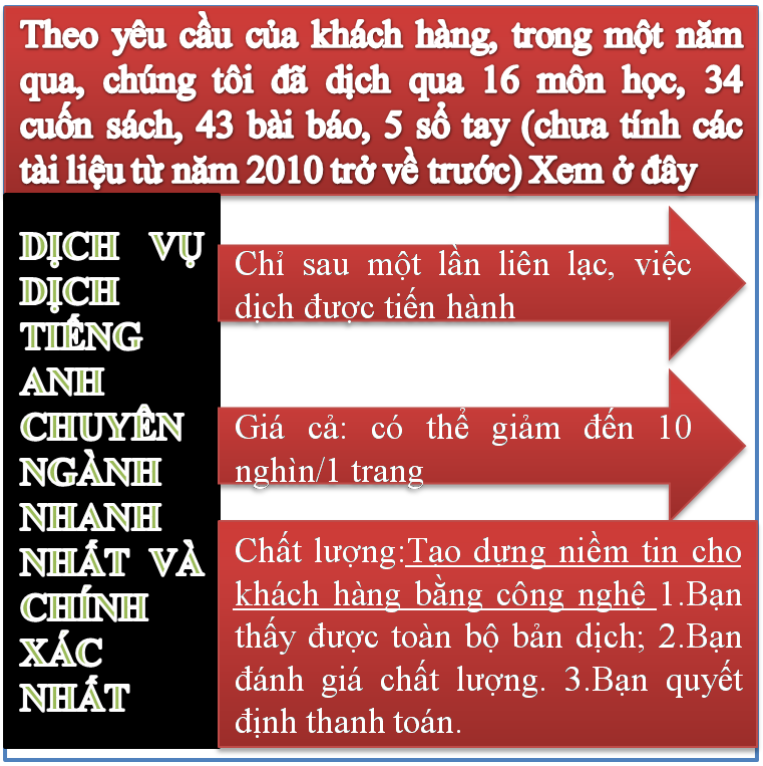

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Beggiatoa, Thiothrix, and ThiopIoca

NỘI DUNG

GIỚI THIỆU

BEGGIATOA

Phân loại

Làm giàu và phân lập

Sinh thái học và phân bố

Hình thái học

Sinh lý học

THIOPLOCA

PHÂN LOẠI

Sinh thái học và phân bố

Hình thái học

Sinh lí học

KẾT LUẬN

GIỚI THIỆU

Mục đích của bài báo này là tổng quan và cập nhật tài liệu về vi khuẩn oxy hóa lưu huỳnh vận động trượt (di chuyển bằng cách trượt). Tuy nhiên, chúng tôi quyết định không đề cập đến Achromatium và Thiospirillopsis trong bài tổng quan này. Vi khuẩn đầu tiên có roi và do đó không thuộc loại sinh vật vận động trượt (20). Loại vi khuẩn thứ hai đã được đề cập đến hai lần trong các tài liệu tham khảo (56, 121) mặc dù việc nghiên cứu nhiều môi trường sống khả dĩ, kể cả việc xem xét lại loại vị trí, làm cho tính hiệu lực của nó có vấn đề (56). Hơn nữa, trong các chủng Beggiatoa thuần, đôi khi chúng ta thấy các sợi xoắn khác biệt với Thiospirillopsis (W.R.Strohl, J.M.Larkin, dữ liệu không xuất bản).

Các thành viên của ba giống còn lại, Beggiatoa, Thiothrix và Thioploca đã từng là chủ đề của một số nghiên cứu gần đây đã được làm rõ, ít nhất là một phần, một số đặc tính cơ bản của những sinh vật này. Có một số sự giống nhau về mặt hình thái học dễ thấy giữa chúng nên có thể gộp chúng vào một bài tổng quan duy nhất. Sự tương tự này bao gồm những điểm sau đây: (a) Tất cả các sinh vật này đều lắng tụ các hạt lưu huỳnh nội tại khi có sunfua; (b) Tất cả đều tạo trichome có thể đạt được chiều dài đáng kể; và (c) tất cả đều di chuyển bằng cách trượt ở một giai đoạn nào đó trong cuộc đời của chúng. Hơn nữa, sự tương tự về mặt sinh lý học của chúng đang bắt đầu lộ diện.

Ngoài việc là đại diện của một nhóm vi sinh vật bất thường và chưa được nghiên cứu nhiều, các sinh vật này thường rất đáng quan tâm ở khía cạnh lịch sử. Chính từ Beggiatoa và Thiothrix mà Winogradsky (126-128) đã xây dựng khái niệm tự dưỡng đầu tiên. Tuy nhiên, sự thiếu chủng thuần và sự hiện diện các vật liệu hữu cơ khả dĩ trong môi trường của ông đã ngăn cản nó thể hiện khả năng tự dưỡng cho đến tận các nghiên cứu sau này của ông ta về vi khuẩn nitrat hóa (130).

