, from 2.5-4 X 5-8μ up to 6.5-7 X 9-11μ, colorless, spherical to mainly ovoid, lightly papillose, mostly filling and randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, color and texture, but vary from 10-12 per cell depending on the cell size.

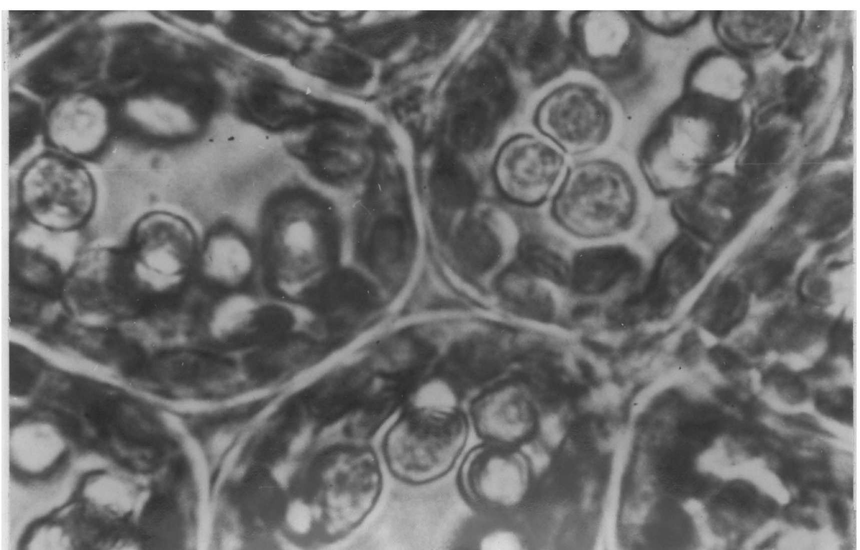

Photo 16. *Jamesoniella autumnalis*, oil-bodies of median leaf cells at 1800X.

Plectocolea crenulata (Sm.) Evans

Median leaf cells 20-25 X 25-35µ, somewhat irregularly shaped with small trigones.

Oil-bodies of median cells 2-6 per cell, from 3.5-4 X 4µ up to 5.5-6 X 10µ, colorless, spherical to ovoid, finely papillose or granular, largely filling and randomly arranged in the cell lumen.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, color, shape, texture and number per cell.

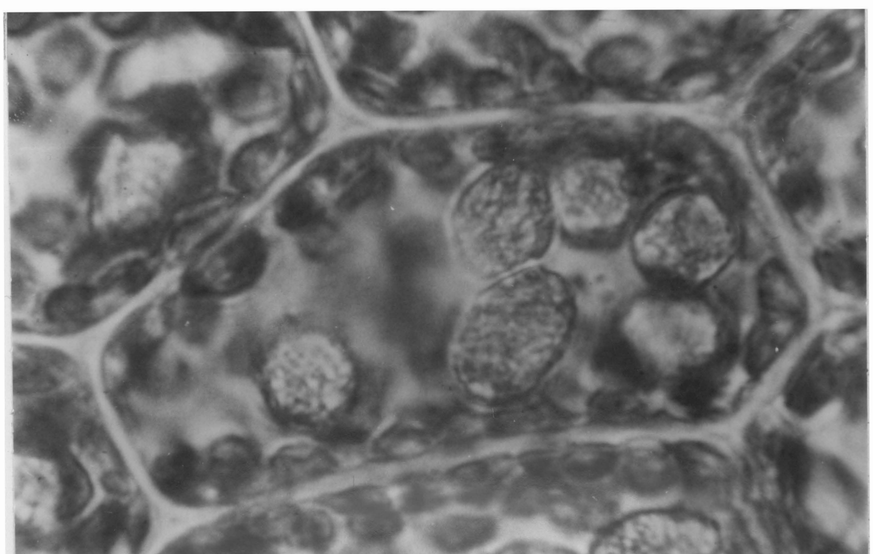

Photo 17. Plectocolea crenulata, oil-bodies of median leaf cells at 1800X.

Plectocolea crenuliformis (Aust.) Mitt.

Median leaf cells 25-28μ, many-sided to irregularly shaped with distinct trigones.

Oil-bodies of median leaf cells 2-8 per cell, from 6-8 X 6-9μ up to 8-9 X 16-20μ (in general the larger the oil-bodies the fewer per cell and vice-versa), colorless, spherical to ellipsoidal, finely papillose, largely filling and randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells absent.

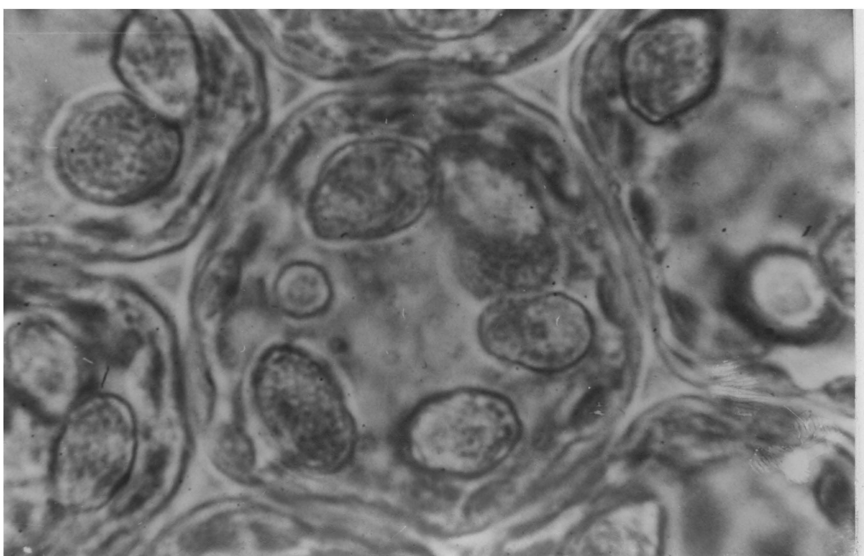

Photo 18. Plectocolea crenuliformis, oil-bodies of median leaf cells at 1800X.

