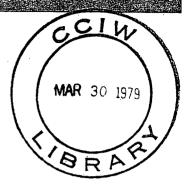




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A SURVEY OF SOME CANADIAN LAKES FOR THE PRESENCE OF ULTRASTRUCTURALLY-DISCRETE PARTICLES INTHE COLLOIDAL SIZE RANGE

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To be published in J. Fish. Res. Bd. Canada March 1979

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1 Running head: Massalski and Leppard: Survey of lake colloids.

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3 A Survey of Some Canadian Lakes for the Presence of

- 4 Ultrastructurally-discrete Particles in the Colloidal Size Range
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- ronment Canada, Burlington, Ontario, Canada L7R 4A6

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- 9 Massalski, A. and Gary G. Leppard. 1979. A survey of some Canadian
- 10 lakes for the presence of ultrastructurally-discrete particles
- in the colloidal size range. J. Fish. Res. Board Can. 00:000-000.

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- 13 Water samples from nine Canadian lakes were centrifuged and the
- 14 pellets were analyzed by transmission electron microscopy. The pellets
- 15 included small organisms, organic colloids and clay particles. In al-
- 16 most all the samples, colloids were the major component revealed following
- 17 thin-section analysis. When viewed at high magnification, much of each
- 18 pellet consisted of morphologically-discrete particles, some of which
- 19 were readily categorized. Electron-opaque fibrils of colloidal size
- 20 were frequently encountered: (1) at different depths; (2) as a coating
- 21 on the surface of algae and bacteria; (3) overlaying the sediments;
- 22 (4) as an apparent adhesive between a variety of particles; and (5) as
- 23 a component of froth at the water-air interface. They were common at
- 24 all times and in lakes of varying trophic levels and sizes.

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1 Key words: water, colloids, fibrils, lakes, electron microscopy.
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Introduction

Limnologically, the word "dissolved" is an operational term:

the term "dissolved organic carbon", or "DOC", refers to all organic

carbon in lake water from large colloids down to small molecules in

true solution. Most "particulate organic carbon", or "POC", is non
living and consists of particles larger than 0.45 µm in smallest dimen
sions (Wetzel 1975), although aggregates of colloids may be operationally

defined as POC depending on their retention by filters. The mean

ratio of DOC to POC in many lakes is on the order of five to one (Wetzel

10 1975). The quantitative importance of DOC in lakes is such that under
standing the functional role of it and of its major components is important.

An understanding of its trophic role in lakes requires knowledge of the

nature and regulation of its biogenesis as well as its interrelationships

with POC.

In 1977 (Leppard et al.), a ribbon-like fibril, of from 3 to 10 nm 16 diameter and having a considerable capacity to bind electron-scattering 17 stains, was shown to be a common colloidal material of the DOC fraction 18 of two lakes. Also, it was found in the POC fraction as a result of its 19 capacity to form large clumps and its capacity to adhere to algae, bacteria, 20 large debris and clay particles. The discovery of these fibrils led to 21 laboratory investigations into the secretion of them by algae and to 22 chemical analyses of fibril-rich materials isolated from lake water 23 (Leppard et al. 1977; Burnison 1978). At the same time, it was realized 24 that transmission electron microscopy allowed us to categorize much of 25 the suspended fine material despite its chemical complexity. As was

