COPROLITES FROM THE BRIDGER FORMATION OF WYOMING: THEIR COMPOSITION AND MICROÖRGANISMS.[1]

W. H. BRADLEY.

ABSTRACT. Remarkably well preserved mammalian and reptilian coprolites are found in parts of the upper Eocene Bridger formation in the southern part of the Bridger Basin of southwestern Wyoming. Most of the coprolites contain a profusion of silicified bacteria that closely resemble the commonest intestinal saprophytes of living animals. One of the mammalian coprolites, inferred to have been produced either by a carnivore or an omnivore, contains in addition an abundance of free-living fresh water algae (principally small desmids) that passed through the alimentary tract with amazingly little injury. A chemical analysis of this coprolite shows that it consists principally of collophane that has the composition of a francolite containing rare earths. Besides cerium and lanthanum it also contains minute amounts of vanadium (V_2O_5) and arsenic As_2O_3. The bacteria of this coprolite are preserved in opaline silica whereas the algae consist of both opaline and chalcedonic silica.

The small desmid cells are extraordinarily well preserved. In many of these such internal structures as pyrenoids, nuclei, and somewhat shrunken chloroplasts have been preserved. Dividing cells, two pairs of conjugating cells, zygospores?, and one monstrosity were found. In addition to the desmids there are two other species of chlorophyceae and one flagellate alga together with minute forms that may also be flagellate algae. Systematic descriptions of 6 microörganisms are given and 3 new species are proposed.

It is concluded that these free-living algae and a few ostracodes were imbibed by the animal in drinking water, that the feces fell on dry ground, and that rather soon thereafter the feces were covered by volcanic ash which yielded siliceous waters to silicify the microörganisms. One analysis of modern canine feces and one of fox feces suggest that the original phosphorus content of the feces may not have changed appreciably during fossilization. The presence of large numbers of desmids suggests that the animal drank from a pool of acid swamp water.

INTRODUCTION.

THE remarkable preservation of the coprolites in parts of the upper Eocene, Bridger formation implies that the original fecal matter was nearly, or quite immune to biological decay and comparatively inert to chemical decomposition. In the petrified remains of such inert material one might expect to find traces of bacterial cells and perhaps other microörganisms. Microscopic examination of several of these coprolites far exceeded the writer's expectations, for most of them contain a

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profusion of silicified bacteria and one (produced by a carnivore or omnivore) contains in addition, a considerable variety and a great number of free-living organisms that had passed through the alimentary tract with amazingly little injury. Accordingly, this particular coprolite was studied in some detail; its microörganisms, insofar as possible, were identified and its chemical composition was determined. The microörganisms reveal a few details of the ecology of the Bridger terrain during the upper part of the Eocene epoch that probably could not have been discovered by other means.

The Bridger formation consists largely of mudstone and volcanic ash, which were laid down on more or less swampy flood plains. Although little is known about the flora of the Bridger terrain during the upper Eocene the rich and varied fauna is well known. Turtles and crocodiles were numerous and the mammalian fauna included animals ranging in size from tiny insectivores to huge titanotheres. As one would expect, the coprolites represent a wide variety of animals including large reptiles (presumably crocodiles), turtles, and many mammals (Plate 1). The large reptilian coprolites and the turtle coprolites were identified by comparison with photographs published by Matley (1939, 1939B). Most of the other coprolites are inferred to be mammalian and to have been produced either by omnivores or carnivores.

EXTERNAL FEATURES OF THE COPROLITES.

Unweathered coprolites are light to dark brown and vitreous on fresh fractures. Those long exposed to the weather have developed a light gray or buff outer layer and some of the smaller ones are nearly white and are chalky throughout. On their outer surfaces many of the coprolites have striae or grooves that were impressed on the feces by muscular pressure (Plate 1, Figs. 6,9). Only one, which was never exposed to the weather, has the smooth glossy or satiny lustre described by Matley (1939B, 539), and interpreted by him as representing the mucous coating of the excrement. Several of the Bridger forms have flattened areas where they struck the ground and a few have impressions of small stems or grass, which they evidently acquired after excretion.

Coprophagous organisms evidently gnawed on the excrement before it was petrified. Scratched and grooved depressions and

channels are rather common. I suppose that these were made by large dung beetles (see Plate 1, Fig. 5). Several of the coprolites have rather large irregular, clay-filled borings that presumably once housed larvae of coprophagus insects.

Attacks on the coprolites were not restricted to the Eocene epoch. One of them has clearly been gnawed by a small present-day rodent for the teeth marks are sharp and cut through the weathered layer so as to expose the brown material below. Apparently rodents gnaw these coprolites, as they gnaw dry bones, for phosphate and lime.

Convolutions, which are so clearly manifest on the outside of the coprolites, are also easily discernible in cross sections (Plate 1, Fig. 2). The lumpy masses are separated from one another by thin partings of chalcedony and carbonates. Smaller veinlets of chalcedony or carbonates reveal the presence of smaller kneaded masses. Pieces of bone, especially the bony scales of ganoid fishes, are numerous in some of the coprolites (Plate 1, Figs. 4, 7) and impressions of hair are locally common on others but most of the coprolites contain no macroscopic objects.

SOURCE OF THE SPECIMENS.

During the summer of 1930 the writer collected several of the coprolites from the Bridger formation a few miles north of Lonetree, Wyoming (T. 13 N., R. 113 W., Uinta County), but most of them were obligingly collected for me by Mr. George Sternberg in the summer of 1941 while he was collecting vertebrate fossils for the U. S. National Museum under the direction of Dr. C. L. Gazin. Sternberg's collection contains specimens from many places in the southern part of the Bridger Basin in both Sweetwater and Uinta Counties, but most of the specimens came from the vicinity of Lonetree from tuffaceous mudstone beds that make up zone C of the Bridger formation, as defined by Mathew (1909).

CHEMICAL AND MINERALOGICAL COMPOSITION.

The brown vitreous mineral that makes up the bulk of the coprolites has the optical properties of collophane. It is isotropic and has a refractive index slightly higher than 1.59. Chemical analysis of the phosphate mineral in one of the coprolites (Plate 1, Fig. 1) reveals several interesting features.

Coprolite from Bridger formation, Uinta County, Wyoming.

(W. H. Bradley, analyst.)

