

TRICHOMONAS HOMINIS: GROWTH IN VITRO AND UTILIZATION OF CARBOHYDRATES

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Hsin-Sheng Lo, Fong-Ling Yueh and Shue-Yueh Liang (1984) *Trichomonas hominis*: Growth *in vitro* and utilization of carbohydrates. *Bull. Inst. Zool., Academia Sinica* 23(2): 137-149. The purpose of this study is to investigate the biochemical nature of *Trichomonas hominis*. Results indicate that the growth of *T. hominis in vitro* is affected by the following factors:

1. Temperature. *T. hominis* grows best at 36°C, next at 30°C and almost no growth at 25°C.
2. pH. The optimal pH for the growth of *T. hominis* was found to reside between 6.6 and 6.8. The decline of pH in spent medium after incubation suggests the production of acid endproducts by the organism.
3. Concentration of horse serum. The optimal concentration of horse serum for supporting *T. hominis* growth is between 5% and 10%. Dialysis of horse serum results in decreased ability of supporting good growth of *T. hominis*.
4. Glucose. The presence of glucose in culture medium is indispensable for the growth of *T. hominis*. A saturation curve between the growth of *T. hominis* and the concentrations of glucose was observed.
5. Panmede. Panmede is an ox-liver extract which is capable of enhancing the growth of *T. hominis*.
6. Carbohydrates. *T. hominis* is able to utilize the following carbohydrates: glucose, fructose, galactose, ribose, maltose, sucrose, glycogen, and amylopectin. Rhamnose, sorbose, mannitol, sorbitol, N-acetyl glucosamine, lactose, cellobiose, trehalose were incapable of supporting the growth of *T. hominis* and glyceraldehyde, 2-deoxy glucose, 2-deoxy ribose, xylose, arabinose, mannose, glucosamine were found inhibitory to the growth of *T. hominis*. A diagrammatic scheme of carbohydrate metabolism in *T. hominis* is postulated.

Trichomonas hominis is an intestinal flagellate commonly found in populations throughout the world. We have isolated a strain of this parasite in Taiwan and that was subsequently maintained in axenic culture (Lo and Shaio, 1981). Despite its widespread existence very few attempts have been made to investigate the biochemical nature of the organism. This study was therefore initiated to explore the growth characteristics of *T. hominis* under axenic cultivation and to detect

its ability of utilizing carbohydrates *in vitro*. Such results will delineate the possible metabolic pathways functioning in *T. hominis* and provide fundamental data for further comparative studies with other parasitic flagellates.

MATERIALS AND METHODS

Organism

Axentially cultivated *Trichomonas hominis*, originally isolated by this laboratory, was maintained in a modified medium identical to

the TYI-S-33 medium of Diamond *et al.* (1978) except that 1,000 U per ml penicillin G and 0.5% Panmede were added, in which calciferol and riboflavin were omitted from the vitamin mixture 107. Cells were grown in screw-capped culture tubes (16×125 mm) each containing 10 ml of the culture medium at 36°C. Routine subculture was made by inoculating 40,000 flagellates into the subsequent culture tube after 48 hr incubation at 36°C.

Harvesting of cells

In large-scale cultivation, cells were grown in 125 ml screw-capped culture flasks each containing 100 ml of the culture medium. The inoculum was 1×10^6 flagellates per flask. Approximately $4-5 \times 10^8$ cells per flask were harvested after 48 hr incubation at 36°C. Cells were washed by centrifugation in a balanced salt buffer, pH 7.0, containing 10 mM potassium phosphate, 20 mM KCl, 0.5 mM MgCl₂, 100 mM NaCl and 0.1 mM Ca(NO₃)₂. The washed cells were then packed in the buffer by centrifugation at $500 \times g$ for 5 min and the cell volume was measured. In some experiments, the packed cells were resuspended in the balanced salt buffer to obtain an optimal cell density.

Cell homogenates

Packed cells were suspended in 15 cell-volumes of cold 50 mM Tris/HCl buffer, pH 7.4, containing 250 mM sucrose and 10 mM dithiothreitol. Cells were then ruptured by a Kinematica Polytron, Model PCU-2, at a setting of 5 for 50 sec for 5 times in an ice-water bath. The homogenates were dialyzed against 500 ml of 20 mM Tris/HCl buffer, pH 7.0, containing 10 mM dithiothreitol for 16 hr and were used for enzyme assays.

Counting of cells

The number of flagellates per culture was determined by a Coulter Counter, Model ZF (Coulter Electronics Ltd.) employing a 100 μ aperture tube: attenuation 4, aperture 16, threshold 9. An aliquot of 0.1 ml of each culture was suspended in 20 ml of Isotone II (Coulter Scientific Japan Ltd.) and four counts were made to obtain an average value.

Carbohydrate determination

Glucose was assayed by an enzymatic method. Cuvettes of 1 cm optical path contained 50 mM Tris/HCl buffer, pH 7.4; 1 mM NADP; 2.5 mM ATP; 1 mM MgCl₂; 10 μ g hexokinase; sample and water to a final volume of 1.0 ml. Reaction was started by the addition of 10 U of glucose 6-phosphate dehydrogenase and was monitored at 340 nm. Calculation was made from the amount of NADP being reduced after reaction was subsided by taking $\epsilon = 6,220 \times \text{cm}^{-1} \times \text{M}^{-1}$.

Extraction of glycogen was carried out according to the method of Good *et al.* (1933). The determination of glycogen and residual carbohydrates in culture medium was made by the method of Montgomery (1957).

