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THE GEOLOGIC IMPORTANCE OF THE LIME-SECRETING ALGAE

WITH A DESCRIPTION OF

A NEW TRAVERTINE-FORMING ORGANISM

BY

MARSHALL A. HOWE

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THE GEOLOGIC IMPORTANCE OF THE LIME-SECRETING ALGAE
WITH A DESCRIPTION OF A NEW TRAVERTINE-FORMING ORGANISM

By MARSHALL A. HOWE

The agency of microscopic algae, especially blue-green algae, in depositing lime in calcareous hot springs and calcareous streams has long been recognized. Ferdinand Cohn¹ was one of the first to investigate the matter in a scientific way, in studying the deposits in the famous hot springs of Carlsbad, in Bohemia.

In America, in 1889, Walter Harvey Weed,² then a member of the United States Geological Survey, published a striking report on the formation of travertine and siliceous sinter by the vegetation of hot springs, with special reference to the remarkable conditions found in the Yellowstone National Park. The deposits of most of the springs in that region are "siliceous sinter," but the extensive one of the Mammoth Hot Springs, covering a total area of about 2 square miles and having a maximum depth of about 250 feet, consists chiefly of calcium carbonate or "travertine," partly precipitated in a mechanical way, but probably to a much larger degree by the action of microscopic algae. The waters of the Mammoth Hot Springs carry a saturated or supersaturated solution of calcium bicarbonate, and much of the lime is deposited by the evaporation and cooling of the water. Yet much or most of what geologists call "travertine" at the Mammoth Hot Springs, as has been demonstrated macroscopically and microscopically by Weed and others, is due to the action of the abundantly present algae or their chlorophyll in consuming or decomposing the CO₂ that is present in the water and thus reducing the amount of calcium bicarbonate that may be held in solution. The precipitated lime is a by-product of the photosynthesis of the little plants. And the same process evidently goes on in both fresh and salt water in which calcium bicarbonate is dissolved in much less than saturation proportions.

In 1895 George Murray³ published critical notes on calcareous pebbles formed by algae, based on material from a pond in Michigan separated from Lake Michigan by a sand bar. Murray found that these pebbles

had been built up by a mixture of blue-green algae, of which the predominating kind was *Schizothrix* (*Inactis*) *fasciculata* (Naegeli) Gomont, as determined by the eminent authority Gomont. However, Gomont⁴ describes the trichomes of *S. fasciculata* as 1.4 μ to 3 μ in diameter, while Murray's figures, according to the magnifications indicated, show trichomes 2.5 μ to 8 μ in diameter. Murray mentions *Dichothrix* as intermingled with his *Schizothrix*, and it seems possible that some of his figures represent *Dichothrix* rather than *Schizothrix*.

In 1897 Josephine E. Tilden⁵ described some new species of Minnesota algae which live in a calcareous or siliceous matrix. Most of the algae formed crusts of various colors, with a maximum thickness of 1 centimeter, on the sides of a large wooden tank on the bank of the Mississippi River. New species were described in the genera *Dichothrix*, *Lyngbya*, *Schizothrix*, and *Chaetophora*, the last a green alga, the others blue-green. An examination of specimens distributed by Professor Tilden indicates the presence also of the plant that is now referred to *Inactis pulvinata* Kützing. It may be the same as the *Lyngbya nana* Tilden, the filaments of which are described as only 1.9 μ in diameter.

In 1900 John M. Clarke,⁶ State paleontologist of New York, published a brief illustrated paper on the water biscuit of Squaw Island, Canandaigua Lake, N. Y. Doctor Clarke states:

The north shores of Squaw Island and the lake bottom about it and over its northward sand bar are covered with flat, whitish calcareous cakes of circular or oval shape, in size ranging from a dime to a half dollar. To pick up one of these, well dried on the surface of the island, and break it in half, seems enough to convince the reflective mind at once of their nature and mode of formation. It often contains as a central nucleus a beach pebble of shale or limestone, a twig, or a bit of charcoal from some youngster's campfire. About this a white or greenish travertine has been deposited in concentric layers, which show themselves with distinctness. * * * On picking one of the water biscuits

¹ Ueber die Algen des Carlsbad Sprudels, mit Rücksicht auf die Bildung des Sprudelsinters: Schlesische Gesell. vaterl. Cult. Abh., Abt. Naturwiss. u. Medicin, 1862, Heft 2, pp. 35-55.

² U. S. Geol. Survey Ninth Ann. Rept., pp. 619-676, pls. 78-87, figs. 52-56, 1889.

³ Phycological Memoirs, pp. 74-77, pl. 19, 1895.

⁴ Monographie des Oscillariées: Ann. sci. nat., Bot., 7th ser., vol. 15, p. 299, 1892.

⁵ Bot. Gaz., vol. 23, pp. 95-104, pls. 7-9, 1897.

⁶ New York State Mus. Bull., vol. 8, pp. 195-198, pls. 13-15, 1900; New York State Mus. 54th Ann. Rept., vol. 3, pp. 195-198, pls. 13-15, 1902.

from the lake bottom, its surface is found to be smooth, slimy, and often greenish; exposure on the shore bleaches it white. The calc-carbonate being dissolved in dilute acid and entirely removed, there remains a soft, spongy organic residuum of precisely the volume of the original biscuit.

C. H. Peck, the State botanist, to whom specimens were submitted, reported that the felted mass was made up of several kinds of fresh-water algae and diatoms. He identified one of the species as "probably *Isa[c]tis fluviatilis*."

In 1903 C. A. Davis,⁷ after the appearance of three shorter papers with similar titles, published a "contribution to the natural history of marl," based chiefly on studies of vast deposits of calcium carbonate in Michigan lakes, which form the basis of the cement industry in that State. In connection with the origin of these extensive accumulations of lime, he ascribes great importance to the green algal genus *Chara*, though admitting that blue-green algae are largely concerned in forming both the massive beds of lake tufa and concentric calcareous pebbles.

The importance of certain lime-secreting marine algae in the building of so-called "coral reefs" has received increasing attention and emphasis since the publication by the Royal Society of London, in 1904, of a large quarto work on Funafuti,⁸ which was selected for this study because it was considered to be a "typical coral" reef or island. Several borings were made here by members of three successive expeditions. The main boring was finally driven down to a depth of more than 1,100 feet. The cores thus obtained were brought back to England for study and analysis. A. E. Finckh, who wrote the chapter on the biology of reef-forming organisms at Funafuti, groups the various lime-secreting organisms at Funafuti in order of their reef-building importance as follows:

1. *Lithothamnium*,⁹ by which Finckh means stone-like, unsegmented, branched or crustaceous red algae (Rhodophyceae) of the family Corallinaceae. These calcareous plants are commonly referred to by geologists and zoologists, and occasionally by botanists, as "nullipores."

2. *Halimeda*. This is a genus of lime-secreting green algae (Chlorophyceae) of the family Codiaceae. It includes several species, of which *Halimeda opuntia* appears to be the one that occurs in most abundance. All are of macroscopic dimensions. Species of *Halimeda* are confined to the warmer seas, while representatives of the *Lithothamnium* group occur in local profusion in Arctic waters also.

3. Foraminifera. Recent studies by T. Wayland Vaughan and J. A. Cushman have emphasized the geologic importance of this group of microscopic animals.

4. Corals. There are doubtless "true coral reefs" and islands that have been actually built in a predominant way by corals, but Funafuti is evidently not one of them.

That Funafuti is not an isolated example of the building of reefs by plants rather than by animals is attested by the observations of Finckh, Gardiner, Setchell, and others. Gardiner¹⁰ remarks that "the importance of the incrusting nullipores in the formation of the reefs of the central Pacific can not be overestimated." Again,¹¹ in discussing the foundation of atolls in general, Gardiner says:

The chief building organism is *Lithothamnium*, the bathymetrical zone of which must be limited to a large degree by the extent to which light can penetrate sea water.

In another publication¹² Gardiner says:

This nullipore [*Porolithon craspedium*], Finckh says, is actually the reef former at Onoatua [Gilbert Islands]. He saw no live coral there, but everywhere on the lagoon and ocean face immense masses of this particular nullipore.

That lime-secreting plants rather than corals are sometimes, at least, the dominant reef formers in the Indian Ocean as well as in the Pacific is attested by the following observation by Gardiner:¹³

The reefs of the Chagos are in no way peculiar save in their extraordinary paucity of animal life. * * * However, this barrenness is amply compensated for by the enormous quantity of nullipores (*Lithothamnia*, etc.), incrusting, massive, mammillated, columnar, and branching. The outgrowing seaward edges of the reefs are practically formed by their growths, and it is not too much to say that, were it not for the abundance and large masses of these organisms, there would be no atolls with surface reefs in the Chagos.

