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ECOLOGICAL INVESTIGATIONS OF ICE WORMS ON CASEMENT GLACIER,  
SOUTHEASTERN ALASKA

by

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## ABSTRACT

(*Oligochaeta*);

A population of ice worms, Mesenchytraeus solifugus, was observed during the summer months of 1967 on Casement Glacier, southeastern Alaska. Live and preserved specimens were brought back for laboratory studies. Casement Glacier specimens are distinguishable from previously described populations mainly on the basis of morphology of internal reproductive organs. On snow, the worm's appearance at the surface is mediated by light intensity. Worms were not seen on snowfields not overlying glacier ice. Their distribution on the glacier seemed related to the distribution of snow and ice algae. Counts were made of various algal forms in ice, snow and water samples. The worms ingest algae. Estimates of standing crop and energy flow in the worm and algal populations indicate the plausibility of the ice worm's subsisting on the algal productivity. Snow buntings, and probably semipalmated plovers, eat ice worms. The ice worm's rate of oxygen consumption at 0 C is 52  $\mu$ l/g hr, and the  $Q_{10}$  is 2.27. Comparison of this respiration rate and  $Q_{10}$  with those of other oligochaetes indicates that the ice worm does not maintain a state that would be predicted from low temperature physiological acclimation in a worm normally living at higher temperatures. This suggests an operational distinction between evolutionary ecological adaptation to temperature and physiological adaptation in the individual. The ice worms begin to autolyze and finally disintegrate at 20 C and above.

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## INTRODUCTION

Worms inhabiting the glaciers on the Pacific coast of North America were first reported by Wright (1887) from the Muir Glacier and Russell (1893) from the Malaspina Glacier. A mountaineering party crossing Malaspina Glacier (de Philippe, 1900) collected a number of specimens which were subsequently described by Emery (1898a, 1898b, 1898c) and named Melanenchytraeus solifugus (Emery, 1898a). At the same time, a second mountaineering party, attempting the same peak over a slightly different route but also crossing the Malaspina Glacier, sent their specimens to Moore who did not publish a description until 1899, at which time he contended that Melanenchytraeus was, in fact, Mesenchytraeus and that Mesenchytraeus solifugus was the first named New World representative of that genus. The points of difference between Emery and Moore are no longer at issue following Eisen's (1904) substantial revision of the Enchytraeidae, in which he redefined the genus and described eighteen new species of Mesenchytraeids collected during the Harriman Alaska Expedition. Eisen in the same publication described specimens of Mesenchytraeus solifugus from Muir Glacier and La Perouse Glacier, showing that the revised genus Mesenchytraeus could unquestionably accommodate the "glacier worms". Welch (1916a, 1916b) described a new subspecies Mesenchytraeus solifugus rainierensis from the upper snowfields and glaciers of Mt. Rainier. Lower snowfields yielded a new and quite distinct species, Mesenchytraeus gelidus. Welch (1917a) published an incomplete description of specimens of Mesenchytraeus solifugus from Grand Pacific Glacier.

The literature on Mesenchytraeus solifugus essentially ends in 1917, but for the studies reported herein, and those of Tynen (1970a, 1970b). Subsequent to that date the species appears in a few keys, and is mentioned in reviews of the literature by Ulke (1917), Stephenson (1930), Gudger (1923), and Altman (1936), but no new information is added. The present neglect of ice worms is not easily understood, as physiological studies of M. solifugus and its relatives might contribute a great deal of information concerning the mechanisms and evolution of low temperature adaptation.

In the summer of 1967, while a member of an Ohio State University Institute of Polar Studies expedition (AEC contract No. AT(11-1)-1473), I was privileged to observe a population of ice worms on Casement Glacier, Glacier Bay National Monument, Alaska. The physical parameters of the environment on and near Casement Glacier have been described by Peterson (1970) and Goldthwait et al. (1966) respectively. The map of Casement Glacier in Figure 1 indicates the positions of our camp, meteorological station, and stake lines as referred to later in this paper. In September, 1967 a number of ice worms were flown to Ohio State University in an ice chest. In the laboratory the worms were successfully maintained for over a year in a B.O.D. cabinet at 0.5 C. A specimen was fixed for electron microscopy 10 days after collection (Goodman and Parrish, 1971). Oxygen consumption rates were measured within a month and a half of collection. Examination of serial paraffin sections of three worms preserved in the field has revealed some differences from previously described specimens of Mesenchytraeus solifugus.

#### TAXONOMIC BACKGROUND

##### Diagnosis of the genus Mesenchytraeus Eisen, 1878

Mesenchytraeid penial bulb (sperm duct penetrates bulb and opens on the center of its surface; bulb single; radial muscle fibers of bulb connect periphery of bulb with body wall). Atrium usually present on sperm duct just before it enters penial bulb. Nephridia with small anteseptal portion, consisting merely of nephrostome; postseptal portion large, plurilobate; nephridial canal closely wound; cell mass greatly reduced. Head pore distinct; usually at or near tip of prostomium. Cardiac body present. Origin of dorsal blood vessel usually postclitellar. Oesophagus merges gradually into intestine. Peptonephridia absent. Intestinal diverticula absent. Chylus cells absent. Testes undivided. Setae sigmoid; singly pointed; approximately equal size in bundle; 4 bundles per segment. Dorsal pores absent.

Table 1 indicates the distribution of these characters within the family Enchytraeidae.

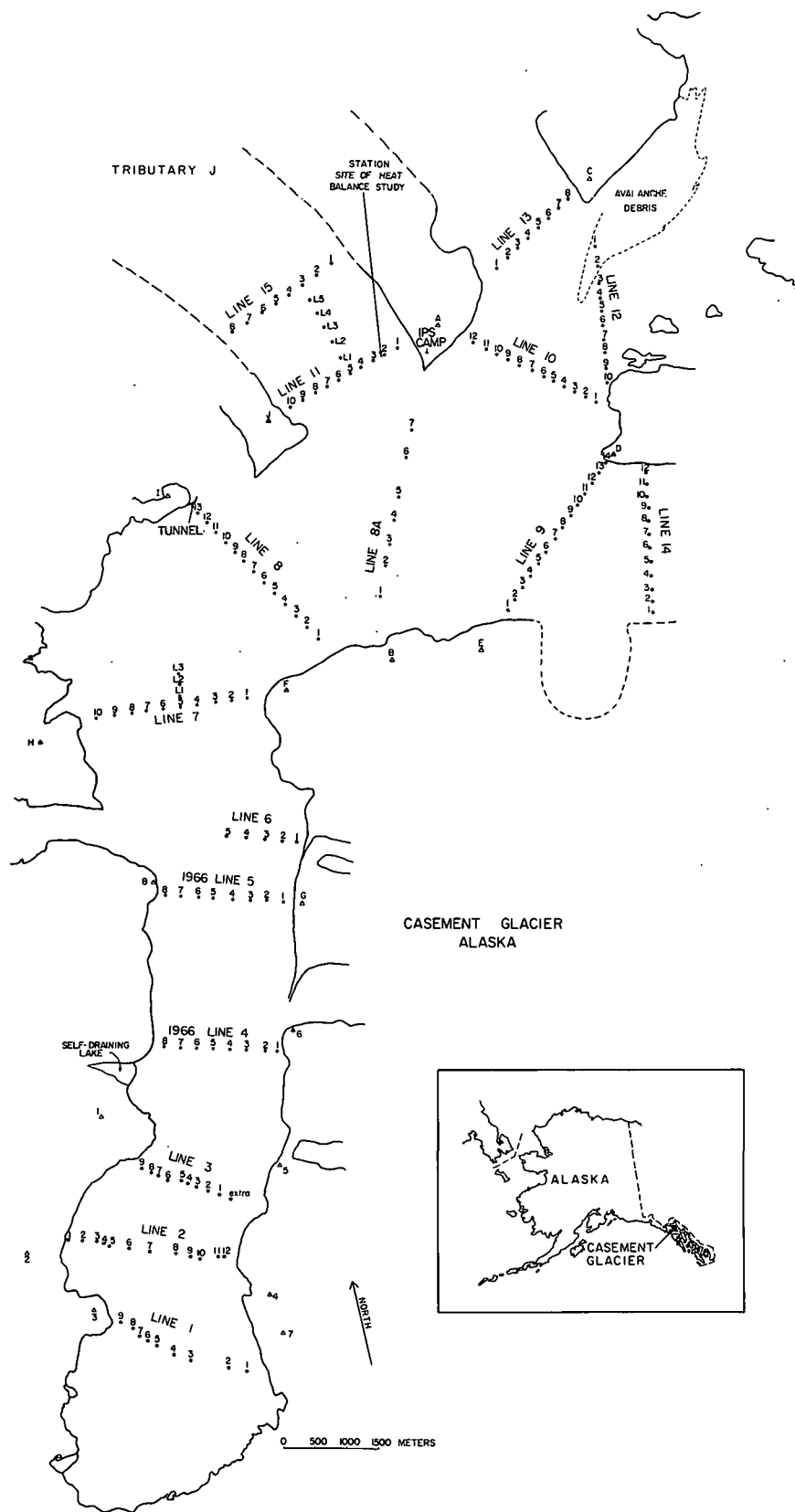


Fig. 1 - Map of Casement Glacier showing the locations of the 1967 camp, meteorological station, survey cairns, rows of movement stakes, and ice tunnel. From Peterson (1970).

Table 1. Comparison of the genera of Enchytraeidae

Genus	Sperm duct opens thru penial bulb	Muscle fibers of penial bulb connect periphery with body wall	Atrium present	Nephridium: anteseptal part small	Nephridial canal closely wound	Nephridial cell mass reduced	Distinct head pore at or near tip of prostomium	Cardiac body present	Sperm sac present	Ovisac present	Dorsal vessel origin postclitellar	Oesophagus merges gradually into intestine	Peptonephridia absent	Intestinal diverticula absent	Chylus cells absent	Testes undivided	Setae sigmoid	Setae singly pointed	Setae of about equal size in bundle	4 bundles of setae per segment	Dorsal pores absent
Mesenchytraeus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Propappus	-	-	+	+	-	-	-	+	-	-	-	-	+	+	+	+	+	-	+	+	+
Henlea	+	-	-	+	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+
Bryodrilus	+	-	-	+	-	-	-	+	-	-	-	+	-	-	+	+	+	+	+	+	+
Buchholzia				+			-	-			-	-	-	+	+		+	+	+	+	+
Marionina	+	-	-	+	-	-	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+
Lumbricillus	+	-	-	+	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+
Enchytraeus	-	-	-	+	-	-	-	+	+	-	+	+	+	+	+	+	+	+	+	+	+
Fridericia	+	-	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	+	+	-
Distichopus	+	-	-	+	-	-	-	+	-	-	+	+	-	+	-	-	-	+	+	-	-
Achaeta				-			+				-	+	+		-		-	-	-	+	+
Michaelsona	-	-	-	+	-	-	-	-			-	+	+	+	+	+	-	+	+	+	+
Stercutus				+	-	-	-	+			-	+	+	+	+	+	+	+	+	+	+
Aspidodrilus				-			-				-	-	-								
Chitrodrilus																	+	+			
Parergodrilus																					
Hydrenchytraeus				+							+	+	-				+	+		+	+

In this chart + indicates that at least some members of the genus concur in a particular feature with Mesenchytraeus, the - indicates that none concur. Blanks indicate absence of data.

The bulk of the information was drawn from Welch's (1920) description of the genera of Enchytraeidae. The descriptions of Aspidodrilus and Parergodrilus were taken from Stephenson (1930). I have also followed Stephenson in treating Hepatogaster Cejka as a subgenus of Henlea.

There is not sufficient information concerning the last five genera listed to assess their position in the family. Chirodrilus, in fact, may be a tubificid. These five genera are but little known and each contains only one or two species. From the remaining more familiar genera, however, Mesenchytraeus emerges as a quite distinctive taxon in the matters of the position of the head pore, the structure of the nephridia, and the composition of the penial bulb.

A head pore at or near the tip of the prostomium occurs only in Achaeta. In this case there need be no confusion, for the genus Achaeta is unique in that setae are wholly absent, and it is one of only two genera in which a considerable portion of the nephridium is anteseptal. The only deviation within Mesenchytraeus is in M. eastwood (Eisen, 1904; p. 50) where the head pore occurs on the upper side of the prostomium near O/I.

The closely wound nephridial canal and the greatly reduced cell mass between folds of the canal are likewise reliable recognition features, and have been reported in no other Enchytraeid. Moreover, the nephridium is generally lobate in Mesenchytraeus, a condition which otherwise has been reported only in Propappus where, however, the canal is arranged in loose adherent loops recalling the postseptal coils of the Tubificidae. The matter of the "small" anteseptal portion of the nephridium may be of greater significance than the chart indicates. In Mesenchytraeus only the nephrostome is anteseptal. The same condition is reported only in Propappus and Michaelsena while in Stercutus the anteseptal portion consists of "little more than a mere nephrostome". These qualifications have not been indicated in other genera where the anteseptal portion is listed as "small". More detail concerning the feature might be revealing. The sole exception

within Mesenchytraeus is Mesenchytraeus grandis (Eisen, 1904) which is credited with "broad" anteseptal parts.

Eisen (1904) first recognized the utility of the penial bulb structures in classification of the Enchytraeidae. On that basis he proposed three subfamilies:

I. Subfamily Mesenchytraeinae. In this group the penial bulb consists of a cushion in which there are radial muscular fibers, running from the body wall to the periphery of the bulb, as well as circular musculature. Glands opening on to the surface of the bulb are often interspersed among the muscle fibers. The sperm duct penetrates the bulb but the glands in the bulb do not open into the duct. Throughout its course in the bulb, the duct is separated by strong longitudinal musculature from the muscles of the bulb.

This subfamily contains only one genus, Mesenchytraeus. In a few members of the genus the penial bulb is degenerate. In M. fontinalis and M. pedatus the bulb is virtually absent and there are only a few glands surrounding the penial pore. In M. orcae and M. kincaidi the bulbs are small and glands are absent but the muscular structure remains distinct.

II. Subfamily Enchytraeinae. In this group there is no large coherent penial bulb, but rather one or more penial papillae, invested with a number of unicellular glands. A few muscle strands penetrate the sets of glands radiating from the base of the papillae to other portions of the body wall within the same somite. Often a layer of muscle forms a thick padding over the glands of the papillae. The sperm duct opens independently of the papillae and is in no way connected with their associated glands. There is never an atrium on the sperm duct.

This subfamily contains two genera, Enchytraeus and Michaelsona. Welch (1914) has noted that in some species of Enchytraeus the bulb is wholly or partly lumbricilline in character.

III. Subfamily Lumbricillinae. In this group there is a single penial bulb which is covered by a thick muscular layer that is a continuation of the body wall and does not invade the glandular portion of the bulb. The sperm duct penetrates one side of the bulb and opens in conjunction with the associated glands. There are no accessory glands nor is there an atrium.