Enzyme assays

The activity of α -amylase was determined by the method of Bernfeld (1955). Substrates employed were glycogen and amylopectin at a concentration of 1%. One ml of sample was incubated for 5 min at 30°C with 1 ml of the substrate solution. Reaction was interrupted by the addition of 1 ml of dinitrosalicylic acid reagent which is composed of 1% 3,5-dinitrosalicylic acid; 30% sodium potassium tartrate and 0.4 N NaOH. The tubes containing this mixture were heated for 5 min in boiling water and then cooled in running tap water. After addition of 10 ml H₂O, the optical density of the solution containing the brown reduction product was determined spectrophotometrically at 540 nm. A blank was prepared in the same manner without enzyme. A calibration curve established with maltose ranging from 0.2 mg to 2.0 mg in 2 ml water was used to convert the optical density readings into milligrams of maltose.

Maltase (or α -glucosidase) was assayed employing the method of Lieberman and Eto (1957). Substrates used were maltose, glycogen and amylopectin at a concentration of 1%. Test tubes contained 20 mM potassium phosphate buffer, pH 6.5; 0.01 ml of substrate solution; 0.1 ml sample and water to a final volume of 1.0 ml. The reaction mixture was

incubated at 36°C for 30 min. Reaction was stopped by heating in a boiling water bath for 3 min. After being cooled in ice, insoluble material was discarded by centrifugation. A blank was prepared by prior heating of the reaction mixture. Liberated glucose was determined by the same enzymatic method as described above.

Sucrase was assayed by the same manner except using sucrose as the substrate.

Radioactivity measurement

Radioactivity was measured with a Konton liquid scintillation spectrometer, Model MR 300 in Aquasol-2 (New England Nuclear).

Reagents used

All carbohydrates employed were purchased from Sigma Chemical Co., St. Louis, Mo., U. S. A. Assaying enzymes, substrates and coenzymes were also from Sigma. [6-³H] Glucose and [1-³H]galactose were from Amersham, Arlington Heights, Ill., U. S. A. Other chemicals were of analytical grade.

RESULTS

Effect of temperature on the growth of *T. hominis*

T. hominis was incubated at three different temperatures. The cell density was determined at varying time intervals. Results presented in Fig. 1 show that *T. hominis* grows best at 36°C while limited growth occurred at 30°C and practically no growth was found at 25°C. When *T. hominis* was incubated at 36°C and 30°C, both lag and log phases could be clearly demonstrated (Fig. 1).

Effect of pH on the growth of *T. hominis*

T. hominis was inoculated into the media of different pH. After incubation for 48 hr at 36°C cell density and final pH were determined. The results are shown in Fig. 2. The optimal pH for the growth of *T. hominis* is between 6.6 and 6.8. The results also reveal that decline of final pH of the media is related to the number of organisms.

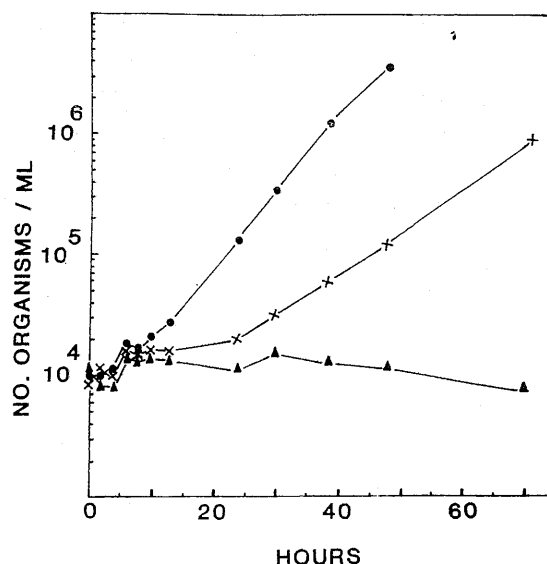


Fig. 1. Effect of temperature on the growth of *Trichomonas hominis*. (▲—▲, at 25°C; ×—×, at 30°C; ●—●, at 36°C).

Effect of glucose on the growth of *T. hominis*

Glucose was omitted from the medium so as to investigate its effect on the growth of *T. hominis*. The results are shown in Table I. After the first subculture, the growth in glucose-omitted medium was limited to approximately one-tenth of that of the glucose-added medium which indicates that glucose is an essential growth factor for *T. hominis*. The presence of residual carbohydrates in the glucose-omitted medium is substantiated by its positive reaction to the phenol-sulfuric acid reagent (Montgomery, 1957). The residual carbohydrates was not glucose had been confirmed by the enzymatic assay. However, it was calculated to contribute approximately 8 mM of glucose to the glucose-omitted medium. The relationship between the growth of *T. hominis* and the concentrations of glucose is shown in Fig. 3. A hyperbolic saturation curve is clearly demonstrated.