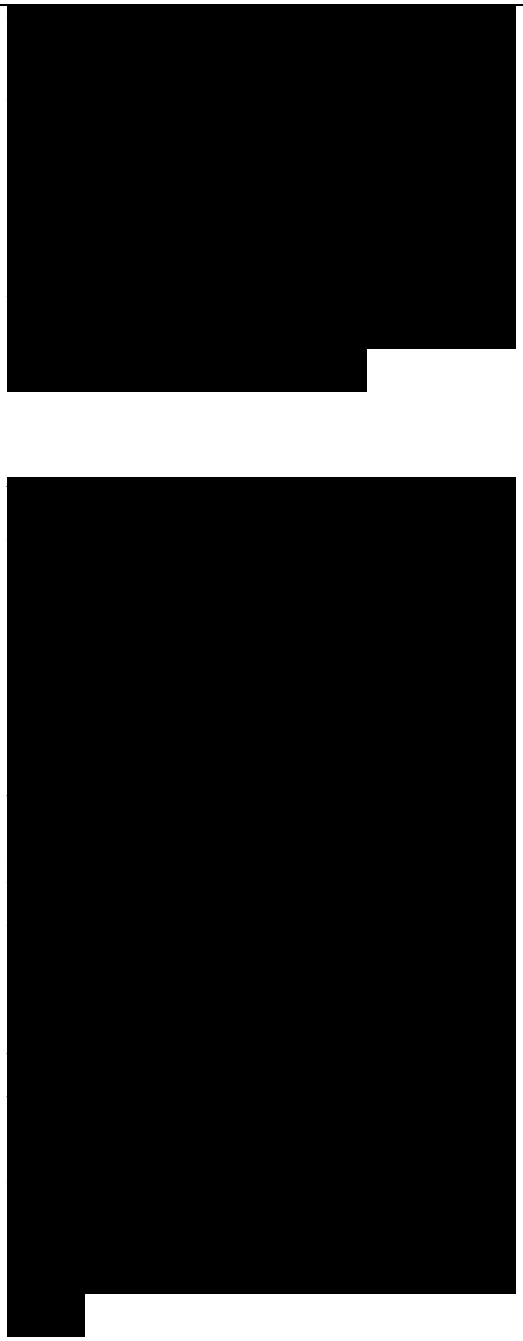
Các dòng Beggiatoa đã được phân lập trong một số nghiên cứu (13, 19, 28, 40, 43, 48, 75, 86, 87, 98, 115) và mỗi dòng được thêm vào kho tàng tri thức của chúng ta. Nhưng chỉ trong khoảng thời gian gần đây chúng ta mới thu được một tập hợp lớn các dòng vi khuẩn phân lập và các nghiên cứu so sánh đã bắt đầu. Trái ngược với Benggiatoa, Thioploca chưa bao giờ thu được dưới dạng chủng thuần, và các chủng Thiothrix thuần chỉ xuất hiện trong một vài năm nay (57). Với nhận thức ngày càng tăng về vai trò của vi khuẩn oxy hóa lưu huỳnh trong tự nhiên và sự xuất hiện của các tập hợp Beggiatoa và Thiothrix, có lẽ đây là thời điểm thích hợp để tổng quan lại các tài liệu trước đây, đây là thời điểm khởi đầu của quá trình nhận thức lại tầm quan trọng của các vi khuẩn này và hoạt động của chúng.

Để xem các mô tả ngắn gọn tuyệt vời về các giống và các loài được mô tả trong bài báo này, cũng như các vi khuẩn oxy hóa lưu huỳnh khác, tham khảo công trình của Fjerdingstad (30).

BEGGIATOA

Phân loại

Giống Beggiatoa bao gồm các sợi bện vào nhau kết tủa lưu huỳnh nội tại, di chuyển bằng cách trượt, và không có vỏ. Chín loài và năm giống đã được đặt tên, nhưng chỉ sáu loài được công nhận trong Sổ tay của Bergey (61). Việc phân biệt các loài được công nhận chỉ dựa trên đường kính trichome, nằm trong khoảng từ 1 micro mét đối với Beggiatoa minima đến khoảng 55 micro mét trong Beggiatoa gigantean.

Because of a lack of pure cultures and definitive descriptions, only Beggiatoa alba is found in the Approved Lists of Bacterial Names (102); B. alba strain B18LD from the Louisiana State University collection is designated as the type strain. The mol% guanine plus cytosine of the DNA of strain B18LD is 41 (69). The morphological similarity between Beggiatoa and the cyanobacterium Oscillatoria has often been pointed out (84, 86,93,94) with the suggestion that Beggiatoa might be an apochlorotic cyanobacterium. The similarity has been recently extended to include the structure of the cell wall (114, 115), the mode of trichome division by the production of necridia (116), and the production of hormogonia (116). Some investigators who have noted the morphological similarities have felt it was too early to suggest that Beggiatoa are apochlorotic cyanobacteria but have felt that future studies may show such a relationship (66,		

107). Nevertheless, one recent proposal (94) suggests that Beggiatoa should be considered as an apochlorotic cyanobacterium. Although future studies may demonstrate the validity of such a relationship, we would like to reserve judgment and point out some of the significant differences in the physiologist of Beggiatoa and Oscillatoria that mediate against accepting such a relationship at this time, (a) Some cyanobacteria can use sugars in the dark.

Glucose is most commonly used and all of the sugars are converted to intermediates; of the oxidative pentose phosphate cycle (109); Beggiatoa does not use sugars (69, 88,98,115), (b) The major reserve material of cyanobacteria is glycogen (109); Beggiatoa stores mainly PHB (88, 115). (c) Cyanobacteria have an incomplete citric acid cycle caused by the absence of oc-ketoglutarate dehydrogenase (109); Beggiatoa has a complete citric acid cycle (W. R. Strohl, manuscript in preparation), (d) Cyanobacteria can photoassimilate acetate and convert it to acetyl-CoA, but it is not respired (\09y,Beggiatoarespires acetate and also uses it as a major source of carbon (15, 28, 52, 77, 87, 98, 115). (e) Some

cyanobacteria autotrophically photoassimilate C02 while oxidizing hydrogen sulfide to sulfur, but they do so only anaerobically (109); Beggiatoa cannot grow autotrophically, photosynthetically, or anaerobically. (/) Cyanobacteria fix CO2 by the ribulosc 1,5-bisphosphatq carboxylase reaction (109); Beggiatoa fixes C02 by heterotrophic mechanisms (112).

Enrichment and Isolation

Several techniques have been developed for the isolation of beggiatoas, and they are all based on the extracted hay medium devised by Winogradsky (126) and adapted effectively by Cataldi (19). From the enrichments, trichomes are washed ar,d blotted dry and are placed on plates of a suitable medium. Filaments that have glided away from the contaminants are then transferred to new plates. The medium may be prescored to provide paths for the migration of the trichomes (13). For additional details, the reader should consult Strohl & Larkin (115). An excellent enrichment for marine beggiatoas was described by Jprgensen (personal communication) and uses the sulfuretum concept of Baas- Becking (4). A 1- to 2-inch layer of sea sand is covered

with a 1-inch layer of sulfide-emanating mud and a few inches of 50-80% seawater. Decaying leaves or extracted hay and CaS04 (about 1 g/liter) are added, about two thirds of the tank is enclosed in aluminum foil, and the unwrapped end is lighted. Within a few weeks the sulfur cycle is well developed, and a combined mat of photo-synthetic bacteria, cyanobacteria, and Beggiatoa develops and remains stable for several months.