	Whole sample (percent)	Insoluble portion (percent)
SiO_2	1.20	5.46
Al_2O_3	1.00	
Fe_2O_3	.86	
FeO, MgO	.81	
CaO	34.24	
H_2O-	1.55	
H_2O+	2.77	
TiO_2	.04	
CO_2	3.46	
P_2O_5	22.78	
MnO	.09	
BaO	none	8.59
SrO	none	none
Cl	none	
F	2.47[a]	
B	none	
SO_3	none	5.94
Ce_2O_3	.28	
ThO_2	tr.	
La_2O_3, etc.	.38	
V_2O_5	.01	
Cr_2O_3	none	
As_2O_3	tr.	
Organic matter		.68[b]
		7.99[c]
Insoluble	28.66	28.66
	100.60	
Oxygen equivalent of F	1.04	
	99.56	

[a] Determined by Dr. Michael Fleischer, U. S. Geological Survey.
[b] Extracted with alcohol and benzol in a Soxhlet extractor.
[c] Other insoluble constituents, not determined.

Partial mineralogical composition of acid-soluble portion (percent).

Rare earth-bearing francolite	87.0
Magnesian calcite	4.7
Opaline silica	1.7

Tests were made for the following elements not listed in the analyses but either they are absent, or present in such small quantities that they were not detected: Zn, Cu, Pb, Zr, Ta, Cb, Co, Ni, and Se.

Neither the formula for collophane ($Ca_3P_2O_8 + H_2O$) nor that for fluorapatite ($3Ca_3P_2O_8 + CaF_2$) gave plausible results in calculating the mineral composition of the acid soluble portion of the coprolite. Michael Fleischer of the Geological Survey suggested that the composition of a carbonate-apatite (francolite) discussed by Gruner and McConnell (1937) be assumed for the predominant phosphate mineral. The partial mineral composition was accordingly determined in the following way. Enough P_2O_5 was first deducted to combine with the rare earths to form (Ce, La, etc.) PO_4 and then all the remaining P_2O_5 was assumed to be present as francolite having the same relative amounts of CaO, MgO, CO_2, F, and $H_2O +$ as given in the analysis reported by Gruner and McConnell. After deducting the proportionate amounts of these constituents there remained virtually no F and only slightly more CO_2 than was necessary to balance all the remaining CaO. The slight excess of CO_2 was assigned to some of the remaining MgO and reported with the calcite as magnesian calcite. The amount of carbonate so calculated (4.7%) agrees well with the amount estimated from thin sections. Soluble silica is reported as opal. All the other constituents whose mineralogic association is uncertain make up 6.6% of the acid-soluble portion of the coprolite. Subtracting these plus the 4.7% magnesian calcite and 1.7% opal from 100 leaves 87% francolite. It is assumed that this hypothetical francolite molecule includes the following constituents $(Ca, Mg, Ce, La, etc.)_{10}$ $(PO_4, CO_3)_6$ $(F, OH)_2$. This empirical approach suggests that the collophane of this coprolite, and presumably also the others, has essentially the same chemical composition as the mineral francolite.

Rare earths, other than zirconium, have been reported in amounts ranging from .01 to .03% in three samples of rock phosphate (Jacob, Hill, Marshall, and Reynolds, 1933, 31). Niggli, however, records (1925, 170-172) a considerable number of analyses of fluorapatite that include rare earths in amounts ranging from a trace to more than 5%. According to Niggli (p. 170), Zambonini synthesized chlorapatite that contained as much as 13% $CePO_4$. Köber and Trömel (1932) prepared an apatite compound having the composition La_2Ca_8 $(PO_4)_6O_2$ and found that it was easier to make synthetic apatite with rare earths than without them.

Only a partial chemical analysis was made of the acid insoluble portion of the coprolites. This sufficed to reveal the pres-

ence of minute barite crystals that were scattered through the material along with equally small particles of clay, feldspar, and quartz. The silica reported in this analysis is unaccountably low, even after allowing for considerable loss as SiF_4 during acid digestion, as thin sections show that chalcedony is apparently abundant enough to account for most of the material insoluble in acid.

PREPARATION OF THE MATERIAL FOR MICROSCOPIC EXAMINATION.

Sections of the coprolites ground thinner than the usual rock sections revealed most of the microörganisms, but some were isolated from the matrix by acid treatment. A small piece was digested in aqua regia to remove the phosphate mineral. Even after digestion the material, though porous, retained its original form. K. E. Lohman of the Geological Survey disintegrated the digested material by repeated freezing and thawing in sodium acetate (Guinard, 1887) and mounted the particles—

PLATE 1.

(Fig. 2 enlarged x 2; all others natural size.)

Fig. 1. Omnivore or carnivore coprolite that contains the remarkable assemblage of microörganisms described in this paper.

Fig. 2. Transverse section of the coprolite shown in Fig. 1. The black veinlets and areas are chalcedony.

Fig. 3. Longitudinally fluted coprolite inferred to be that of a turtle.

Fig. 4. Coprolite containing an abundance of thick bony scales of gar pike. Producing animal unknown.