Effect of horse serum on the growth of *T. hominis*

T. hominis was inoculated into the medium containing various concentrations of horse serum. The results presented in Fig. 4 show

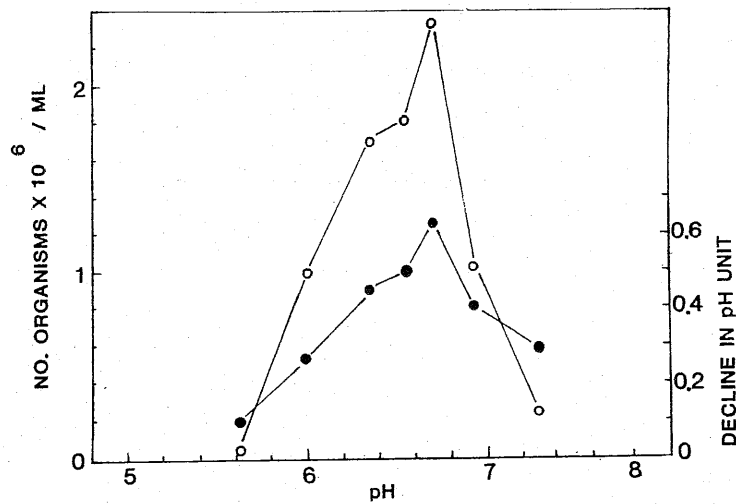


Fig. 2. Effect of pH on the growth of *Trichomonas hominis* (○—○). The pH of each culture was determined before inoculation and after 48 hr incubation at 36°C. The decline of pH (●—●) was the difference between the initial and the final pH of the culture medium.

TABLE I
Serial subcultures of *Trichomonas hominis*
in glucose-omitted medium and
glucose-added medium

Subculture number	Average flagellates/ml	
	glucose-added*	glucose-omitted
1	5,429,600	596,700
2	5,192,200	529,800
3	3,527,500	390,325
4	4,103,600	365,400
5	3,121,600	388,800
6	3,901,600	339,800
7	3,198,100	440,000

* Glucose, 1% was added to the medium.

The inoculum was 4,000 flagellates per ml. Each subculture was made in four culture tubes. Incubation was for 48 hr at 36°C.

that horse serum is absolutely needed for the growth of the organism. Almost no growth was obtained in culture medium supplemented with horse serum less than 2%. The results also show that the growth of *T. hominis* is proportional to the horse serum concentrations between 2% and 5%. The optimal horse serum concentration for *T. hominis* growth *in vitro* ranged

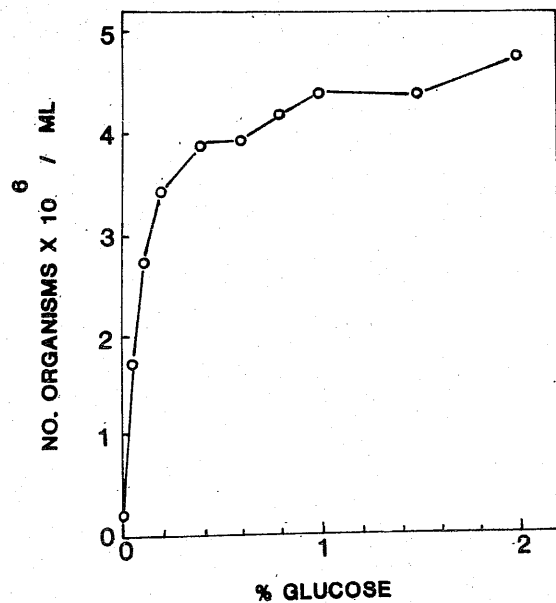


Fig. 3. The growth of *Trichomonas hominis* at various concentrations of glucose.

between 5% and 10%. Dialyzed horse serum was not as good as the undialyzed in the support of *T. hominis* growth (Fig. 5).

Enzymic assays reveal that horse serum contains α -amylase and maltase activities which are capable of hydrolyzing polysaccharides into monosaccharides (Table II).

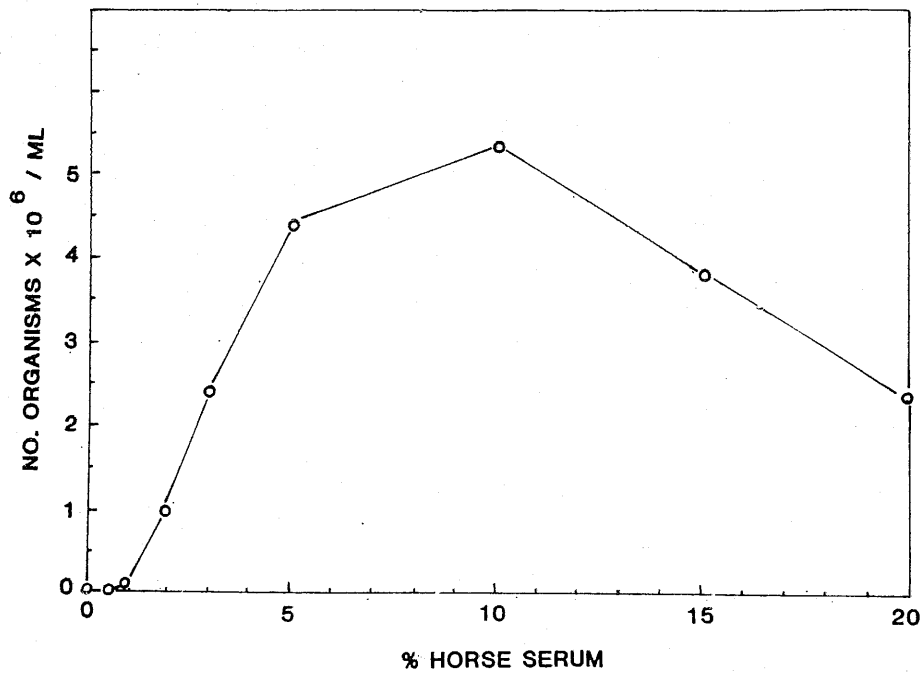


Fig. 4. Effect of horse serum on the growth of *Trichomonas hominis*.