Plagiochila asplenioides (L.) Dum.

Median leaf cells 25-30 X 30-32μ, somewhat round to irregularly shaped with well-defined trigones.

Oil-bodies of median leaf cells 4-6 per cell, from 4-5μ spheres up to 4.5-5 X 8-8.5μ, colorless, spherical to ovoid, papillose or granular, very consistent throughout every cell, randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells the same as the oil-bodies of the median leaf cells with the exception that the great majority are 4 X 4μ spheres, and there tend to be more per cell (5-10).

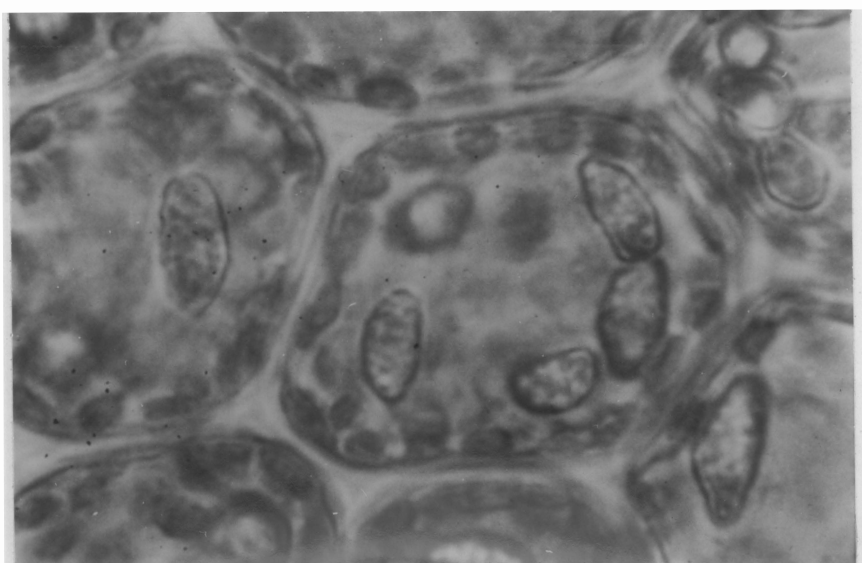

Photo 19. Plagiochila asplenioides, oil-bodies of median leaf cells at 1800X.

Diplophyllum apiculatum (Evans) Steph.

Median leaf cells 8-10 X 12-20μ to 12-14μ and isodiametric with moderate trigones.

Oil-bodies of median leaf cells 8-10 per cell, from 3-4 X 3-4μ up to 3-4 X 6-7μ, colorless, ovoid to slightly irregular, ranging from coarsely papillose to slightly segmented, randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells the same as the oil-bodies of the median leaf cells except fewer per cell (1-3 or lacking).

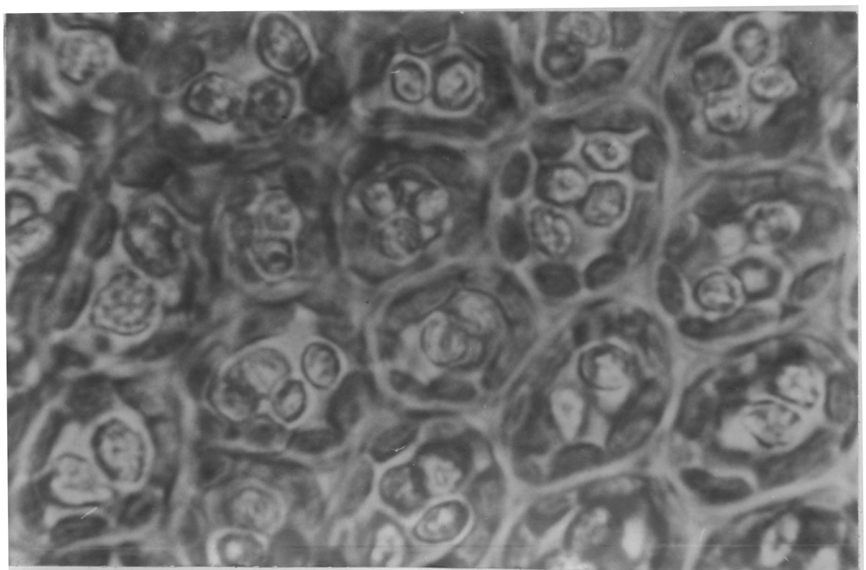

Photo 20. Diplophyllum apiculatum, oil-bodies of median leaf cells at 1800X.

Scapania nemorosa (L.) Dum.

Median leaf cells 20-30μ, somewhat irregularly shaped with trigones.