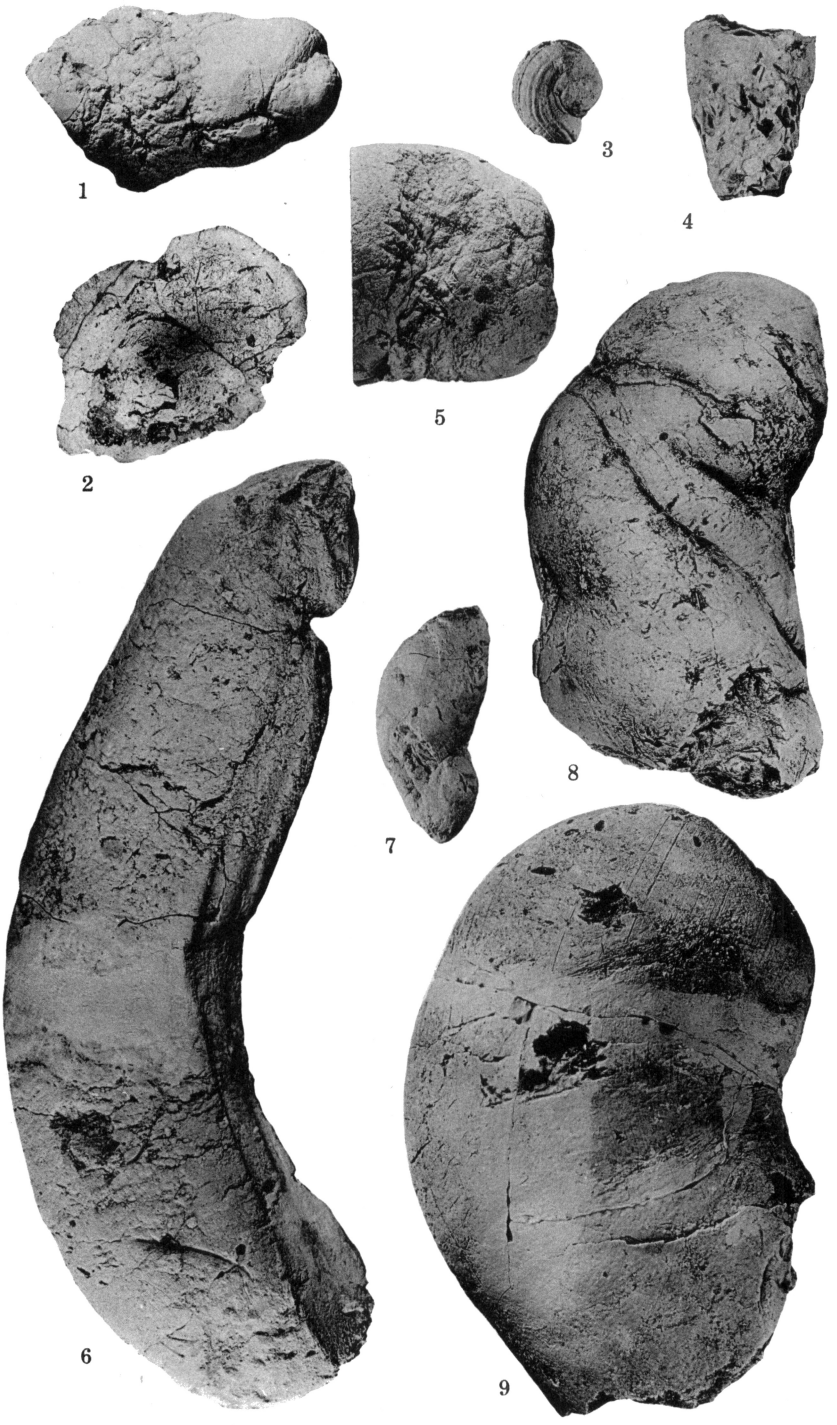
Fig. 5. Portion of the coprolite shown in Fig. 6 showing a diagonally scratched furrow that was excavated from the original feces by a coprophagus organism, presumably a dung beetle.

Fig. 6. Complete coprolite of an omnivore or carnivore showing a deep furrow impressed in the original feces by an irregular feature of the anal anatomy. Near the lower end are several deep impressions of small twigs or grasses. Producing animal unknown but possibly it was *Paleosyops*, a common animal in the Bridger fauna. A wide crack in the coprolite a little below the center has been filled with plaster.

Fig. 7. Complete coprolite of a small carnivore. This one contains many bone fragments and at least some small gar pike scales.

Fig. 8. One of the largest of the mammalian coprolites. Part of its surface has a satiny sheen that is interpreted as a remnant of a mucous coating on the original feces. At the lower end is a deep furrow excavated by a coprophagus organism.

Fig. 9. Reptilian coprolite, presumably crocodilian. The upper end is the terminus which is marked by a system of fine striae that tend to converge in a roughened area (back of the side shown in the photograph) where this lump parted from the following mass. The texture of this roughened end suggests that the material had the consistency of a stiff paste.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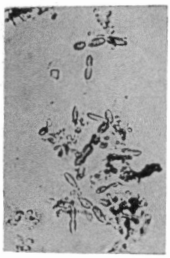

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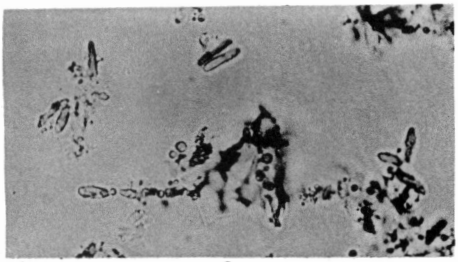

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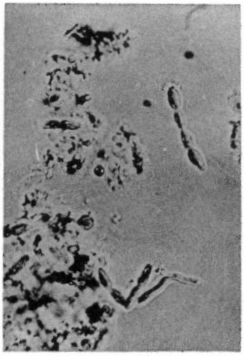

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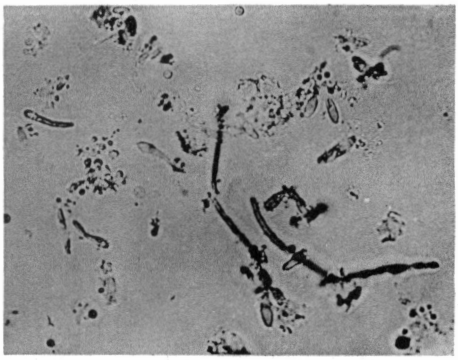

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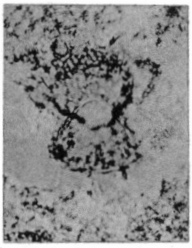

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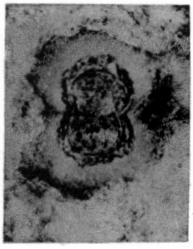

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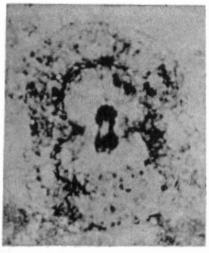

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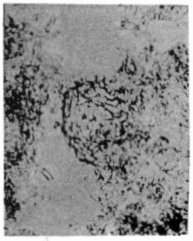

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mostly silicified bacterial cells—in Aroclor, a synthetic resin whose refractive index is 1.66 (see Plate 2, Figs. 1-4). A few mounts were also made in Hyrax, another synthetic resin whose refractive index is approximately 1.8.

MICROÖRGANISMS.

Of the coprolites examined microscopically one in particular contained the greatest number and most varied assemblage of microörganisms. This coprolite (Plate 1, Fig. 1) was collected in 1930 a few miles north of Lonetree, Wyoming (T. 13 N., R. 113 W., Uinta County). Its chemical and mineralogical composition are discussed on the preceding pages. Because the conclusions reached are based principally upon the extraordinary group of microörganisms in this coprolite the remainder of the paper will be restricted to a discussion of this specimen and its contents. The specimen is in the National Museum.