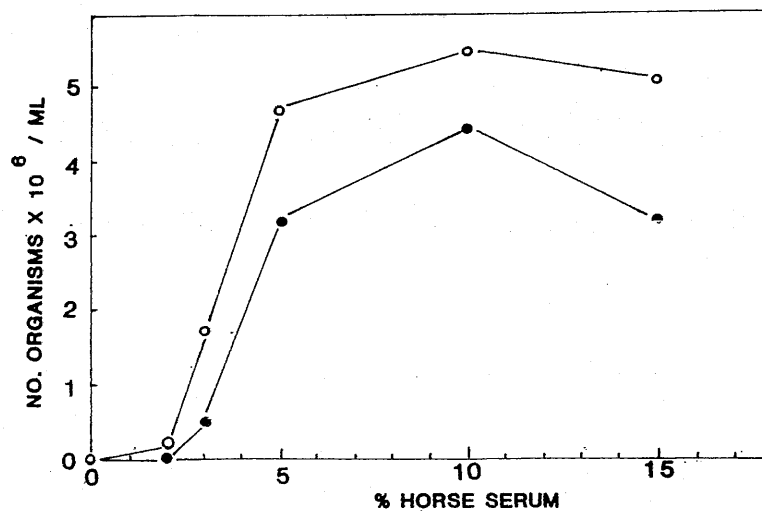


Fig. 5. The effects of dialyzed (●—●) and undialyzed (○—○) horse serum on the growth of *Trichomonas hominis*.

TABLE II
α-Amylase and maltase activities
in horse serum

Activities determined	Substrates used	Product released/hr/ml horse serum
α-Amylase	Glycogen	4 mg maltose
	Amylopectin	5 mg maltose
Maltase	Maltose	3.4 μmol glucose

Effect of Panmede on the growth of *T. hominis*

The effect of Panmede, an ox-liver extract, on the growth of *T. hominis* was investigated by its omission from the culture medium. The results are given in Table III. When Panmede was omitted from the medium, a significant decrease in cell density was found. This may suggest that Panmede is capable of providing

TABLE III
Serial subcultures of *Trichomonas hominis*
in Panmede-omitted and Panmede-
added medium

Subculture number	Average flagellates/ml	
	Panmede- added*	Panmede- omitted
1	5,020,500	2,667,700
2	4,664,500	1,908,800
3	4,984,400	2,327,300
4	5,130,300	1,797,600
5	3,206,300	1,872,900

* Panmede, an ox-liver extract, 0.5% was added. The inoculum was 4,000 flagellates per ml. Each subculture was made in three culture tubes. Incubation was for 48 hr at 36°C.

certain supplement(s) to enhance the growth of *T. hominis in vitro*.

The capability of *T. hominis* to utilize carbohydrates

A number of carbohydrates and their derivatives were used at a concentration of 1% to replace glucose in the culture medium. Their abilities to support *T. hominis* growth were compared and the results are shown in Fig. 6. Among monosaccharides, glucose > fructose > galactose > ribose in support of *T. hominis* growth while mannose, arabinose, xylose glyceraldehyde, 2-deoxy glucose, 2-deoxy ribose and glucosamine were inhibitory to the growth. Rhamnose, sorbose, mannitol, sorbitol, N-acetyl glucosamine were incapable of supporting *T.*

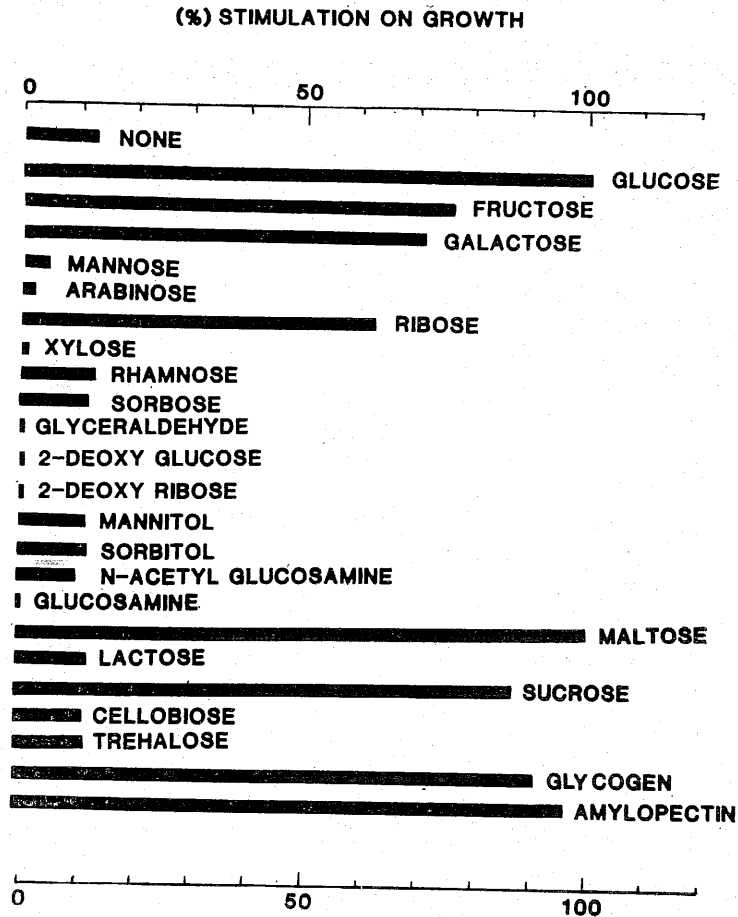


Fig. 6. Effect of various carbohydrates on the growth of *Trichomonas hominis*. The growth in glucose-added medium was taken as 100%.

hominis growth. Among disaccharides, maltose was better than sucrose in supporting *T. hominis* growth while lactose, cellobiose and trehalose failed to support the growth of the parasite. Two polysaccharides, glycogen and amylopectin, were also capable of supporting the growth of *T. hominis*.