Mme. Dr. A. Weber-van Bosse¹⁴ describes and publishes photographs of extensive *Lithothamnium* banks near the southwest point of Timor, in the Dutch East Indies.

In 1921 Mayor,¹⁵ writing of Rose Atoll, American Samoa, states that

There are a few fossil corals, chiefly *Pocillophora*, embedded in the rock of the atoll rim and the boulders, but the whole visible rock of the atoll consists so largely of *Lithothamnium* that we may call it a "*Lithothamnium* atoll" rather than a "coral atoll."

⁷ Michigan Geol. Survey, vol. 8, pt. 3, pp. 65-96, 1903.

⁸ The atoll of Funafuti—borings into a coral reef and its results, being the report of the coral-reef committee of the Royal Society.

⁹ This is the original and now commonly used spelling of the generic name that has often appeared in print as *Lithothamnton*. In the broad sense in which the name is employed by Finckh, it is doubtless intended to include species that would now be referred not only to *Lithothamnium* but also to *Lithophyllum*, *Porolithon*, *Goniolithon*, etc. These are all plants of considerable size.

¹⁰ Gardiner, J. S., The coral reefs of Funafuti, Rotuma, and Fiji, together with some notes on the structure and formation of coral reefs in general: Cambridge Philos. Soc. Proc., vol. 9, p. 477, 1898.

¹¹ Idem, p. 501.

¹² Gardiner, J. S., The fauna and geography of the Maldives and Laccadive Archipelagoes, vol. 1, p. 462, 1901.

¹³ Quoted by Foslie, M., The Lithothamnia: Linnean Soc. London Trans., Zoology, 2d ser., vol. 12, pp. 177, 178, 1907; The Percy Sladen expedition in H. M. S. *Sealark*: Nature, vol. 72, pp. 571, 572, where a photograph of this *Lithothamnium* reef is published.

¹⁴ Siboga-Exped. Mon. 61, p. 4, 1904.

¹⁵ Mayor, A. G., Am. Philos. Soc. Proc., vol. 60, p. 67.

Setchell,¹⁶ who has made several visits to the South Sea Islands, largely for the purpose of studying the reefs, has in a succinct paper summed up the present status of our knowledge of the origin of so-called "coral reefs" in part as follows:

In closing his article on the building of coral reefs Howe¹⁷ says: "Much evidence has accumulated tending to show that the importance of corals in reef building has been much overestimated and that final honors may yet go to the lime-secreting plants." It seems to me that the final honors can now be bestowed, and, without minimizing the contributions of the corals, there may be added:

1. That without nullipores no "coral reefs" can be or would have been formed.

* * * * *

5. That the animal components of the reef of next importance after the nullipores are the various incrusting species, especially of *Polytrema*, a genus of Foraminifera.

Later James B. Pollock,¹⁸ in a paper on the fringing and fossil reefs of Oahu, states that

The organisms chiefly contributing calcium carbonate to both fossil and fringing reefs are corals and coralline algae. The algae contribute more than the corals. The algae are called by the general name of *Lithothamnium*.

Calcareous algae of the coralline group occur as well-preserved fossils in limestone rock of Tertiary and Quaternary strata. There is evidence¹⁹ that the *Lithothamnium* structure may become gradually obliterated, perhaps by the action of percolating water, resulting in a structureless limestone.²⁰ In America beautifully preserved fossils of the *Lithothamnium* group have been described and figured by the present writer²¹ from Oligocene and Pleistocene strata of the Panama Canal Zone, from the Eocene of St. Bartholomew, the middle Oligocene of Antigua, the upper Oligocene of Anguilla, and the lower Miocene of Trinidad. *Lithothamnium jurassicum* Gümbel²² has been described from the Jurassic of Switzerland, and the more or less doubtful *Lithothamnium? ellisianum* Howe and Goldman²³ from the Jurassic Ellis formation of Montana. *Archaeolithothamnium marmoreum* (Munier-Chalmas) Foslie and *Lithophyllum belgicum*

Foslie²⁴ have been currently referred to the Calcaire Carbonifère of Namur, Belgium, but Mme. Lemoine has shown that *L. belgicum* came in reality from the Aptian (Cretaceous) of the French Pyrenees.²⁵

Fossil organisms of Silurian and Cambrian origin that have been described under the generic name *Solenopora* have usually been referred to the coralline algae, but in the writer's opinion the Ordovician type of the genus does not belong in this family, if it is, in fact, an alga. However, there can be no serious doubt that Urganian and Jurassic fossils more recently placed under *Solenopora*²⁶ are true algae, closely related to *Lithothamnium*.

Although rhodophyceous algae of the coralline (*Lithothamnium*) group may not be of great antiquity, in a geologic sense, algae of a lower group, the Myxophyceae (or Cyanophyceae), more popularly referred to as the "blue-green algae," were probably among the first forms of life. There is superficial evidence that many, at least, of the most ancient limestones, of Cambrian and pre-Cambrian age, were laid down by the agency of these blue-green algae and that in mass production of limestone these lowly organisms were much more active than they are at the present time. The existence of several kinds of blue-green algae in hot springs²⁷ shows their adaptation to the higher temperatures that doubtless prevailed in the earlier stages of the development of life on the earth.

The blue-green algae are always of colonial habit. The individuals are of microscopic size, and individuality is often poorly defined, but the colonial masses of the present age are commonly of macroscopic dimensions, and in the geologic past such masses apparently helped to make deposits of lime that are now conspicuous features of extensive geologic formations. It is to be freely conceded, however, that no one of these supposed algal limestones of Cambrian or pre-Cambrian age, when examined microscopically, either decalcified or in ground section, shows any incontestable evidence of an algal nature. In view of the extreme age of these supposed plants and the extreme delicacy of the gelatinous cell walls of the Myxophyceae, even when more or less calcified, it seems unreasonable to expect any preservation of their microscopic cell structure. The firm, always strongly calcified cell walls of the Lithothamnieae, so perfectly

¹⁶ Setchell, W. A., Nullipore versus coral in reef formation: Am. Philos. Soc. Proc., vol. 65, pp. 136-140, 1926.

¹⁷ Howe, M. A., Science, new ser., vol. 35, pp. 837-842, 1912.

¹⁸ Bernice P. Bishop Mus. Bull. 55, pp. 1-56, pls. 1-6, 1928.

¹⁹ Seward, A. C., Algae as rock-building organisms: Sci. Progress, vol. 2, pp. 10-26, 1894.

²⁰ Walther, J., Die gesteinsbildenden Kalkalgen des Golfes von Neapel und die Entstehung structurloser Kalke: Deutsch. Geol. Gesell. Zeitschr., Bd. 37, 1885. See also Science, vol. 7, pp. 575, 576, 1886.

²¹ Howe, M. A., On some fossil and recent Lithothamnieae of the Panama Canal Zone: U. S. Nat. Mus. Bull. 103, pp. 1-13, pls. 1-11, 1919; Tertiary calcareous algae from the islands of St. Bartholomew, Antigua, and Anguilla: Carnegie Inst. Washington Pub. 291, 1919; Two new Lithothamnieae, calcareous algae, from the lower Miocene of Trinidad, British West Indies: U. S. Nat. Mus. Proc., vol. 62, art. 7, pp. 1-3, pls. 1-4, 1922.

²² Gümbel, C. W., Die sogenannten Nulliporen: K. bayerisch. Akad. Wiss., Math.-phys. Klasse, Abh., vol. 11, Abt. 1, p. 43, pl. 2, figs. 9a, 9b, 1871.

²³ Howe, M. A., and Goldman, M. I., Am. Jour. Sci., 5th ser., vol. 10, pp. 314-324, figs. 1-11, 1925.

²⁴ Foslie, M., Remarks on two fossil Lithothamnia: K. Norske Vidensk. Selsk. Skr., 1909, No. 1, pp. 3-5.

²⁵ Lemoine, Mme. Paul, Contribution à l'étude des Corallinacées fossiles, VIII, Mélobésiées de l'Aptien et de l'Albien: Soc. géol. France Bull., 4th ser., vol. 25, pp. 5-6, 1925.