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1 predicted earlier (Leppard et al. 1977), ribbon-like, "electron-opaque"
2 fibrils and other kinds of electron-opaque fibrils of similar dimensions
3\, are shown here to be common to the water and sediments of a variety
  of lakes in a variety of situations. Illustrated here is a survey of
5 lakes for such fibrils, including a preliminary attempt to document
6 other common, distinctive, colloidal particles. The word "fibril" is
   used in the standard dictionary sense meaning a "small filament or thread".
                        Materials and Methods
10.
         Water samples were taken from nine Canadian lakes selected
12 because of current and previous limnological investigations and
13 variety in lake type.
1) Lake Ontario (8 km offshore from Oshawa at the OOPS 11 IFYGL
15 Station);
         2) St. George Lake (near Toronto, Ontario);
         3) Thompson Lake (near Toronto, Ontario);
         4) Jack Lake (50 km northeast of Peterborough, Ontario);
        5) Lake Erie (both the Western Basin and Central Basin);
        6, 7 and 8) Erickson-Elphinstone District Lakes, numbers L255,
21 L318 and L885 (in southwestern Manitoba, west of Lake Manitoba);
22 \cdots
         9) Kootenay Lake, British Columbia (at midlake station S-23).
         Table 1 shows the sampling program. We defined two separate
24 colloid fractions, one of particular interest to us here and a second
                       the latter
25 for future analyses, Vderived by high speed centrifugation of the
```

- I remaining fluid. Preliminary comparative studies on a variety of
- 2 samples from St. George Lake (see also Leppard <u>et al.</u> 1977) revealed
- 3 that the more readily characterized colloids were present in both
- 4 fractions. This paper describes the readily sedimented fraction
- 5 which contained some small organisms, many colloid-sized particles,
- 6 as defined by Vold and Vold (1964), and complex aggregates of colloids.
- $\bar{\tau}$ Because of the potential significance of observations on the physical
- 8 relationships of natural fibril aggregates (Leppard 1975; Leppard and
- 9 Ramamoorthy 1975; Leppard et al. 1977) and because of potential dis-
- 10 ruption of these aggregates by ultracentrifugation, no attempt is made,
- 11 in this early study, to describe the colloidal aggregates derived by
- 12 sedimentation at great centrifugal forces.
- Replicate portions of each freshly-taken sample were centrifuged
- 14 at 1,000q to give loosely-packed pellets which were prepared for
- 15 electron microscopy and stained with heavy metals according to Leppard
- 16 et al. (1977). The general approach to the microtomy of the pellets
- 17 was as outlined in Leppard et al. (1977). Several consecutive sections
- 18 of approximately 50 nm thickness were cut from each pellet, followed by
- 19 removal of several micrometers of pellet, then further cutting of
- 20 consecutive "thin" sections and so on. This approach provides a gross,
- 21 semiquantitative evaluation of the abundance of any given distinctive
- 22 structure (see Discussion). Observations on stained sections and photo-
- 23 graphs of them were made with a Siemens 101 transmission electron
- 24 microscope. The data collection for this study consisted of about
- 25 1600 micrographs derived from approximately 100,000 different discrete

l images on the microscope screen. Serial sections were searched at 2 4,000x with interesting grid windows searched later at 20,000x. Depending 3 on the heterogeneity shown by a given pellet, the ratio of images 4 studied to images photographed ranged from about one in ten to about 5 one in one hundred. If a given distinctive morphological entity was 6 found readily and if it was also the most frequently encountered entity, 7 it was given an abundance rating of 3. If not detected at all within 8 the time frame of the initial search, it was given an abundance rating of 0. 11 Results 12 All of the water samples revealed a variety of distinctive colloids 13 (as defined by Vold and Vold 1964) which tended to fall into categories according to their dimensions, form, and electron opacity after staining with heavy metals. These categories included electron-opaque fibrils, clay particles, cell wall fragments, diatom frustules, fragments of invertebrate exoskeleton, electron-lucent fibrils, complex slimes, viruses, tripartite structures resembling membranes, algal scales, unusually small prokaryotes and a variety of granules. Of the 30 different kinds of samples, 29 revealed electron-opaque 21 fibrils as shown in Table 1. Of the nine lakes studied, eight had such fibrils, with five of these lakes showing evidence that they were quantitatively important. Fifteen of the 30 kinds of samples revealed