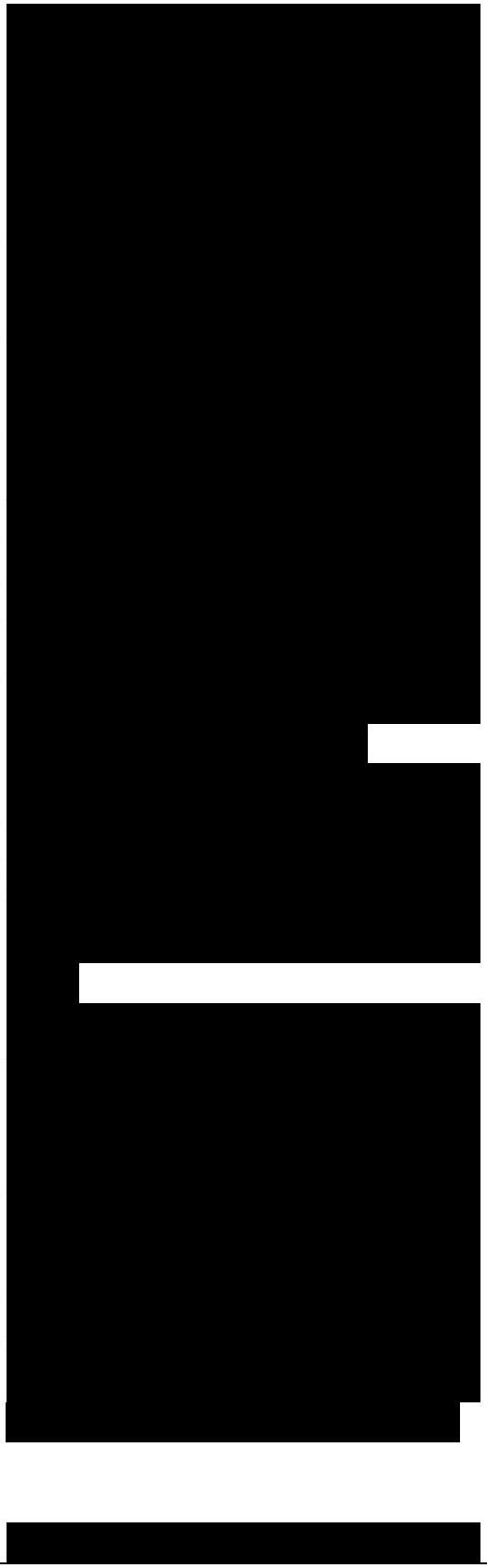
Ecology and Distribution

Many reports describe the occurrence of Beggiaioa in the sediments of lakes, streams, and ditches (28, 98, 115, 124), in brackish marshes (115), in coastal waters (41, 109), in association with cyanobacterial mats (78), in freshwater and estuarine sulfur springs (5, 56, 121), in association with coral (23, 33), in the rice rhizosphere (44,83), and in giant cobweb-like mats on the sea floor (3, 108). Beggiatoa is also found in sewage (13, 40), in activated sludge (25), and on the submerged decaying remains of plants or animals from which sulfide is produced during decomposition (5). Recently, large beggiatoas of up to 100 jim in diameter have been observed at the sulfide-

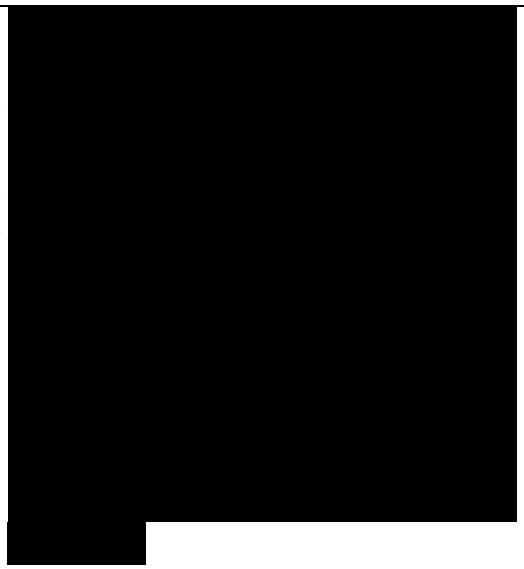
emanating hydrothermal vents on the ocean floor (38). Sediments that contain suitable concentrations of sulfide, oxygen, and C02 provide proper conditions for Beggiatoa growth (87). The p-polysaprobic zone (29) Beggiatoa inhabits has comparatively few species but often has large numbers ofindividuals; blooms of certain bacteria may occur in this zone (124). Beggiatoa and Thiothrix differ ecologically in that the former exists in the sediments where it glides to its optimum habitat (42) and the latter grows in flowing waters where it attaches to a solid substrate (see section on Thiothrix).

Beggiatoas are often found in polluted waters, but they are not good indicators of pollution because of their ubiquitous nature (55, 103).

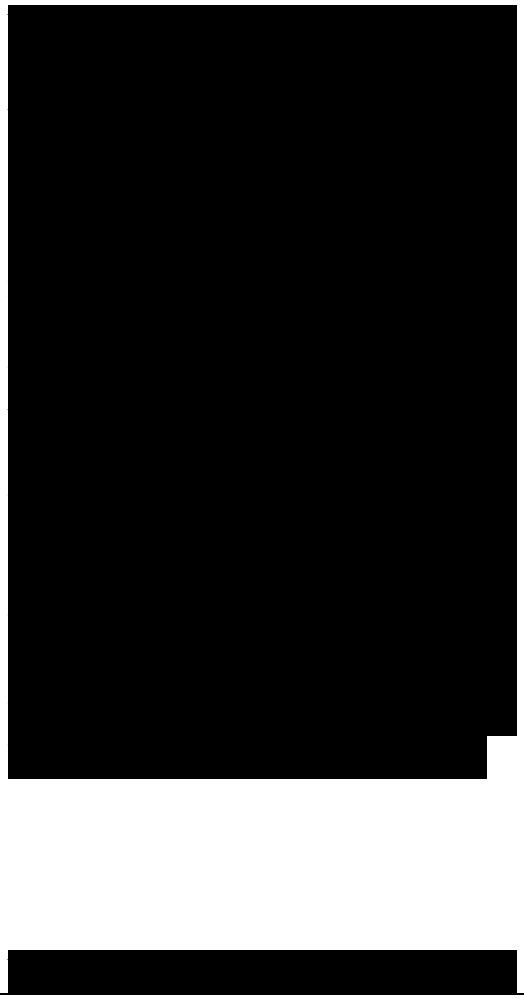
Beggiatoas are generally considered to be mesophilic (56), although several strains of B. alba grow at WJC (115). Beggiatoas have been observed in thermal springs (56, 82) with temperatures of 69.5°-72.0°C (82). However, microenvironments that beggiatoas inhabit in hot springs may be of a cooler temperature (D. C. Nelson, personal



communication).
Beggiatoa normally exists at the interface (transition) between an anoxic sulfide-emanating lower sediment and the oxic interstitial waters or environments above them (41,42). In the laboratory, their growth at an interface can be demonstrated by the thin layer they form below the surface of liquid (52, 90) or soft agar (115) if sulfide and oxygen are supplied from the bottom and top, respectively.