²⁶ Pfender, J., Sur la présence d'une Solénopore dans l'Urganien du sud-est de la France—*Solenopora urgoniana*, n. sp.: Soc. géol. France Bull., 4th ser., vol. 30, pp. 101-105, pl. 8, 1930; Les Solénopores du Jurassique supérieur en Basse-Provence calcaire et celles du Bassin de Paris: Idem, pp. 149-164, pls. 16-19.

²⁷ Setchell, W. A., The upper temperature limits of life: Science, new ser., vol. 17, pp. 934-937, 1903.

preserved in various Tertiary and Quaternary strata, are in a very different category. In the calcareous travertine or tufa now being laid down by various blue-green algae in lakes and streams in the United States, it is commonly difficult to demonstrate and identify the contributing organisms except in the superficial layers. Why should one expect their delicate structure to persist for millions of years? Nevertheless, one who is accustomed to see and to handle the algae of the present day may feel convinced from their macroscopic characters that certain laminated ancient limestones were laid down by algae, even while admitting more or less subconsciously the possibility of being deceived.

In Great Britain the writings of A. C. Seward²⁸ and E. J. Garwood²⁹ have emphasized the geologic importance of the algae, though Seward is dubious as to the algal nature of so-called organisms referred to the genus *Cryptozoon* and of the Algonkian limestones described and figured by Walcott. The literature relating to the geologic significance of the algae is becoming extensive, and it is not the writer's purpose to attempt any complete review of it at this time. A valuable bibliography of the subject, even though notably incomplete in its American references, is given by J. Pia.³⁰

In the United States, in 1913, Eliot Blackwelder³¹ made a notable contribution to the subject, in which he published photographs showing a remarkable resemblance of deposits of Ordovician dolomite to modern reefs of calcareous algae of the *Lithothamnium* group. The probability of calcareous algae having something to do with the formation of magnesian limestone and dolomite is heightened by chemical analyses³² of various lime-secreting marine organisms, showing high percentages of magnesium carbonate in the lithothamnioid algae, whereas the madreporian corals are notably deficient in magnesium. A similar inference may be drawn from the biologic and chemical analyses of the borings at Funafuti, to which reference has already been made. Clarke and Wheeler³³ have already stated that

In short, all the evidence goes to prove the importance of the algae as limestone builders and the subordinate character of the corals. This importance is now fully recognized by students of marine limestones and by paleontologists generally.

²⁸ Op. cit.; Fossil plants, pp. 122, 123, 1898; The earlier records of plant life: Geol. Soc. London Proc., vol. 79, pp. lxxi-civ, 1923; Plant life through the ages, 1931.

²⁹ On the important part played by calcareous algae at certain geological horizons: Geol. Mag., new ser., dec. 5, vol. 10, pp. 440-446, 490-498, 545-553, 1913; Nature, vol. 92, pp. 111-121, Sept. 25, 1913.

³⁰ Geologisches Alter und geographische Verbreitung der wichtigsten Algengruppen: Oester. Bot. Zeitung, Band 73, pp. 174-190, 1924.

³¹ Origin of the Bighorn dolomite of Wyoming: Geol. Soc. America Bull., vol. 24, pp. 607-624, pls. 28-35, 1913.

³² See Clarke, F. W., and Wheeler, W. C. The inorganic constituents of marine invertebrates: U. S. Geol. Survey Prof. Paper 102, 1917. Pages 44-50 are devoted to analyses of calcareous Rhodophyceae and Chlorophyceae, none of which are properly "invertebrate."

³³ Op. cit., p. 54.

In 1914 G. R. Wieland,³⁴ accepting the various species of *Cryptozoon* as algae, refers to the pre-Cambrian, Cambrian, and Ordovician ages as characterized by the "reign of algae" and adds:

Nor does it even seem too much to say that no dominant organisms of later ages, whether plant or animal, ever exceeded the Paleozoic seaweeds or left a bulkier record.

A little later in 1914 Charles D. Walcott, distinguished Secretary of the Smithsonian Institution, published his striking paper on pre-Cambrian Algonkian algal flora,³⁵ in which he takes the ground that the extensive (nonmarine?) magnesian limestones of Algonkian age (chiefly in the Belt Mountains of Montana) were laid down by algae of the blue-green group, much as deposits of lime are now being made, on a smaller scale, by blue-green algae in fresh-water streams, ponds, and lakes in various parts of the United States. Walcott gave several new generic and specific names to these supposed fossil algae, although there seems to be scarcely any definitely conclusive evidence in their microscopic structure that these formations are due to algae at all. However, from their general macroscopic characteristics it seems probable to the present writer that some, perhaps most, of these new generic names were applied to real algae or to their very ancient forerunners. The magnitude of some of these limestone deposits is indicated by Walcott's remark that "in the Camp Creek section of Montana *Collenia* was found to range up through 2,500 feet (760 meters) of strata."³⁶ There are also extensive deposits of Algonkian limestones in Arizona, in the Grand Canyon of the Colorado. The study of the supposed fossil algae of that region, begun by Walcott and by Dawson, is being continued by David White.³⁷

E. S. Moore³⁸ has directed attention to massive strata of ancient presumably algal limestones, more or less silicified, on the Belcher Islands, Hudson Bay, and the adjacent mainland. These strata attain a thickness of 428 feet and are considered to be of pre-Cambrian age. The contributing organism shows concentric layers, somewhat as in the *Cryptozoon proliferum* from the Cambrian of Saratoga County, N. Y., and the *Collenia frequens* from the pre-Cambrian of Meagher, Mont. Professor Moore has found³⁹ similar calcareous concretions in pre-Cambrian rock from the vicinity of Port Arthur, Ontario.

³⁴ Further notes on Ozarkian seaweeds and oolites: Am. Mus. Nat. Hist. Bull., vol. 33, pp. 237-260, Apr. 14, 1914.

³⁵ Smithsonian Misc. Coll., vol. 64, pp. 77-156, pls. 4-23, July 22, 1914.

³⁶ Idem, p. 98.

³⁷ Study of the fossil floras of the Grand Canyon, Arizona: Carnegie Inst. Washington Yearbook Nos. 26, 27, 28, and 29; Algal deposits of Unkar Proterozoic age in the Grand Canyon, Arizona: Nat. Acad. Sci. Proc., vol. 14, No. 7, pp. 597-600, 1928.

³⁸ The iron formation on Belcher Islands, Hudson Bay, with special reference to its origin and its associated algal limestones: Jour. Geology, vol. 27, pp. 412-438, 1918.

³⁹ Letters of April 10 and April 26, 1924.

A very important recent contribution to the literature of algal reefs is W. H. Bradley's beautifully illustrated paper on algal reefs and oolites of the Green River formation.⁴⁰ These reefs and beds are of the Eocene epoch and they show manifest algal structure, microscopically as well as macroscopically. Bradley identifies the dominant alga as *Chlorellopsis coloniata* Reis, originally described in 1923 from the Miocene lake beds of the Rhine Valley. The limestone beds formed by these algae in the Green River region of Wyoming, Colorado, and Utah are locally as much as 18 feet thick.

The deposition of lime in Green Lake, near Kirkville, N. Y., a few miles east of Syracuse, has been referred to by C. D. Walcott⁴¹ and W. H. Bradley.⁴² Walcott published photographs illustrating the external appearance of the deposits and sections, without magnification. Bradley illustrated the gross appearance (op. cit., pl. 29, B) and sections under low magnifications (op. cit., pl. 30, A, B). He also ventured to name the various algae that are disclosed by dissolving out the calcium carbonate. "Of these," he says, "*Microcoleus* [*paludosus* Kützing], by reason of its greater bulk, predominates, yet the minute cells and colonies of *Palmella* are vastly more numerous. *Palmella* cells are probably the unidentified 'rounded or oval, very small cells' that C. A. Davis referred to in his notes on the lime deposits of Green and Round Lakes, N. Y., published in Walcott's description of some pre-Cambrian algal deposits."

The writer has examined excellent material of this calcareous deposit collected in Green Lake by William R. Maxon October 21, 1914. The mass, or its surface, is distinctly blue-green, and several species and genera of Myxophyceae are represented in it and on it. The dominant form appears to be a filamentous one, much more delicate than *Microcoleus paludosus* mentioned by Bradley, having trichomes only 1μ to 2μ broad; it is coarser, more entangled, less compacted, less erect than the similar plant from Furnace Creek, W. Va., that is referred below to *Inactis pulvinata* Kützing. It is probably to be identified with *Inactis fasciculata* (Naegeli) Grunow [= *Schizothrix fasciculata* (Naegeli) Gomont], which is normally a lime precipitator. Associated with it are species of *Gloeocapsa*, *Gloeotheca*, and *Aphanocapsa*, and very numerous minute brownish or nearly colorless cells which appear to be identical with the organism described on page 63 as new from Furnace Creek, near Harpers Ferry, W. Va. These may well be the "rounded or oval, very small cells" mentioned by C. A. Davis.