Oil-bodies of median leaf cells 3-6 per cell (as high as 9-11 depending on habitat variation), from 3.5-4 X 3.5-4μ up to 6-7 X 10-12μ, light brown, ovoid to egg shaped, very papillose, largely filling the cell lumen, arranged close to the cell wall.

Oil-bodies in the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, color, and texture but vary from 3-9 per cell depending on the cell size.

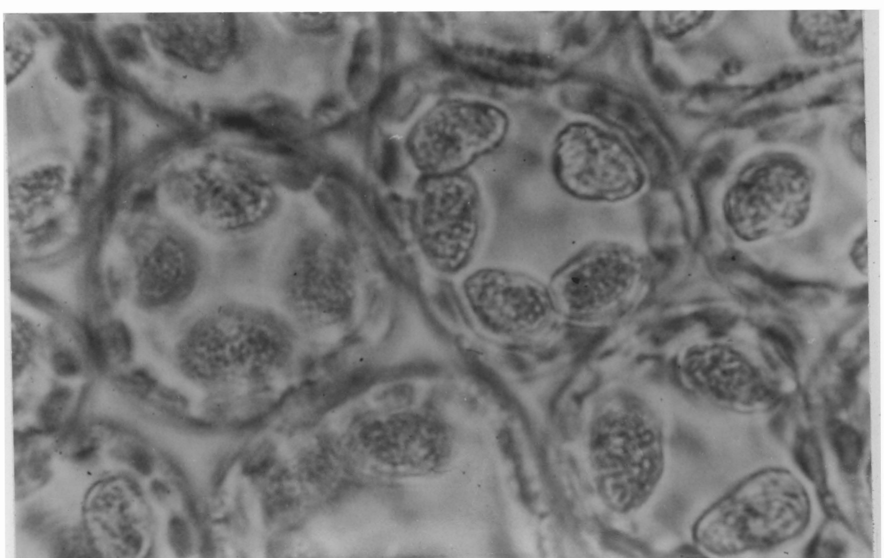

Photo 21. Scapania nemorosa, oil-bodies of median leaf cells at 1800X.

Scapania curta (Mort.) Dum.

Median leaf cells 20-25 X 20-30µ, spherical to irregularly shaped without trigones.

Oil-bodies of median leaf cells 3-6 per cell, from 3-4 X 3-4µ up to 6-7 X 10µ, colorless, spherical to ovoid to irregularly sausage shaped, coarsely papillose, largely filling and randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, texture, color, but about twice as many per cell (10-12).

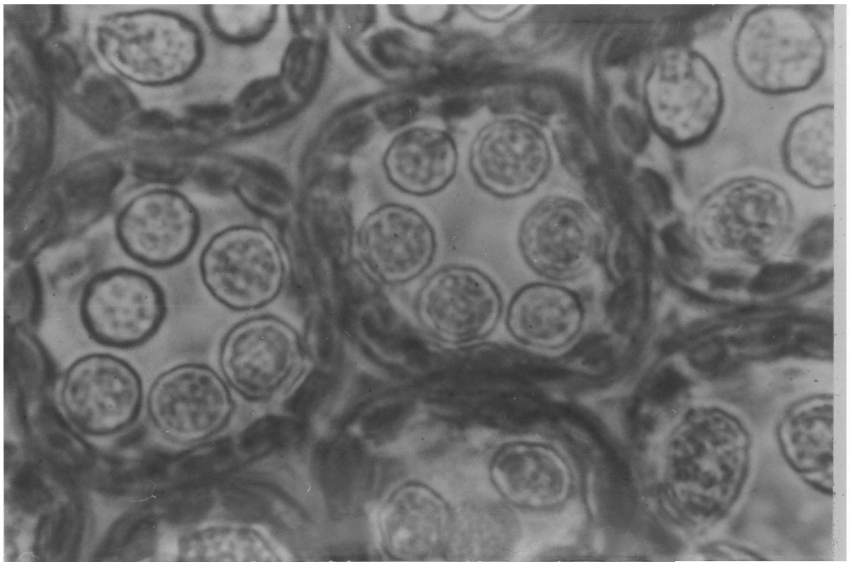

Photo 22. Scapania curta, oil-bodies of median leaf cells at 1800X.

Porella platyphylla (L.) Lindb.

/ Median leaf cells 25-28μ, many-sided to irregularly shaped with trigones.

Oil-bodies of median leaf cells 11-25 per cell from 1-2 X 1-2μ up to 1-2 X 3-4μ, colorless, spherical to disc or lens shaped, smooth, small, largely filling and randomly arranged within the cell lumen.