This subfamily contains the genera Lumbricillus, Marionina, Bryodrillus, Henlea, Fridericia, and Distichopus. Eisen, though lacking information concerning the penial bulb in Buchholzia, Chirodrilus, and Stercutus, still appended them to the subfamily: Buchholzia on account of its relationship to Henlea; Chirodrilus for "convenience sake" (Eisen, 1904, p. 6); while for Stercutus, no reason at all was given. Welch (1914) noted minor exceptions among some species of Marionina.

A fourth subfamily, Achaetinae, was considered to receive the genus Achaeta which is quite unlike the other genera, though the details of its penial bulb are unknown and, in fact, it may be of the lumbricillid type.

#### Synonymy of the Genus Mesenchytraeus Eisen

Mesenchytraeus + Neoenchytraeus (part.) Eisen, 1878.

"  
Öfuerst af Konglia Vetenskaps-Akademiens Forhandlingar 35 n. 3 pp. 67, 74.

(Established Mesenchytraeus and Neoenchytraeus as subgenera of Enchytraeus. No type specimen was designated. The subgenus Mesenchytraeus included 3 species: M. primaevus Eisen, M. mirabilis Eisen, and M. falciformis Eisen. This paper translated and expanded by Eisen, 1879. Synonymy of Neoenchytraeus falciformis with M. falciformis by Michaelsen, 1889).

Analcus Levinsen, 1884. Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn. 1883 p. 230.

(No type species was designated. The genus included 3 species, A. armatus Levinsen, A. flavus Levinsen, and A. glandulosus Levinsen. Synonymy by Michaelsen, 1889).

Enchytraeus (part.), Vejdovsky, 1884. System und Morphologie der Oligochaeten. p. 41.

Mesenchytraeus, Michaelsen, 1886. Untersuchungen über Enchytraeus Möbii, Mich., und andere Enchytraeden. p. 44.

(Not seen. Redefined the subgenus).

Pachydrilus (part.), Michaelsen, 1886. Archiv für mikroskopische Anatomie. 28 p. 294.

(Not seen. N. sp. Pachydrilus beumeri Michaelsen.

Synonymy by Michaelsen, 1887).

Mesenchytraeus, Michaelsen, 1887. Archiv für mikroskopische Anatomie. 30 p. 369.

(Redefined as genus. Included, in addition to Eisen's 3 species, M. flavidus Michaelsen and M. beumeri Michaelsen, the latter formerly Pachydrilus).

Mesenchytraeus, Michaelsen, 1889. Abhandlungen aus dem Gebiete der Naturwissenschaftlichen Verein in Hamburg. 11 Heft 1 pp. 15-20.

(Equated Analycus with Mesenchytraeus showing A. glandulosus to be Eisen's former Neoenchytraeus fenestratus).

Subgen. Neoenchytraeus (part.) + Subgen. Mesenchytraeus (part.) + Pachydrilus (part.), L. Vaillant, 1889. Histoire naturelle des Annelés marins et d'eau douce. 31 pp. 251, 252, 234.

(Synonymy by Michaelsen, 1900).

Melanenchytraeus (nomen nudum) Emery, 1898. Revue Suisse de Zoologie et Annales du Musée d'Histoire naturelle. 5 suppl. p. 21.

Melanenchytraeus, Emery, 1898. Atti della Reale Accademia dei Lincei.- Rendiconti della classe di scienze fisiche, matematiche e naturali. 7 p. 110.

(Type M. solifugus by monotypy. Synonymy by Moore, 1899).

Mesenchytraeus, Moore, 1899. Proceedings of the Academy of Natural Sciences, Philadelphia. 1899 pp. 125-144.

Mesenchytraeus, Michaelsen, 1900. Oligochaeta, in Das Tierreich. 10 p. 84. (Complete synonymy of the Oligochaeta).

Mesenchytraeus, Eisen, 1904. Enchytraeidae of the West Coast of North America, in Harriman Alaska Expedition. 12 pp. 10, 14.

(Redefined on basis of penial bulb, also established subfamily Mesenchytraeinae. Added 18 new species).



Diagnosis of the Species  
Mesenchytraeus solifugus (Emery) 1898

Body darkly pigmented. Forty-three to 60 somites, usually about 50. Two to six setae in the preclitellar ventral bundles. Clitellum indistinct or absent. Spermathecae confined to V, with 2-3 diverticula.

Discussion of Diagnosis

The only other so intensely pigmented New World mesenchytraeid is M. gelidus Welch (1916a) which has 66 to 77 somites; 7 to 9 setae in the preclitellar ventral bundles; a uniformly yellow clitellum on 3/4 XI-XII; and belongs to the group of mesenchytraeids whose spermathecal ampullae are greatly enlarged and extended posteriorly through several segments.

Most mesenchytraeids are white or yellow. M. harrimani and M. maculatus have some dorsal brown pigmentation, and M. obscurus is dark brown to yellowish brown (Eisen, 1904).

Of the Old World species described prior to 1900, only Mesenchytraeus mirabilis Eisen (1878) is darkly pigmented. The spermathecae in this species terminate in conical ampullae and have 4 to 5 globular diverticula. Nielsen and Christensen (1959), in any event, consider M. mirabilis a dubious species.

Synonymy of the Species Mesenchytraeus solifugus (Emery)

Melanenchytraeus sp. Emery, 1898. *Revue Suisse de Zoologie et Annales du Musée d'Histoire naturelle.* 5 suppl. p. 21.

(Malaspina Glacier)

Melanenchytraeus solifugus Emery, 1898. *Atti della Reale Accademia dei Lincei.-Rendiconti della classe di scienze fisiche, matematiche e naturali.* 7 p. 110.

(Malaspina Glacier)

Mesenchytraeus solifugus, Moore, 1899. Proceedings of the Academy of Natural Sciences of Philadelphia. p. 125.

(Malaspina Glacier)

Mesenchytraeus nivus Moore, 1899. Proceedings of the Academy of Natural Sciences of Philadelphia p. 130.

(Malaspina Glacier)

Mesenchytraeus nivus corr. niveus Michaelsen, 1900. Das Tierreich. 10 p. 87.

(M. niveus is considered perhaps to be immature  
M. solifugus)

Mesenchytraeus solifugus, Eisen, 1904. Enchytraeidae of the West Coast of North America, in Harriman Alaska Expedition. 12 pp. 59-61.

(Muir Glacier, La Perouse Glacier)

Mesenchytraeus solifugus rainierensis Welch, 1916. Transactions of the American Microscopical Society. 35 pp. 103-105.

(Mt. Rainier)

Mesenchytraeus solifugus, Welch, 1917. McGill University Bionomical Leaflets. No. 2 pp. 5-8.

(Grand Pacific Glacier.)

Equates M. nivus with partially mature M. solifugus)

#### DESCRIPTION OF SPECIMENS FROM CASEMENT GLACIER

Dermal epithelium intensely pigmented; dark brown, almost black. Length 15-17 mm. Somites 46-50. Body cylindrical, tapers gradually anterior to XII as far as I which is somewhat swollen; width about 0.6 mm constant posterior to XII, narrowing abruptly just ahead of truncate anal ring; external annulation indistinct except in anterior-most segments. Prostomium spheroidal, head pore at tip. Dorsal pores absent. Four bundles of setae per segment; anterior to XII, ventral row 3-5, average 4.25 setae per bundle, lateral row usually 2-3, rarely 1 or 4,

average 2.36 setae per bundle; posterior to XII, ventral row usually 2-4, lateral row usually 1-2 setae per bundle; ventral bundles absent on XII, dorsal bundle reduced or absent, ventral setae on XI not enlarged; setae bluntly pointed, sigmoid, distal angle acute, proximal curve shallow, nodulus absent. Postpharyngeal bulbs present. Chloragogue cells present from IV posteriad. Nephridia with small narrow anteseptal part, postseptal portion a trilobate mass of closely wound tubules, anterior-most lobe connects to nephrostome, ventral-most lobe leads to nephridiopore duct, ectal portion of which is pigmented; first nephridia on septum VI/VII, present on successive septa except XI/XII and XII/XIII. Septal glands present in IV, VI, VII and VIII. Dorsal blood vessel arises between XIII and XIV, narrows abruptly in V; small cardiac body present from V to XII. One pair of transverse vessels present in IV. Lymphocytes ellipsoidal, not pigmented. Brain notched anteriorly. Spermathecae confined to V, no unicellular glands attached to duct; 2 diverticula; ampullae of spermathecae join dorsal to oesophagus, common ampulla connects laterally to oesophagus. Penial protuberance prominent on XII, clitellum not detectable externally, thickened glandular hypodermis present in XII/XIII. Spermiducal funnel in XI, cylindrical, length roughly 3x diameter, only slightly bent in middle, opening directed cephalodorsally; small ciliated collar present. Long coiled sperm duct folded on itself extends back to XV/XVI, lying inside sperm sacs past XII/XIII. Atrium present just outside penial bulb, 6 large atrial glands. Penial bulb laced with muscle fibers; about 14 penial glands arranged radially around penial pore; accessory glands absent. Paired sperm ducts arise as caudal outpocketings of septum XI/XII; lie within ovisac posterior to XII/XIII; both sperm sacs long, terminate in XVI. Ovisac originates as caudal outpocketing of XII/XIII, bifurcates in XV, and extends back several more segments.

COMPARISON OF CASEMENT GLACIER SPECIMENS  
WITH PREVIOUS DESCRIPTIONS OF MESENCHYTRAEUS SOLIFUGUS

Maturity

Comparison and evaluation of differences between the various accounts of M. solifugus is greatly hindered by the fact that so many characteristics are related to the reproductive system and are thus subject to variability with respect to the degree of sexual maturity. Unfortunately there is no independent character on the basis of which one can reliably determine the precise state of maturity, especially since no specimens seem to develop a really distinct clitellum. We can at least, however, stipulate that all described specimens be sufficiently mature that developing spermatozoa and ova can be found. Moore (1899), for example, found among his specimens of M. solifugus a number of lighter colored individuals whose spermathecae were simple club-shaped sacs, lacking diverticula and communicating neither with one another nor with the oesophagus, and whose penial bulb and associated structures were reduced - these were given species status as M. nivus. Michaelsen (1900) suggested that M. nivus ("corr. niveus") is perhaps immature M. solifugus. Welch (1917a) found in immature specimens from Grand Pacific Glacier that the spermathecae do unite and join the oesophagus but lack diverticula, so he considered the synonymy of M. nivus and M. solifugus established, especially since earlier studies (Welch, 1914) had shown that in some Enchytraeidae the spermathecae are among the last of the reproductive organs to reach maturity, and that 1) the duct, 2) the ampulla, and 3) the diverticula seem to develop in that order.

Welch's (1917a) Grand Pacific Glacier specimens were designated "partially mature" (p. 5), though actual criteria were not given. None of the specimens showed a clitellum (p. 7), but sections of one "approaching maturity" exhibited "a very slight thickening of the hypodermis on XI/XII."

Emery's (1900) specimens likewise were not completely mature. Even in the most developed individuals, having extensive sperm sacs filled

with developing spermatozoa, the eggs were "minute" (p. 224) and no mention is made of an ovisac. "In one specimen unfortunately injured in the genital region, I could recognise the beginning of development of glandular cells in the hypoderm of the twelfth segment," (p. 225). The most mature individual was described from serial sections: the spermathecae have diverticula, the ampullae unite dorsally, but there is no connection with the oesophagus. The very short, almost rudimentary, spermiducal funnel figured (Emery's Fig. 15) is further evidence of only partial maturity, though the sperm duct itself is very long.

Eisen (1904) unfortunately made no reference to the testes, ovaries, sperm sacs or ovisacs of the specimens he described. The clitellum (p. 59) was said to be "probably confined to XII".

Welch (1916a) described the sperm sacs and ovisac in the mature individuals of M. solifugus rainierensis as containing masses of developing spermatozoa and ova (p. 107), though no clitellum was apparent and sections showed no increase in the thickness of the hypodermis.

Moore (1899) likewise found masses of developing spermatozoa and ova in the sperm sacs and ovisac (p. 125), and found the clitellum not "distinctly developed, but on the contrary [it] is thin and scarcely extends beyond the limits of the twelfth somite". Moore also described a pair of conspicuous elliptical swollen glandular areas surrounding the ectal opening of the spermathecae, as well as enlarged setae ("one third longer and much thicker") in the ventral bundle of XI. Both these features may be copulatory accessories. Welch found them absent in the Mt. Rainier specimens and they are not mentioned by other authors. Considering that Moore's specimens are also the largest recorded we must admit the possibility that no one else has ever described fully mature individuals of M. solifugus.

The more mature individuals from Casement Glacier do have sperm sacs and ovisacs containing masses of developing spermatozoa and ova, including some clusters of much larger ova. Sections through XII-XIII show the hypodermis to be glandular and somewhat thickened, though the clitellum is not detectable externally.

Only Moore (1899) described the testes (p. 128) which he found to be attached to the body floor in segment XI close to the root of septum X/XI near the middle line. I have not found such structures in the Casement Glacier specimens, but instead there is a pair of outpocketings of septum X/XI forward into segment X. These sacs are situated laterally to the oesophagus, and contain spermatozoa in various stages of development. Whether or not material collected in another season would have exhibited characteristics consistent with more advanced maturity is at the moment an open question.

Of the two collections of worms made on September 8, 1967, one, from a snowfield on line 13 (Fig. 1), heavily populated with worms, consisted entirely of worms with undeveloped penial protuberances. Paraffin sectioning of one proved it to be, as suspected, immature. A smaller sample of worms from a water-filled crevasse near the meteorological station, 2 km away, consisted of 6 worms with well developed penial protuberances, 3 with undeveloped protuberances, and 1 intermediate. Three of the worms with well developed protuberances were sectioned and proved to contain sperm and ova. None of the other worms collected on other occasions in 1967 showed more outward signs of development than the foregoing three upon which the description of the Casement Glacier population is based.