A most important contribution to the field of the present paper was made in 1915 by H. Justin Roddy,⁴³ who described the calcareous concretions of Little Conestoga Creek, in Lancaster County, Pa., from the points of view of both botanist and geologist. In his introduction he states:

My search was amply rewarded by finding them [concretions] in great quantities and distributed throughout nearly the entire length of the Little Conestoga. I found also that they not only occur in the creek itself, but that quite large deposits of the concretions underlie the flood-plain meadows along the creek banks. One of these, in Kendig's Woods, 2 miles southwest of Millersville, Pa., is made up wholly of concretionary materials on the top of which forest trees of large size and considerable age are growing. This deposit covers nearly an acre to the depth of about 8 feet in the middle, thinning out lenslike toward its edges. Another deposit along the same stream near Fruitville, in Evans's Meadow, more extensive in area but of slighter depth, forms a substratum under a thick soil cover and has an average depth of about 2 feet. * * * The concretions, both in the stream and in the deposits, vary in size from peas to masses nearly a foot in diameter.

Later Donegal Creek, another stream in the same county, was found to possess these objects in even greater abundance.

One meadow of fully 12 acres bordering the stream about 1 mile northeast of Marietta was found to be underlain with a bed of concretions not less than a foot in average thickness throughout its entire extent.

In 1918 James B. Pollock⁴⁴ published a scholarly and exhaustive paper on blue-green algae as agents in the deposition of marl in Michigan lakes. He traversed, from a more strictly botanical viewpoint, the ground previously covered by C. A. Davis, and he reached somewhat different conclusions, minimizing and localizing the importance of *Chara* and emphasizing the importance of the blue-green algae. From the calcareous incrustations on the shells of living clams, having a life span of 8 to 10 years, he estimated that the blue-green algae deposit marl at the rate of about 1 foot in thickness in 75 years.

Other known instances of the more or less manifest agency of the algae in forming limestones might be mentioned, but the above, with others that are referred to in the literature cited, may suffice for the present occasion. Evidence of the important, often dominant rôle of the algae in this connection is cumulative.

In February, 1930, David White, of the United States Geological Survey, brought to the writer concentrically laminated calcareous pebbles from Furnace Creek, a tributary of the Potomac River about $1\frac{1}{2}$

⁴⁰ U. S. Geol. Survey Prof. Paper 154, pp. 203-223, pls. 28-48, 1929.

⁴¹ Pre-Cambrian Algonkian algal flora: Smithsonian Misc. Coll., vol. 64, p. 86, pl. 4, figs. 3, 4, 1914.

⁴² Algae reefs and oolites of the Green River formation: U. S. Geol. Survey Prof. Paper 154, pp. 203-223, pls. 28-48, 1929.

⁴³ Concretions in streams formed by the agency of blue-green algae and related plants: Am. Philos. Soc. Proc., vol. 54, pp. 246-258, figs. 1-2, 1915.

⁴⁴ Michigan Acad. Sci. Ann. Rept., vol. 20, pp. 247-260, pls. 16, 17, 1918.

miles above Harpers Ferry, W. Va. He brought also, from more rapidly flowing water in the same stream, more extensive rocklike deposits of lime, of the general kind commonly known to geologists as "travertine." The first microscopic examinations of ground sections and of decalcified preparations showed a mixture of minute plants—diatoms, unicellular Chlorophyceae, unicellular and filamentous Myxophyceae (Cyanophyceae), and possibly bacteria—and, in parts exposed to rapid water, the filamentous prothallus of a *Lemanea*. In parts of the deposit there was a dominance of a minute filamentous blue-green alga, with colored parts (trichomes) only 1μ or a little more in width. These apparently belong to the genus *Inactis* (a section of *Schizothrix* of some authors) and to the species *Inactis pulvinata* Kützing, originally described from Germany in 1849, since reported from cataracts in North America, and known to form hard deposits of lime. Mixed with the more or less erect filaments of the *Inactis* and in places predominating were much coarser filaments (trichomes 6μ to 7μ in diameter) with firm, rigid sheaths; these filaments appear to be referable to *Lyngbya martensiana calcarea* Tilden, originally described from Minnesota. There are, however, wide areas of this Furnace Creek deposit that show no traces of either the *Lyngbya* or the *Inactis*, and further studies indicated that very numerous minute particles which had at first been passed over as bacteria or granules of an inorganic nature often showed in mass traces of a light blue-green or yellowish-green color. The conviction grew that they were representatives of the Myxophyceae, smaller, perhaps, than any previously known, and that they were the actively important agents in precipitating lime and in forming a kind of limestone. In the older layers of the deposit the chlorophyll doubtless vanishes, and on the lower shaded surfaces of the irregularly eroded or built-up rock in rapids its presence is difficult or impossible to demonstrate, yet, a priori, it may be assumed to be there, for lime is precipitated, and the precipitation of lime is held to be linked with photosynthetic action of chlorophyll in decomposing the CO_2 (apparently HCO_3 in this case) in the water and thus reducing the amount of calcium bicarbonate that may be held in solution.

On December 7, 1930, under the guidance of David White and Charles B. Read, of the United States Geological Survey, the writer enjoyed the privilege of visiting Furnace Creek and inspecting the deposits

in place. An extreme deficiency of rainfall during the preceding six months had left the stream very low, and the calcareous pebbles in the slower parts and the expansive calcareous travertine in the more rapid parts were readily accessible. There had been a rain (about one-third of an inch in Washington) the afternoon and evening before, and the stream was higher than the former low levels, though the water was still clear. A sample of the water, thus presumably diluted from the concentration of the preceding day, was taken to Washington by Mr. White for analysis, which showed the following constituents, in parts per million:

| | |
|----------------------|-----|
| CO_2 | 0 |
| HCO_3 | 237 |
| Iron..... | .1 |
| Mn..... | .7 |
| Ca..... | 66 |
| Total hardness..... | 255 |

In the rapids, especially in the shaded recesses, the superficial crust is conspicuously black or at least dark or rust-colored. Mr. White states (in a letter) that the lime is here associated with manganiferous iron oxides. Sections show a laminated structure, with dark layers occurring at irregular intervals, and Mr. White suggests that the deposits of iron and manganese accompany the greater concentrations of these metals in the water in seasons of drought, the year 1930, in which the deposit was very notable, being one in which the annual rainfall in the Washington region was only about half the normal.

In spite of the differences in appearance between the olive-brown, ash-colored, or subfuscous concentric pebbles of the moderately quiet water and the expanded harder black or ferruginous crusts of the rapids, the writer believes that the organism that is chiefly responsible for the precipitation is specifically the same in both situations. In the well-aerated rapids, for some reason, especially in the shaded caverns, the iron and manganese are deposited more obviously and copiously than on the pebbles of the better-lighted floor of the quiet stream. The organism seems to differ only in being browner or yellower, and this is apparently due to the presence of the darker metals.

In view of the manifest importance of this minute organism in depositing lime and the difficulty of trying to identify it definitely with previously described genera, it seems desirable to give it a new generic as well as a new specific name. Descriptions follow.

Class MYXOPHYCEAE

Family CHROOCOCCACEAE

Genus LITHOMYXA, n. gen.⁴⁵

Cells subglobose, ovoid, or short cylindrical, very minute, associated in great numbers in an extended layer, precipitating lime and forming a rocklike crust. Cell membranes soft, very inconspicuous, confluent. Cell division apparently in one direction; cells solitary, in twos, irregularly in fours, or often few or many conglobate. Chromatophore not definite; chlorophyll very little, in dark places perhaps wanting.

The genus shows points of contact with *Aphanothece*, *Aphanocapsa*, *Synechococcus*, *Synechocystis*, *Oncobyrsa*, and *Chlorogloea*. Perhaps it may be placed provisionally between *Oncobyrsa*⁴⁶ and *Chlorogloea*, from both of which it differs in the essential lack of radial arrangement of its cells. The type and only known species is described below:

Lithomyxa calcigena Howe, n. sp.