Microelectrodes (42, 96) have been used to measure the pH and the concentrations of oxygen and sulfide in 500- to 700-^.m thick mats of marine Beggiatoa. Sulfide was present in the sediment below the mats and oxygen was in the water above them. The region where sulfide and oxygen overlapped was 50 thick, and all of the sulfide oxidation took place in this zone. The rate of sulfide oxidation by the beggiatoas was 100-1000 times the chemical oxidation rate, showing that it was the beggiatoas that removed the sulfide and the oxygen through their respiratory activities. It is obvious these organisms exert an enormous influence on the sulfur cycle in



the marine sediment (42).

Beggiatm is one of several filamentous microorganisms shown to cause bulking of activated sludge, but it is often of minor importance; Thiothrix and Sphaerotilus are usually the dominant forms (25).

Beggiatoa has been seen in association with “black line” disease of coral, prompting the suggestion that it is involved in the etiology of the disease (33), but this involvement has not been proven (23).

Plants that grow in flooded soils may be protected from sulfide-induced diseases by Beggiatoa. In an attempt to discover why rice plants growing in paddies do not suffer from sulfide toxicity (37), Hollis and co-workers (36,37,43, 44, 83) discovered a mutualistic symbiotic association in which the bacterium removes the sulfide from the plant rhizosphere, and the plant roots excrete catalase, which protects the bacterium from its own metabolically produced peroxides. Moreover, oxygen is conducted downward through the plant and is excreted by the roots to produce an oxidised area in the rhizosphere. Beggiatoa has also been observed in the rhizosohere of Svartina, a plant that is physiologically very similar to

rice and is the dominant and most important plant in the marsh ecosystem (115). The ability of Beggiatoa to fix nitrogen in both marine and fresh water (78, 79) and to remove sulfide may make it a very important part of the fiooded-soil ecosystem.

Several investigators have observed a photophobic response by Beggiatoa (54, 78, 126). The trichomes may form thick mats on the sediment surface at night and may migrate down into the mud during the daytime. A potential photoreceptor with an action spectrum similar to a cytochrome was observed (78) and may be responsible for the photophobic response. The cytochrome may act as a photosensitizer that in the presence of oxygen produces the singlet-state-oxygen free radical. In the absence of carotenoids or other singlet-state oxygen quenchers, photodynamic death could ensue. The movement of Beggiatoa from the photic to the aphotic zone would eliminate this photodynamic effect.

The movement of Beggiatoa into the sediments in daytime may also be due, in part, to an aversion to the oxygen produced by adjacent plants during sunlit periods. The decreased oxygen

tension below the mud surface would allow the cell to produce less of the toxic peroxide and superoxide. Beggiatoa has a superoxidt: dismutase (W. R. Strohl, unpublished data) but it has no catalase. Thus, in normal oxygen tensions, Beggiatoa may produce superoxide and peroxide; if sunlight is also present, triplet-state oxygen may be produced (111). The movement of Beggiatoa from a photic aerobic zone to an aphotic microaerophilic zone should protect the organism from the combined effects of sunlight and oxygen. If this microaerophilic habitat also contains sulfide, additional protection of the cell may occur through the detoxification of the environment by the reaction H202 + H2S —> S° + 2H20. This reaction has generally been considered to produce no energy (15, 76). However, the reduction of peroxide (Eo= 300 mV) by sulfide (Eo~ —200 mV) could be an energy-yielding process (G<pr -23 kcal mol-1) if mediated by cytochrome c.

Morphology

Beggiatoa (Figures 1 and 2) is a multicellular bacterium that produces trichomes that may attain great lengths. The cells within the trichomes are separated by the membranes and the peptidoglycan layer of the

cell wall (114,115). The remaining cell wall layers do not form part of the septa but instead are continuous along the length of the trichome.

Beggiatoa stains gram negatively (115), but its cell envelope is more complex than that of typical gram-negative bacteria (66, 114). The best procedure used for the observation of cell wall structure by electron microscopy (66,113, 114) was a fixation with gluteraldehyde and ruthenium red, followed by an osmium tetroxide with ruthenium red post-fixation. Depending on the strain……..

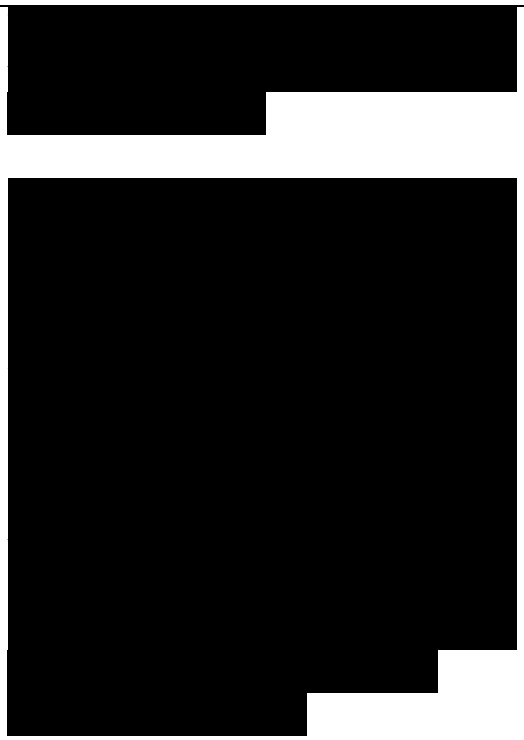
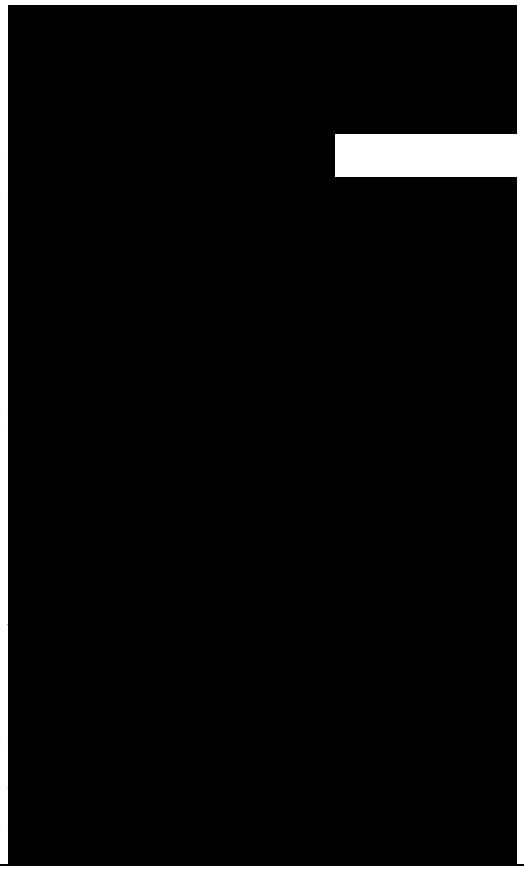