#### Preservation

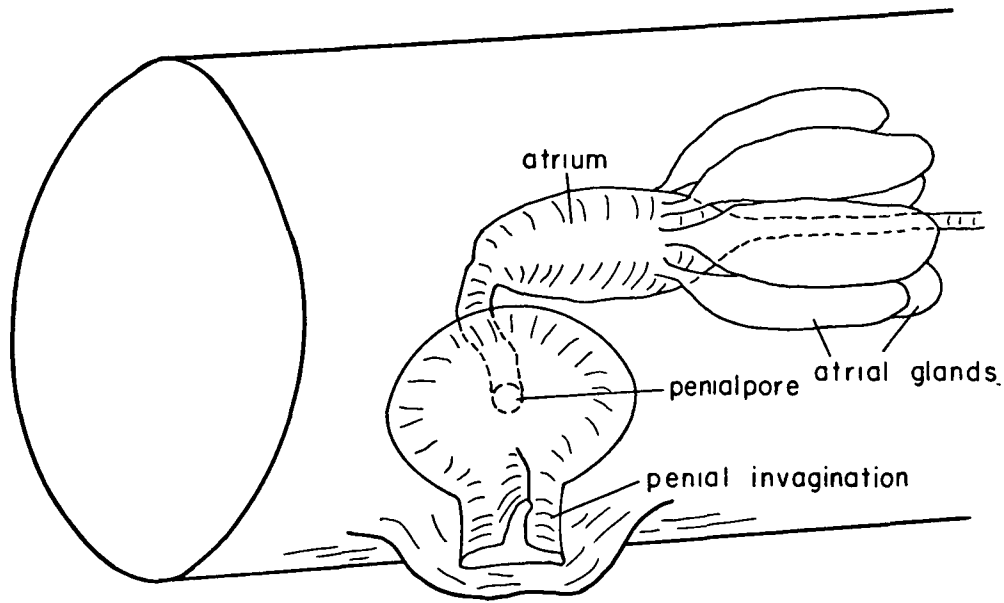
Both Moore (1899) and Welch (1916a) describe whitish rings or bands formed by ruptures of the epidermis, primarily in some of the intersegmental grooves. It has been my experience that such lesions occur on specimens that have been warmed; they are absent from all specimens that were preserved in 70% ethanol immediately upon collection. In the laboratory, live specimens began to degenerate after a few hours at 20 C. Hence, all glacier worms allowed to remain in vials of water in the collector's pocket, pack, tent, etc., prior to fixing are considered to be in a doubtful state of preservation.

## Penial Bulb

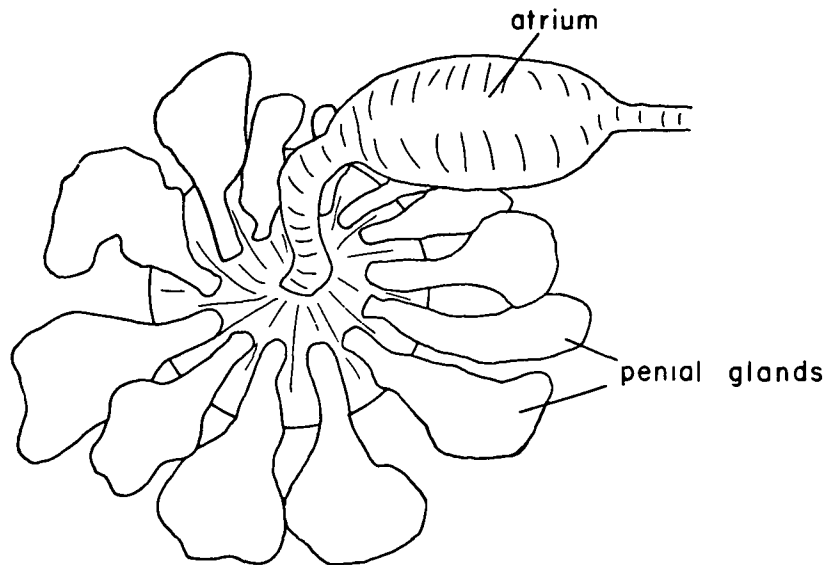
I have tried to follow Eisen's (1904) terminology for the structures associated with the penial bulb. A fuller description should elucidate their meaning:

Externally the penial bulbs appear as a pair of protuberances on the ventral surface of somite XII. The center of each corresponds in location to that of the ventral bundles of setae which in this segment are absent. On the apex of the protuberance, a triradiate slit marks the opening of the penial invagination. The two mesial limbs of the slit form a shallow crescent at right angles to the ectal slit which is fairly straight and oriented parallel to the circumference of the worm. The internal chamber formed by the invagination is shaped like a shallow dish, concave side facing the body wall. This chamber opens to the surface via a channel shaped like an inverted 'T' in cross section. The base of the channel extends from the ventral-most rim of the dish-shaped chamber and emerges as the two mesial limbs of the external slit. The vertical portion of the channel runs from the lower part of the ectal face of the chamber and emerges as the ectal limb of the external slit. The width of the vertical portion of the channel is less than half the diameter of the internal chamber, so the penial pore (the opening of the sperm duct into the center of the ental face of the penial invagination) is not opposite the external pore of the invagination (Fig. 2).

Welch's statement (1916a, p. 113), "this inner chamber caps the ental part of the invagination like the top to a mushroom", as well as the diagrams of Emery and Moore, leave the impression that, on the contrary, the penial pore is opposite the ectal channel. Perhaps this difference is just a difficulty of three-dimensional representation. Eisen's (1904) plate VII, depicting a transverse section of the worm through the plane of the vertical limbs of the external channel, concurs with my observations.



LATERAL VIEW OF PENIAL BULB ASSEMBLY  
(PENIAL GLANDS OMITTED)



MESIAL ASPECT OF PENIAL BULB ASSEMBLY (ATRIAL GLANDS OMITTED)

Fig. 2 - Structure of the penial bulb in Casement Glacier specimens of Mesenchytraeus solifugus



The wall of the invagination is a thickened extension of the body wall, consisting of a cuticle, a pigmented epithelium and muscular layers. There are small unicellular glands scattered among the epithelial cells lining the invagination. These gland cells do not penetrate the muscle layers as do the "unicellular glands" in M. solifugus rainierensis (Welch, 1916a). About 14 multicellular glands (more properly fascicles of unicellular glands each with a long extension, as there seems to be no common lumen), arranged radially in a single circle around the penial pore, open into the penial invagination. The gland fascicles are narrowest where they penetrate the muscular coat of the invagination wall and they are most easily counted from sections at that level, for with Azan triple stain the glands take a blue color while the muscle appears red. The expanded distal ends of the multicellular penial glands are irregularly lobed and crowded together, so I doubt that a reliable count can be made from dissections.

Muscular fibers, some connected to the muscular layer of the invagination, are interspersed among the penial glands. A peritoneum seems to cover this cluster of glands and muscle fibers, but it is too delicate for its extent to be actually traced.

Eisen (1904) described accessory glands lying outside the penial bulb and opening via extremely long ducts onto the body surface around the opening of the penial invagination.

Welch (1916a) described pear-shaped accessory glands opening into the invagination, commonly at its origin.

In the Casement Glacier specimens I have found ducts of glands associated with the bulb leading only to the mesial face of the invagination chamber, none open onto the ectal face of the chamber nor around the opening of the invagination, so accessory glands are absent. Owing to the extreme delicacy of the peritoneum surrounding the bulb, whether all, part, or none of a lobate gland lies within its boundaries is a largely gratuitous distinction. Isolated muscle fibers from around the base of the penial bulb extend towards, and may attach to, some of the atrial and penial glands. In unstained sections one might mistake these fibers for gland ducts and

perhaps describe the combination as accessory glands. Unfortunately, neither Eisen nor Welch recorded the details of their microscopic preparations.

Within the limits of the penial bulb the sperm duct is surrounded by a thick layer of longitudinal muscle. Just outside the bulb the duct widens into a fusiform chamber, the atrium. The lumen of the atrium is lined with columnar blue-staining gland cells. The glandular layer is covered by a continuation of the muscular coat of the ectal portion of the sperm duct. The atria are disposed approximately parallel to the long axis of the worm. Six atrial glands, each a fascicle of glandular cells without a common lumen, are arrayed radially about the atrium and all are connected to the atrium in the same transverse plane. Each bundle of ducts is surrounded by a whorl of muscle fibers where it penetrates the muscular coat of the atrium. Inside the atrium the individual ducts disperse among the glandular cells and I believe that the duct tips extend a short distance into the atrial lumen, for those projections stain a somewhat reddish color and look a little too thick for cilia. The expanded end of each atrial gland is about as large as the body of the atrium. Most are deflected posteriorly though a few extend forward.

Publications prior to Eisen's (1904) revision lack both detail and uniformity of terminology in their descriptions of the penial bulb. I hereby reproduce the accounts of Emery and Moore, including in brackets my interpretation of their terms:

Moore (1899, p. 129) writes, "Before entering the atrium [penial invagination] in somite XII the recurrent limbs of the sperm ducts expand into narrow fusiform sacs [atria] (figure 3, ss), having glandular, epithelial, and muscular walls, which receive the ductules of a group of unicellular spermiducal glands [atrial glands]. This structure probably serves to form and eject the spermatophores. A narrow curved duct which is also provided with some unicellular glands [?], perforates the mesial wall of the atrium [penial invagination] and opens into its lumen.

"...the atrium [penial invagination] is in part of ectodermal origin as is indicated by the pigmented lining epithelium. It is a spheroidal

thick walled partly eversible sac, with an internal cavity having a mushroom shape in the retracted organ. Its walls are composed of a cuticle covered, rather deep, pigmented and perhaps glandular epithelium, surrounded by a thick muscular layer in which the fibers are partly longitudinal, but largely radial, especially about the place of entrance of the sperm duct. A number of groups of unicellular glands [penial glands] are attached to the organ and probably empty into its lumen."

Moore's reference to "figure 3, ss" is apparently an error as "ss" points to the sperm sacs in his plate while "se" labels the atrium. A more serious point of difference is that he finds glands in or connected to the duct between the atrium and the penial pore. No such glands have been reported by the other authors. Accessory glands, if present, were not distinguished from penial glands.

Emery (1900, p. 227-228) finds that "the last tract [of the sperm duct] forms a spherical bulb [penial invagination] (a), but before reaching it the tube presents a fusiform swelling [atrium] (c) whose wall is very thick and made of long cells, directed radially in its transverse section, the lumen not being widened. Bundles of prostatic (spermiducal) glands [penial glands] (b) are related to the bulb; another little group of glands [atrial glands] (c) lies around the tube, above its fusiform thickening."

The figure referred to seems to have been reconstructed from sagittal sections. Again, no distinction is made between penial and accessory glands.

#### Postpharyngeal Bulb

The matter of postpharyngeal bulbs is likewise obscured somewhat by terminology. Emery (1900, p. 228) states that "salivary glands" are absent and Moore (1899, p. 127) also states that "there are no salivary glands (peptonephridia of Benham)." The term peptonephridium applies to organs that superficially resemble nephridia but are connected to the digestive tract rather than opening to the outside. In two genera of

	Spermathecae					Spermiducal funnel		Penial bulb																	
<u>M. solifugus</u> Casement Glacier	15-17	46-50	3-5	2	+	+	+	+	6	14	-	+	+	XIII- XIV											
	Length (mm)	Somites	Setae per preclitellar ventral bundle	Diverticula	Ampullae fused	Connected to oesophagus	Swollen area around opening	Glands on duct	Longer than broad	Opens posteriorly	Collar present	Posterior extent of sperm ducts	Atrial glands	Penial glands	Accessory glands	Both sperm sacs long	Posterior extent of sperm sac	Ovisac encloses sperm sac	Ovisac bifurcates	Bifurcation in segment	Ovisac encloses both sperm ducts	Lymphocytes pigmented	Salivary glands present	Origin of dorsal blood vessel	
<u>M. solifugus rainierensis</u>	12-18	51-60	2-4	2	-	+	-	+	+	-	-	XX	5	>25	+	+	XV	+	+	XIII- XIV	+	-	XIII- XIV		
<u>M. solifugus</u> Emery's (1900) description, Malaspina Glacier	"a little over 10"	53	4	2-3	+	-	-	-	-	-	-	XV												XII	
<u>M. solifugus</u> Moore's (1899) description, Malaspina Glacier	15-20	43-58	3-6	3	+	+	+	+	+	+		XVIII													
<u>M. solifugus</u> Eisen's (1904) description, Muir and/or La Perouse Glaciers	12	50	3-5	3	+				+	+			8	15	+										

Table 2. Comparison of published accounts of Mesenchytraeus solifugus

Enchytraeidae they are rather large and conspicuous organs. Stephenson (1930) uses the term postpharyngeal bulb to designate the less extensive but otherwise quite similar organs found in some other enchytraeid genera including Mesenchytraeus. In the Casement Glacier specimens of M. solifugus there is, on each side of the oesophagus, behind the pharyngeal plate, an irregularly lobed organ which greatly resembles in both size and composition the folded mass of nephridial tubules except that it acquires a slightly bluish tinge on staining while the nephridia are a bluish gray. Part of the tubule on the side nearest the oesophagus stains bright red. In no part is it ciliated. The organ connects laterally to the oesophagus. I do not know whether Moore or Emery would have considered this postpharyngeal bulb a salivary gland or peptonephridium, but I suppose it would have been given some name if they had observed it.

#### Summary of Comparison

Comparison of the Casement Glacier specimens with other published accounts is summarized in Table 2. Only subspecies rainierensis (Welch, 1916a) has been described in sufficient detail for a satisfactory analysis. The original description of M. solifugus (Emery, 1898a, translated and expanded by Emery, 1900) was from only partially mature specimens. Moore's (1899) fuller description of mature specimens from the same glacier might have provided the solution but neither he nor Emery gave detailed information concerning important features of the penial bulb assembly. Eisen (1904) described the penial bulb in specimens from a glacier other than Malaspina and failed to describe the sperm sacs and ovisacs. For purposes of comparison I have lumped Eisen's description with those of Emery and Moore though it may describe yet another subspecies.

The Casement Glacier specimens are distinct from M. solifugus rainierensis by virtue of more setae, fewer penial glands, no accessory glands on the spermathecal duct, and fused spermathecal ampullae. The Casement Glacier specimens are distinguished from other described M. solifugus by a vastly different arrangement of sperm sacs and ovisacs, postclitellar origin of the dorsal blood vessel, and fewer spermathecal diverticula.

Owing to the small numbers of specimens examined by myself or other investigators, excluding Welch (1916a), only M. solifugus rainierensis has been adequately characterized. Hence, I have not proposed new nomenclatural status for the Casement Glacier population of M. solifugus despite its apparent distinctness. Future more extensive investigations of the distribution and anatomy of ice worms very likely will lead to the warranted characterization of distinct subspecies.

#### DISTRIBUTION OF ICE WORMS

Darkly pigmented worms inhabiting ice or snow have been reported in the older literature from Geikie Glacier (Odell, 1949), La Perouse Glacier (Eisen, 1904), Malaspina Glacier (Russell, 1893; Emery 1898a; Moore, 1899), Muir Glacier (Wright, 1887; Eisen, 1904), Grand Pacific Glacier (Welch, 1917a), and the Seward Firnfield (Odell, 1949) in southeastern Alaska; and on Mt. Olympus (Gudger, 1923) and Mt. Rainier (Welch, 1916a) in Washington. More recently Tynen (1970a, 1970b) reported ice worms from Cliffe Glacier on Vancouver Island, and on the basis of collected personal communications from people visiting glacial areas, indicated the presence of ice worms on 3 additional glaciers in southeastern Alaska, 1 on Vancouver Island, 32 in the coast range of British Columbia, and 13 in Washington. Tynen (1970b) personally did not find ice worms in the Canadian Rocky Mountains, the Selkirks and the Cariboos, and received negative reports concerning the American Rockies and Mt. McKinley, Alaska; he concluded that ice worms are confined to the coastal glaciers of western North America, and probably only those coastal glaciers within the compass of the Cordilleran ice sheet.