BACTERIA.

In the large intestine of man, and omnivores and carnivores in general, definite types of bacteria multiply enormously. This

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PLATE 2.

Figs. 1-4. *Escherichia bridgerana*, n. sp., isolated from the phosphatic matrix of the coprolite. 1. Cells undergoing binary fission, x 650. 2. Normal rods, ovoids, and coccoids with cell at the lower left showing terminal fission, x 1000. 3. Pair of exceptionally large cells undergoing binary fission. At the left and in the lower part of the field are normal sized cells some of which are still embedded in siliceous matrix, x 1000. 4. Club-shaped cells and greatly elongated rods with a few normal rods, ovoids, and coccoids, x 1000.

Figs. 5-9. *Staurastrum enteroxenum*, n. sp., in thin sections of the coprolite. 5. Oblique view from above showing the two triangular semicells alternating with one another. The cell walls are partly obscured by tufts of acicular crystals of the chalcedony that makes up the cell, x 600. 6. Front view (or vertical section) of the alga showing the broad isthmus and open sinus. The cell wall appears to be granulate, x 740. 7. Dividing pyrenoids replaced by opal in a vegetatively dividing cell of chalcedony. The cell walls are nearly everywhere obscured by the opaque matrix of the coprolite which has been painted out on the negative, x 740. 8. Slightly oblique view from below showing two cup-shaped bodies of opal that are inferred to be shriveled remains of the axile chloroplasts, x 740. 9. Vertical section showing dividing pyrenoids or nucleus (?) connected by a highly refringent band. The zone around the cell apparently is chalcedony that has grown outward in optical continuity with the chalcedony that makes up the cell, x 740.

Fig. 10. Zygospore, perhaps belonging to *Staurastrum enteroxenum*. The matrix of the coprolite has been partly painted out on the negative, x 175.

accounts for the homely but nonetheless astonishing fact that the feces of such animals consists principally of bacterial cells—most of them dead (Zinsser and Bayne-Jones, 1937). Perhaps it is not surprising, therefore, that the most abundant microörganisms found in this coprolite are bacteria and that, furthermore, nearly all of them resemble the colon bacillus and other closely related intestine-dwelling or enteric bacteria that abound in normal feces. Neither the form of the coprolite nor any of the fossilized microörganisms suggest that the animal was in any wise abnormal.

Doubtless it is impossible to identify silicified bacterial cells, however faithfully preserved, with any specific living forms. Nevertheless, certain broad relationships of these ancient coprolitic bacteria may be inferred. The fact that they occur in great abundance in feces makes it probable that they belong in the genus *Escherichia*, aerobic, non-sporing rods of both saprophytic and parasitic habit that are found in the intestines under normal and diseased conditions. These and other closely related bacilli are all so much alike that they cannot be distinguished by morphology alone (Zinsser and Bayne-Jones, 1937, 552-553). All the discernible morphologic details of the fossil bacterial cells agree with those of the bacilli included under *Escherichia.*

For example, of the thousands of fossil bacterial cells isolated from the coprolites and examined at high magnification with critical illumination[2] no spore-forming cells were found although cells showing binary fission are numerous and other characteristic forms of gemmation were also found (see Plate 2, Figs. 1-4). Moreover, the bacilli in *Escherichia* do not have enveloping capsules and no suggestion of capsules was found on any of the fossil bacteria.

The resemblance between the fossil bacteria and the forms found in Hort's cultures (1917) of several enteric bacilli is particularly striking. The fossil bacteria have in common with the bacilli cultured and observed by Hort the following characteristics: a considerable range in cell size and shape, numerous fusiform cells in various stages of binary fission, coccoid and ovoid forms, detached buds, greatly elongated and curved rods, clubs, and branched or budding forms (see Plate 2, Figs. 1-4). Branched or budding forms, however, are rare among the fossils

[2] Leitz fluorite oil immersion objective with yellowish light filtered through a Wratten B (green) filter.

and no cells showing undoubted cruciform budding, such as Hort described, were found.

The probability that these fossil bacteria represent some of the commonest saprophytic bacilli, such as those of the colon group, rather than any of the disease-producing bacilli is suggested by the fact that in feces the colon and several similar bacilli greatly predominate over all the other forms (Zinsser and Bayne-Jones, 1937, 1140-1141). This probability, however, is clearly of little value for fixing the taxonomy of the bacteria. Perhaps all that can be concluded from this, and the foregoing considerations, is that the fossil bacteria illustrated in (Plate 2, Figs. 1-4), may be placed with more or less assurance in the genus *Escherichia.* For convenience of reference they may be designated *Escherichia bridgerana.*[3] The name will serve as a tie both to the Bridger formation and to the Bridger Basin. Renault and Bertrand (1894, 1898, 1900, 1903), described a considerable variety of fossil bacteria from coprolites of Permian age found at Cordesse, Lalley, and Ignornay in France, and Bertrand (1903), described still others in his exhaustive monograph on the coprolites of Lower Cretaceous age from Bernissart, Belgium. Of these fossil bacteria several unnamed varieties described by Bertrand (1898), and *Bacillus permiensis* Renault (1894, 1900), appear to be most nearly similar to *E. bridgerana* though they are all considerably larger. Bertrand regarded his unnamed varieties of bacteria as close relatives of *E. coli* (1903, 73-76). Many of the fossil bacteria described by Bertrand and Renault are empty molds in the matrix but some of the bacteria were replaced by calcium phosphate (1894, 586-587).

GREEN ALGAE (CHLOROPHYCEAE).

Although the presence of fossilized bacteria might have been expected in coprolites the presence of innumerable desmids, which are free-living microscopic green algae, is astonishing. Moreover, the desmids are not only abundant but they are well-preserved and are accompanied by smaller numbers of other fresh water algae and a few minute aquatic animals that evidently all lived together (see Plates 2-4).

The desmids in this coprolite are rather simple dumbbell-

[3] Systematic descriptions of the microörganisms are grouped at the end of the article under the heading "Systematic descriptions."

shaped cells 0.02 to 0.025 mm. in diameter and about 0.03 mm. long. Seen from above each semicell has the form of a rounded triangle. A peculiarity, shared by these desmids with several living species, is that the angles of the upper semicell alternate with those of the lower (see Plate 2, Fig. 5).