these fibrils to be the most abundant of the morphologically distinctive

- 1 colloids, with St. George Lake being a particularly good source
- 2 regardless of situation. Considering individual samples, the fibrils
- 3 were most dominant in the six meter summer sample from Jack Lake,
- 4 followed by the 0.5 meter summer sample from Lake 318 and then by
- 5 several different samples from St. George Lake. They were found in
- 6 the summer surface froth of St. George Lake and in the metalimnia
- 7 of both Jack Lake and St. George Lake.
- All sediment traps contained fibrils. Two water samples
- 9 (Thompson Lake and Lake 885) were characterized by an extreme wealth
- 10 of algal cells; one showed the fibrils while the other did not. In
- 11 the case of Thompson Lake, all the fibrils in the surface water were
- 12 part of bacteria-alga associations. The sole lake which was sampled
- 13 extensively (St. George Lake) revealed fibrils in abundance in all
- 14 four seasons. The sole lake (Lake 885) showing a fibril abundance
- 15 rating of 0 (see Table 1) was reinvestigated to give a second rating
- 16 of 0. 1.1
- 17 The electron-opaque fibrils came in several distinctive varieties,
- 18 although long ribbon-like types were the most frequently encountered.
- 19 The next most abundant category of colloidal material consisted of
- 20 irregular, angular, electron-opaque tablets and leaflets of various
- 24 kinds suggestive of different kinds of clay particles. Such particles
- 22 were particularly abundant near lake bottoms; they had a patchy dis-
- 23 tribution as did those categories of colloids found infrequently. There
- 24 were some revealing physical associations between fibrillar colloids
- 25 and the biota; these are described in detail and discussed in Massalski

1 and Leppard (1979).

- Fig. 1 illustrates a common situation in lake water, an algal 3 cell with a surface coating of fibrils whose thickness is similar 4 to the diameter of the cell proper. Sometimes such a thick coating 5 is associated with encystment. Extensive examination with the electron 6 microscope reveals many fibrils to be of great length, a feature not 7 often conveyed by the micrographs. Fig. 2 shows some fibrils having 8 little curvature and running in the plane of the section. 9 sectioning results and views such as Fig. 2 indicate that many electron-10 opaque fibrils of ribbon-like aspect are very long with respect to 11 their diameter. Diameters of approximately 5 nm are commonly associated 12 with lengths of thousands of nanometers. Fig. 3 illustrates thick 13 fibrils having thin branches. These fibrils are all associated with 14 one side only of a fragment of algal cell wall, in this case the distal 15 side (external surface). Such asymmetry of wall fragments was common. Interlaced branched fibrils forming a porous three dimensional network are shown in Fig. 4. Such aggregates are found frequently on the surface 18 of algae and as an apparent adhesive between fragments of debris. Surface 19 froth at the lakewater-air interface of St. George Lake in summer 20 contains extremely fine fibrils as shown in Fig. 5. These fibrils are the thinnest which can be clearly distinguished as electron-opaque fibrils.
 - Electron-opaque fibrils, although typically distinctive, can be confused on rare occasions with other categories of colloid. Fig. 6 is an example of a granular slime layer on the surface of a green

Where the packing of the granules is less dense, there are indications of fine fibrils whose diameter is at the resolution limit Thus, one cannot be certain whether densely-packed for sections. portions of this mucilage consist entirely of small granules or a mixture of granules plus curved fibrils whose images in cross-section appear as granules. Fig. 7 presents another problem in categorization Found occasionally. Enmeshed in a cell wall coating of at least two varieties of electron-opaque fibril are some electron-lucent (Leppard and Colvin 1978) fibrils with an electron-opaque sheath (see arrows). Under suboptimal viewing conditions and at low magnifications, such sheathed fibrils appear entirely electron-opaque. The cell wall proper shown in Fig. 7 presents many electron-lucent fibrils arranged in a criss-cross pattern characteristic of cellulosic walls; small aggregates of these were noted rarely in the survey as were algal surface scales of similar texture. 15 Fig. 8 illustrates clay particles cross-connected by fine fibrils 16 and Fig. 9 illustrates a cell wall fragment connected to clay particles via fibrils attached to one side only of the wall. Similar observations have been made recently by botanists on samples not subject to centrifugation (Guckert et al. 1975; Leppard and Ramamoorthy 1975). Fig. 10 shows virus-like particles embedded in a meshwork of fine fibrils 21 giving rise to an aggregate of "viruses" whose diameter is ten times 22 that of an individual virus. As one would expect, individual viruses, free of associated material, were not seen in the pellets of the readily 25 sedimented fraction. Figs. 8, 9 and 10 are three of many kinds of examples of