The entire family Enchytraeidae is widely distributed in polar and temperate regions (Michaelsen, 1900; Welch, 1914). The genus Mesenchytraeus includes many species which are apparently found only in cold regions (Ude, 1901; Welch, 1916a). Within the genus, a few species are reported in thermal habitats whose severity approaches that of the ice worm: M. gelidus inhabits seasonal snow (Welch, 1916a), M. altus is reported from moss and litter near and under snow in July (Welch, 1917b), and M. hydrius is found in slow meltwater streams close to melting snow (Welch, 1919).

## HABITAT AND BEHAVIOR OF ICE WORMS

Glacier worms generally are not active on the surface during the daylight hours (Russell, 1893; Emery, 1900; Moore, 1899; Tynen, 1970a). The Mt. Rainier subspecies is the only known exception to this pattern (Welch, 1916a). This behavior pattern on Casement Glacier was most rigidly adhered to by worms in snow. At no time during the period of our stay, June 24 to September 9, were worms seen on snow surfaces from late morning till early evening, yet as the evening light dimmed, swarms of worms, commonly more than  $25/m^2$ , were seen on the snow. Such observations were recorded on the entire upper glacier from line 8 to lines 12, 13, 14 and about 2 km upglacier from line 11 (Fig. 1). I had no opportunity to make other than daylight observations on the lower glacier until after the snow there had melted. During the day, in deep snow on line 10, worms were brought up in drill cores from as deep as 2 m. Early in the season when the snow cover was less than 1 m deep around the meteorological station, I dug several pits down to glacier ice without finding any worms, though the surface there swarmed with worms at an average density of about  $35/m^2$  that same evening; so the worms during the day either burrowed into ice, or more likely, retreated into the deeper snow in crevasses. The snowbridge surfaces were even more densely populated with worms at night. There was usually a longitudinal furrow bottomed with discolored, generally yellow-brown or pink snow, running down the center of each snowbridge. The color generally penetrated the snow to a depth of 2 or 3 cm, and during the day some worms could be found just under the colored layer. At midday a hole about 10 cm in diameter was dug through a snowbridge near the meteorological station. The top of the hole was on clean snow halfway between the midline furrow and the snowbridge margin. The hole began to scrape the crevasse wall at a depth of 44 cm and the hole broke through to the crevasse cavity at 52 cm. The distribution of worms encountered in this vertical transect was as follows:

23	cm	2 worms
25-27	cm	1 worm
29	cm	1 worm
36	cm	1 worm
38	cm	1 worm
40	cm	2 worms
42-44	cm	5 worms
45-47	cm	1 worm

Thus the greatest daytime concentration was near the bottom of the snow-ice interface in the crevasse wall. On three occasions worms were not seen on snowbridge surfaces at night; two of these were during unusually heavy rain and the worms could be exposed by scraping away 1/2 to 1 cm of snow; the third was an exceptionally clear bright night and the snow surface had crusted by 2200 hours local time. From noon July 31 until midnight August 3, worms visible in a quadrat on the surface of a snowbridge near the meteorological station were counted at 30-min intervals. Concurrently the net radiation flux was measured with a Funk net radiometer (Instrument no. 274). The ice-worm density and the absolute value of the net radiation are plotted on log scales against time in Figure 3. The second curve of worm density beginning on August 3 represents data from a second quadrat on a neighboring snowbridge. Figure 3 indicates a high degree of synchrony in the glacier worms' vertical migration. On four consecutive evenings the worms first appeared on the surface between 1800 and 1900 local hours reaching densities of at least  $25/m^2$  within an hour of first appearance and reaching densities of at least  $50/m^2$  within an hour and a half of first appearance. In each case the density reached  $25/m^2$  less than one hour after the net radiation had first dropped below  $0.115 \text{ cal/cm}^2 \text{ min}$ . The first two mornings the density dropped to  $25/m^2$  within half an hour after net radiation exceeded  $0.06 \text{ cal/cm}^2 \text{ min}$ . Throughout July 31, August 1 and most of August 2 the cloud cover had been 100% as is usual for this region. Figure 4, taken from Peterson (1970), summarizes daily ablation



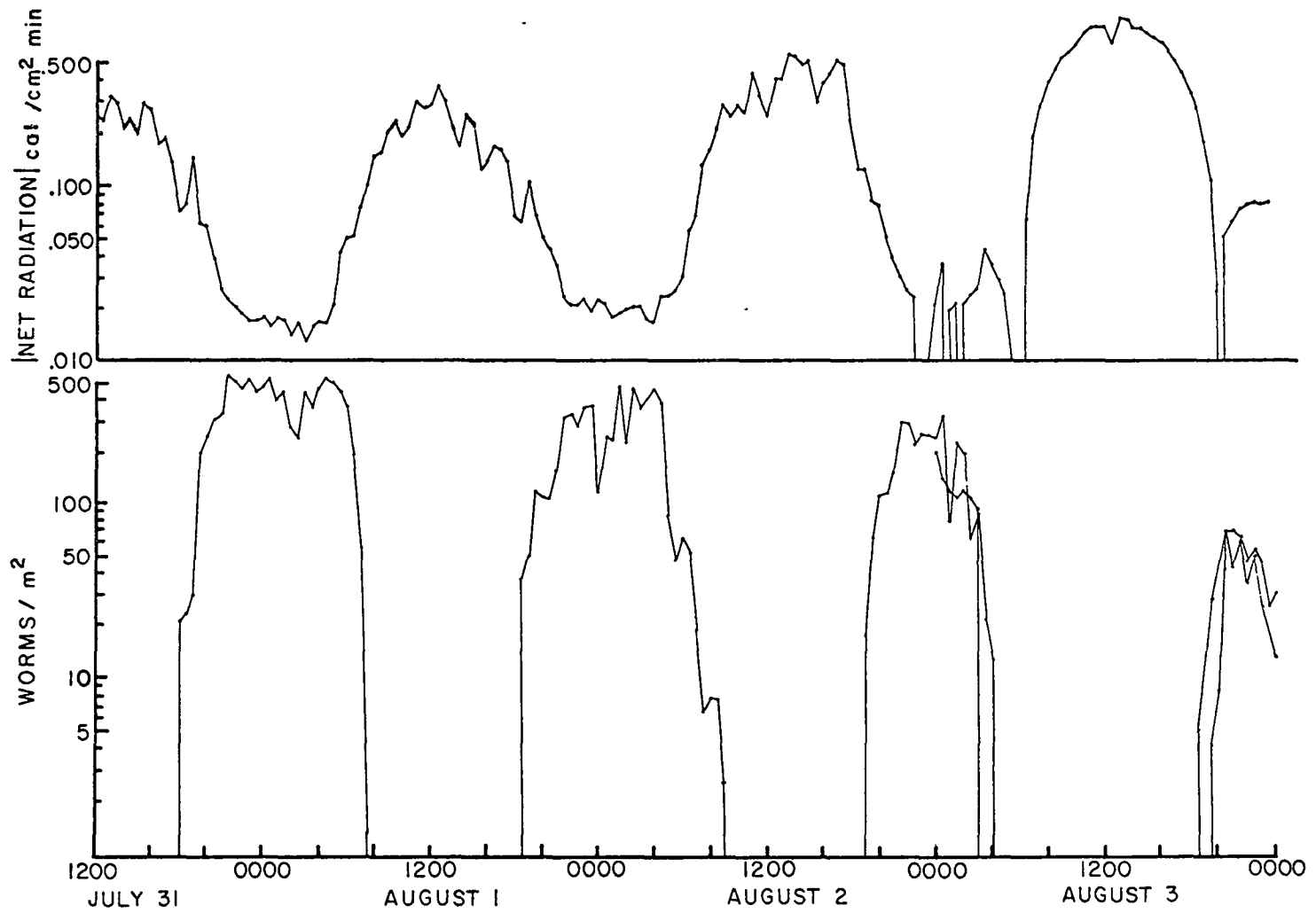


Fig. 3 - Concurrent measurements of the absolute value of net radiation and ice-worm concentration at the surface of a snowbridge.

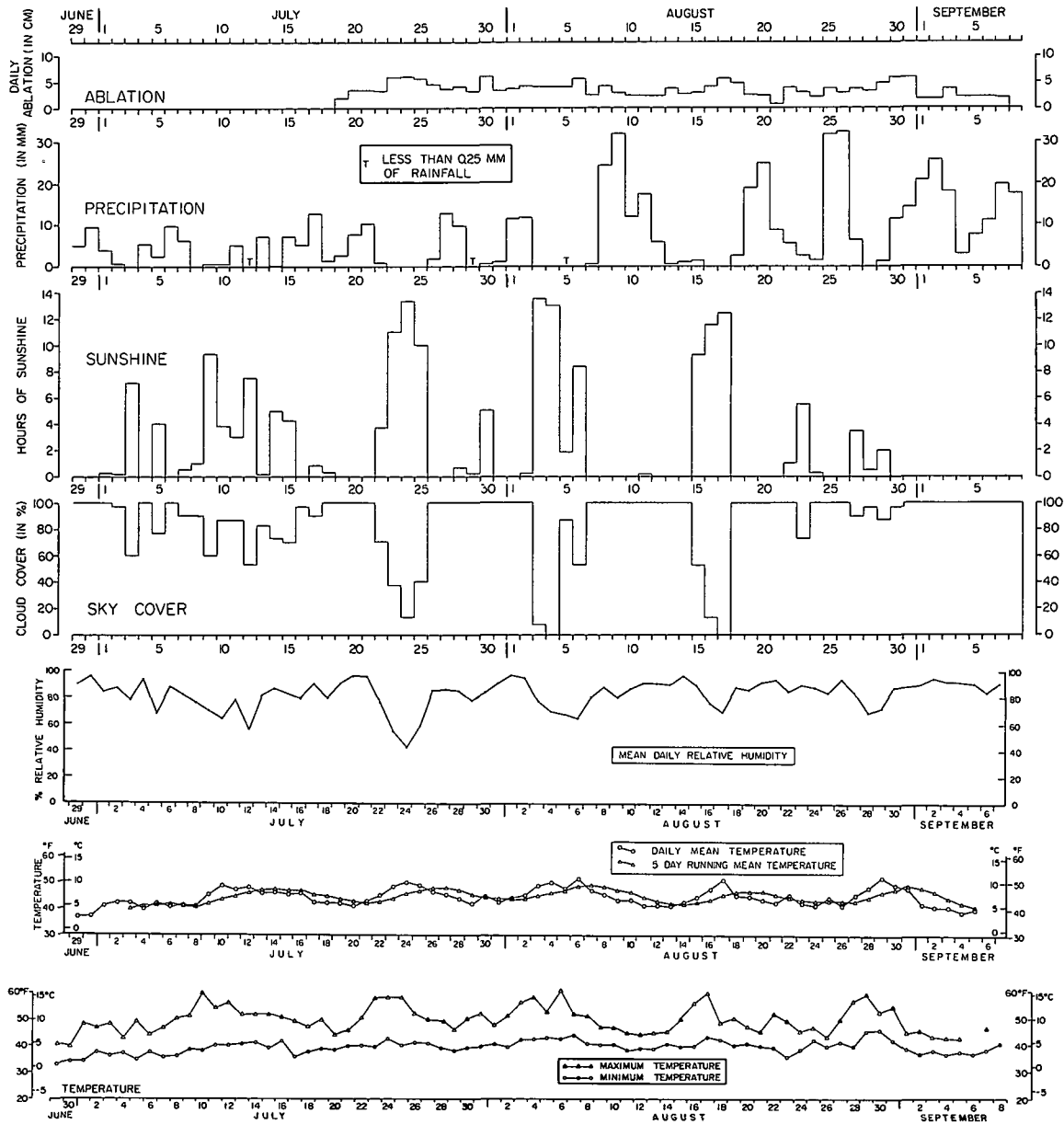


Fig. 4 - Daily ablation and meteorological conditions at the station on upper Casement Glacier, 1967. From Peterson (1970).

and meteorological conditions at upper Casement Glacier in 1967. At 2230 local hours on August 2 the cloud cover lifted and net radiation became negative as the glacier radiated heat into the night sky. The log graph, of course, goes off scale each time the net radiation changes sign. The response of the worms to the clear sky of the early morning of August 3 was to retire about three hours earlier than they had the previous two mornings. The night of August 3 was also clear and bright and the worms did not reach their usual density peak. Hence the worm's daily vertical migration was not governed solely by endogenous circadian rhythm but was influenced by meteorological conditions.

Worms were not seen on snowbanks not overlying glacier ice, even though many of the snowbanks near our main camp were continuous with the snow cover of the glacier when we arrived in June.

Worms were not seen on bare ice surfaces during the day, though they were brought up in drill cores from depths of up to 1.5 m on lines 4, 5, and 8. In the evenings worms would appear on some bare ice surfaces but their distribution was confusingly patchy. It seemed that the density of worms seen on glacier ice around the meteorological station was considerably less than their density on the snow surface there earlier in the season. It was my impression on 4 occasions that worms appearing on ice surfaces in the evening were most numerous around crevasses. Worms often could be seen in crevasse walls considerably below the glacier surface; they were particularly concentrated near dark annual layers.

Worms were regularly seen on the floors of cryoconite holes during the daytime. While worms in snow moved by weaving between grains, the worms on the cryoconite material simply lay on the surface and progressed with a serpentine motion which appeared quite inefficient owing to obvious slippage. Worms placed on wet glass made what appeared to be attempts at forward motion by inching, longitudinal extension and contraction of the anterior part of the body with the main bearing surface a few segments behind the prostomium. Progress on glacier ice was much more efficient: the worms presumably wound their way along the small irregularities caused by differential melting along ice crystal boundaries.

As snow melted in poorly drained regions of the glacier, slush puddles of varying extent were formed. Considerable numbers of worms could be seen in slush throughout the day. They were most numerous in red or brownish-tinted slush puddles where their density often exceeded  $100/m^2$ .

Worms were seen in the ice walls of cryoconite holes, water-filled crevasses and in small rivulets throughout the day. The worms in water-filled crevasses and rivulets were generally less numerous than the populations seen on snow, though one small crevasse near the meteorological station contained over 100. The worms under still water were always well embedded in the ice wall with only the anterior portion of the body, perhaps one-half to one-third, free in the water. The free end often waved back and forth in an erratic series of arcs roughly totaling a circular motion through the water. Much less frequently a worm on the snow or ice surface would rear back in the air in a similar, though more jerky, waving performance. The current in some of the rivulets on ice was sufficient to form riffles, yet worms in the rivulet beds were not swept away. I deliberately dislodged a few and they were carried only a few cm before gaining a new hold. The sigmoid setae probably are very helpful in this regard. On one occasion in a slow rivulet on the lower glacier I saw a number of worms tangled in a loose ball two or three cm in diameter. Another member of the party reported seeing a somewhat larger ball of worms. When several worms were placed in a cylindrical tank of water they would quickly congregate in a similar writhing mass with a number of free ends waving back and forth.

Since worms were seen under water and in slush during the daytime, if the vertical migration on snow is in response to light intensity then the worms must be most sensitive to the longer wavelengths which would be filtered out by water.