Two pairs of conjugating desmid cells were found in this coprolite (Plate 3, Fig. 5). Among desmids conjugation results in the formation of a thick-walled and usually highly ornamented resting spore or zygospore. Several ornamented objects inferred to be zygospores of desmids, were found but, like the conjugating pairs, they are difficult to photograph because of the depth of focus required (Plate 2, Fig. 10).

In the normal vegetative division of the desmids a cross wall forms at the isthmus between the semicells. The semicells then move apart and each semicell grows a new semicell. Sometimes, however, a monstrosity is developed—instead of two new semicells forming, a single large globular cell develops and the old semicells remain firmly attached to it (Turner, 1922, 61; Smith, 1933, 567). One such monstrosity was found (Plate 3, Fig. 6).

Many, but not all, of these fossil desmids, which now consist of chalcedonic silica, have paired or dumbbell-shaped central bodies of opaline silica within them that resemble the internal structures of living desmids. These central bodies are always located in the isthmus between the two halves of the cell and are always oriented along the long axis of the cell, as are the internal structures—the pyrenoids, nuclei, and chloroplasts—of the living plants (Plates 2-3). Furthermore, several of these dumbbell-shaped central bodies are hung on a thin cross-wall such as forms between the semicells of desmids about to begin vegetative division.

These paired central bodies within the desmid cells have a variety of shapes. Some are closely appressed and have short protuberances; others have long protuberances that either are of various lengths or that are distinctly crooked. Some are connected by a clear, rather highly refringent isthmus (Plate 2, Fig. 9). In living desmids both the nucleus and the pyrenoids divide in this manner and occupy this position in the cell. Perhaps the best evidence, however, for believing that some of the desmid cell contents have been preserved is shown in (Plate 2, Fig. 7). The internal structure resembles very much two pyrenoids dividing. According to this interpretation the pair of dark globular central bodies correspond to the viscous pro-

tein globules of the pyrenoids of the living cell and the irregular zone around them represents the sheath of starch granules. In living desmids the pyrenoids divide when the cell divides vegetatively. The fairly well-defined transverse wall suggests that this fossil desmid was about to divide.

The contents of another of the fossil desmids are also of exceptional interest. In this individual the central body consists of two cup-shaped elements back to back (Plate 2, Fig. 8). The chloroplasts of similar living desmids are cup-shaped but in most species are larger. At least one desmid, however, (*Staurastrum inconspicuum* Nordstedt) has decidedly small chloroplasts (Lükemüller, 1902). Because of the striking similarity with the chloroplasts of living desmids I am inclined to believe that the cup-shaped central bodies in this fossil desmid are fossilized remains of somewhat shrunken chloroplasts of the original living cell.

Not all the central bodies in these desmids, however, are believed to be faithful petrifactions of original organic structures. Many of them seem rather to be dumbbell-shaped aggregates of minute mineral fibers whose form was determined by the growth habit of the fibers and by the medium in which they grew (Plate 3, Fig. 4, Plate 4, Fig. 1). More than 100 different inorganic salts, if combined under the proper conditions, will yield microscopic dumbbell-shaped aggregates of fibers (Morse, Warren, and Donnay, 1936; Morse and Donnay, 1936). If one salt is mixed with a gel and the reacting salt solution is allowed to diffuse slowly into the gel, bundles of fibers begin to form. As the reaction continues the bundles swell out at the ends into spheroidal masses. The ultimate form is either a dumbbell-shaped body or, with some compounds, two hemispheres separated by an equatorial furrow.

In many of the fossil desmids the central dumbbell-shaped bodies are perfectly symmetrical and are made up of very fine fibers of opaline silica (Plate 4, Fig. 1). It seems that these may be mineral idiomorphs[4] that formed within the desmid cell early in the stage of mineralization. According to this supposition the fixed or hardened cell protoplasm was the gel and the

[4] Idiomorph—the noun of the familiar adjective idiomorphic—a term suggested by C. H. Dane for inorganic objects other than crystals but having a distinctive and characteristic form which is determined by the growth habit of the constituent particles and by the medium in which they grew. The term is useful specifically for objects whose form is more or less complex and, therefore, cannot be described in a single word.

silica in solution outside the cell was the diffusing electrolyte. The dilute silica solution, derived by leaching volcanic ash, was alkaline and after diffusing through the gel precipitated its silica in the central part of the cell where the solution was neutralized by the tannins which are inferred to accumulate there (along with iron salts) when the desmid cell is about to conjugate (Tiffany, 1924, 88). Whether or not this is the precise mechanism by which these opal idiomorphs came into being we may be reasonably sure the desmids internal cell structures, or their remains, exerted a decisive influence, because the opal idiomorphs are always centrally located within the cell and their long axes are always parallel to the long axis of the cell.

It appears, therefore, that some of fossil desmids contain central bodies of opal whose form happens only by chance to resemble the original pyrenoids or nuclei whereas others contain true petrifactions (also in opal) of the original internal structures (chloroplasts, pyrenoids, and nuclei). Perhaps the stage of disintegration of these internal structures at the time of silicification determined whether the true form would endure or a false one develop.

Virtually all the desmids found in the coprolite belong to one species which is referable to the living genus *Staurastrum* Meyen. This species is given the name *enteroxenum*—intestine stranger. The systematic description is given at the end of the paper. A few of the desmids in the coprolite should be referred to the genus *Cosmarium* Corda (Plate 3, Figs. 10, 11). In a letter to me Prof. G. W. Prescott, of Albion College, called attention to the similarity between these desmids and *C. pachydermum* Lund. Unfortunately too few of these individuals are present to reveal the characters desirable either for this specific reference or to serve as the basis for a new species. The observable features of circularity, great relative width of isthmus, and overall dimensions are all restricted to one front view of the desmid. The cell wall is apparently, though not surely, thick; whether it is punctate or not, as in *C. pachydermum* is not determinable from the fossil specimens available. A few others are referable to some unidentified genus of small desmids (Plate 3, Fig. 8).

Only two other green algae, both free-living fresh water forms, were found in this coprolite and each is represented by a single individual. One is referable to the living genus *Closteridium* Reinsch and is regarded as a new species (*Closteridium*

bulliforme). Its systematic description is given at the end of the paper. The other evidently belongs to the living genus *Chlamydomonas* Ehrenberg.

FLAGELLATE ALGAE (CHRYSOPHYCEAE).