- 1 fibrils apparently acting as adhesives.
- Many distinctive varieties of cell wall fragments, exoskeleton
- 3 fragments, frustules, granule aggregates and membrane-like structures
- 4 could be characterized according to dimensions and morphology, but
- 5 not to species (Figs. 11, 12).
- Rarely, electron-opaque fibrils are found on the proximal side
- $\overline{}$ of a cell wall. This is shown in Fig. 13 as another example of the
- ⁸ unusual asymmetry of cell walls with respect to the attachment of
- 9 fibrillar coatings. The wall (Fig. 13) is an apparently disintegrating
- 10 wall but one can find examples of normal walls, associated with
- ll healthy-appearing cells, which have a coating of fibrils on the
- 12 proximal side. In every example of the latter case, however, there
- 13 was a much more extensive coating on the distal side. Thus, the
- 14 proximal coating may not have represented an attached coating but may
- 15 possibly have represented, instead, fibrils in transit from the cell
- 16 to the external milieu. This topic is treated more fully in Massalski
- 17 and Leppard (1979).
- Fig. 14 shows strips of algal cell wall (peeling away from an
- apparently healthy green alga, not shown) associated with electron-
- 20 opaque fibrils displaying a great range of diameters and an extremely
- 21 coarse appearance. If the more typical fibrils were not present, then
- 22 the coarse fibrils might not have been recorded as fibrils per se.
- 23 Both Figs. 14 and 15 illustrate fibrils which just barely fit the
- 24 dictionary definition (Webster's New Collegiate Dictionary, 1974) of
- 25 the word "fibril".

1	Figs. 15, 16 and 17 illustrate a feature of Jack Lake worthy
2	of further inquiry. In one 18 m sediment trap sample, three distinct-
3	ive types of electron-opaque fibrils were recorded frequently. Fig.
4	15 shows apparently short, irregularly-shaped fibrils, Fig. 16 shows
5	apparently rigid, long, fine fibrils arrayed almost geometrically, and
6	Fig. 17 shows curved ribbon-like fibrils which are the most common type
7	yet encountered.
8	As a result of this survey, it is now clear that electron-opaque
9	fibrils can be subcategorized into many well defined types with some
10	occurring frequently in nature. We have documented individual fibrils
11	as fine as 2 nm and, rarely, as thick as 40 nm. Within this range there
12	are long, short, straight and curved ones. They can be subcategorized
13	as: branched or unbranched; tapered or uniform in diameter; rod-like,
14	ribbon-like or irregular in longitudinal view; with tip differentiation
15	or without it. Some appear to have a granular substructure and there
16	is considerable variation from one sample to another in their ability
17	to take up stains. Additional documentation of the various subcategories
18	can be found in Leppard et al. (1977) and Massalski and Leppard (1979).
19	
20	
21	Discussion
22	Electron-opaque fibrils of various types, whose diameters fall
23	in the range of 2-40 nm (.002040 µm), are common in Canadian lakes.
24	They are found throughout the water column of at least some lakes and
25	they form coatings on many kinds of particles including cells. As

ı shown earlier (Leppard et al. 1977) ribbon-like fibrils can be separated 2 from other kinds of particles by physical techniques. This survey $_{
m 3}$ suggests that the "dissolved organic carbon" fraction of lake water, 1 as defined operationally, might also be separated into other distinct-5 ive categories of colloids, using the electron microscope as an instrument for confirming purification steps. Because of the shape and dimensions of the fibrils and the large numbers of pellets (and their replicates) to be sectioned, we were unable to calculate exact fibril contributions to the volume of the pelleted materials. Preliminary experiments indicate that many of the electron-opaque fibrils do not become part of a pellet unless centrifugal forces on the order of 100,000 g are applied for several hours. Thus, quantitative estimates of fibril abundance will depend on further 13 development of separation techniques permitting direct weight measurements accompanied by accurate estimates of purification losses. Some steps have been taken in this direction (Burnison 1978). Two problems in estimating fibril abundance were observed. 17 fibrils having a diameter near 2 nm are too fine to be resolved unless 18 they are extremely well stained. Even when successfully stained, they still escape detection at low magnifications. Consequently, our survey technique tends to underestimate the abundance of the finest fibrils. Second, we encountered several types of electron-lucent (Leppard and Colvin 1978) fibrils having electron-opaque coatings whose $_{24}$ appearance at search magnifications (4,000x) on the viewing screen