Plates 19-23

Cells mostly 0.4μ to 1.5μ long and 0.3μ to 1μ wide, before division usually about twice as long as wide,

⁴⁵ *Lithomyxa*, gen. nov. (fam. Chroococcearum, class. Myxophycearum).

Cellulae subglobosae, ovoideae, vel brevi-cylindricae, minutissimae, in strato expanso numerosissimae confertae, calce induratae, crustam lithoideam efficientes. Membranae mollissimae, valde inconspicuae, confluentes. Cellularum divisio per speciem in directionem ad unam dimensionem, cellulis solitariis, binis, irregulariter quaternis, saepe paucis, vel multis conglobatis. Chromatophora haud definita, chlorophyllo minimo, in locis obscuris forsitan carente. Genus specie *Aphanothece*, *Aphanocapsae*, *Synechococco*, *Synechocystidi*, *Oncobyrsae*, et *Chlorogloea* affine est. *Lithomyxa calcigena*, species typica.

Lithomyxa calcigena sp. nov.

Cellulis plerumque 0.4μ - 1.5μ longis, 0.3μ - 1μ latis, juvenilibus pallide aerugineo-viridibus, luteis, vel luteo-brunneis, in aetate pallescentibus, crustam duram laminatam, 1 mm. ad mult. cm. crassam, superficie sordidam, olivaceam, cineream, fuscam, vel nigram, sublaevem, verrucosam, foveolatam, scrobiculatam, irregulariter nodosam, aut plus minusve grosse mammillatam efficientibus.

In rivulo "Furnace Creek" dicto ad "Harpers Ferry" Virginiae Occidentalis: in aquis placidioribus lapillos olivaceos, cinereos, vel subfuscus concentricae laminatos; in locis obscuris in aquis rapide fluentibus crustam latam crassam fuscam vel nigram *Lithomyxa* effecit. In aquis plus rapide fluentibus cum *Inacti pulvinata* Kuetzing, *Gloeocapsae* specie, et *Lemaneae* prothallo saepe consocia est. Species lapillos laminatos quoque in rivulo "Little Conestoga Creek" dicto in comitate "Lancaster" Pennsylvaniae (J. P. Roddy legit) effecit.

⁴⁶ Kützing (Phycologia generalis, p. 172, 1843) states that *Oncobyrsa fluviatilis* Agardh, the monotype of Agardh's genus *Oncobyrsa*, which Agardh himself placed among the Diatomeae, is the same as *Inoderma lamellosum* Kützing, a member of the Chlorophyceae. If this is true, the name *Oncobyrsa* (1827) should replace *Inoderma* (1843), and the genus Myxophyceae now currently known as *Oncobyrsa* should receive a new name, which may possibly be found among its alleged synonyms. A critical examination of Agardh's type specimen of *Oncobyrsa fluviatilis* is desirable.

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the young very pale blue-green, losing color with age, forming a hard laminate crust 1 millimeter to a few or many centimeters in thickness, the surface sordid, olivaceous, ash-colored, fuscous, or black, nearly smooth, verrucose, foveolate, scrobiculate, irregularly nodose or clivulose, or coarsely mammillate.

In a stream known as Furnace Creek, a tributary of the Potomac River, $1\frac{1}{2}$ miles above Harpers Ferry, W. Va. Type in the herbarium of the New York Botanical Garden, collected by David White, Charles B. Read, and Marshall A. Howe, December 7, 1930. The technical type is considered to be one of the concentric pebbles found on the bed of the stream in rather quiet water. The more extensive and more massive, usually black or fuscous crusts found in the more rapidly moving water may be considered as deposited by the form *ferrifera*, if a distinctive name is required. This appears to differ from the type only in color (which may be looked upon as a sort of stain) and in its ability to precipitate considerable quantities of iron and manganese, which may be conditioned on its occurrence in rapidly moving, well-aerated, and perhaps well-shaded water. The same organism in different surroundings appears to have different physiological or chemical effects. In ground vertical or radiovertical sections the margin (surface) sometimes shows 2, 3, or 4 cells in an anticlinal row, but in general the cells are without order, their longer axes lying in any direction.

In the quiet water the *Lithomyxa* is often associated with Diatomaceae, Protococccaceae, and Chroococccaceae, rarely with *Inactis*. In the rapid water it is frequently found with *Gloeocapsa*, the filamentous protonema of *Lemanea*, *Inactis pulvinata* Kützing, and *Lyngbya martensiana calcarea*. The *Inactis* and *Lyngbya* sometimes occupy extended areas in more or less pure culture. Occasionally fields of the *Inactis* and *Lyngbya* and of the ferriferous form of the *Lithomyxa* meet and are sharply delimited at the line of juncture, as is often the case with crustaceous lichens. Plate 20, A, shows the black crust of the *Lithomyxa* impinging on the gray or ash-colored crust of the *Inactis* and *Lyngbya*, the line of demarcation being especially sharp at the top and bottom of the photograph and more broken in the middle.

That both iron and manganese are relatively much more abundant in the dark crusts than in the gray is shown by analyses kindly supplied by R. C. Wells, chief chemist of the United States Geological Survey. In the black crusts, in which *Lithomyxa calcigena* is the dominant organism, the analysis shows 12.3 per

cent of Fe_2O_3 and 4.5 per cent of MnO ; in the gray crust, in which *Inactis pulvinata* and *Lyngbya martensiana calcarea* are dominant, Fe^{47} is only 0.14 per cent and MnO is only 0.03 per cent.

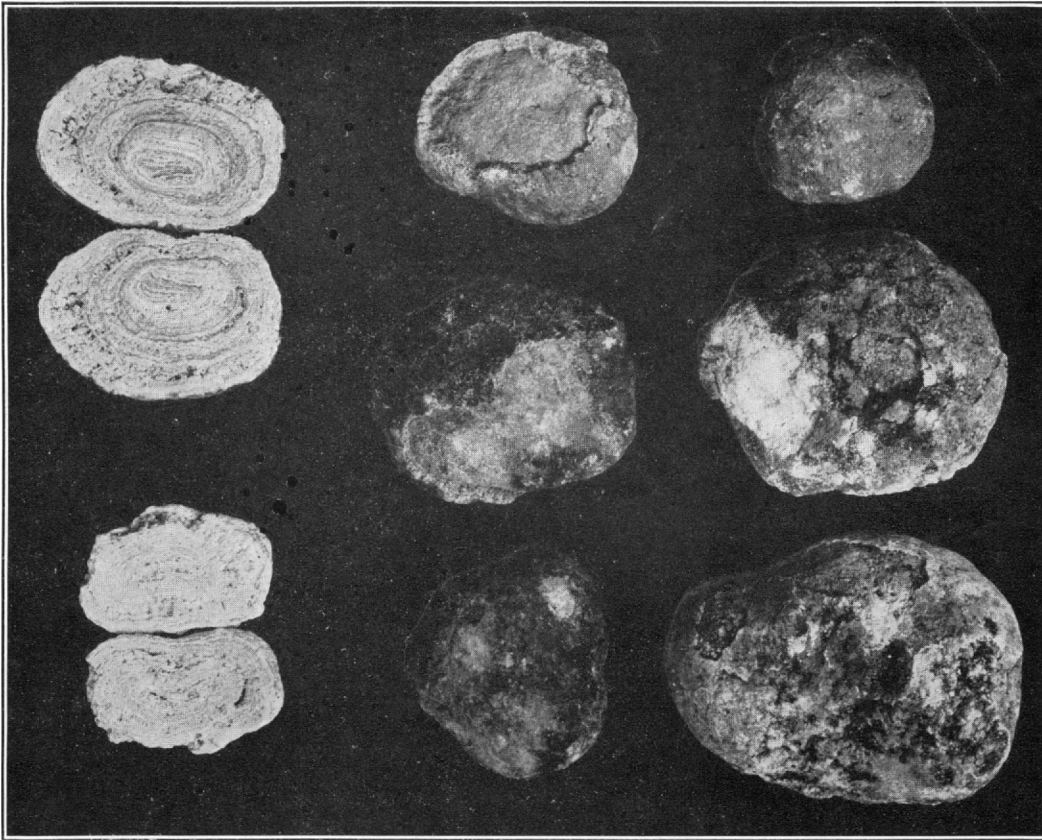
The concentrically laminated calcareous pebbles described by Roddy as occurring in two streams in Lancaster County, Pa., are evidently more abundant there than in Furnace Creek, near Harpers Ferry, W. Va.

⁴⁷Equivalent to 0.17 per cent FeO . The iron is probably in the ferrous condition, but the differentiation of ferrous and ferric iron is uncertain in the presence of organic matter.—R. C. Wells.