Hydrolysis of disaccharides and polysaccharides by *T. hominis* in vitro

The ability of *T. hominis* to hydrolyze maltose and sucrose *in vitro* is shown in Table IV. The results indicate that *T. hominis* possesses maltase and sucrase activities. The ability of *T. hominis* to hydrolyze glycogen and amylopectin into maltose and glucose suggests the presence of α -amylase activity in the organism (Table V).

TABLE IV
Hydrolysis of disaccharides
by the homogenates of
Trichomonas hominis

Substrates used	μ mol glucose/hr/ml packed cells
Maltose	2.3
Sucrose	6.3

Each reading was an average of 3 determinations. One ml packed cells represents $3.2 \pm 0.4 \times 10^9$ cells.

TABLE V
Hydrolysis of polysaccharides
by the homogenates of
Trichomonas hominis

Substrates used	mg maltose released/hr/ml packed cells	μ mol glucose released/hr/ml packed cells
Glycogen	10.5	5.8
Amylopectin	34.1	1.4

Each reading was an average of 3 determinations. One ml packed cells represents $3.2 \pm 0.4 \times 10^9$ cells.

Glycogen content in *T. hominis*

Glycogen content in *T. hominis* grown in

TABLE VI
Glycogen content in *Trichomonas hominis* grown in medium with various carbohydrates

Carbohydrates in medium	Glycogen content (mg/ml packed cells) \pm S. D.
None	8.8 \pm 1.8
Glucose	17.2 \pm 2.4
Maltose	16.3 \pm 1.6
Galactose	37.7 \pm 8.7
Sucrose	13.7 \pm 1.0
Fructose	49.1 \pm 4.0

Each reading was an average of 3 determinations \pm S. D.

medium with various carbohydrates is given in Table VI. It appears that the ability of *T. hominis* to restore glycogen varies with the carbohydrate species provided in the culture medium.

Uptake of glucose and galactose by *T. hominis*

The uptakes of glucose and galactose were determined by the incorporation of radiolabeled substrates into *T. hominis* cells.

The time-course of uptake of [6 - 3 H]glucose and [1 - 3 H]galactose are shown in Fig. 7 and Fig. 8, respectively. Both glucose and galactose were incorporated into *T. hominis*.

The modes of uptake of glucose and galactose were investigated by determining the incorporation of radiolabeled substrates as a function of their unlabeled substrates. The results are shown in Fig. 9 and Fig. 10. In both cases, the incorporation of radioactivity decreased as the concentrations of unlabeled substrates increased. Such results indicate that the incorporation of radiolabeled substrates is inhibited by the presence of unlabeled substrates and may suggest the existence of specific transport systems for glucose and galactose in *T. hominis*.

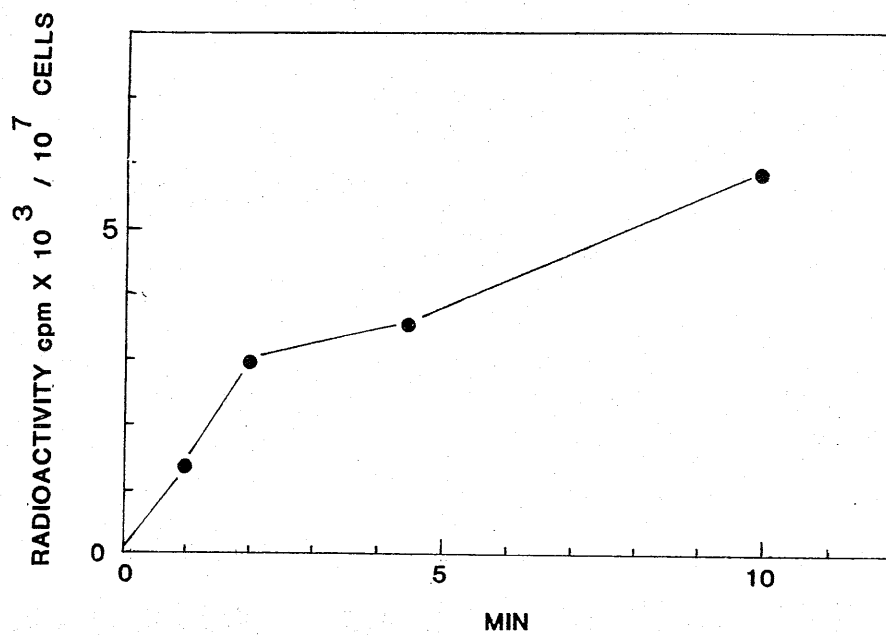


Fig. 7. The time-course of uptake of [6-³H]glucose by *Trichomonas hominis*.