Oil-bodies in the outer stem cells the same as the oil-bodies of the median leaf cells in size, shape, color, texture, and number per cell

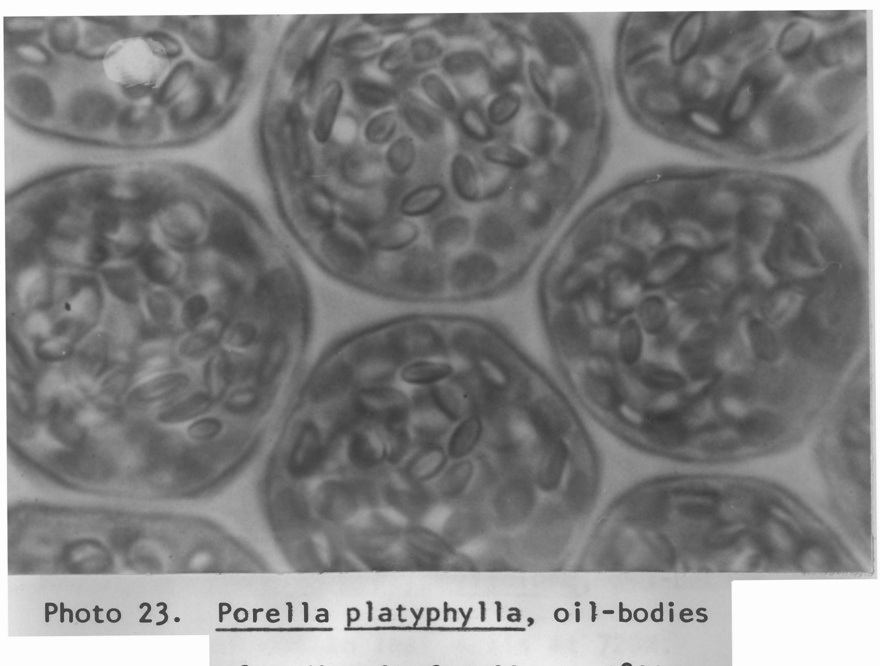

Photo 23. Porella platyphylla, oil-bodies of median leaf cells at 1800X.

Porella platyphylloidea (L.) Lindb.

Median leaf cells 15-25µ, somewhat irregularly shaped to spherical with trigones.

Oil-bodies of median leaf cells 14-35 per cell, 1.5-2 X 1.5-2µ up to 1.5-2 X 5µ, colorless, spherical to disc or lens shaped, smooth, small, largely filling and randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells similar to the oil-bodies of the median leaf cells in size, shape, color, texture and number per cell.

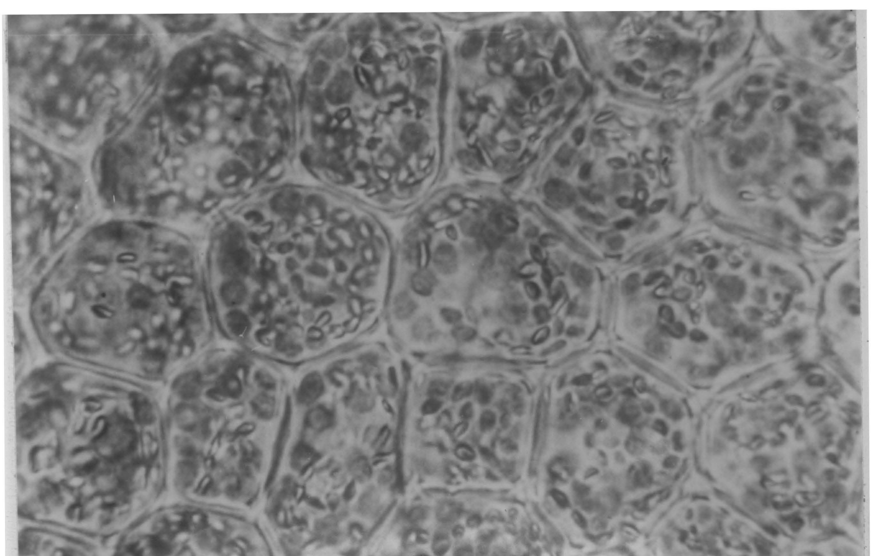

Photo 24. Porella platyphylloidea, oil-bodies of median leaf cells at 720X.

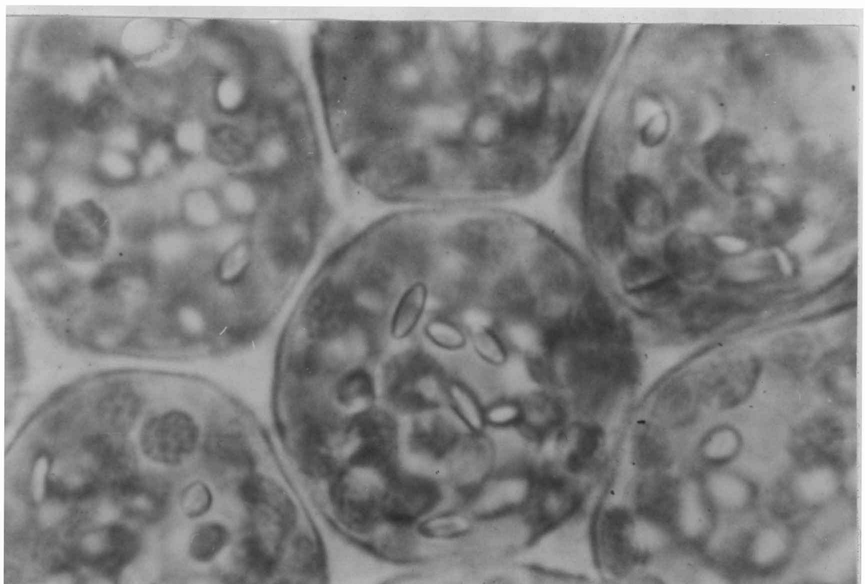

Photo 25. Porella platyphylloidea, oil-bodies of median leaf cells at 1800X.

Frullania asagrayana Mont.