#### ALGAE

As the snow cover melted, much of its surface developed a pocked pattern. This topography was characterized by closely spaced shallow

depressions, usually 5 to 15 cm deep and 0.3 to 0.6 m rim to rim. The bottoms of all such depressions were discolored, the hue ranging from a pale yellowish brown to a distinct red. Each depression usually contained a few sand-size mineral particles as well as finer detritus and mineral matter. Large areas of this type of snow were observed at some period over most of the upper glacier from line 8 to the snow pit on the main divide (pit 1, Fig. 5). The snow pattern preceding this was generally a closely rippled topography. In a few places in the region circumscribed by lines 8, 11, 13, 12, and 14, some restricted patches of rippled surface snow persisted, mostly on steep banks. Rippled snow generally was not discolored. I observed only one red patch of rippled snow: this was a snowbank above and behind cairn A. The red color was restricted to the ripple troughs. On September 4 when we walked up tributary J for a snow pit survey (pit 3), the snow surface there was rippled (Fig. 5). The snow looked rather fresh and was very white.

In general, then, the rippled pattern was characteristic of relatively new snow surfaces; as the surface ablated a pocked topography with its associated algal populations would develop. It is conceivable that the increased energy absorption of pigmented algae may contribute to or even initiate the formation of the typical depressions. As the snow ablated further, some slush puddles formed and some of these were tinted brownish or red. Almost all ablating snowbridges had a somewhat discolored midline furrow, and some were quite pink.

No red or brown discoloration other than fine mineral patches was seen on glacier ice. On one occasion a party returning from line 8A reported seeing a bright green patch of ice on the wall of a moulin about 2 m below the rim. The width of the green patch seemed confined to ice over which water was running. A core of the green ice was collected, and when I examined it later in camp it was about 10 cm long and olive green throughout.

Samples of snow and ice for microscopic examination were melted and filtered on Millipore HA filters (0.45  $\mu$  pore size). The filters were next dehydrated in isopropanol followed by xylene. The filters were then cut

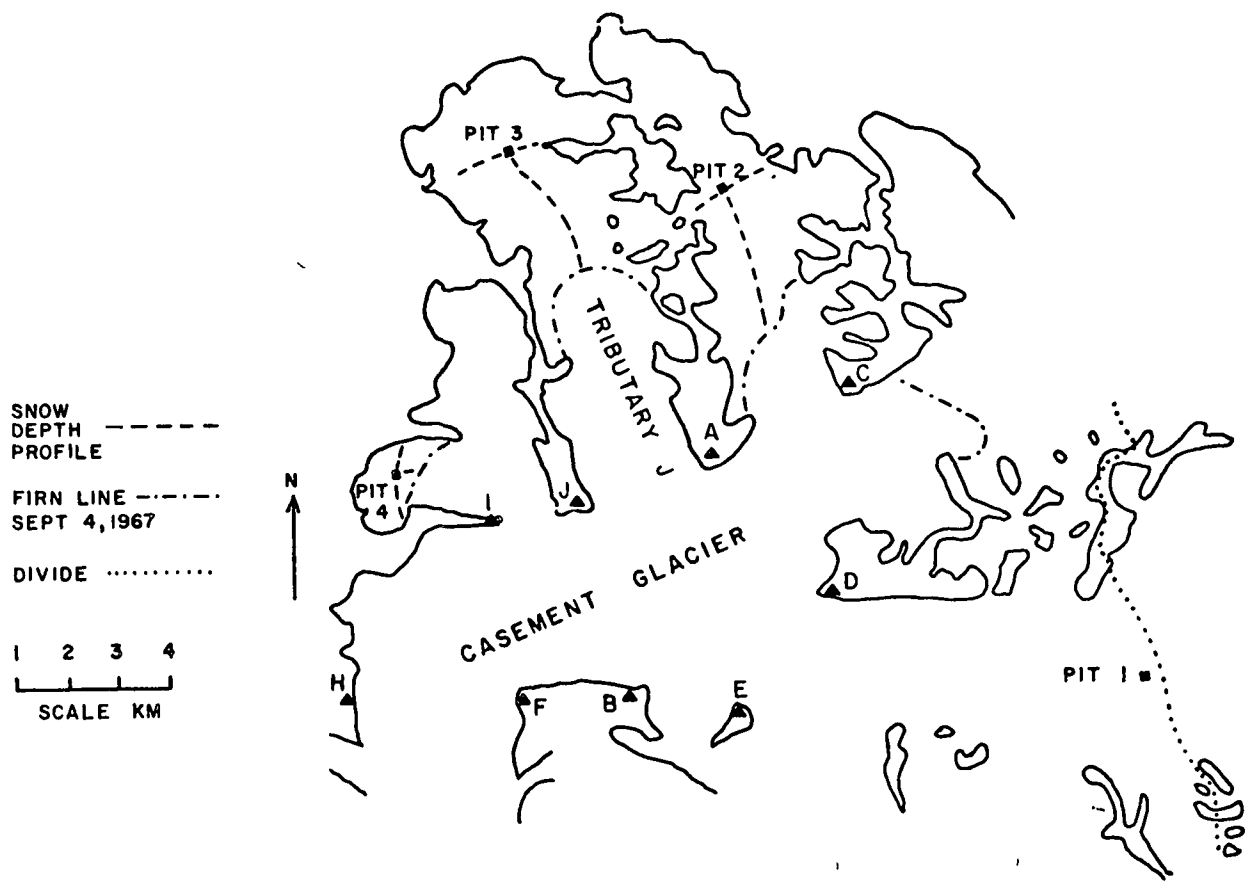


Fig. 5 - Map of upper portion of Casement Glacier showing the locations of the snow pits and the snow depth profiles made in September, 1967. From Peterson (1970).

in half and each half was mounted in picolyte. Owing to the considerable amounts of mineral particles, the preparations were thicker than ideal, but the resulting slides were quite viewable, and pigmented algae were easily counted. Except for a few poorly sealed slides the preparations have shown no signs of degradation over the past three years. The slides and a copy of field notes are now in the data collection of the Institute of Polar Studies, The Ohio State University.

Table 3 indicates the results of algal counts in a variety of samples from Casement Glacier. The most numerous algae were tentatively named on the basis of comparison with Kol's (1942) descriptions, though in the absence of pure cultures rigorous identification is impossible.

There were three morphologically distinguishable types of red cells present. In 19 of the samples the red cells were exclusively spherical. The size range was considerable. In one sample the mean diameter was  $16.4 \mu$ , the range of 99 cells was from  $8 \mu$  to  $34 \mu$  with 52.5% of the cells between  $13 \mu$  and  $20 \mu$ . Most of the cells were not invested with a mucilaginous envelope, though most of the largest cells were. The spherical cells conform most closely to Kol's description of Chlamydomonas nivalis, admittedly a catchall category. In seven of the samples, at least 10% of the red cells were ovoid and almost all of these had a mucilaginous envelope. The mean length and width of red cells in sample 17 were  $14.6 \mu$  and  $10.7 \mu$  respectively. The size range was not as broad as for the spherical cells. The range in length of 50 cells was from  $11 \mu$  to  $19 \mu$  with 68% between  $13 \mu$  and  $15 \mu$ . The range in width was from  $8 \mu$  to  $14 \mu$  with 64% between  $10 \mu$  and  $11.5 \mu$ . The ovoid red cells best conform to Kol's description of Chlamydomonas sanguinea. In three samples at least 1% of the red cells were provided with a peculiar star-shaped envelope which I have not seen described elsewhere. The red cells so embellished were all spherical, typically  $20 \mu$  in diameter, though the same samples all contained at least 10% ovoid red cells (Fig. 6).

The brown cells were cylindrical, typically  $11 \mu$  in diameter and  $24 \mu$  long. Many were seen in filaments several cells long. Most of the brown cells conform to Kol's description of Ancyclonema nordenskioldii, but some of the smaller ones may have been Mesotaenium berggrenii.

Table 3. Algal counts from snow, ice and water samples

Sample	Location	Time of Collection	depth of sample, cm	no. of ice worms	no. of snow fleas	conc. of algae (cells/cc snow)	% red	% other spherical	% bacum	% fusiform
1	Red patch of snow from midline furrow of large snowbridge on line 11 near camp	1200 Aug 5	0-2.5	2	6	$1.76 \times 10^4$	99.2	0.0	0.4	0.4
2	Same snowbridge, halfway between midline furrow and margin, not detectably pink	1115 Aug 6	0-2.5	0	0	$4.32 \times 10^2$	99.2	0.3	0.0	0.0
3	Halfway between midline furrow and margin of snowbridge near station, vertical core	1545 Aug 6	0-2.0	0	0	$1.37 \times 10^2$	98.7	0.0	1.3	0.2
4	Same core	1545 Aug 6	2.0-4.0	0	0	$0.31 \times 10^1$	85.6	7.1	0.0	0.0
5	Same core	1545 Aug 6	4.0-6.0	0	0	$2.38 \times 10^1$	83.0	6.4	9.6	0.0
6	Same core	1545 Aug 6	6.0-8.0	0	1	$3.82 \times 10^1$	61.0	17.2	17.9	3.3
7	Same core	1545 Aug 6	8.0-10.0	0	0	$6.89 \times 10^1$	84.2	2.9	10.1	2.9
8	Same core	1545 Aug 6	10.0-12.0	0	0	$6.29 \times 10^1$	42.6	30.1	10.1	16.6
9	Same core	1030 Aug 7	25.0-27.0	1	8	$7.96 \times 10^2$	54.4	11.8	1.7	31.9
10	Same snowbridge, second core 10 cm farther from margin	1045 Aug 7	35.0-37.0	0	11	$1.48 \times 10^2$	63.3	7.0	4.5	25.1
11	Same core	1100 Aug 7	42.0-44.0	5	7	$6.09 \times 10^2$	49.7	7.8	30.9	10.0
12	Same core	1100 Aug 7	45.0-47.0	1	8	$6.28 \times 10^2$	49.1	7.7	24.2	14.4
						(cells/cc water)				
13	Snowbridge below icefall near snowfield on line 13, snowbridge was swarming with ice worms (>100/m <sup>2</sup> ) at time	1930 Aug 24	0-3.0	13	20	$9.71 \times 10^3$	93.3	0.0	0.0	0.2
14	Clean bluish-looking slush in narrow depression near site of sample 13, swarming with ice worms (>100/m <sup>2</sup> ) at time	1930 Aug 24	0-5.0	0	0	$4.50 \times 10^2$	38.4	11.8	30.3	19.1
15	Reddish-brown slush in a puddle upglacier from station on tributary J	1600 Aug 19	0-3.0	0	1	$2.89 \times 10^3$	81.5	7.9	2.2	6.3
16	Slush and snow from the margin of the same puddle	1600 Aug 19	0-3.0	2	67	$1.00 \times 10^4$	93.0	1.1	0.4	4.6
17	Clean generation of snow from snowfield above icefall on line 13, depth to ice 18 cm	1600 Aug 21	0-1.0	0	0	$5.79 \times 10^3$	97.6	1.2	0.0	0.2
18	Same spot, deeper layer at boundary between light snow and underlying more granular snow	1600 Aug 21	4.0-6.0	0	0	$4.14 \times 10^2$	81.8	7.1	0.0	10.1
19	Dark generation of snow (slightly reddish cast) from same snowfield, depth to ice 12 cm, dark-colored snow only 0.5 cm deep	1600 Aug 21	0-1.0	0	0	$2.33 \times 10^4$	99.4	0.3	0.0	0.3
20	Same spot, deeper layer	1600 Aug 21	4.0-6.0	0	0	$3.32 \times 10^1$	44.5	9.3	41.6	4.6
21	Brilliant red snow from a shallow depression west of the snow pit on the tributary J snowfield, red color extended 6 cm down	1530 Sept 4	0-1.5	0	0	$1.36 \times 10^5$	89.4	10.4	0.1	0.1
22	Clean-looking snow alongside tributary J, snow pit	1530 Sept 4	0-1.5	0	2	$0.67 \times 10^1$	31.5	60.5	0.0	2.6
23	White ice atop a small hummock near station on line 11	1730 Aug 7	0-4.0	0	0	$2.11 \times 10^2$	8.16	1.0	85.6	4.9
24	Water from cryoconite hole near station on line 11; there were ice worms on the hole floor	1200 Aug 16	water depth 9.5	0	0	$8.66 \times 10^{-1}$	18.0	0.0	67.4	14.5
25	Water from crevasse near station; there were worms in the crevasse wall	1500 Aug 9	just below water surface	0	0	$1.00 \times 10^1$	5.27	2.2	21.6	70.2
26	Ice from green patch on wall of moulin over which water was running on line 8A	Aug 14	-	0	0	$3.75 \times 10^4$	0.431	0.07	0.0	0.0