 $_{25}$ of the electron microscope was that of an electron-opaque fibril.

1 Any departure from the highest standards of microscopical and photo-2 graphic technique led to an incorrect categorization of such fibrils. Prior to this survey, we had focussed on ribbon-like fibrils 1 because of their abundance in St. George Lake and in the Bay of Quinte, 5 a eutrophic bay on the northern shore of Lake Ontario. However, the 6 presence of a variety of electron-opaque fibrils other than ribbon-7 like types from several of our surveyed lakes has caused us to make conceptual adjustments in trying to understand their chemistry and 9 biological roles (see Leppard et al. 1977). It is clear now that considering all electron-opaque fibrils to be chemically and physiologically similar is a dangerous assumption. Furthermore, one should 12 not ignore less abundant categories of distinctive colloids (as defined microscopically) in future attempts to understand the roles of fibrils in lakes. This is emphasized by Figs. 8, 9 and 10 which illustrate physical relationships between fibrils and other colloids having poten-16 tially important roles. The nature of these relationships is such that they are not likely to have been created by the sedimentation step in sample preparation and they are subject to verification by more specialized technology (see Guckert et al. 1975). As documented in Fig. 8, an examination of aggregates of clay leaflets reveals a fibrillar linkage between some of them. A study of cell wall fragments 22 reveals them to be cross-connected occasionally to somewhat distant 23 clay particles by means of fibrils (Fig. 9). Fig. 10 suggests that 24 viruses may be present in lake water as aggregates which will not pass 25 fine filters in filtration procedures used in sampling for viruses.

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1 Further microscopical surveys are needed to assess the significance
^{\circ} of these viral aggregates as well as some of the other components of
3 DOC.
                            Acknowledgements
         We thank the following scientists from the National Water
8 Research Institute for their invaluable assistance: Dr. D.R.S. Lean,
9 Dr. B.K. Burnison, Dr. B. Brownlee, Mr. T.P. Murphy and Mr. M.N.
   Charlton.
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24	
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TABLE 1. Sampling program for a microscopical analysis of sedimentable colloids in lake water.

Lake	Time	Depth from Surface	Notes ¹	Abunda electron fib	nce ² of -opaque rils
Lake Ontario	June 1976	1 m		1	
		10 m		1	
		40 m		. 1	
		2 m above bottom	sediment trap -	3 days 1	
				· · · · · · · · · · · · · · · · · · ·	
St. George Lake	February 1976	bottom	sediment trap	3	3
30. 430. 30	March 1976	1 m above bottom	sediment trap -	5 weeks 3	3
	April 1976	5 m		3	3
		1 m above bottom	sediment trap -	2 weeks 3	3
	May 1976	0 m		`	3
		4 m			3
		13 m			3 -
	July 1976	0 m	surface froth	. ;	3
	September 1977	Om			3
		7 m	•		3

TABLE 1. (continued)

St. George Lake	September 1977 6 m metalimnion	2
Second Basin	September 1377	
Thompson Lake	August 1978 0 m dominated by Anabaena	1
	<u>spiroides</u>	
Jack Lake	August 1978 6 m sediment trap - 1 week	3
	8 m metalimnion	1
	11 m sediment trap - 1 week	2
	18 m sediment trap - 1 week	. 3
Lake Erie		•
Central Basin	September 1976 1 m above bottom sediment trap - 6 days	2,
	3 m above bottom sediment trap - 6 days	2
Lake Erie		
Western Basin	September 1976 1 m above bottom sediment trap - 2 1/2 days	2
	October 1977 2 1/2 m	1
	5 m	1

TABLE 1. (continued)

Erickson-Elphinstone District Lakes								
L255	* 	July 1977		1/2 m				3
L318		July 1977		1/2 m				3.
L88 5	ta e e	July 1977		1/2 m	,	dominated by	Aphanizomenon	0
Kootenay Lake		July 1977	,	2 m				3
	•			8 m			•	1

¹Samples are conventional water samples unless indicated as being from a sediment trap. The time that the sediment trap was suspended in the water column is indicated.

²A rating of 3 for abundance means that the electron-opaque fibrils were both readily encountered and the single most common material observed. A rating of 0 for abundance means that they were not observed during the initial stages of the search.

Figure Legends

1		
2	A11	figures were produced from material fixed in glutaraldehyde-
3		postfixed in osmium-ruthenium, and poststained with uranium
4	and lead.	All printing was done deliberately at maximum contrast to