Two flask-shaped cells were isolated from the coprolite that strongly resemble the hard shells or loricae of a small, fresh water, epiphytic alga, *Lagynion* Pasher. The more nearly perfect of these algae (Plate 4, Fig. 5) is described, though it is not given any specific designation.

Minute, feathery bell-shaped objects in considerable numbers were isolated from the coprolite (see Plate 4, Figs. 6-12). Many of these resemble superficially the scales from the wings of small insects but their conical or bell-form evidently rules this out. Several features suggest that they may be the loricae or hard protecting shells of minute fresh water algae. Two kinds of these objects are apparently distinguishable, though it is possible that one is a more advanced growth stage of the other. The smaller kind (Plate 4, Fig. 6) is represented by five complete individuals that are nearly identical in size and structure. The larger kind (Plate 4, Figs. 7-12) comprises individuals that differ from one another in form and size but appear to fit into an integrated series.

Although these objects are not surely identifiable and have not been given names they are nevertheless described and discussed.

RADIOLARIA?

Minute objects of opaline silica that have a striking resemblance to diatoms were found in two thin sections of the coprolite (Plate 4, Fig. 3). K. E. Lohman obligingly studied these objects and found that they are not diatoms and that the resemblance is superficial. Instead of being hollow discoid or spheroidal shells they are highly porous spheres, the mesh structure being apparently homogenous in all planes through the sphere. The photomicrograph is an optical section approximately on an equatorial plane. This structure also rules out the possibility of their being either siliceous cells or cysts of chrysophycean algae, which are hollow shells. Lohman suggested that the structure of certain radiolarian skeletons is somewhat simliar to the fossil porous spheres. None of the Radiolaria figured by Haekel (1887), resembles the fossils

closely either in structure or size though certain genera in the order Sphaeroidea (e. g. *Plegmosphaera*) suggest a possible relationship.

All the known Radiolaria are marine, and if these fossils are marine they must have been derived from marine formations around the margin of the Bridger Basin. Although Radiolaria were found in the Upper Cretaceous Mowry shale of the Black Hills region in northeastern Wyoming (Rubey, 1929), Lohman found no siliceous microörganisms in two samples of the Upper Cretaceous Hilliard shale which I collected a few miles south of the Bridger Basin near Manila, Utah. It seems more probable that these minute siliceous spheres belonged to some unidentified fresh water organism and that they grew in the pool along with the other fresh water organisms found in the coprolite. Their original composition is inferred to have been siliceous but this is by no means certain.

OSTRACODES.

A few shells and shell fragments of small cyprid ostracodes were found in the coprolite. These apparently lived in the same place as the Algae.

FOSSILIZATION.

The fossilization or petrification within a coprolite of such delicate things as desmids and their cell contents involves four factors: the way the organisms got into the animal's alimentary

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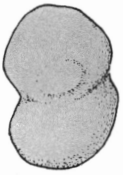
PLATE 3.

Figs. 1-7, 9. *Staurastrum enteroxenum*, n. sp.; camera lucida drawings from individuals in thin sections and photomicrographs from thin sections. 1. Front view, x 570. 2. Side view of another and slightly smaller individual showing the narrow isthmus when viewed from the side, x 570. 3. Oblique view from above; dotted line indicates area obscured by matrix, x 570. 4. Oblique view from above showing opal idiomorph in axile position within chalcedony cell, x 570. 5. Two conjugating cells, x 570. 6. Monstrosity consisting of abnormal central globular cell with two semicells firmly attached, x 570. 7. Front view of cell showing opal idiomorph or remnants of dividing pyrenoids within a cell replaced by chalcedony, x 740. 9. Axile body of opal, either an idiomorph or shriveled remains of dividing pyrenoids or chloroplasts; cell wall obscured by matrix and painted out, x 740.

Fig. 8. Front (or side?) view of an unidentified desmid considerably smaller than *S. enteroxenum*, x 570.

Figs. 10-11. Front view of a desmid belonging to *Cosmarium* Corda, closely similar to *C. pachydermum* Lund, x 740. Fig. 11 shows an opal idiomorph or dividing pyrenoids preserved in opal in a cell of chalcedony, x 740.



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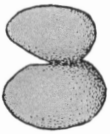

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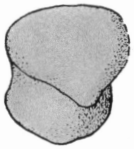

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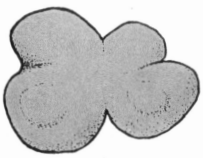

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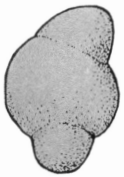

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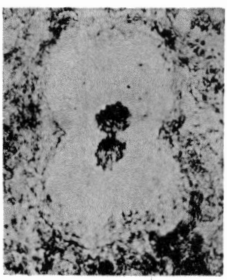

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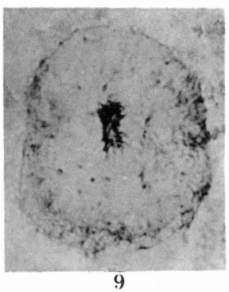

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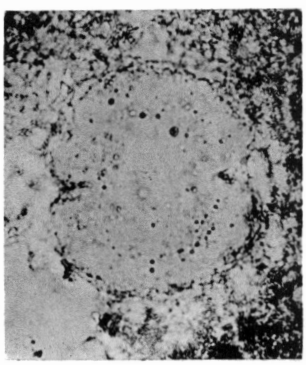

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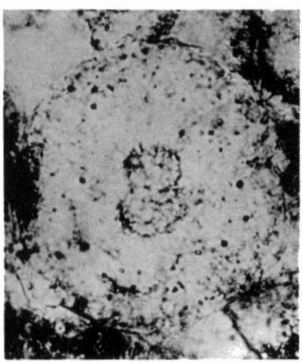

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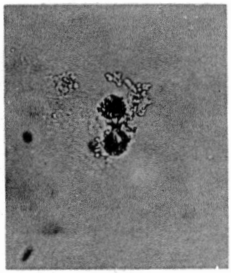

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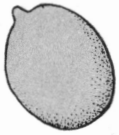

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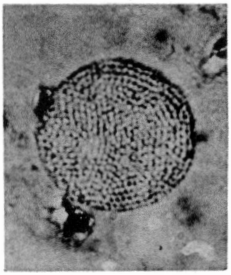