However, Roddy's description and published photographs and a sample pebble that he has kindly sent to the writer show that the pebbles of these two not very widely separated areas are essentially the same in physical characteristics and that they have been built up by essentially the same kinds of blue-green algae, of which *Lithomyxa calcigena* is the principal or dominant lime-precipitating organism.⁴⁸

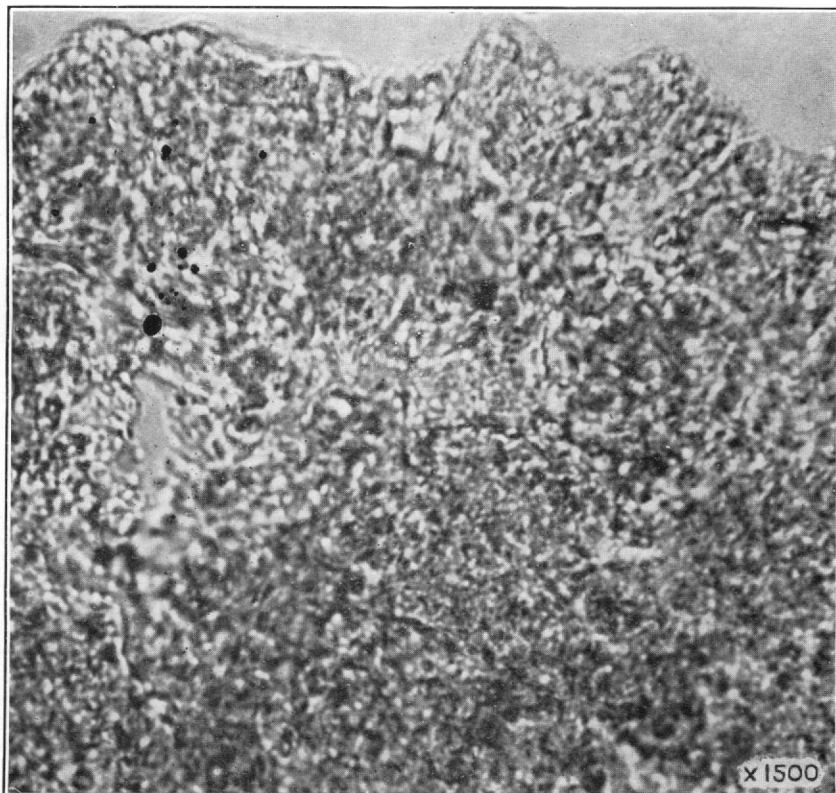
⁴⁸The above paper, in a condensed form and illustrated by lantern slides, was presented at a meeting of the National Academy of Sciences held at Washington April 28, 1931.

PLATES 19-23



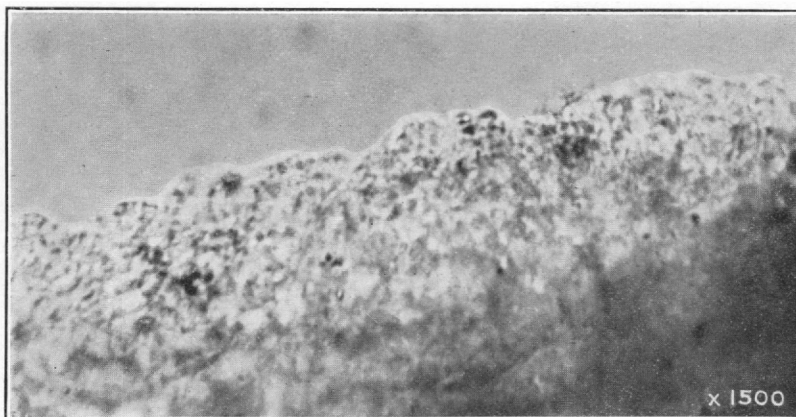
A. CALCAREOUS CONCRETIONS FORMED CHIEFLY BY *LITHOMYXA CALCIGENA*

From bottom of Furnace Creek, in rather quiet water, near Harpers Ferry, W. Va.; collected by White, Howe, and Read December 7, 1930. A decalcified preparation, made from the superficial crust of the bisected pebble shown in the upper left-hand corner and preserved in the herbarium of the New York Botanical Garden, is specified as the technical type of *Lithomyxa calcigena*.



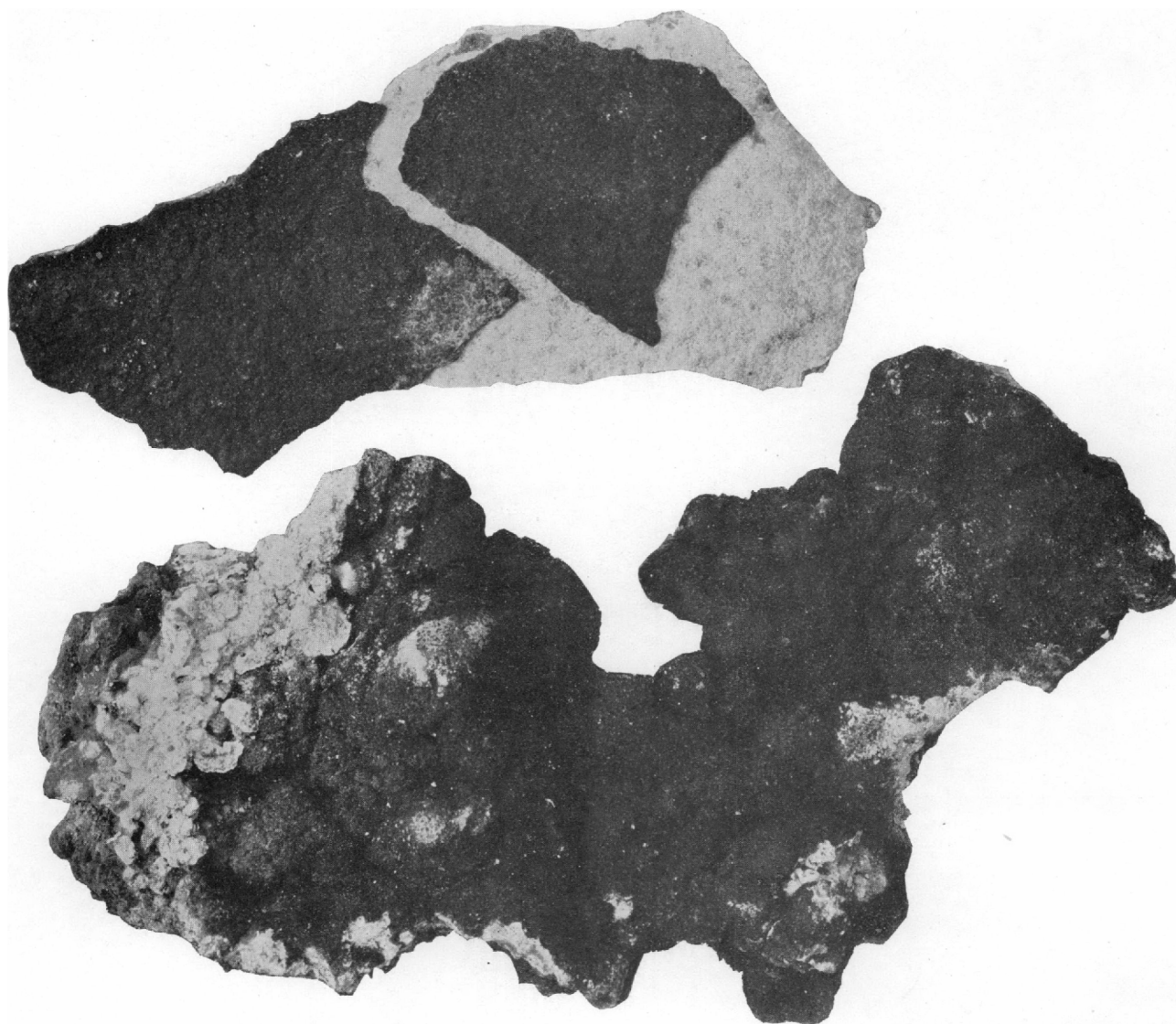
B. A PORTION OF A GROUND SECTION OF ONE OF THE PEBBLES FROM FURNACE CREEK

Showing, especially in the lower central region, outlines of the *Lithomyxa* cells, with incrusting lime; at the upper margin (surface) the cells sometimes appear to be in rows of two, three, or four.