Figure I A circuitans-type colony of Beggiatoa alba on a heterotrophic growth medium.



……contained four or five layers external to the cytoplasmic membrane, giving an appearance similar to that of the cyanobacterium Oscillatoria (22,45). The innermost cell wall layer is interpreted as the peptidoglycan because of its appearance and the sensitivity of the organism to lysozyme in the presence of ethylenediaminetetraacetic acid (66, 70). The next layer has the "railroad track" appearance of a typical gram-negative cell envelope. There may be two or

three additional layers (Figure 3) (66,113, 114), the most external of which usually has a longitudinally fibrillar pattern (22, 114).

Beggiatoa moves by gliding on a trail of excreted slime; the mechanism of this movement is unknown (11). Speeds of gliding as high as 8 |i.m sec 1 have been seen (39). On an agar surface, the trichomes exhibit two distinct patterns of gliding. In the circuitans (87) pattern, one or more trichomes produce a doughnut-shaped coil (Figure 1) in which the entire coil rotates on the agar. In the other pattern, called linguiformis (87), the trichomes produce tongue-like extensions from the edge of the colony. These patterns are strain specific and may be species specific (69). The trichomes glide in the direction of the long axis and have been said to rotate about their long axis as they move (78, 120). However, it is difficult to see how a trichome that is coiled, as in the circuitans- type of colony, can glide if rotation about its long axis is obligatory.

The extracellular slime that Beggiatoa produces is a polysaccharide (115) that does not stain with ruthenium red (113, 114). It is composed primarily of neutral sugars, consisting of about 89-92%

mannoside in two B. alba strains and 58-64% glucose in a third B. alba. The composition of the slime remained the same in either heterotrophic or mixotrophic growth conditions (S. Seuferer, W. R. Strohl, J. M. Larkin, unpublished data).

Figure 3 An idealized drawing of Beggiatoa alba B I5LD under mixotrophic (/1) and heterotrophic (B) growth conditions. (From 14.)

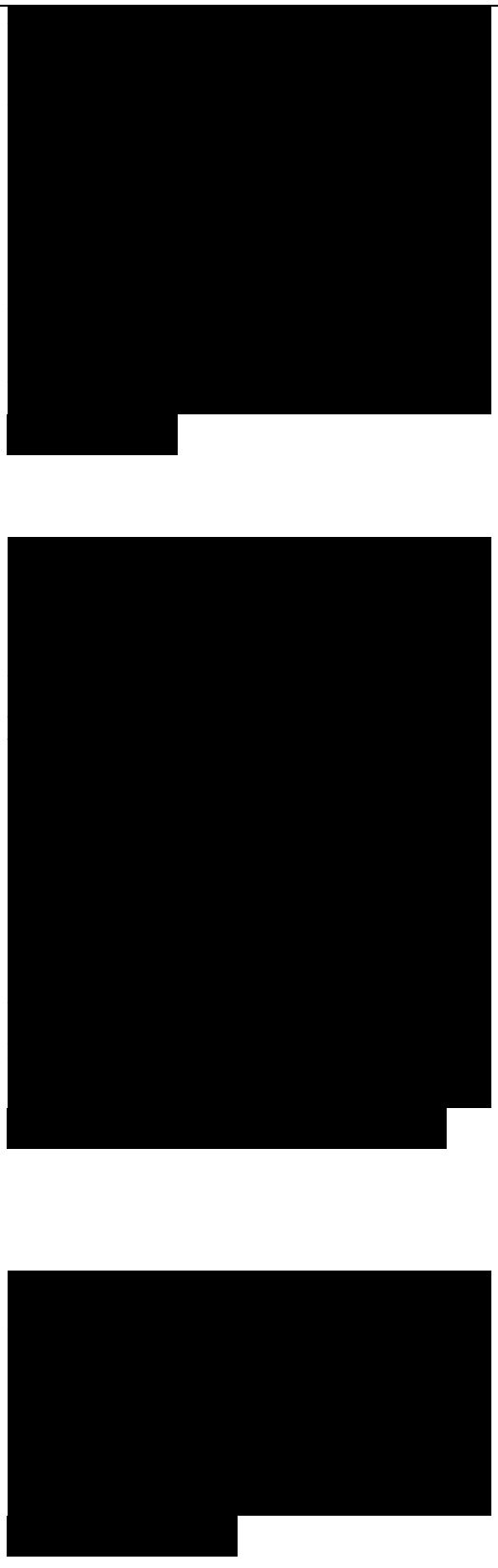
The function of the slime in gliding is unknown (11). Other trichomes may follow in the slime trail of a pioneer trichome (10) and the slime trail may be used by other species of bacteria (12). The slime does not have a pheromone effect (12). Trichomes of B. albaB 15LD have tufts of fimbriae (W. J. Dobson, personal communication), but their function is unknown. Other strains of Beggiatoa have not been examined for the presence of fimbriae. The major theories concerning the mechanisms of gliding have recently been reviewed (11) and are not covered here.