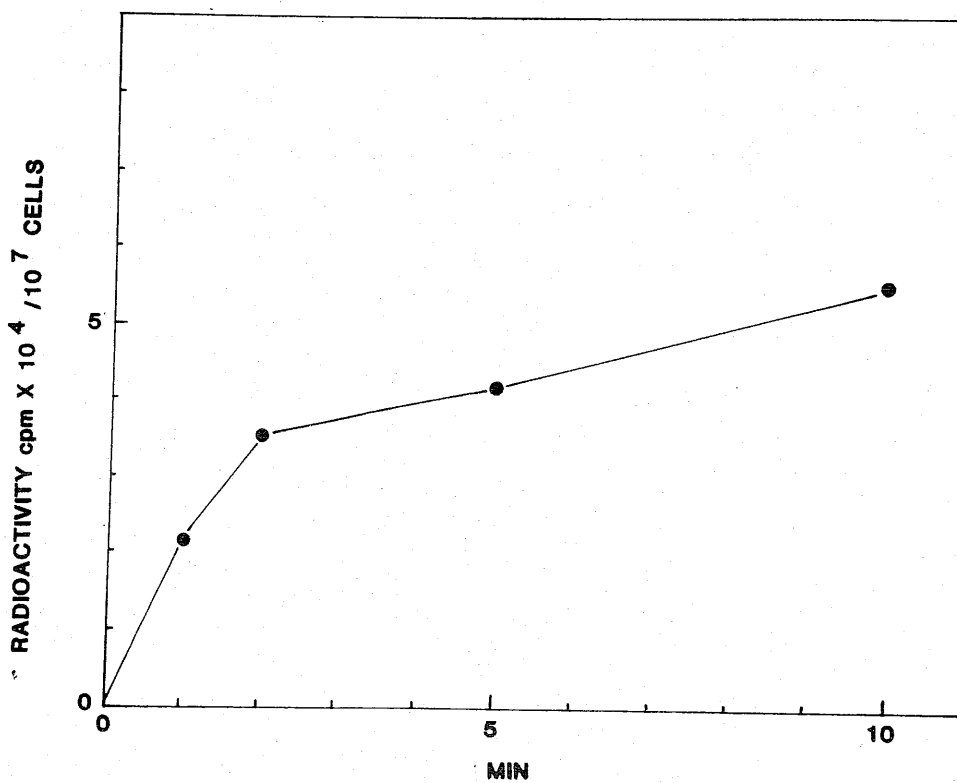


Fig. 8. The time-course of uptake of [1-³H]galactose by *Trichomonas hominis*.

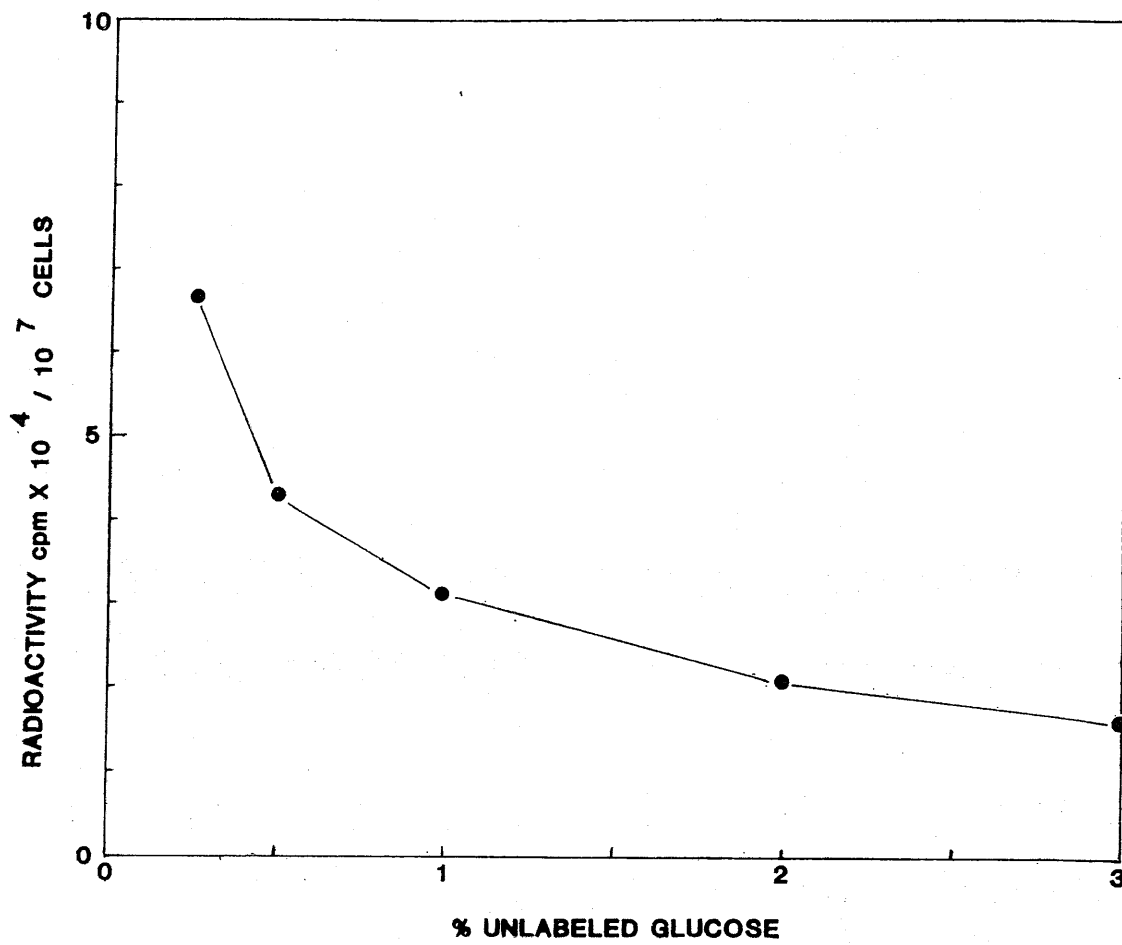


Fig. 9. Effect of unlabeled glucose on the uptake of [6-³H]glucose by *Trichomonas hominis*.