Median leaf cells 9-11 X 18-20μ, somewhat irregularly shaped with trigones.

Oil-bodies of median leaf cells 2-4 per cell, from 1.5-2 X 2μ up to 2.5-3 X 4μ, colorless, spherical to ovoid, lightly papillose, somewhat inconspicuous, randomly arranged within the cell lumen.

Oil-bodies in the outer stem cells similar to the oil-bodies of median leaf cells in size, shape, color, texture and number per cell.

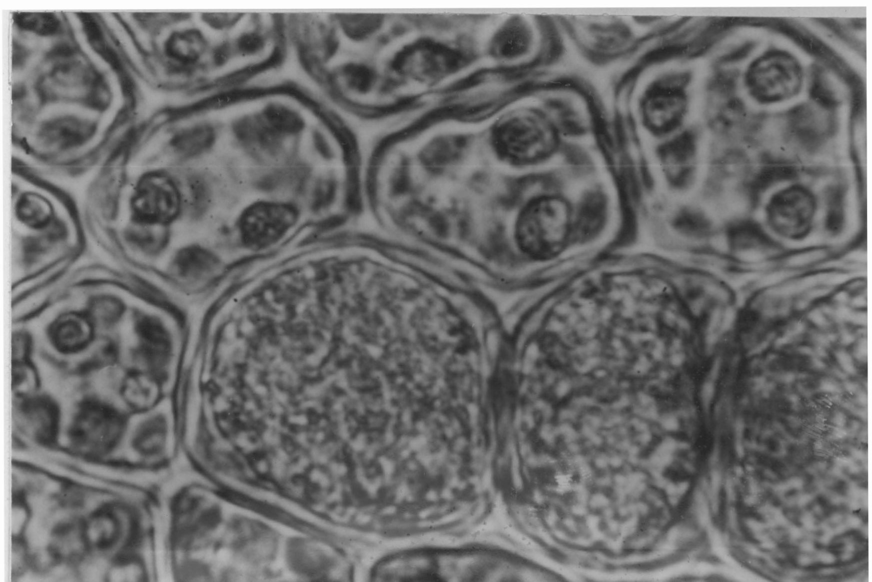

Photo 26. Frullania asagrayana, oil-bodies of median leaf cells at 1800X (note paracysts).

Frullania inflata Gott.

Median leaf cells 25-30µ, somewhat irregularly shaped, without distinct trigones.

Oil-bodies of median leaf cells 3-5 per cell, from 3.5-4 X 4µ up to 4-5 X 8-10µ, light brown, from spherical to ovoid with a few sausage shaped, strongly papillose, scattered throughout the cell lumen.

Oil-bodies in the outer stem cell 3-4 per cell, smaller (2.5-3 X 3µ), ranging from spherical, papillose and small to segmented, appearing in clumps of 3-4 or even in chains 4-6 segments long.

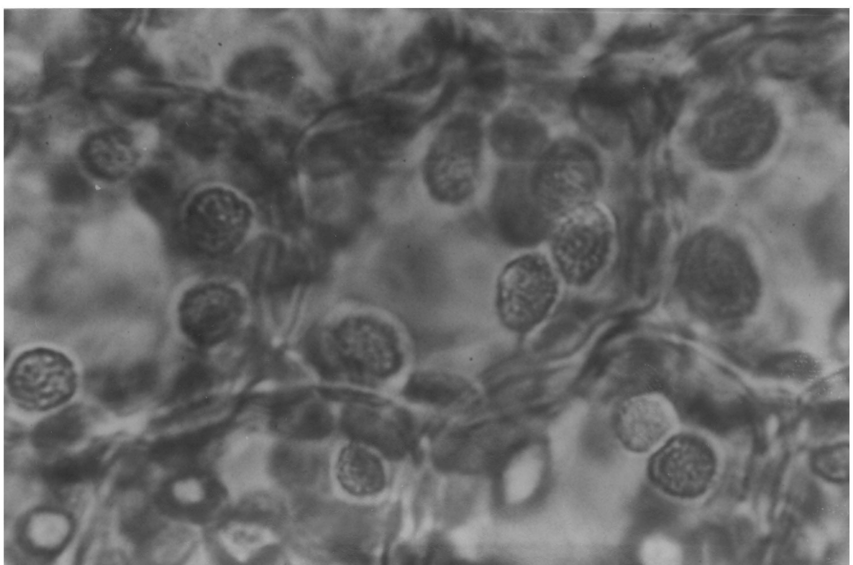

Photo 27. Frullania inflata, oil-bodies of median leaf cells at 1800X.

Frullania riparia Hampe

Median leaf cells 18-20 X 30-35μ, irregularly shaped with irregular trigones.

Oil-bodies of median leaf cells 3-4 per cell (as high as 5-6), from 3.5-4μ spheres up to 4.5-5 X 9-10μ, colorless, irregularly spherical to ovoid, papillose or granular, randomly arranged within the cell lumen.

Oil-bodies of the outer stem cells the same as the oil-bodies of the median leaf cells except that they are smaller, from 2μ spheres up to 3-5μ.