Beggiatoa cells contain three types of inclusions, PHB (90, 114, 115), volutin (66,115), and sulfur(22,40,60,66,75,113-115, 120,126-129). The latter inclusion separates the genera of Beggiatoa and Vitreoscilla (61,

110, 115) and has been the subject of much interest. Sulfur granules are produced by Beggiatoa in the presence of sulfide and they may slowly disappear after sulfide is removed (19, 28, 86, 126, 128). The granules are refractile in the light microscope (40, 115), and they may be extracted with a number of organic solvents, such as carbon disulfide, pyridine, and others (19, 115). The appear-ance and solubility have often been used for tentative identification of sulfur granules (40, 101, 115). In an electron microscope, the sulfur granules of unfixed cells are more electron dense than the other cellular constituents (40, 60).

The sulfur in the granules is dissolved away by the ethanol or acetone during dehydration of the cells for electron microscopy, leaving electron-translucent areas (99, 113). In thin sections these "spaces" have been observed to be external to the cytoplasmic membrane but internal to the cell wall (22, 66, 75, 114, 115), and they nearly filled the entire cell of one B. alba strain (22). Sulfur inclusions in Beggiatoa and Thioploca were interpreted as being enclosed by the cytoplasmic membrane (66). Other investigators have also

shown that the sulfur inclusions were membrane bound (22, 113-115, 120). The sulfur inclusions of three mixotrophically grown strains of B. alba had single-layered -'"tron-dense envelopes about 4 nm thick (113). The sulfur granule membrane of mixotrcphically grown B. alba B15LD had three electron-dense layers, 2.1, 3.5, and 2.i nm in thickness, separated by two electron-light layers to give atotal thickness of 12-14 nm (113-115). Similar pentalaminar envelopes were observed in the same location in cells grown without added sulfide, but they were folded and compacted into rather small spaces (114). Figure 3 shows the cell wall structure, cytoplasmic membrane, PHB granules, and sulfur granules of B. alba B15LD. Sulfur granules maybe noticeable in Beggiatoa cells within a very short time after exposing them to sulfide (14,126,128). The speed with which this occurs may not allow enough time for the cells to synthesize sulfide-oxidizing systems, so other mechanisms for sulfide oxidation have been sought. It is known that sulfide and peroxide will react to yield water and molecular sulfur; this reaction bias been postulated to account for the deposition of sulfur by a peroxide-producing

catalase-negative strain of B. leptomitiformis (14) and by Thioploca (74). Cytochromes were not detected in the B, leptomitiformis strain, forcing the conclusion that the oxidation of sulfide is not an energy-yielding reaction (14) but instead is a mechanism by which the Beggiatoa was able to destroy its endogenously produced hydrogen peroxide, All strains of Beggiatoa examined since then are catalase negative (76, 115), but none have been examined to see if they produce hydrogen peroxide. Therefore, it is not possible to conclude that the detoxification of peroxide is the only possible function of sulfide utilization by Beggiatoa. Moreover, many strains of Beggiatoa, including the B. leptomitiformis strain used in the original investigation, are now known to possess a functional sulfide-reducible electron transport system (see section on physiology). It is possible that heterotrophically grown beggiatoas contain the mechanism for sulfide oxidation even in the absence of added sulfide. Heterotrophically grown B. alba strain B15LD contains folded and compacted pentalaminar membrane vesicles, which in		

mixotrophically grown cells were shown to contain sulfur (114; Figure 3). If the mechanism for sulfide oxidation is associated with those membranes, a switch from heterotrophic to sulfide-oxidizing growth conditions could lead to the very rapid appearance of sulfur granules. In Thiobacillus, the oxidation of sulfide is mediated by cytochrome c (104), and all strains of Beggiatoa examined so far have a cytochrome c (118; S. Burton, personal communication). The location of cytochrome c in Beggiatoa has not been determined. It will be of interest to see if any cytochrome c activity is associated with the sulfur granule membrane. The cytological evidence that sulfur granules are discrete membrane-enclosed structures in specific sites within the cell indicates that sulfide oxidation is a metabolic function and is not random, as would be the case if detoxification were its only function.

Sulfur granules of Beggiatoa in freeze-etched preparations had the same morphology as the sulfur granules of Chromatium (95), and the enclosing membranes were visible (113). A conclusive demonstration that these granules in Beggiatoa

contain sulfur was recently provided (60).

The sulfur granules in Thiothrix and Thioploca are external to the cytoplasmic membrane, just as in Beggiatoa (see below). This has at least two important consequences. It indicates that it may not be necessary for sulfide to diffuse across the membrane to the cytoplasmic side where it could disrupt metabolism, which may explain how these organisms avoid the toxic effects of the sulfide ion. Secondly, the oxidation of sulfide on the external surface of the cytoplasmic membrane may aid in establishing a proton gradient for the synthesis of ATP.

The amount of PHB contained within a cell of Beggiatoa is proportional to the amount of acetate in the medium (52). About 50-55% of the cell dry weight under heterotrophic conditions can be PHB (34, 112). Nearly 50% of the [l4C]acelate assimilated by heterotrophically grown B. alba was incorporated into PHB (112). In a continuous culture under mixotrophic conditions, the PHB made up only 8-14% of the cell dry weight (34). Stored PHB may allow Beggiatoa to survive in starvation conditions (52).

Physiology ENERGY METABOLISM Winogradsky first studied the nutrition of Beggiatoa using slide cultures (126, 128, 129) in which he observed sulfur granule formation in the trichomes after the addition of hydrogen sulfide. When sulfide XEM ẢNH THỨ I VÀ PHẦN DỊCH BÊN DƯỚI	[redacted]	

trophically and deposited sulfur but could not grow autotrophically. All beg- giatoas isolated since then have been capable of heterotrophic growth, and most could deposit sulfur (11, 28,52,76, 87,98, 115). A few isolates lack the ability to deposit sulfur and may be genetic or physiological variants of Beggiatoa that have lost the ability to oxidize sulfide (70). This loss could occur if the genetic control of sulfur oxidation was carried on an extrachromosomal element such as the plasmids recently isolated from Beggiatoa (70). The B. leptomitiformis strain used by Morita and co-workers (14, 15, 73) is on deposit with the

American Type Culture Collection with the accession number of 15551. This culture does not now deposit sulfur (69) or oxidize Na235S (W. R. Strohl, unpublished data).