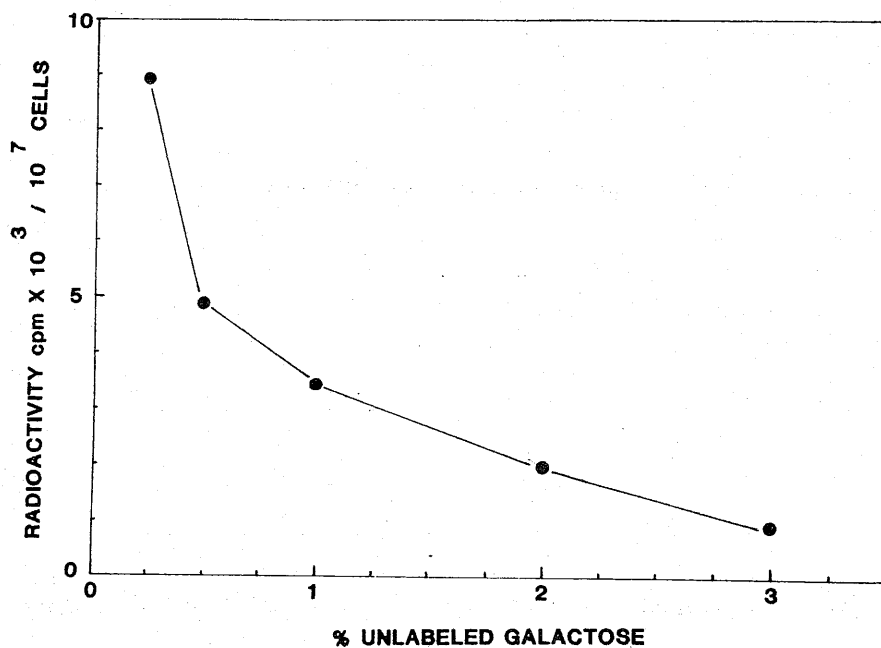


Fig. 10. Effect of unlabeled galactose on the uptake of [1-³H]galactose by *Trichomonas hominis*.

DISCUSSION

The purpose of studying *T. hominis* growth *in vitro* is to establish optimal conditions for its cultivation so as to increase yield of the organism and to reveal some of its nutritional requirements for further investigation.

The temperature-dependent growth of *T. hominis* indicates the parasitic nature of the organism. The optimal pH for growth of *T. hominis* resides between 6.6 and 6.8 which is comparable to the pH of its natural habitats in human intestine. The significant drop of medium pH associated with the growth of the organism suggests the production of appreciable amount of acidic endproducts. The nature of these endproducts requires further identification. Kupferberg *et al.* (1953) reported that the growth of *T. vaginalis*, a flagellate found in human urogenital tracts, is related to the production of lactic acid and the decline of medium pH. Solomon (1957) found that optimal growth of *T. hominis* was obtained at pH of 6.5 to 7.0 and at temperatures of 35°C to 37°C which are similar to our

findings.

Horse serum (or other sera) is usually an indispensable component of all culture media for *in vitro* cultivation of eukaryotic organisms. As to the precise role that serum plays in support of cell growth still remains obscure. In our study, we found that horse serum is essential for the growth of *T. hominis*. We have done preliminary work on the fractionation of horse serum by gel-filtration chromatography to identify the active ingredient(s) which support the growth of *T. hominis*. It was found that the active fractions associated with the growth-promoting activity have a relatively high molecular weight (Lo, unpublished data). Whether these fractions render biological activities or supplements nutritional requirements to the organism is uncertain. However, enzymic assays reveal that horse serum does possess α -amylase and maltase activities which are capable of hydrolyzing maltose or glucose-polymers into free glucose. In the glucose-omitted medium employed in our experiments, the residual carbohydrates can thus be readily hydrolyzed

and utilized by *T. hominis* in the presence of horse serum.

Panmede is an ox-liver extract which provides various nutrients and growth-stimulating substances. Its role in supporting a better growth of *T. hominis* is now under further investigation.

The requirement of glucose for the growth of *T. hominis* indicates that glycolysis is the main pathway functioning in the organism to provide energy to maintain its viability. Besides glucose, our work reveals that *T. hominis* is also capable of utilizing fructose, galactose, maltose, sucrose, ribose, glycogen, and amylopectin but not lactose, mannose, trehalose, arabinose, xylose and many other carbohydrate derivatives. Solomon (1957) reported that *T. hominis* can utilize glucose, galactose, maltose,

lactose, and sucrose. The discrepancy between our results is lactose. Examination of previous reports dealing with the carbohydrates utilization of other trichomonad protozoa reveals variable capability of each species to utilize different carbohydrates. *T. gallinae*, a pigeon parasite, is capable of utilizing glucose, glucose-polymers, fructose, galactose, mannose, sucrose, lactose, turanose, arabinose, and ribose (Daly, 1970; Daly *et al.*, 1974; Honigberg and Pierce, 1963; Read, 1957; Shorb, 1964). Other sugar or sugar alcohols were either utilized minimally or not at all. *Trichomonas foetus*, a cattle parasite, has been shown to utilize 21 carbohydrates for growth. Among these, glucose, galactose, mannose, maltose, and sucrose were found to be the most readily metabolized (Shorb, 1964). Read (1957) reported that *T.*