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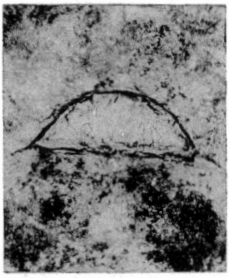

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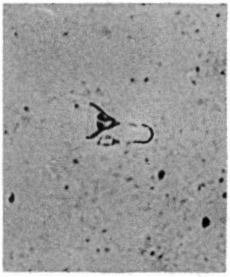

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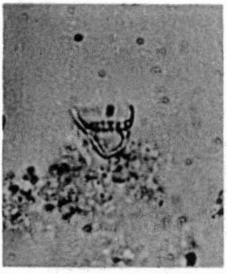

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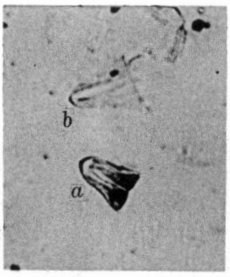

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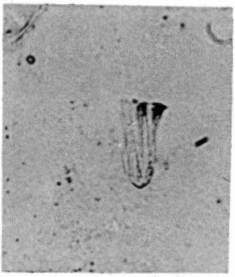

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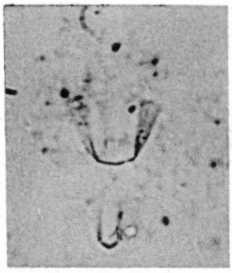

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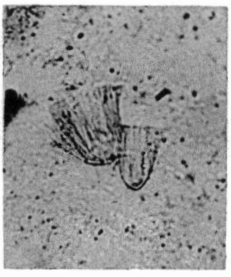

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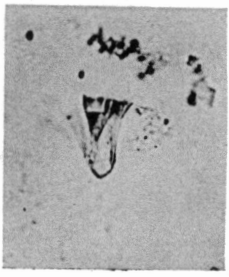

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tract, how they escaped destruction there, how the cell contents were fixed or hardened before mineralization, and, finally, the source of the mineralizing solutions.

It is inferred that the desmids and the associated aquatic organisms were a purely chance constituent of material within the animal's gut. This seems to follow from the fact that they were so little digested. If the algae did not serve as food they probably were taken up in drinking water. To have taken up so great a number of desmids it seems probable that the animal must have drunk deeply from a pool at low water stage wherein the desmids were concentrated in great abundance.

If the desmids got into the animal's stomach in drinking water they probably did not stay long in the stomach nor is it likely that they were subjected to anything but dilute solutions of the acids and strong digestive ferments in the stomach and small intestines because, when omnivores and carnivores drink, the drastic digestive system is not set in operation. Instead, the pyloric valve at the lower end of the stomach opens and allows the water to pass right along until it is absorbed through the walls of the small intestine. Particles thus introduced into the intestinal tract become mixed with thoroughly digested food which is already well along in the gut. Furthermore, desmids are well suited to survive passage through an animal's digestive system, for their cell walls consist of cellulose and cellulose is not digested by animals. Cellulose, to be sure, is decomposed by bacteria in the large intestines of certain herbivores but there is no evidence either from the form of the coprolite or from the identifiable remains within it that it was dropped by an herbivorous animal. Indeed, the argument might quite as well be reversed and say that because the desmids were not

PLATE 4.

Fig. 1. Opal idiomorph isolated from the coprolite, x 484.

Fig. 2. *Chlamydomonas* sp., a flagellate alga resembling *C. gloeocystiformis* Dill. Camera lucida drawing, x 570.

Fig. 3. Unidentified siliceous organism resembling a diatom, x 900.

Fig. 4. *Closteridium bulliforme*, n. sp., in a thin section of the coprolite, x 364.

Fig. 5. *Lagynion sp.*, isolated from the coprolite. Siliceous fragments of the matrix and bacterial cells have been partly painted out on the negative, x 650.

Figs. 6-12. Minute organisms isolated from the coprolite that are inferred to be the loricae of flagellate algae, possibly related to either *Dinobryon* Ehrenberg or *Cyrtophora* Pascher. Figs. 6, 8-10, and 12 are enlarged x 1000; Figs. 7 and 11 are enlarged x 1100.

destroyed the animal probably was not an herbivore. No bacterial cells were found within any of the desmids.

Although the passage of desmids through an animal's alimentary tract and their subsequent fossilization may be accounted for, it is more difficult to explain the preservation of the ephemeral structures within these desmids. The first requisite for the preservation of such delicate things is prompt killing and fixing of the cell contents. The most plausible fixing agent that may be called upon is heat. A temperature of 70° C. will effectively set the cell contents of minute organisms. Ground temperatures of 60° to 80° C. have been recorded in Old World deserts (Walther, 1924, 26, 65). Although the Bridger terrain was not desert during the upper Eocene the summer insolation may have been intense because the region was remote from the ocean and therefore had a continental climate. Consequently, it seems within reason to suppose that if the feces laid for hours in the direct sun it may have absorbed sufficient heat to harden the cell contents of the contained microörganisms. That the ground where the excrement lay was dry is indicated by the absence of either mycelia or spores of fungi in the outer parts of the coprolite.

Once the cell contents were fixed, the subsequent mineralization was a purely geologic process. Judging from the excellent preservation of the microörganisms it probably was not long after exposure to the hot sun that the feces were covered by a protecting blanket of sediment. I infer that the protecting sediment was volcanic ash whose small particles of metastable glass soon gave up silica to form the siliceous waters that converted the microörganisms to opaline and chalcedonic silica.

Just how the fecal matter was converted to the phosphate mineral francolite is not known but it is certain that the conversion must have happened before the overlying sediment was thick enough to flatten the coprolite. If the original fecal matter was as rich in calcium phosphate as certain modern dog feces no great chemical changes occurred during the process. The following analysis of dog feces, which Prof. G. Evelyn Hutchinson of Yale made after reading the manuscript of this paper, suggests that carnivores that gnaw bones may excrete feces containing a remarkably high percentage of calcium phosphate.

Weathered canine feces (dried at 110° C).