5	present an	optimal view of the fibrils. The bar represents 0.5 μm .
6	FIG. 1.	Surface of a green alga showing densely-packed, fine
7		fibrils external to the cell wall. 0.5 m water sample
8		from Erickson-Elphinstone District Lake 318.
9	FIG. 2.	Loosely-packed fibrils extending a great distance into
10		the water from an eukaryote alga. Note the fact that some
'n		fibrils can be traced individually for up to several micro-
12	· · · · · · · · · · · · · · · · · · ·	meters. Also note, in the center, a rare case of several
13	·	coalesced fibrils giving the impression of a thicker straigh
14		fibril. 0.5 m water sample from Erickson-Elphinstone Dis-
15		trict Lake 318.
16	FIG. 3.	➡ Detached cell wall in the process of disintegration showing
17	•	an attachment of surface fibrils on one side only. 13 m
18		water sample from St. George Lake.
19	FIG. 4.	Thick branched fibrils and their thin branches. Note the
20		apparent, three-dimensional network formed by the associa-
21		tion of the branches. 2 m water sample from Kootenay Lake.
22	FIG. 5.	# Sample of surface froth revealing extremely fine fibrils.
. 23		These are the thinnest fibrils which can be clearly dis-
24		tinguished. Note the magnification and compare with the

fibrils in Fig. 3 and Fig. 4. Surface water sample from

1	* 1	St. George Lake.
2	FIG. 6.	The Surface of a green alga surrounded by an electron-opaque
3		slime layer which, at its edges, rarely reveals some
4		extremely fine fibrils approaching the resolution limit of
5		the electron microscope for sections. Erickson-Elphinstone
6	•	District Lake 318.
7	FIG. 7.	⋣ Discarded mother cell wall of a green alga showing several
8		distinctly different fibrillar materials. The wall proper
9		reveals a typical cellulosic wall pattern, in which layers
10		of rigid fibrils appear oriented in a criss-cross manner.
11		Projecting into the external milieu is a layer of at least
12	•	two varieties of electron-opaque fibrils attached to the wal
13		proper. Some fibrils are electron-lucent with an electron-
14		opaque coating - see arrows. Erickson-Elphinstone District
15	i •	Lake 318.
16	FIG. 8.	Near the bottom of a lake, many of the colloidal particles
17		can be tentatively identified as clay. Sometimes a network
18		of fibrils is found between these clay particles. 40 m
19	v.	water sample from Lake Ontario.
20	FIG. 9.	- 全 Cell wall fragment showing fibrils extending from one
21	. '	side only. These fibrils appear to penetrate adjacent
22		colloidal particles. Some of the adjacent particles may be
23		tentatively classified as clay. Sediment trap, 2.5 day
24		sample taken 1 m above botton, Lake Erie, Western Basin.
25	FIG. 10.	Virus-like particles embedded in a meshwork of fine fibrils.

Note the clear regions of different dimensions around some particles. Sediment trap, 5 week sample taken 1 m 2 3 above bottom, St. George Lake. 4 FIG. 11. 🖴 Example of a distinctive particle of probable biological origin. Note the highly organized geometrical 5 substructure. Ill-defined fibrillar extensions can be seen 7. attached to each structure. Sediment trap, 6 day sample taken 1 m above bottom, Central Basin of Lake Erie. 8 Another example of readily characterized particles FIG. 12. 9 10 (readily categorized according to dimensions and form) which may be tentatively identified as fragments of exo-11 12 skeleton. Sediment trap, 5 week sample, taken 1 m above 13 bottom, St. George Lake. 14 FIG. 13. ➡ Empty cell whose wall is in the process of disintegration. The internal layer of wall reveals a multitude 15 of electron-opaque fibrils projecting into the lumen. This 16 is an unusual case; such fibrils found either on the surface 17 of the walls of living cells or on decomposing cell walls 18 19 are usually associated with the outer surface of the wall. Sediment trap, 1 week sample, 18 m, Jack Lake. 20 Thick and thin fibrils attached to a wall layer which is 21 FIG. 14. 22 being released into the external milieu from the cell wall 23 of a green alga (not shown). Surface water sample, Thompson 24 Lake.

A Electron-opaque, fibrillar material associated with a

25

FIG. 15.

1		blue-green alga. Sediment trap, 1 week sample, 18 m, Jack
2		Lake.
3	FIG. 16.	## Unique example of an aggregate of electron-opaque fibril:
4		which are arrayed geometrically. These fibrils are
5		unusually straight and frequently cross at right angles.
6		Sediment trap, 1 week sample, 18 m, Jack Lake.
7	FIG. 17.	One of the most common varieties of electron-opaque
8		fibrils. These are found frequently in many locations.
9		At least some of the granular structures are cross-sections
10		and near cross-sections of fibrils. Sediment trap, 1 week
11	•	sample, 18 m, Jack Lake.
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