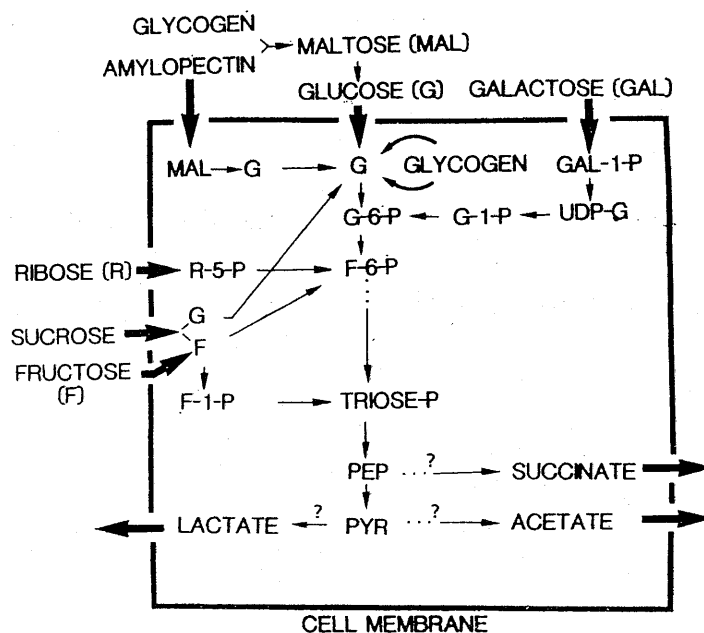


Fig. 11. Postulated pathways of carbohydrate metabolism in *Trichomonas hominis*.

Abbreviations used are:

UDP-G	uridine diphosphate-glucose
G-1-P	glucose 1-phosphate
G-6-P	glucose 6-phosphate
F-6-P	fructose 6-phosphate
F-1-P	fructose 1-phosphate
TRIOSE-P	triose phosphates
PEP	phosphoenolpyruvate
PYR	pyruvate
R-5-P	ribose 5-phosphate

vaginalis utilizes glucose, galactose, mannose, fructose, arabinose, xylose, maltose, trehalose, lactose, sucrose, starch, and glycogen for growth. It is apparent that parasitic trichomonads exhibit different capabilities of utilizing carbohydrates. Such capability characterizes unique metabolic pathways and enzyme systems for the parasites to utilize various carbohydrates.

According to our results, the pathways of carbohydrate metabolism in *T. hominis* can be postulated as shown in Fig. 11. Glucose and galactose are transported through specific transport systems into the cells and catabolized via glycolysis to acquire energy. The utilization of galactose presumably proceeds through the following enzyme system consists of galactokinase, UDP-glucose: galactose 1-phosphate uridylyltransferase, UDP-glucose 4-epimerase and phosphoglucomutase. In addition to catabolism, glucose can also be anabolized into glycogen as stored polysaccharides. Accumulation of glycogen by microorganisms is believed to be affected by their growth conditions. Our results indicate that *T. hominis* is capable of altering its glycogen content with respect to the carbohydrate species provided in the growth medium. There might be a delicate machinery exists in *T. hominis* to control the on-and-off switch of glycogen synthesis and degradation and is worthy of further pursuing. Maltose, amylopectin, and glycogen can be either ingested by phagocytosis and pinocytosis directly or hydrolyzed by horse serum α -amylase and maltase into glucose before entering the cells. The ingested glucose-polymers are then hydrolyzed by α -amylase and maltase present in *T. hominis* for further degradation. Fructose utilization indicates the presence of ketohexokinase, fructokinase, aldolase, and triose kinase activities in *T. hominis*. Utilization of ribose by *T. hominis* for growth suggests the presence of a rather complicated enzyme system: ribokinase, ribosephosphate isomerase, ribulosephosphate 3-phosphate epimerase, transketolase, and aldolase. Sucrose utilization is accom-

plished by the sucrase activity found in *T. hominis*. The capability of *T. hominis* to utilize the above carbohydrates further substantiates the essential role of glycolysis in the energy metabolism of *T. hominis*.

The endproducts of glucose catabolism can be narrowed down to be lactate, acetate, and succinate as suggested by the pathway illustrated in Fig. 11. Our next step is to identify those enzyme activities responsible for the formation of acidic endproducts found in *T. hominis*.

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腸道鞭毛蟲之生長及醣類之利用

羅新生 岳鳳玲 梁素月

本研究的主要目的，在於探討腸道鞭毛蟲之生化特性及生長情形。影響腸道鞭毛蟲生長的因素有下列幾項：一、溫度。腸道鞭毛蟲的生長情形，於 36°C 最佳；30°C 次之；25°C 幾無生長可言。二、培養基之酸鹼值。腸道鞭毛蟲之生長以介於酸鹼值 6.6 及 6.8 間最理想。當蟲體繁殖生長後，培養基之酸鹼值明顯下降，顯示蟲體排出大量酸性終產物。三、馬血清濃度。培養基之馬血清濃度，以介於 5% 及 10% 之間最適合蟲體之生長，透析後的馬血清對生長有不利之影響。四、葡萄糖。葡萄糖是蟲體生長必要的因素，生長情形與葡萄糖濃度呈一飽和曲線關係。五、牛肝萃取物 (Panmede)。牛肝萃取物能提供某些養份，促進蟲體的生長繁殖。六、醣類化合物。腸道鞭毛蟲能利用之醣類，除葡萄糖外，有果糖、半乳糖、核糖、麥芽糖、蔗糖、肝醣、支鏈澱粉；無法利用之醣類有：鼠李糖、山梨糖、甘露糖醇、山梨糖醇、N-乙酰胺基葡萄糖、乳糖、纖維雙醣、漏蘆糖；對生長有抑制作用的醣類有：甘油醇、去氧葡萄糖、去氧核糖、木酮糖、阿拉伯糖、甘露糖、胺基葡萄糖等。腸道鞭毛蟲之醣類代謝途徑可據以設定。