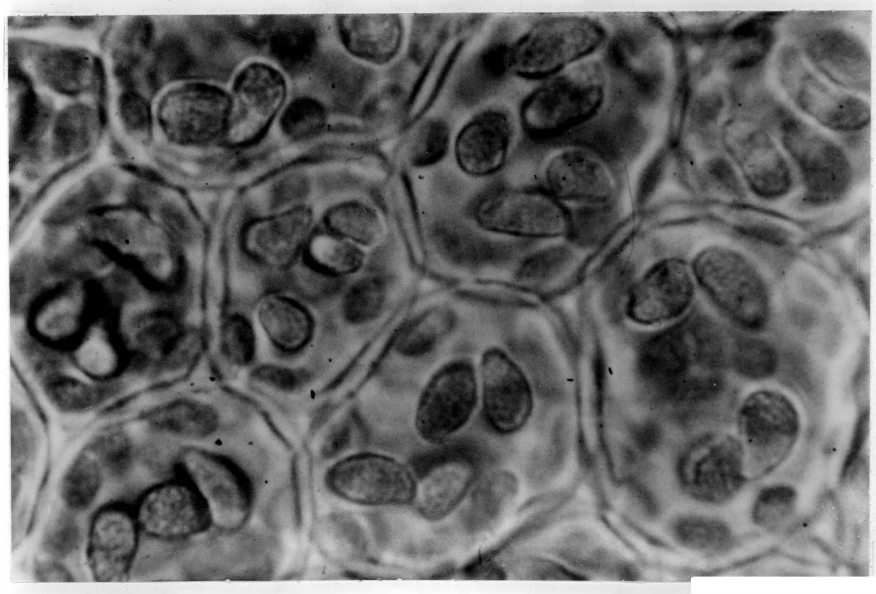

Photo 28. Frullania riparia, oil-bodies of median leaf cells at 1800X.

Frullania eboracensis Gott.

Median leaf cells 25-30μ, irregularly shaped with small trigones.

Oil-bodies of median leaf cells 2-5 per cell, from 2.5-3 X 3μ up to 3.5-4 X 9-10μ, colorless, spherical to ovoid and at times sausage shaped, very papillose or granular, clustered together in the center of the cell. In general, the fewer the oil-bodies per cell, the larger they tend to be.

Oil-bodies of the outer stem cells very homogenous, smaller (2-3μ spheres) and many more per cell (4-18).

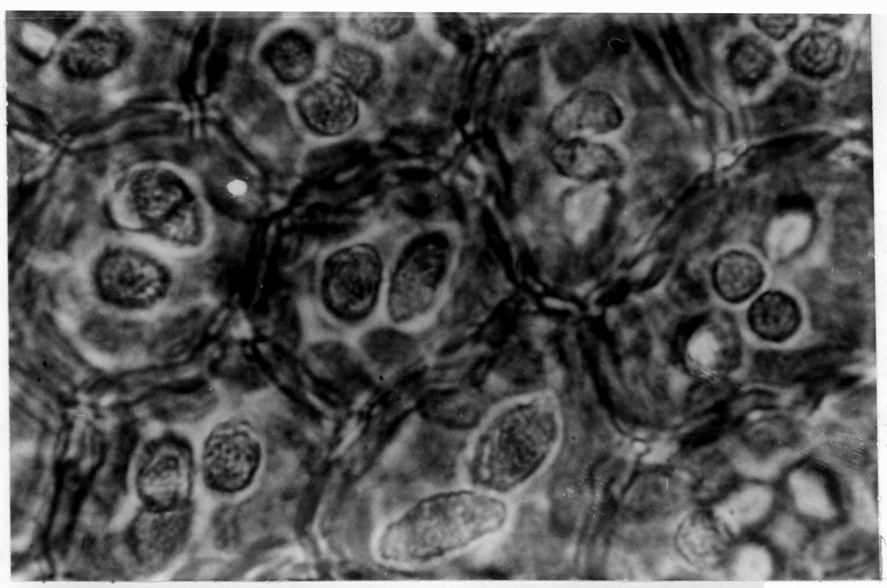

Photo 29. Frullania eboracensis, oil-bodies of median leaf cells at 1800X.

DISCUSSION

Considering the fact that oil-bodies are found in the great majority of leafy liverworts, it seems strange that there is little mention of them in many bryophyte and hepatic descriptions and keys. Until recently interest has not been great enough to mention them at all. In the early 1900's two leading bryologists Mueller (1939) and Garjeanne (1903) wrote some of the first descriptions of European liverwort oil-bodies. Except for these relatively few works the oil-bodies had been virtually ignored in leafy liverwort descriptions. Two of the more recent researchers who have paid considerable attention to the oil-body as an important part of liverwort morphology are R. M. Schuster (1954, 1966, 1969, 1974) and S. Hattori (1953, 1954). Together and separately they published a large number of papers on the morphology of North American and Japanese oil-bodies.

In this study the number of oil-bodies per cell of the liverworts examined range from as few as 2-4 per cell in the Frullaniaceae to as many as 14-35 in the Porellaceae. *Blepharostoma trichophyllum* exhibited the largest individual range from as few as two oil-bodies in some cells to as many as twenty-five in other cells. In most cases the size of the cell is proportionate to the number of oil-bodies in the cell but not in every instance. One exception is *Porella platyphylla* and *Porella platyphylloidea*. Each has median leaf cells of approximately the same size, but *P. platyphylloidea* has an average of 10-15 more oil-bodies per cell than *P. platyphylla*.