Another explanation for the inability of some isolates to deposit sulfur is that they may oxidize sulfide to sulfate without the intermediate production of sulfur granules. It is also possible that the isolates are really a Vitreoscilla beggiatoides (84, 85,115) or similar organism and that other types of granules, such as PHB, have been mistaken for sulfur. We have received several strains labeled as Beggiatoa that deposited large refractile PHB granules but did not deposit sulfur (69) or oxidize Na235S (W. R. Strohl, unpublished data).

There are several possible functions for the oxidation of sulfide by beg- giatoas. One possibility is that Beggiatoa requires a reduced sulfur source for biosynthetic purposes, as has been observed with some thiobacilli (105). Secondly, it has been proposed that sulfide detoxifies endogenously produced hydrogen peroxide (14). The recent work of Nelson & Castenholz (76) supports this concept. However, it has been

improperly stated that Beggiatoa requires catalase for growth (36). A third possibility is that sulfide, and possibly thiosulfate, serve as electron donors for energy production and reducing power via the electron transport system (17, 34, 112, 115, 118) as has been shown with the thiobacilli (1). Several Beggiatoa cultures were shown to be sensitive to cyanide and azide (115), which led to the observation that B. alba B18LD contains a cyanide, sulfide, and dithionite alterable c-type cytochrome (17). Recently, c-, b-, and a-type cytochromes have been observed in three strains of B. alba and in three B. leptomitiformis strains (118; W. R. Strohl, manuscript in preparation). Moreover, ubiquinone no.8 (18; W. R. Strohl, manuscript in preparation), traces of a naphthaquinone (18), NADH dehydrogenase (15; W. R. Strohl, manuscript in preparation), NADPH dehydrogenase and reduced flavins (W. R. Strohl, manuscript in preparation), and a CO*binding o-type cytochrome (117,118; W. R. Strohl, manuscript in preparation) have also been observed in Beggiatoa strains. Thus, the heggiatoas, including one strain previously reported to	[redacted]	

have no cytochrome (14), appear to have a full complement of respiratory chain components. Respiration studies nave united tne oxidation of several trichloroacetic acid cycle intermediates (98; G. W. Luli, W. R. Strohl, unpublished data) as well as pyruvate (W. R. Strohl, unpublished data) and acetate (112) to the electron transport system.

The oxidation of Na235S to 35S° and sulfide-dependent oxygen consumption by B. alba B18LD were inhibited by the electron transport inhibitors 8-hydroxyquinoline, 1,10-o-phenanthroline, 2-/i-heptyl-4-hydroxyquinoline-N- oxide (HOQNO), cyanide, and azide, suggesting that a sulfide respiration system is present in that strain (117, 118; W. R. Strohl, manuscript in preparation). The presence of sulfide caused a marked decrease in the rate of acetate oxidation (112) and approximately a twofold increase in growth yield in continuous cultures (34). All of these features meet the requirements suggested (76) as criteria for mixotrophy of Beggiatoa and support the view that mixo- trophic strains of Beggiatoa exist (34, 115).

Different strains of Beggiatoa may use sulfide for different

purposes. Some may use sulfide for biosynthetic purposes, although this has not been suggested for any specific strain. The strains used by Morita and co-worker (14, 15, 73) and by Nelson & Castenholz (76) may have used sulfide to detoxify the environment by removing peroxides.

However, in the former studies the strain was incorrectly thought to lack an electron transport system, and the latter authors assumed, but did not demonstrate, that their strain produced peroxide. The strains isolated by Strohl & LaTkin (115) appear to use sulfide for energy production and thus come the closest to fulfilling Winogradsky's (126, 128) original concept of Beggiatoa. Additionally, the oxidation of sulfide may help to maintain a proper redox equilibrium for microaerophilic growth (111). The work of Nelson & Castenholz (76) suggests the possibility that stored sulfur can be used as an electron acceptor to allow anaerobic respiration of Beggiatoa and perhaps allow anaerobic growth.

carbon and nitrogen metabolism

A central issue of Beggiatoa physiology is its, utilization of carbon compounds (112, 124). Most beggiatoas can grow with acetate as the sole added carbon

source (15, 28, 52, 77, 78, 87, 91, 115). Several others can grow on lactate (69, 77, 87), pyruvate (69, 87), ethanol (69,77), and several C-4organic acids (14, 69, 87); none can grow on C-5 or C-6 organic acids or on hexose sugars (64, 69, 87). If Beggiatoa is autotrophicas suggested (48, 52, 127), or if it is a cyanobacterium that has lost its chlorophyll (84, 93, 94), it should fix large amounts of CO2 (77, 112, 124), predictably by either the Calvin-Bensen or the serine cycles (112), or perhaps by the reductive citric acid cycle (24).

An examination of B. leptomitiformis (15) showed that C02 was fixed via a reversal of the isocitrate dehydrogenase reaction, one step of the reductive citric acid cycle. However, four other enzymes [aconitase, fumarase, phos-phoenolpyiuvate (PEP) carboxylase, and a-ketoglutarate synthase] important to the reductive citric acid cycle were not observed. An unusual and unsatisfying biosynthetic cycle for acetate and C02 utilization was postulated from these results (15). Three of the four enzymes missing inB. leptomitiformis were found to occur inB, alba, but in such low activities as to require very sensitive assays with l4C-

labeled substrates (W. R. Strohl, manuscript in preparation). The fourth missing enzyme was present in B. alba in greater amounts (W. R. Strohl, manuscript in preparation). Thus, a reexamination of the metabolism of B. leptomitiformis should be undertaken. B. alba B18LD fixes C02 via an NADPH-linked malic enzyme and by isocitrate dehydrogenase (reversed) activities, but not by ribulose-1,5- bisphosphate carboxylase, PEP carboxylase, pyruvate carboxylase, or a-ketoglutarate synthetase (112). Thus, it appears that B. alba fixes C02 by typical heterotrophic methods and does not use autotrophic pathways. Low levels of C02 are apparently required for the growth of B. alba (112), but the amount of 14C02 fixed is too low to account for much cell carbon (77, 112). The fixation of C02 is dependent upon the presence of acetate (77, 112), and some of the C02 requirement may be met by acetate oxidation (112). Three strains each of B. alba and B. leptomitiformis oxidized 16-18% of the C-2 and 2S-A9% of the C-l carbons of acetate to C02 (W. R. Strohl, manuscript in preparation).	[redacted]	

The available data indicates that B. alba B18LD (W. R. Strohl, manuscript in preparation) and perhaps other Beggiatoa strains (77, 124) have normal citric acid and glyoxylate cycles for their intermediary metabolism.