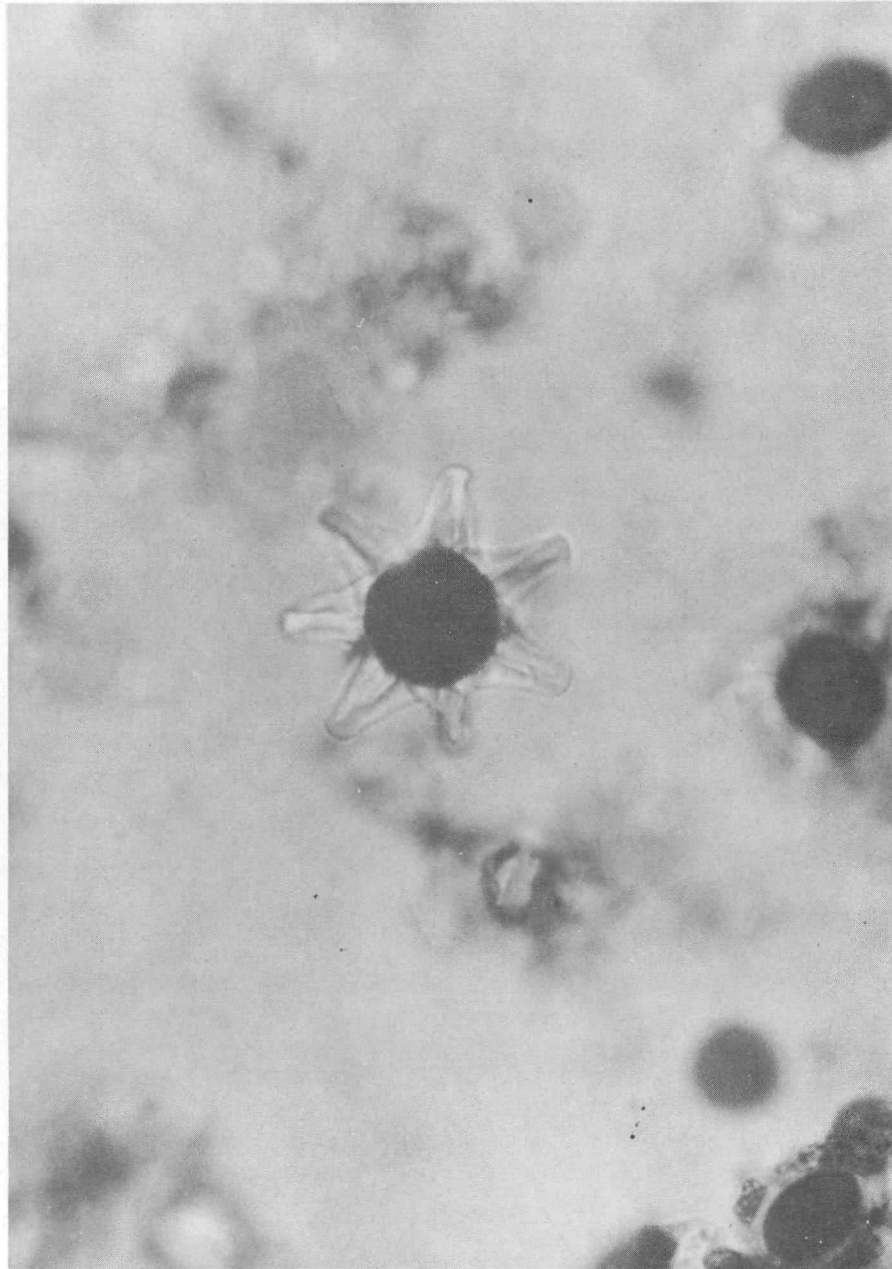


Fig. 6 - Photomicrograph of red Chlamydomonas cell with a star-shaped envelope

Most of the elongated cells seemed to be various forms of Scotiella nivalis as described by Kol. These appeared as fusiform cells typically 18  $\mu$  long and 9  $\mu$  wide in the middle with a more or less central chloroplast, some with and some without the spiral ribs, and as cylindrical cells typically 17  $\mu$  long and 10  $\mu$  wide, often with a clear sheath. A third type of elongated cells, spindle-shaped, typically 48  $\mu$  long and 11  $\mu$  wide, was present in samples 6, 11, 12, 15, 16, 18 and 23 with a frequency ranging from 0.2% to 1.4% of the total. These latter did not conform to any known phase of S. nivalis. I was unable to determine in counting whether some or all of the fusiform unribbed cells were not, in fact, small diatoms. The identity of the ribbed cells and the cylindrical forms is more certain.

Little can be said about the clear or green round cells; most could have belonged to any number of species, including phases of Chlamydomonas nivalis. A few conformed to Kol's descriptions of Trochiscia cryophila and Smithsonimonas abbotii on the basis of spines and warts respectively.

The category 'other' consisted mostly of larger diatoms, fungal spores and a few fern spores. Sample 26 was from the previously mentioned green patch on a moulin wall, and in it more than 99% of the cells were narrow, variously curved, pale blue-green cells averaging 26.6  $\mu$  long and 18  $\mu$  wide, similar to Kol's description of Dactylococcopsis alaskana.

Samples 13, 15, 16, 21 and 25 contained a few (less than 1%) brown ovoid objects, of varying internal detail, typically about 70  $\mu$  long with a clear sheath with one or more small spikes at each end (Fig. 7). Larger brown ovoid objects, about 140  $\mu$  long, with a small curved protuberance at one end, were seen in sample 24. Neither of these forms has been identified.

The ecology and distribution of the more abundant algae according to Kol (1942) follows:

Chlamydomonas nivalis is a typical snow alga found on nearly every Alaskan snowfield, and present in samples from 7 of the 13 Alaskan sites sampled by Kol.

Chlamydomonas sanguinea was first described from Pichincha and was present in samples from 4 of the 13 Alaskan sites sampled by Kol.



Fig. 7 - Photomicrograph of an unidentified object found in some snow and water samples.

Ancyclonema nordenskioldii is also known from Greenland, Franz Josef Land, Spitsbergen and Norway. In Alaska it was a characteristic glacialis-cryobiont found on every Alaskan glacier, and was present in samples from 6 of the 13 Alaskan sites sampled by Kol.

Mesotaenium berggrenii is the most abundant ice alga in the northern hemisphere and is also found in the Andes and Antarctica. It is a characteristic plant of permanent ice fields and was present in samples from 7 of the 13 Alaskan sites sampled by Kol.

Scotiella nivalis is a nivalis-cryobiont appearing frequently over the whole world. It appears to be the first microorganism to settle on the snowfields and is one of the most common organisms on Alaskan snowfields. It was found in samples from 8 of the 13 Alaskan sites sampled by Kol.

Contrary to Kol's designation of Ancyclonema nordenskioldii as a glacialis-cryobiont, cells fitting its description were also abundant in some snow samples from Casement Glacier, e.g. 11, 14 and 20. Cells conforming to Kol's descriptions of Chlamydomonas nivalis and Scotiella nivalis were both present in an ice surface sample (23) though they are said to be typically "nivalis-cryobionts".

In general, the Casement Glacier flora was comprised essentially of extremely common and cosmopolitan algae. Therefore this algal community in itself is not sufficient to account for the apparently restricted distribution of ice worms.

It was noted previously that worms were often numerous in regions of the glacier that were not detectably tinted by algae; however, we see from Table 3 that clean-looking ice and snow in some instances contained very substantial populations of algae, including the red Chlamydomonas. Samples 13 and 17 with concentrations of  $9.71 \times 10^3$  and  $5.79 \times 10^3$  cells/cc respectively were the most heavily populated samples that did not appear noticeably pink. The least densely populated snow samples to appear pink or reddish brown were samples 1 and 19 with concentrations of  $1.76 \times 10^4$  and  $2.33 \times 10^4$  cells/cc respectively. So the threshold density for visual detection of a red-cell-dominated algal population is around  $1 \times 10^4$  cells/cc.

## TROPIC DYNAMICS

The complete absence of pollen and the sparsity of fern spores (0.48% in sample 11, 0.015% in sample 15, and 0.0066% in sample 16) in the Casement Glacier preparations indicates that windblown material originating off the glacier is quite insignificant as a source of organic material on the glacier.

Filtering 120 liters of air on August 9 and 500 liters of air on August 16 failed to trap any pollen grains, spores or other organic particles. Therefore the primary production of the algal community must directly or indirectly support the remainder of the glacial life forms, though the glacier was very infertile in terms of nutrient minerals. The following chemical determinations were made with a Hach water engineer's test kit (model DR-EL) on crevasse water collected August 9 and 12 and September 6, 1967 (the same site as sample 25):

pH	6.84	
O <sub>2</sub>	13	ppm
CO <sub>2</sub>	0.12	ppm
PO <sub>4</sub> <sup>=</sup> (ortho)	0.11	ppm
PO <sub>4</sub> <sup>=</sup> (poly)	0.11	ppm
NO <sub>3</sub> <sup>-</sup> nitrogen	0.089	ppm
NO <sub>2</sub> <sup>-</sup> nitrogen	0.009	ppm
Si	0.04	ppm
Fe	0.08	ppm
Cl <sup>-</sup>	< 1.5	ppm
CaCO <sub>3</sub>	< 3	ppm

From the data of Richman (1958) and Ketchum and Redfield (1949) the average caloric value of 7 cultures of chlorophyceae, representing 6 species from 4 genera including Chlamydomonas, was 5,230 calories per gram of dry weight, with the range from 5,158 cal/g to 5,507 cal/g.

Ketchum and Redfield found the average dry weight per unit volume of algal cells in their 6 cultures to be  $2.305 \times 10^{-4} \text{ g/mm}^3$ . I found the average red cell diameter in sample 1 to be  $16.4 \mu$ , so, treating it as a sphere, the average red cell volume is  $2.32 \times 10^{-6} \text{ mm}^3$ . The average red cell dimensions in sample 17 were  $14.6 \mu$  long by  $10.7 \mu$  wide, so, treating these as ellipsoids of revolution, the average volume of an ovoid red cell is  $8.74 \times 10^{-7} \text{ mm}^3$ . The average measurements of the clear and green elongate cells (mostly Scotiella nivalis) from several samples were  $18.36 \mu$  long by  $9.26 \mu$  wide, so, treating these cells as ellipsoids of revolution, the average cell volume was  $8.3 \times 10^{-7} \text{ mm}^3$ . The average measurements of the brown cells from several samples were  $23.6 \mu$  long by  $10.66 \mu$  wide, so, treating these cells as cylinders, the average brown cell volume was  $2.12 \times 10^{-6} \text{ mm}^3$ . This information is sufficient to calculate the approximate caloric content of the standing algal crop in the Casement Glacier samples.

Thus the caloric content of the red cells in the sample of the top 2-1/2 cm of the noticeably red midline furrow of a snowbridge (sample 1) was  $4.96 \times 10^{-2} \text{ cal/cc}$ , or, just considering this 2-1/2 cm layer, the crop was  $1.24 \times 10^3 \text{ cal/m}^2$ . By comparison, the caloric content of the red cells in the top 2-1/2 cm of clean-looking snow half way between the midline furrow and the snowbridge margin (sample 2) was  $1.22 \times 10^{-3} \text{ cal/cc}$  or for the top layer  $3.05 \times 10^1 \text{ cal/m}^2$ . Comparing sample 3 with 4, 17 with 18, and 19 with 20, we see that the top 1 or 2 cm of snow contained at least an order of magnitude more algae than the underlying snow (the denser populations in the lower 4 samples of the vertical transect represented in samples 3 through 12 were probably enriched by drainage from above following the crevasse wall, for this core began scraping the crevasse side at 27 cm), so the top 2 cm probably do account for most of the algae in the snow samples that were not from red patches. Thus, calculating the caloric content of all the algae from samples 2, 3, 13, 17 and 19, the typical snow surface crop gives  $1.23 \times 10^{-3}$ ,  $3.75 \times 10^{-4}$ ,  $2.75 \times 10^{-2}$ ,  $6.2 \times 10^{-3} \text{ cal/cc}$  and  $2.51 \times 10^{-2} \text{ cal/cc}$  respectively with the average  $1.21 \times 10^{-2} \text{ cal/cc}$ . Assuming on this basis that the average

crop of the snow covering remaining on the upper glacier in mid-August is represented by a layer 2 cm thick, whose caloric content is  $1.21 \times 10^{-2}$  cal/cc, the standing crop of producers on this surface is  $2.42 \times 10^2$  cal/m<sup>2</sup>. This is probably a lower limit, for it neglects the red midline furrows of snowbridges and isolated patches of red snow whose algal densities were much higher and some of which were demonstrably deeper than 2 cm.

Sample 3 was from the same snowbridge on which the quadrat count of ice worms was 200 worms/m<sup>2</sup> on August 2 and 70 worms/m<sup>2</sup> on August 3. On August 29 at 1930 local hours I found more than 100 worms/m<sup>2</sup> on the snowbridge which was the site of sample 13, and I estimated the average density of worms on the snowfield from which samples 17 and 19 were taken to be 25 worms/m<sup>2</sup> in most places, with patches a few square meters extent where the density was over 100 worms/m<sup>2</sup> at 1930 on September 8. If for purposes of calculation a rough figure of 100 worms/m<sup>2</sup> is accepted as a probably high estimate of the average worm density on the snow surfaces remaining in mid-August, the caloric equivalent of this population may be calculated as  $1.51 \times 10^2$  cal/m<sup>2</sup> using my laboratory measurement of  $3.08 \times 10^{-3}$  g as the average wet weight of an ice worm, and Johnson's (1942) figure of 0.106 for the ratio of dry weight to wet weight of earthworm tissue, and French, Liscinsky and Miller's (1957) figure of  $4.617 \times 10^3$  calories per gram dry weight for the caloric content of earthworms.

While these standing crop estimates are interesting, they alone are not sufficient for analyzing the biological energy budget of the glacier, for such a budget requires figures pertaining to turnover time of the standing crops and rates of energy utilization.

Of the 53 worms collected and preserved on Casement Glacier, including those encountered in filter mounts, only 8 were less than 1 cm long, of which 5 were 3 mm long or less (28 of these worms were from filter and core samples; 25 were collected from surface swarms in a collective effort to "collect worms" that may have biased the results in favor of conspicuous and therefore larger worms). This relatively low frequency of ostensibly young individuals in the population, coupled with the observation that the ice worms can live over one year in the laboratory,

indicates that the amount of energy the worm population utilizes for growth and reproduction is very small relative to the maintenance energy; that is, the energy consumed in normal metabolism measured as respiration in the individual worms should adequately represent the rate of energy consumption by the ice-worm population.

The average rate of oxygen consumption of ice worms at 0 C was 52.05  $\mu\text{l/g}$  wet weight per hour as determined from 24 worms in 2 flasks of a Warburg respirometer over a period of six hours. If we assume that all the consumed  $\text{O}_2$  was utilized in the metabolism of carbohydrate, each  $\mu\text{l}$  of  $\text{O}_2$  represents  $5.007 \times 10^{-3}$  cal (this is a high estimate, therefore, since metabolism of fat or protein would yield less energy,  $4.686 \times 10^{-3}$  cal and  $4.500 \times 10^{-3}$  cal respectively). Using my previous figures of  $3.08 \times 10^{-3}$  g as the average wet weight of an ice worm, and the probably high estimate of 100 ice worms per  $\text{m}^2$  as the average density, we can compute the energy consumption of the ice-worm population on the glacier as  $9.65 \times 10^{-1}$  cal/ $\text{m}^2$  per day.

Since the glacier surface was continually melting, and since this meltwater was continually washing algae away from the surface, if the algal population were to maintain a steady state, its rate of production of biomass must equal the rate of loss by ablation plus the rate of loss through death of cells that do not wash away. Therefore the net productivity of the algal population is at least the caloric equivalent of the rate of biomass loss to drainage. If we accept sample 25, water from a crevasse into which a rivulet was flowing, as representative of the drainage water, we may compute the caloric loss incurred through drainage as  $1.492 \times 10^{-2}$  calories per liter of meltwater, on the basis of the algal densities given in Table 3 and the information used in the calculation of the caloric equivalent of standing crops. Sample 25 was collected on August 9, 1967. The following conditions obtained on August 8 and 9:

	August 8	August 9
daily ablation	4.5 cm	3.0 cm
daily rainfall	2.4 cm	3.3 cm
mean relative humidity	88%	81%
cloud cover	100%	100%



Ignoring evaporation then, each square meter of glacier surface during this period melted down 37.5 liters/day and in addition caught 33.5 liters/day rain, so each square meter of glacier releases 71 liters of water/day. Therefore, multiplying the standing crop in crevasse water by this figure, we find that the productivity of the algal population on upper Casement Glacier was at least  $1.492 \times 10^{-2}$  cal/liter  $\times$  71 liters/m<sup>2</sup> day =  $10.58 \times 10^{-1}$  cal/m<sup>2</sup> day.