The size of individual oil-bodies range from the very minute and inconspicuous 1μ spherical oil-bodies of Blepharostoma trichophyllum to the 16-20μ ovoid "monsters" of Plectocolea crenuliformis. It appears that in most cases the size of the oil-bodies is not proportionate to the size of the cell. It is not unusual to observe very large cells containing many small oil-bodies in one liverwort and also observe another species with similar size cells containing fewer larger oil-bodies. It is also just as common to find a wide variety of sizes of oil-bodies in one cell of one liverwort such as in Lepidozia reptans.

Most oil-bodies are colorless. Some exceptions to this observed in this study are Lepidozia reptans, pale grey; Lophocolea minor, reddish-brown; Lophocolea bidentata, brown; Jungermannia lanceolata, light brown; Scapania nemorosa, light brown; Frullania asagrayana, light brown; Tricholea tomentella and Bazzania trilobata, somewhat shiny.

The most important diagnostic characteristic of oil-bodies is their shape. Oil-body shapes found in this study are spherical, ovoid, sausage shaped, lens shaped, or irregularly shaped. It is not uncommon to find three or more oil-bodies of diverse shapes in one cell.

Texture of the oil-body is probably the second most important characteristic which makes individual oil-bodies distinctive. The textures observed in this study are smooth, finely to coarsely papillose and 1-3 rows of segmentations. It is also not uncommon to find a variety of textured oil-bodies in one cell.

In most of the cells observed the oil-bodies are randomly arranged in the cell lumen. However, in the cases of Calypogeia muelleriana, Lophocolea minor, Jungermannia lanceolata and Scapania nemorosa the oil-bodies definitely tend to be grouped around the perimeter of the

of the cell in close proximity to the cell wall. Also Frullania asagrayana typically exhibits a single cluster of oil-bodies in the center of the cell.

By analyzing the information in Table 1 some statements may be made concerning the taxonomic significance of the oil-bodies of the leafy liverworts studied here. In some cases variation in oil-body morphology is so great within a family or even a genus that no natural taxonomic significance can be assigned. On the other hand, some families may be considered to be very natural groups by the consistency of their oil-body characteristics. However, in the cases where oil-body morphology within a family or genus varies greatly, oil-bodies can possibly be used with a good deal of success to separate genera or species.

Both genera examined in the Ptilidiaceae have oil-bodies that are similar in size, number per cell and texture. However, the oil-bodies of Blepharostoma are colorless, at times segmented, and randomly arranged, whereas Trichocolea has definitely shiny oil-bodies that are never segmented and tend to group at the ends of the filament-like cells.

Both genera described in the family Lepidoziaceae exhibit similarly shaped, textured, colored and arranged oil-bodies. Lepidozia reptans has oil-bodies that are about twice as many per cell and slightly larger than the oil-bodies of Bazzania trilobata. With just these minor differences it seems that in this family the oil-bodies show some indication of being a useful taxonomic criterion.

The two species examined in the family Calypogeiaceae share basically all the same characteristics. Calypogeia muelleriana shows slightly more oil-bodies per cell, more well-defined segmentations in the oil-bodies and a definite grouping of the oil-bodies close to the cell walls, as

TABLE-1 SUMMARY OF IMPORTANT OIL-BODY CHARACTERISTICS

Family	Species	oil-bodies/cell	
Ptilidiaceae	*Blepharostoma trichophyllum*	2-6 (25)	1u X 1µ
	Tricholea tomentella	4-8 (10)	2-3 X 2-3µ
Lepidoziaceae	*Lepidozia reptans*	10-25 (7-25)	3.5-4 X 5µ
	Bazzania trilobata	3-8	3-4 X 3-4µ
Calypogeiaceae	*Calypogeia mulleriana*	6-13	2.5-3 X 5µ
	Calypogeia fissa	4-8	2.5-3 X 4µ
Harpanthaceae	*Lophocolea heterophylla*	4-7	2.5-3 X 3µ
	Lophocolea minor	6-8 (14-17)	3-4 X 4µ
	Lophocolea bidentata	10-18 (4)	3-3.5 X 3µ
Jungermanniaceae	*Jungermannia lanceolata*	5-10 (15)	5.5-6 X 6µ
	Jamesoniella autumnalis	8-18	2-4 X 5-8µ
	Plectocolea crenulata	2-6	3.5-4 X 4µ
	Plectocolea crenuliformis	2-8	6-8 X 6-9µ
Plagiochillaceae	*Plagiochila asplenioides*	4-6	4-5 X 4-5µ
Scapaniaceae	*Diplophyllum apiculatum*	8-10	3-4 X 3-4µ
	Scapania nemorosa	3-6	3.5-4 X 4µ
	Scapania curta	3-6	3-4 X 3-4µ
Porellaceae	*Porella platyphylla*	11-25	1-2 X 1-2µ
	Porella platyphylloidea	14-35	1.5-2 X 2µ
Frullaniaceae	*Frullania asagrayana*	3-5	3.5-4 X 4µ
	Frullania inflata	2-4	1.5-2 X 2µ
	Frullania riparia	3-4 (5-6)	3.5-4 X 4µ
	Frullania eboracensis	2-5	2.5-3 X 3µ