Ammonia is used as a nitrogen source by every Beggiatoa strain isolated to date. An increase in growth yield of B. alba B18LD in the presence of excess

Figure 1 Beggiatoa and chemolithotrophy.
Drawings made by Winogradsky of Beggiatoa and translation {from the French) oi the legend accompanying these figures. "Fig. I. The tip of a filament of Beggiatoa alba, (a) in sulfurous ¡sulfide-containing! water, (b) after 24 h in water nearly depleted in H2S. (cI after 48 h in water without H2S [note depletion of sulfur globules with time]. Fig. 2. The tip of a filament of Beggiatoa media. Fig. 3. The lip of a filament of Beggiatoa minima." From Winogradsky. S. 1949. Mtcrobiologie du Sol. Masson. Paris.

• Figure 17.26 Sulfur bacteria, (a) Deposition of internal sulfur granules by Beggiatoa. (b) Attachment of the sulfur-oxidizing archaeon

Sulfolobus acidocaldarius to a crystal of elemental sulfur. Cells are visualized by fluorescence microscopy after staining them with the dye acridine orange. The sulfur crystal does not fluoresce. See Figure 17.27 for how sulfide and sulfur are oxidized to yield ATP. • Figure 17.27 Oxidation of reduced sulfur compounds by sulfur chemolithotrophs. (a) Steps in the oxidation of different compounds. The sulfite oxidase pathway accounts for the majority of sulfite oxidized. |b) Electrons from sulfur compounds feed into the electron transport chain to drive a proton motive force; electrons from thiosulfate and elemental sulfur enter at the level of cytochrome c. NADH must be made by energy-consuming reactions of reverse electron flow since the electron donors have a more electropositive E0' than does NAD'/NADH. Cyt, cytochrome; FP, flavoprotein; Q. quinone. For the structure of APS. see Figure 17.38. ……. ……..	[redacted]	

was depleted, the granules disappeared and sulfate appeared in the medium (126, 128).

Using spring water and a defined atmosphere with partial pressures of hydrogen sulfide, oxygen, carbon dioxide, and nitrogen, Keil (48) probably obtained pure cultures of *Beggiatoa*. However, the claim that his strains were autotrophic have gone unsubstantiated (88, 89), and Pringsheim (Keil's professor) later questioned the validity of the results, stating that Keil's "technique was too clumsy for comparative experiments and suffered from the fact that the conditions in the culture fluid were rather obscure" (89). Keil tried but was unable to grow his beggiatoas heterotrophically, perhaps because he used very rich organic media containing high concentrations of glucose and/or peptone. We know today that beggiatoas generally do not grow in such media (19, 28).

Bavendamm (6) did not isolate *Beggiatoa* or *Thiothrix*, contrary to what has sometimes been stated in the literature (52, 124). He did obtain enrichments of both organisms, but he stated that he was then satisfied with Keil's observations and he went no further with his isolations. Another claim of the isolation and growth of *Beggiatoa* in autotrophic culture (52) was later retracted (88, 89), and it is doubtful that autotrophic beggiatoas have yet been isolated.

Cataldi (19) was the next to isolate a strain of *Beggiatoa*. It grew heterotrophically and deposited sulfur but could not grow autotrophically. All beggiatoas isolated since then have been capable of heterotrophic growth, and most could deposit sulfur (11, 28, 52, 76, 87, 98, 115). A few isolates lack the ability to deposit sulfur and may be genetic or physiological variants of *Beggiatoa* that have lost the ability to oxidize sulfide (70). This loss could occur if the genetic

acetate was linear with concentrations of 0.1–2.0 mM ammonium ion—10 mM ammonium and above was toxic. With a low ammonium concentration (0.1 mM), glutamine synthetase and glutamate synthetase were active but glutamate dehydrogenase was inactive (122). With a high ammonium concentration (2.0 mM), glutamate synthase was very active, glutamate and alanine dehydrogenases had low activities, and glutamine synthetase activity was absent. (112).

Early reports indicated that *Beggiatoa* could not use nitrate as a nitrogen source (48, 122), but recent evidence indicates that some strains may use nitrate (79, 122) or nitrite (A. Vargas, W. R. Strohl, unpublished data) as sole nitrogen sources. Glutamate, aspartate, and asparagine can be used as sole nitrogen, carbon, and energy sources by some beggiatoas (87). However, glutamate cannot be used as a sole carbon source by *B. alba* B18LD, and it is a poor nitrogen source for that strain; glutamate may be used as an energy source by *B. alba* B18LD (122).

THIOTHRIX

Taxonomy

The first description of the organism we now know as *Thiothrix* was made in

Acctate phụ thuộc tuyến tính vào nồng độ 0.1-2.0 mM ion amoni-10 mM amoni và trên giá trị này là ngưỡng độc hại. Với nồng độ amoni thấp (0.1 mM), glutamine synthetase và glutamate synthetase hoạt động nhưng glutamate dehydrogenase không hoạt động (122). Với nồng độ amoni cao (2.0 mM), glutamate synthetase rất hoạt động, glutamate và alanine dehydrogenase có hoạt tính thấp, hoạt tính glutamine synthetase không xuất hiện.

Các báo cáo gần đây chỉ ra rằng Beggiatoa không thể dùng nitrat như một nguồn nitơ (48,122), nhưng những bằng chứng gần đây cho thấy rằng một số dòng có thể sử dụng nitrat (79,122) hoặc nitrit (A Vargas, W.R.Strohl, dữ liệu không xuất bản) như một nguồn ni tơ duy nhất. Glutamate, aspartate, và asparagine có thể được sử dụng như các nguồn nitơ, cacbon và năng lượng duy nhất bởi một số beggiatoa (87). Tuy nhiên, glutamate không thể được sử dụng như một nguồn các bon duy nhất bởi B.alba B18LD, và nó là một nguồn nitơ nghèo đối với dòng đó; gluatamate có thể được sử dụng như một nguồn năng lượng bởi B.alba B18LD (122).

THIOTHRIX

Phân loại

Mô tả đầu tiên về sinh vật này hiện nay được gọi là….