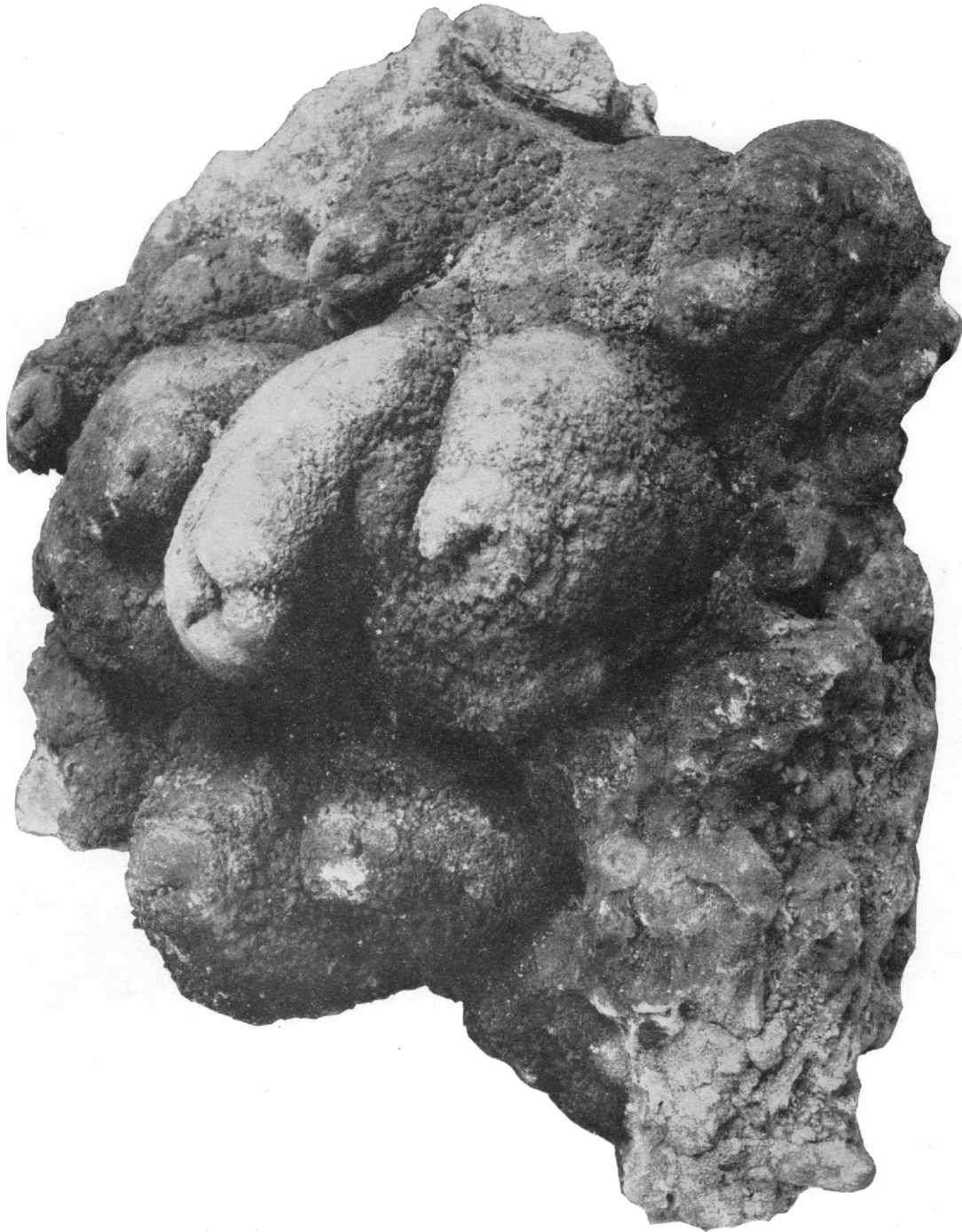
A. A PORTION OF A GROUND VERTICAL SECTION OF THE BLACK CRUST ILLUSTRATED IN B

Showing outlines of the calcified *Lithomyxa* cells.



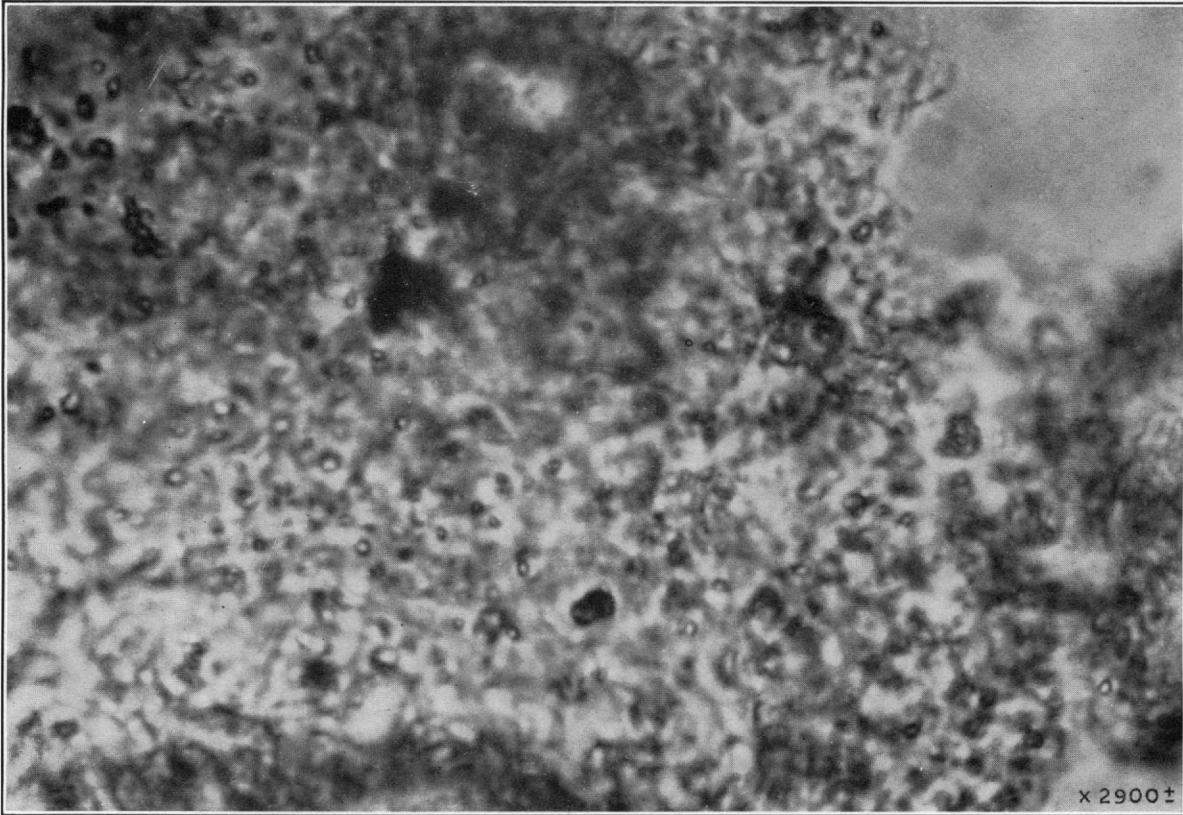
B. DARK OR BLACK CRUST, FORMED CHIEFLY BY *LITHOMYXA CALCIGENA* FORM *FERRIFERA*, IN SHADED OR PARTLY SHADED PLACES IN RAPIDLY MOVING WATER, FURNACE CREEK, W. VA.

Collected by White, Howe, and Read December 7, 1930. The darkening of the crust is apparently due to the presence of iron and manganese. The upper view indicates the readiness with which the superficial dark crust (a loose fragment here dislocated) separates from the underlying white crust, which also has been laid down by the *Lithomyxa*.