size range	color	shape	texture	rows of seg.	arrangement
2-2.5 X 3-3.5µ	colorless		1-pap.----3-4 seg.	1	random
3-4 X 6µ	shiny		1-pap.	X	ends
6-7 X 10-11µ	grey		smooth----3-4 seg.	X	random
4-5 X 6µ	shiny		smooth----seg.	1	random
2-5 X 11µ	colorless		3-5 (8-15) seg.	2	CW
3-4 X 7-8µ	colorless		1-seg.	2	random
3.5-4 X 7-8µ	colorless		r-pap.	X	random
3-4 X 8µ	red-brown		1-pap.	X	CW
4.5-5 X 10µ	brown		pap.	X	random
5.5-6 X 10-11µ	tan		pap.	X	CW
6.5-7 X 9-11µ	colorless		1-pap.	X	random
5.5-6 X 10µ	colorless		1-pap.	X	random
8-9 X 16-20µ	colorless		1-pap.	X	random
4.5-5 X 8-8.5µ	colorless		pap.	X	random
3-4 X 6-7µ	colorless		r-pap.----1-seg.	X	random
6-7 X 10-12µ	tan		r-pap.	X	CW
6-7 X 10µ	colorless		r-pap.	X	random
1-2 X 3-4µ	colorless	disc	smooth	X	random
1.5-2 X 5µ	colorless	disc	smooth	X	random
4-5 X 8-10µ	tan		r-pap.	X	random
2.5-3 X 4µ	colorless		1-pap.	X	random
4.5-5 X 9-10µ	colorless		pap.	X	random
3.5-4 X 9-10µ	colorless		r-pap.	X	random

compared to *Calypogeia fissa* with its randomly arranged, slightly smaller and less-defined segmented oil-bodies.

Three species in the family Harpanthaceae were examined. All three are members of the genus *Lophocolea* and all exhibit very similar numbers per cell, size, color, shape and texture. *Lophocolea bidentata* has a slightly different arrangement of oil-bodies within the cell. The vast similarities shown by the oil-bodies of these three species of *Lophocolea* suggest that reasonable taxonomic significance may be assigned to their oil-bodies.

Four different genera were examined from the family Jungermanniaceae. The only oil-body characteristics these four have in common are their shape and texture. *Jungermannia lanceolata* has light brown oil-bodies that are arranged close to the cell wall. On the other hand, *Jamesoniella autumnalis*, *Plectocolea crenuliformis* and *Plectocolea crenulata* have colorless oil-bodies that are randomly arranged within the cell. All four also show slight variations in size and numbers. As mentioned earlier the two most important characteristics that make an individual oil-body distinctive are shape and texture. Even though these four species have only two characteristics in common, they are very relevant.

In the family Porellaceae, *Porella platyphylla* and *Porella platyphylloidea* were examined. Both had almost identical oil-bodies except for the fact that almost twice as many oil-bodies occur per cell in *P. platyphylloidea*, a species which some bryologists regard as a variety of *P. platyphylla*.

In the family Scapaniaceae three genera were examined, two species of *Scapania* and the genus *Diplophyllum*. *Scapania nemorosa* and *Scapania curta* show very similar oil-bodies except for a slight color difference

and small variation in their arrangement. Diplophyllum apiculatum tends to have different shaped oil-bodies that are approximately the same size but have a few more per cell.

In the Frullaniaceae four species of Frullania were found to contain very similar oil-bodies. Aside from F. asagrayana having light brown and sometimes sausage shaped oil-bodies, F. eboracensis having similarly shaped, colorless oil-bodies and F. riparia and F. inflata having colorless and only spherical or ovoid oil-bodies, all three exhibit remarkable similarities, especially in their shape and texture. It is in this family that the greatest continuity can be found among its oil-bodies.

Since only one species was examined in the family Plectocoleaceae little can be said about the relevance of characteristics in this family.

SUMMARY

In the early literature of the Hepaticae oil-body characteristics were rarely used for taxonomic purposes or in morphological descriptions of liverworts. This paper describes a method for describing oil-bodies of the median leaf cells of leafy liverworts. Written descriptions and photomicrographs of the oil-bodies of twenty-three common east-central Illinois leafy liverworts in the following families are included: Ptilidiaceae (two species), Lepidoziaceae (two species), Calypogeiaceae (two species), Harpanthaceae (three species), Jungermanniaceae (four species), Plagiochilaceae (one species), Scapaniaceae (three species), Porellaceae (two species), and Frullaniaceae (four species).

The diagnostic characteristics recorded for each species were the number of oil-bodies per cell, size range of the oil-bodies, color, shape, texture, number of rows of segmentations, if segmentations are present, and arrangement of oil-bodies within the cell.

It was found that the families Lepidoziaceae, Calypogeiaceae, Jungermanniaceae, Scapaniaceae, Porellaceae and Frullaniaceae, are composed of genera and species that show homogeneous oil-body characteristics. The Ptilidiaceae contain two species with oil-bodies of different shapes, colors and numbers per cell. In the family Harpanthaceae it was found that colors vary among the three species observed along with widely varying textures. Only one species from the family Plagiochilaceae was studied.

Because oil-bodies are easy to find in fresh material and contain several distinguishing characteristics, their morphological descriptions can aid taxonomists and phylogeneticists in the systematic arrangements of leafy liverworts and in the construction of keys for their identification. It is the opinion of this author that further descriptive and taxonomic work and morphological studies of the leafy hepatics should include detailed oil-body descriptions. Oil-bodies are much too unique a structure to be ignored.

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