The energy relationships of the ice worms and algae may be summarized thus:

ice worm standing crop	$1.51 \times 10^2$ cal/m <sup>2</sup>
algal standing crop	$2.42 \times 10^2$ cal/m <sup>2</sup>
ice worm energy consumption	$9.65 \times 10^{-1}$ cal/m <sup>2</sup> day
algal productivity	$10.58 \times 10^{-1}$ cal/m <sup>2</sup> day

Bearing in mind that the ice worm estimate is probably high and the algal estimate is probably low, these figures indicate that it is energetically plausible for the ice-worm population to subsist on algal production. Now, the productivity measured as loss through drainage represents algal material that in any event is not available to ice worms. However, these calculations do show that if the ice worms subsist exclusively by grazing the snow and ice algae, then the cost of this grazing to the algal community is less than the loss through drainage. This does not, however, prove that ice worms do, in fact, eat snow and ice algae. To investigate this matter I macerated a number of ice worms and filtered the resultant tissue pulp and gut contents in the same manner as algal preparations and scanned the filters in search of red pigmented algae. The results are as follows:

- (1) 10.3 red cells per worm from ice worms collected in a core through a snowbridge (the same site as samples 3-12) at 1100 local hours August 7; this may be a low figure since the coverslip was not sealed properly on one of the slides and as a consequence some of the algae may have been oxidized.

- (2) 22.0 red cells per worm from ice worms collected from the wall of a water-filled crevasse (the same site as sample 25), 1500 August 9.
- (3) 12.5 red cells per worm from ice worms collected from a cryoconite hole (the same site as sample 24) noon August 16.

Clearly, the ice worms do ingest algae. From these same slides as well as serial sections it became apparent that the worms also ingested just about everything else that may be found in the ice or snow, provided that it is sufficiently small, for their alimentary tracts contained quantities of brown detritus and mineral particles. Therefore, while it is certain that algae are the worm's ultimate source of food energy, the proximate source may be algal cells or decomposed algal matter or both, depending on the digestive enzymes available to ice worms. When some melted red snow was examined with an oil immersion microscope it was swarming with rod-shaped bacteria.

The serial sections of ice worms revealed single-celled organisms (Fig. 8), roughly cylindrical, about 120  $\mu$  long by 23  $\mu$  wide, inhabiting the oesophagus from segments VIII to X. Emery (1900) described similar organisms in the gut and assigned them to the genus Anoplophyra. I found no such organisms living free on the glacier, so they are an endosymbiont of some sort. Conceivably they may secrete enzymes which aid in the assimilation of refractory algal material.

#### BIRDS

Snow buntings, Plectrophenax nivalis, were frequently seen on all regions of the glacier and its surroundings. During the course of the summer, I observed one or more snow buntings land on ice or snow and peck at the surface on nine occasions. In addition, I observed one or more snow buntings flying over the glacier on six more occasions. Toward the end of the season it was discovered that small flocks of snow buntings regularly flew over the remaining snowfields at dusk. This suggested that they fed on ice worms, since the worms were especially abundant on these snowfields. At 1915 local hours August 24 I shot and dissected a female



Fig. 8 - Photomicrograph of a cross section of the ice worm's oesophagus showing several symbiotic microorganisms in the lumen

snow bunting that was hopping about on a snowbridge at the foot of an icefall below line 13. There was an ice worm in her oesophagus and her gizzard contained part of a springtail, some lepidopteran wing scales and a number of red algal cells.

While crossing the lower glacier on July 26 I saw several semi-palmated plovers, Charadrius semipalmatus, on the ice. Peterson reported that a previous summer, when the main camp was situated on the lower glacier, plovers were frequently seen pecking on the ice surface, as if they also feed on ice worms. Odell (1949) similarly reported a "phalarope" feeding ostensibly on ice worms as it swam about some meltwater and ran over floating ice on the Seward Firnfield.

On July 13 I observed a hummingbird fly over the ice on line 7. A second was seen on August 11 between cairn J and the tunnel. These were probably rufous hummingbirds, Selasphorus rufus, which were also seen on various mountain slopes near the glacier.

#### SNOW FLEAS

Springtails or snow fleas (Collembola) were exceedingly numerous on and around the glacier. Their incidence in snow and ice samples is shown in Table 3. The greatest concentrations of snow fleas seemed to be associated with snow patches and puddles that were colored with algae. At times, toward evening, regions of snow swarmed with the little insects. Their hopping ability is prodigious: snow fleas often were trapped in the rain gauge situated 75 cm above ground at our main camp.

#### OTHER ANIMALS

On July 10 a surveying party saw a mountain goat on the ice near line 4. On July 14 I saw some fecal pellets, which I suspect were goats', on the ice upglacier from the station on tributary J. A band of mountain goats occupied the mountain behind camp most of the summer.

On July 27 I found a lynx skeleton on the ice near line 8A.

On August 22 the party working at the tunnel reported seeing a black bear.

PHYSIOLOGY OF LOW TEMPERATURE ADAPTATION IN THE  
ICE WORM

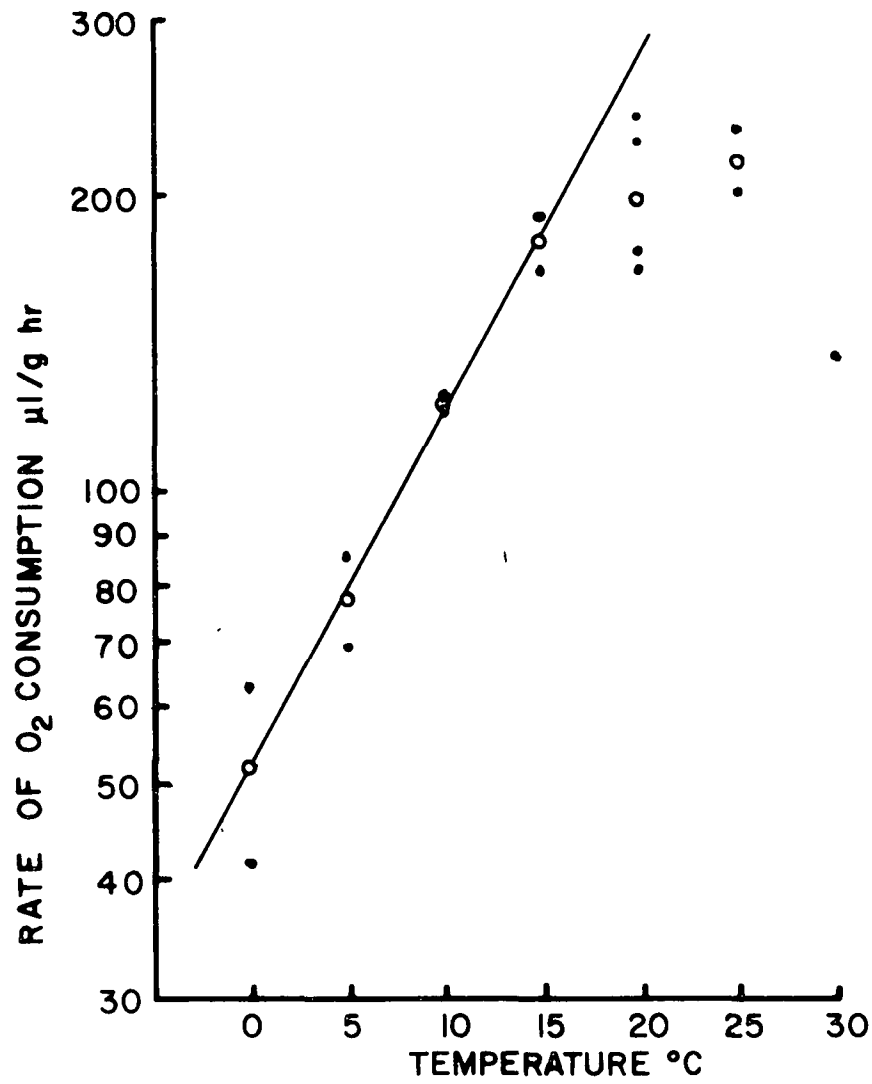
Temperature Dependence of Respiration

Within some temperature range including the normal environmental temperature, the rates of biological functions commonly conform to the Arrhenius equation of chemical kinetics, according to which the logarithm of the rate should be linearly related to temperature. Rates of respiration, usually the rate of oxygen uptake, have been studied most in this regard. It has been widely observed (Prosser and Brown 1961) that, in poikilotherms this rate rises about two and one half times for each  $10^{\circ}$  C rise in temperature (that is,  $Q_{10}$  is equal to some number around 2-1/2).

Figure 9 presents the results of determinations of the rate of oxygen uptake in the ice worm measured at 5 C intervals from 0 C to 30 C in a Warburg respirometer. Each data point represents the stabilized rate of a single flask containing 10 to 12 ice worms. From Figure 9 it is evident that the response is linear to 15 C. The  $Q_{10}$  within this range is 2.27.

Acclimation

When a poikilotherm is moved from one stable temperature regime to another, the first response of the respiration rate is, as described above, a linear response to the antilog of the temperature, the rate increasing with higher temperature and decreasing with lower temperature. This new stabilized rate usually does not persist indefinitely, but is replaced by an acclimated rate, the period of adjustment lasting from a few hours to a few days. Once acclimation is accomplished, measurement of the logarithm of stabilized rates of respiration as functions of temperature will again yield a linear plot, but the new rate line is displaced either by translation, rotation, or both, relative to the former rate line. The most common pattern of acclimation to lowered temperature is clockwise



ICE WORM - RESPIRATION

- ONE WARBURG FLASK
- AVERAGE AT ONE TEMPERATURE

Fig. 9 - Ice-worm respiration rates as a function of temperature

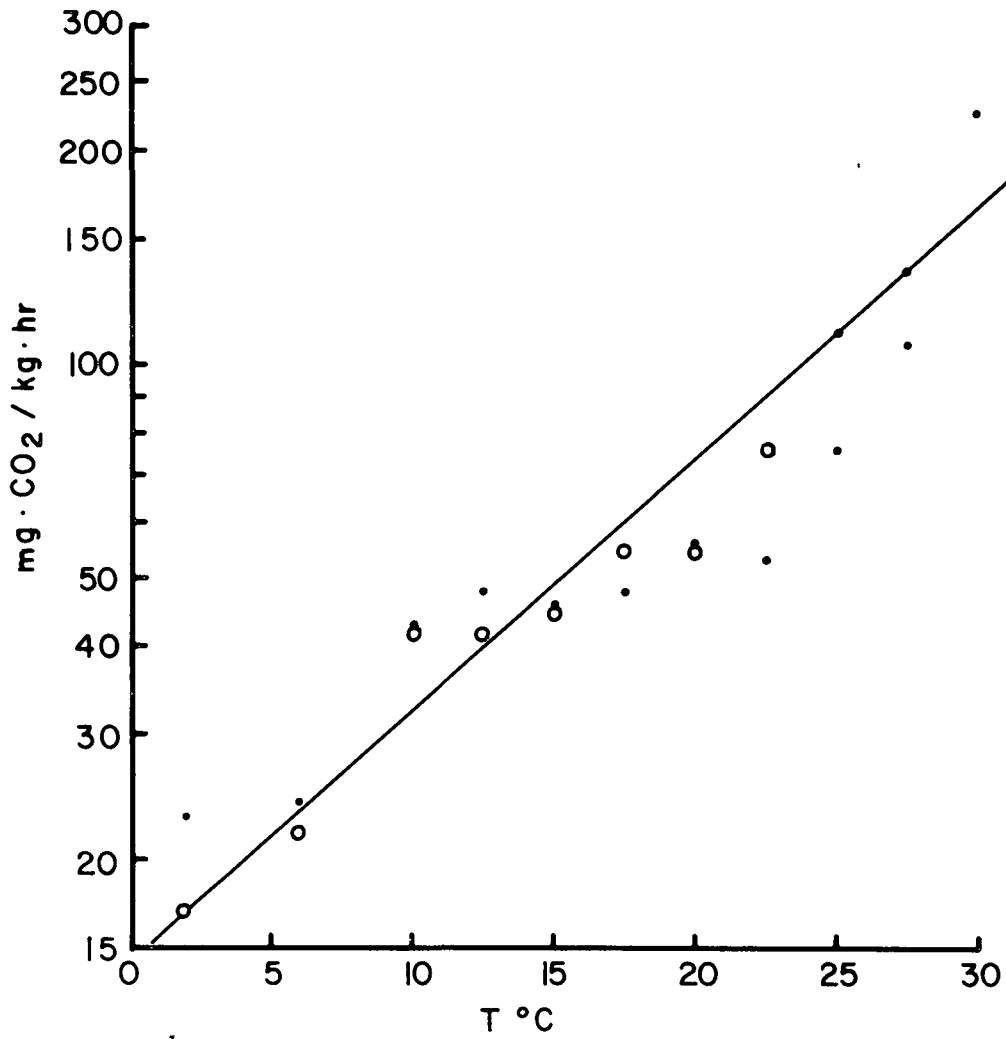
rotation combined with translation so as to intersect the original rate line at a temperature higher than the normal temperature (Prosser and Brown, 1961; Bullock, 1955), though there are many well documented exceptions. The consequence of this pattern of acclimation is a compensatory shift in rate of respiration to a figure closer to the original and a lower  $Q_{10}$  so that the respiration rate is less sensitive to changes in temperature.

If the ice worm's adaption to its low temperature environment evolved in a manner identical with, or analogous to, the mechanism of acclimation, we would therefore expect that:

- (a) the ice worm should exhibit a  $Q_{10}$  which is significantly lower than that of other oligochaetes which live at more usual temperatures, and
- (b) the ice worm's respiration rate at 0 C should be higher than the respiration rate at 0 C of an oligochaete acclimated to a higher temperature, and
- (c) the ice worm's stabilized respiration rate at higher temperatures should be higher than the respiration rate of oligochaetes which normally live at these temperatures.

From the fact that the ice worm's  $Q_{10}$  is 2.27, a figure that is quite typical for poikilotherms, expectation (a) evidently does not obtain.

Comparative data on the  $Q_{10}$  in oligochaetes is exceedingly sparse. In Figure 10 I have plotted Vernon's (1897) figures for  $CO_2$  production in Lumbricus terrestris, as a function of temperature. A least squares regression on this data yielded a  $Q_{10}$  of 2.02. An attempt to fit a  $Q_{10} = 2.27$  line to the data, as in Figure 10, indicates that 2.27 is a bit too high. The reality and significance of the apparent plateau in the midrange of this plot is controversial (Davies and Tribe, 1969). If we do consider this 10 C to 20 C range as most representative of the earthworm's temperature response, a still lower  $Q_{10}$  is indicated. Kirberger (1953) conditioned specimens of Lumbriculus variegatus at 10 C, 16 C and 23 C and then measured the resultant  $Q_{10}$ 's over the range 14 C to 24 C as 2.0, 2.0, and 1.83 respectively. In Figure 11 I have plotted the results of Kirberger's (1953) measurements of respiration rates in Eisenia foetida, and fitted  $Q_{10}$  lines. The  $Q_{10}$  values are 2.17, 1.72, 1.60, and 1.39.