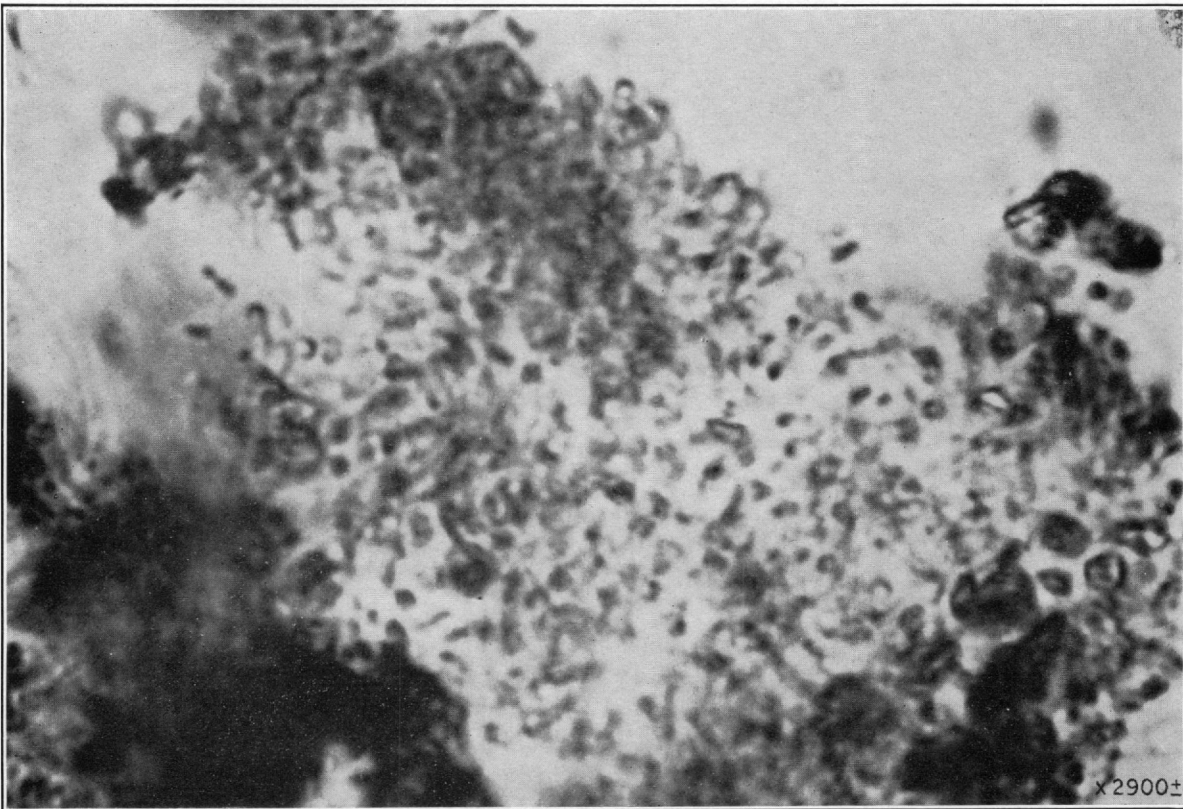


CALCAREOUS TRAVERTINE FORMED CHIEFLY BY *LITHOMYXA CALCIGENA* FORM *FERRIFERA*, IN MORE OR LESS SHADED PLACES IN RAPIDLY MOVING WATER, FURNACE CREEK, W. VA.

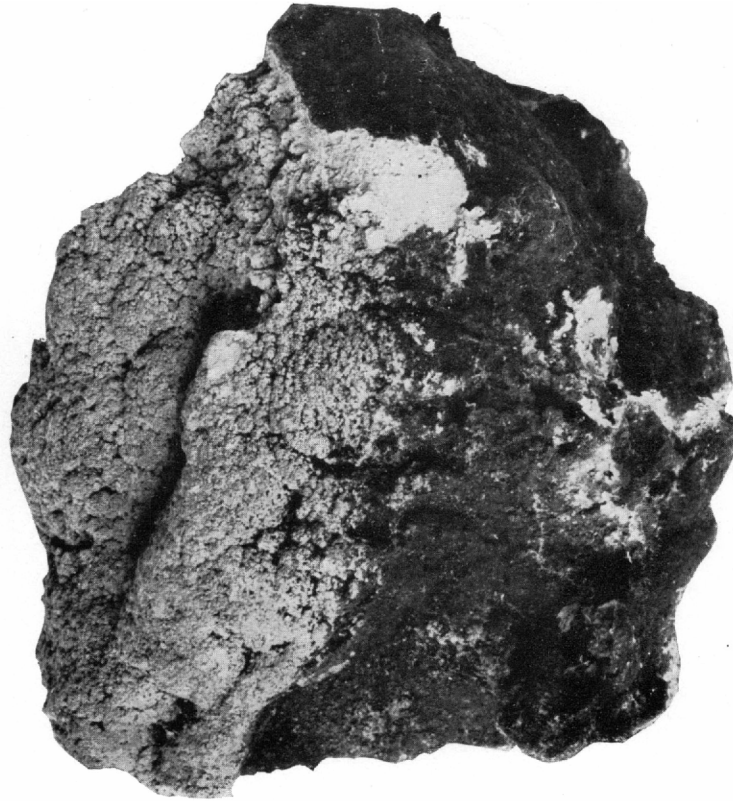
Collected by White, Howe, and Read December 7, 1930.



A. *LITHOMYXA CALCIGENA*, DECALCIFIED, MORE OR LESS EMBEDDED IN COLLOIDAL JELLY, FROM SURFACE LAYER OF A CALCAREOUS PEBBLE, FURNACE CREEK, W. VA.
Collected by White, Howe, and Read December 7, 1930.

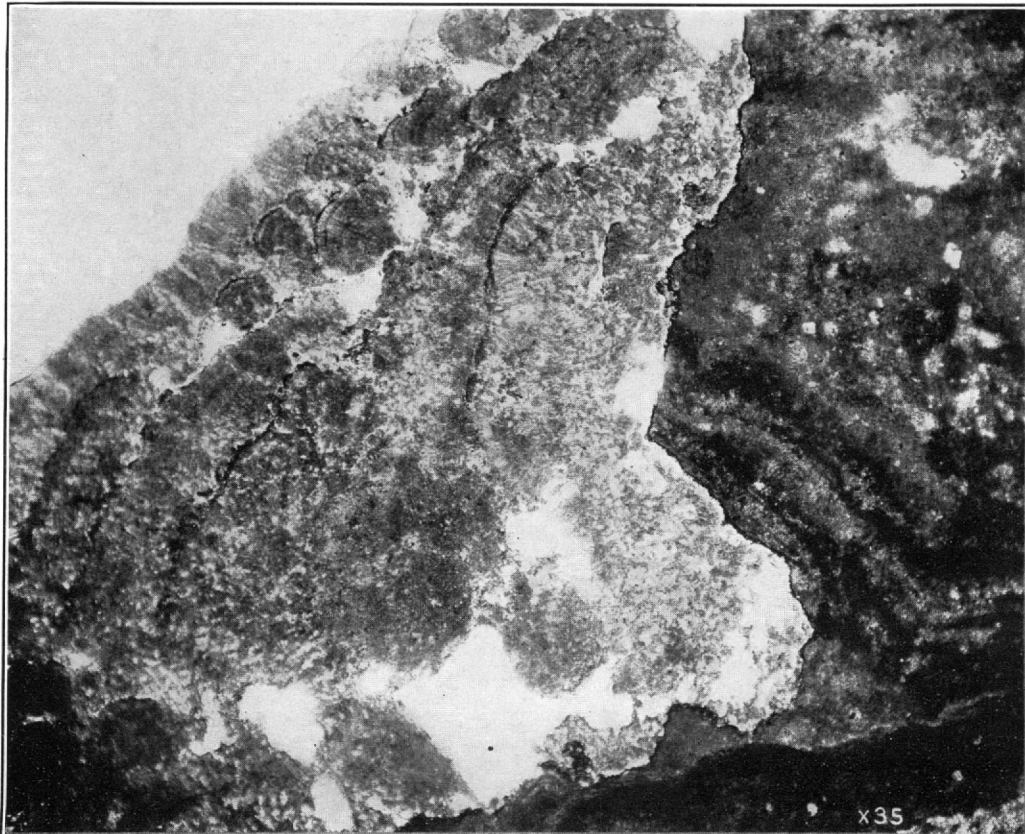


B. A SIMILAR PREPARATION OF *LITHOMYXA CALCIGENA* FORM *FERRIFERA*, FROM THE BLACK CRUST



A. SPECIMEN OF TRAVERTINE

The gray travertine at the left is made chiefly by two filamentous blue-green algae, *Lyngbya marlesiana calcarea* and *Inactis pulvinata*; the black travertine at the right was laid down chiefly by the more minute unicellular organism, *Lithomyza calcigena*.



B. A GROUND SECTION AT THE LINE OF JUNCTURE OF THE GRAY TRAVERTINE AND THE BLACK. The *Lyngbya* and *Inactis* form the looser and (in section) flabellate crusts at the left. The *Lithomyza* forms the more compact and homogeneous crust at the right.

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