• INCREASING  
 ○ DECREASING  
 SUPERPOSED  $Q_{10} = 2.27$

Fig. 10 - Rate of CO<sub>2</sub> production in Lumbricus terrestris from data of Vernon (1897)



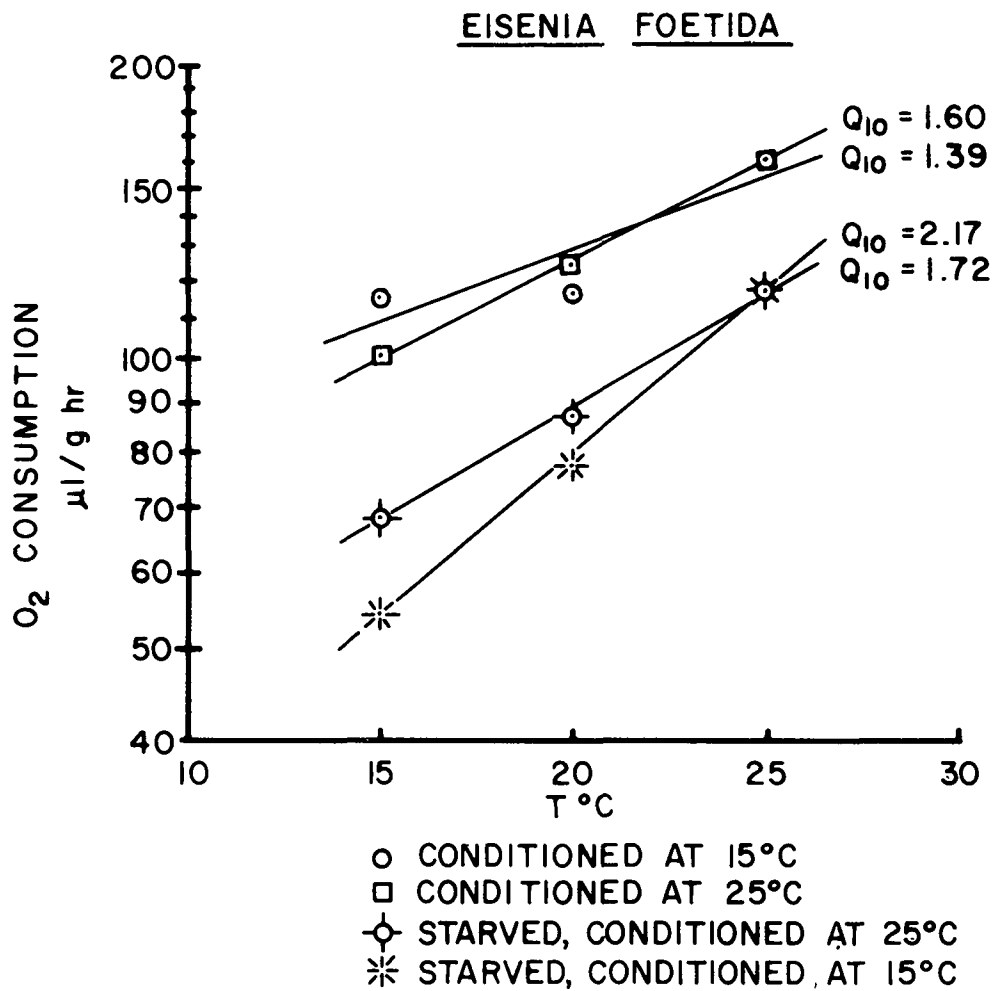
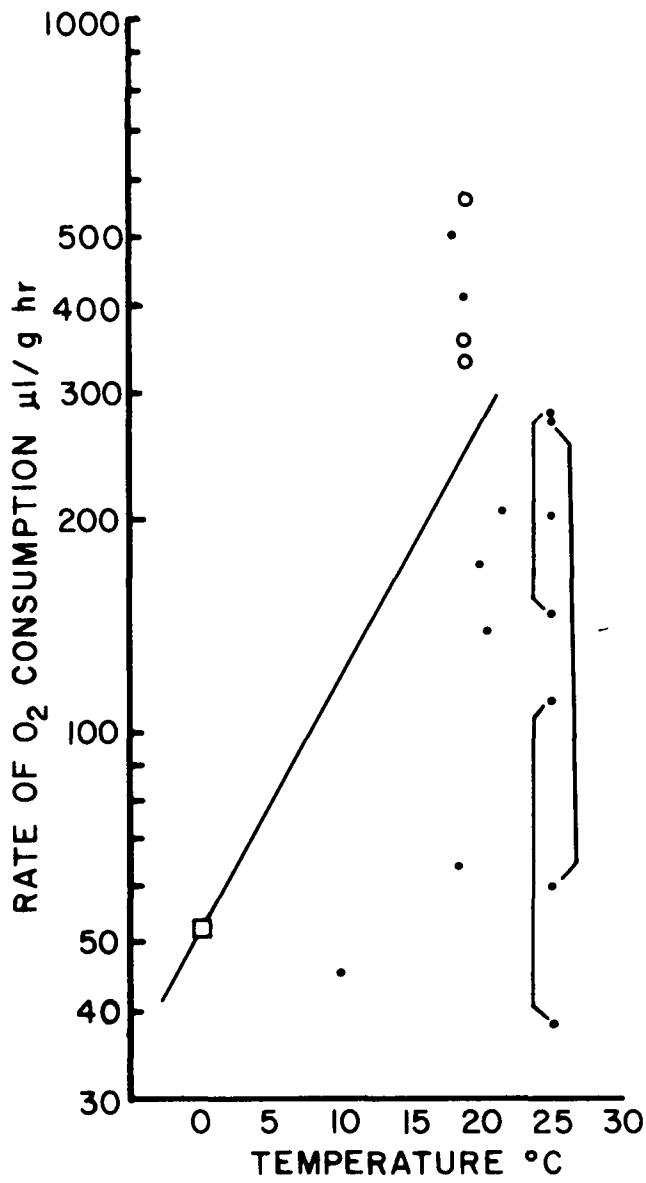


Fig. 11 - Rate of respiration in Eisenia foetida from data of Kirberger (1953)

Rao and Bullock (1954) found that  $Q_{10}$  commonly increases with organism size as well as with habitat temperature. The ice worm is smaller than the earthworms studied by Vernon and Kirberger, so if any correction factor were to be applied for purposes of comparison, it would increase the ice worm's  $Q_{10}$  to a figure that is higher yet. On the basis of this limited information, the  $Q_{10}$  value of the ice worm is, in fact, high relative to other oligochaetes.

In Figure 12 I have plotted the respiratory rates, and the temperatures at which they were measured, for all the oligochaetes for which there are data in the Handbook of Respiration (National Academy of Sciences, 1958). The extreme scatter makes interpretation difficult. The scatter probably is largely due to size differences in the organisms studied; the bracketed pairs of data points represent measurements of "large" and "small" individuals of the same species. The scatter may be exacerbated by the range of methods employed in measurements by 10 different authors. Owing to these difficulties, I shall rely mostly on Kruger's (1955) respiration data for three enchytraeids in an assessment of expectations (b) and (c). Kruger's experimental organisms were the only members of the ice worm's family for which data were available. They were Enchytraeus albidus, Pachydrilus lineatus, and "einer sehr kleinen weissen Enchytrae". At least the first two species are about the same size as the ice worm. According to Michaelsen (1900), the length of Enchytraeus albidus is 10 to 35 mm, and the diameter is 0.5 to 1.0 mm, while for Lumbricillus (= Pachydrilus) lineatus the length is 15 to 20 mm. In Figure 12 I have included the ice worm's respiration rate at 0 C and a line representing its  $Q_{10}$ , 2.27, from which it is apparent that the ice worm's stabilized respiration rate at a higher temperature (19 C) as predicted from its  $Q_{10}$  is lower than the rates of three enchytraeids which very likely normally live at or near this temperature; thus expectation (c) is not supported.

If either Enchytraeus albidus or Pachydrilus lineatus were to have a stabilized respiration rate at 0 C the same as the ice worm, its respective  $Q_{10}$  would be determined by a straight line drawn between the point representing the respiration rate of the ice worm and a point



OLIGOCHAETE RESPIRATION

- OLIGOCHAETA - HANDBOOK OF RESPIRATION 1958
- ENCHYTRAEIDAE - KRÜGER 1955
- ◻ ICE WORM

Fig. 12 - Oligochaete respiration rates at various temperatures

representing the respiration rate of E. albidus or P. lineatus on the semilog rate-temperature plot, in this case the points (352  $\mu$ l/g hr, 19 C) and (330  $\mu$ l/g hr, 19 C). These lines would imply  $Q_{10}$ 's equaling 2.75 and 2.65 respectively. For either of these two enchytraeids to have a lower respiration rate at 0 C than the ice worm, would require  $Q_{10}$ 's that were higher still--that is, their  $Q_{10}$ 's would have to be somewhat higher than is to be expected for a poikilotherm, and significantly higher than known  $Q_{10}$ 's in oligochaetes. I have not seen data on the usual  $Q_{10}$ 's in the Enchytraeidae, but until such information is available, expectation (b) should be considered improbable.

Accordingly, from measurements of respiration rates in the ice worm and data available on other enchytraeids, the hypothesis that the ice worm's low temperature adaptation is accomplished through the maintenance of a physiological state similar or identical to low temperature acclimation in a typical oligochaete is not supported.

#### Cold Stress

Low temperatures do pose physiological problems for living things. In a survey of the temperature at which various biological activities (including protoplasmic movement, ciliary movement, cellular multiplication, development and growth, metabolic processes, muscular movement, heartbeat, excitability and nervous functions) cease in a wide range of organisms, Bělehrádek (1935) lists 112 out of 137 as having their "biological zero" above 0 C, eight cease at 0 C and 17 persist below 0 C. The actual cause, or causes, of this stress is not well understood.

Several degrees below 0 C, much of the damage is a consequence of freezing and attendant dehydration (Luyet and Gehenio, 1940; Lovelock, 1953). Casement Glacier in summer is, in effect, an ice bath whose temperature never deviates from 0 C. In winter, owing to the high heat of fusion of water (79.7 cal/g) and the insulating properties of snow, the glacier temperature probably never does fall below 0 C, except for a surface layer. Therefore, since protoplasm freezes at a few degrees below 0 C, ice worms may never be confronted with the problems of freezing.

Evidently, the mere fact of lower rates of metabolism is not the cause of cold stress at low temperatures above freezing, for the ice worm does indeed have a low rate of respiration, and relative to the respiration rates of other oligochaetes it does not seem to have undergone a permanent acclimation to compensate for lowering of the rate of respiration in accord with a commonplace  $Q_{10}$  value; yet the ice worm does survive at low temperatures.

Of course, the rate of oxygen consumption is but a gross index to the rates of a large number of biochemical reactions involved in complex and, in some cases, branching pathways. The rates of each of these reactions will be affected by temperature according to the Arrhenius equation where  $k$ , the rate constant, is equal to:

$$Ae^{-\frac{u}{RT}}$$

But the values of  $A$  and  $u$  are specific to each reaction, so the amount of change of rate with respect to a change in temperature will differ from one reaction to the next. Hence, the problem may be a matter of enzymatic balance, where cooling may disproportionately reduce the rate of one reaction to the extent that the ensuing excess or deficiency of some intermediate in the pathway becomes critical.

Ushakov (1967) has discovered an intriguing relationship among enzymes that may be construed to support this theory of enzymatic balance. In a survey of the "thermostability" (measured as the temperature causing 50% inactivation in 30 min) of six enzymes in 19 species of poikilotherms from 6 phyla, he found that for any pair of enzymes considered over this array of organisms a plot of the thermostability of one enzyme against the thermostability of the other yields a straight line. Therefore, knowing the slopes and intercepts of one such plot for every enzyme, and given a value for the thermostability of one enzyme in a certain organism, one could predict the thermostabilities of all the other enzymes in that organism. In other words, Ushakov's work indicates that the thermostabilities of the enzymes in any poikilotherm are related through a series of linear equations,

$$T_1 = A_2 T_2 + B_2 = A_3 T_3 + B_3 = A_4 T_4 = \dots = A_n T_n + B_n$$

where  $T_j$  is the thermostability of the  $j^{\text{th}}$  enzyme considered in a particular organism and  $A_j$  and  $B_j$  are constants relating  $T_j$  to  $T_1$  for any poikilotherm.

While this relationship of enzyme thermostabilities does not prove a relationship involving enzyme activities, it is very suggestive.

#### Heat Stress

During the course of respiration measurements with the Warburg apparatus, the effects of heat stress on the ice worm were evinced at temperatures over 15 C both by the falling respiration rate and by gross physical deterioration.

Worms in one flask contracted longitudinally and were immobilized after 2-3/4 hr at 20 C preceded by a period of 2-1/2 hr to raise the temperature from 15 C to 20 C preceded by 2-3/4 hr at 15 C. Twenty minutes after their return to an ice bath, six of the worms recovered normal motions, 2 moved only slowly, 1 only flexed slightly and 1 did not recover. This latter had begun to disintegrate at one end which turned a yellow-gray color and appeared swollen. Of the two partially recovered worms, one was similarly afflicted with a disintegrating extremity while small bubble-like eruptions appeared in the integument of the second. Some of the worms in a second flask subjected to the same temperature regimen were also immobilized and the rest moved in an unusually abrupt and jerky manner. All these recovered normal motion 10 minutes after their return to an ice bath.

When two flasks of ice worms were placed directly in a 20 C bath for three hr, their motions were slowed, and some contracted. Over a period of 1/2 hr the temperature was raised to 25 C and the worms then

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moved only by slow curling and uncurling. After 2 hr at 25 C most of the worms lay in loose coils. After 3-1/2 hr at 25 C, one flask was returned to an ice bath: all of the worms were tightly curled, 3 out of 10 had fragmented and most of the worms had puffy yellow-gray sections; none recovered after 1/2 hour. The second flask was kept at 25 C for 3-1/2 hr; its temperature was raised to 30 C over a period of 1/2 hr. After 1/2 hr at 30 C all the worms had fragmented into short sections and there was much suspended gray-brown material in the flask. This suspended matter did not exhibit any interpretable structure when viewed under the oil immersion microscope.

It is to be expected for a poikilotherm to succumb at temperatures 10 C to 20 C above that of its normal habitat. This can be attributed to both denaturation of enzymes and loss of enzyme balance. The effect of heat stress is subject to modification by acclimation. Grant (1953) found that heat tolerance (measured as that temperature causing 50% mortality in 48 hr) in the earthworm, Pheretima hopeiensis, was lowered an average of 0.3 C for each 1 C decrease in the conditioning temperature, e.g., worms kept at 15 C had a heat tolerance of 22.7 C, worms kept at 4 C had a tolerance of 19.4 C. Therefore, it is not surprising that exposure to temperatures of 20 C and above caused some damage to ice worms; however, I have not encountered in the literature specific reference to autolysis. Bell (1959) describes a peculiar enchytraeid, Enchytraeus fragmentosus, lacking sex organs, which reproduces by fragmentation: mature individuals break into 3 to 11 sections, each of which fully regenerates in a period of about 10 days.

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