Ignition loss	23.7
P_2O_5	31.5
CaO	40.3
Sand	1.1
Indet.	3.4
	100.0

Professor Hutchinson wrote[5] that the material had weathered white and must have lost much of its organic matter by leaching but had retained its original fecal form. He added that the analysis indicates "that most of the material is calcium phosphate of about the composition of hydroxylapatite" and that it was probably derived from bone meal in the dog food. Subsequently Mr. H. S. Siegele obtained a specimen of fox-dung from the Yale Natural Preserve. This material was somewhat weathered, though retaining its original form, and contained white material as well as remains of the chitinous exoskeletal parts of insects. Much of the white material consisted of macroscopically recognizable bone splinters. Analyses of two samples gave

$H_2O - 110°$	8.9	8.4
$H_2O + 110°$ organic	38.3	39.3
sand	13.9	25.3
CaO	17.5	13.5
P_2O_5	18.5	11.0
indet. ash, loss etc.	2.9	2.5

In the first sample, low in sand, some phosphorus must have been present in a form other than bone.

If the original feces, both mammalian and reptilian, contained as little phosphorus as some other dungs for which analyses are available, then considerable quantities of both calcium and phosphorus, as well as other elements, must have been added during the diagenetic changes. On a dry weight basis hog manure contains only about 0.66% and steer manure about 1.49% P_2O_5 (Thorne, 1917). Human feces is exceptionally rich in phosphorus (Wheeler, 1914), yet, according to data published by Wolff (1892), it contains, on a dry weight basis, only 4.55% P_2O_5. The feces of certain uricotelic reptiles may have contained 10 to 20% P_2O_5, amounts comparable to the phosphate content of guano (Wolff, 1892, 140-141). If large

[5] Personal communication, May 1945.

percentages of phosphorus were added some may have come from the decomposing shards of volcanic glass but perhaps the greater part would have been derived from the fluid and solid excreta and bones that decomposed during Bridger time, for none of the urine (which contains more phosphorus than feces) and surely only a small percentage of the dung and bones produced were petrified. Phosphatic material thus decomposed returns its phosphorus to the soil and soil water.

Why phosphorus should concentrate in fecal matter is an intriguing question for which I have found no satisfying answer. Nevertheless, it seems to be rather general that the mineralizing substance of coprolites is largely tri-calcium phosphate (Mattey, 1939; 1939 B; Bertrand, 1903; Stocklasa, 1880). The analyses of carnivore feces that are given above perhaps suggest that only such fecal matter as is exceptionally rich in calcium phosphate becomes fossilized. This might account for the absence of coprolites that were unmistakably derived from herbivores.

Minute quantities of fluoride are probably present in most ground waters,[6] and presumably this is the source of the fluorine that is combined with the tri-calcium phosphate in the coprolites. The source of the rare earths in the coprolite is obscure but calcium is so common a constituent of ground waters that its part in the mineralization of the coprolite warrants no comment.

ECOLOGIC SIGNIFICANCE OF THE MICROÖRGANISMS.

Unfortunately little is known, or at least little has been published, about the ecology of the Bridger terrain during the upper Eocene, when the region was populated by a great number and variety of animals. Swamps are indicated by a few rather widely spaced beds of carbonaceous sediments in the Bridger formation and a general wetness of the terrain is indicated by the abundance of aquatic turtle and crocodile bones. The presence of large numbers of desmids indicates that some of the ponds had a low concentration of dissolved solids and were probably acid swamp waters, for only in such waters do desmids prosper. According to Prof. G. M. Smith (1933, 565), desmids usually abound only in waters whose pH ranges between 5 and 6. Acid swamp waters low in electrolytes generally occur in regions that have poor drainage and a consid-

[6] Margaret D. Foster, U. S. Geological Survey; oral communication.

erable supply of ground water derived directly from rainfall and from inflowing streams. Such an environment would have provided an abundance of vegetation to serve as the basic food supply for the Bridger fauna. Comparatively dry hot summers may be inferred from the location of the area in a continental interior and possibly also from the desmids, if their great concentration in the coprolite indicates a low-water stage of the pool from which the animal drank.

ACKNOWLEDGMENTS.

It is a pleasure to acknowledge the helpful suggestions of my friend G. Evelyn Hutchinson, of the Osborn Zoölogical Laboratory at Yale, who reviewed the complete text and who, very generously, collected and made a chemical analysis of dog feces so as to provide a better basis for interpreting the geochemistry of the coprolites. Equally pleasurable is it to acknowledge the generous assistance of Prof. G. W. Prescott, of Albion College, and Dr. Hannah Croasdale, of Hanover, New Hampshire; Professor Prescott for his authoritative criticism and suggestions concerning the identification and systematic treatment of the algae, and Doctor Croasdale for translating descriptions of the new species into Latin.

Here I wish also to express thanks to my colleagues of the Geological Survey. At considerable inconvenience to himself, the late Dr. R. C. Wells, Chief Chemist, generously shared his own laboratory space with me while the chemical analysis of the coprolite was being made. He also gave me much-needed advice on analytical procedures. I am particularly indebted to Dr. K. E. Lohman who made all the photomicrographs, disintegrated the acid-treated specimens and mounted the washed residues in synthetic resins, and who studied certain of the microörganisms. As upon many previous occasions, I am grateful to Dr. C. H. Dane who read the manuscript critically and gave general counsel during its preparation.

SYSTEMATIC DESCRIPTIONS.

Bacteria.

ESCHERICHIA BRIDGERANA, Bradley, n. sp.

Plate 2, Figs. 1-4.

Cellulae cellulis *E. coli* atque formarum affinium entericarum consimiles; plerumque circa 3 micra long. atque 1 micron diam.

sed exspatiatae longitudine a minus quam 2 ad circa 17 micra. Formae cellularum variant a corporibus brevibus ovatis atque coccoideis per breves virgulas obtusas, cellulas fusi- atque claviformes usque ad virgulas elongatissimas curvatasque. Capsulae atque sporae ignotae. Gemmatio magna ex parte per fissionem binariam necnon autem per gemmationem terminalem atque lateralem.

Cells resembling those of *E. coli* and related enteric forms; usually about 3 microns long and 1 micron in diameter but having an extreme range in length from less than 2 to about 17 microns. Cell shape ranges from short ovoids and coccoids, through blunt-ended short rods, fusiform cells, and clubs, to very much elongated and curved rods. Capsules and spores unknown. Gemmation mostly by binary fission but also by terminal and lateral budding.

ALGAE.

CHRYSOPHYCEAE.

Lagynion Pascher.

LAGYNION. sp.

Plate 4, Fig. 5.

Lorica flask-shaped, robust, and rather short necked (unless some of the neck has been broken off). Height 31 microns, maximum diameter about 29 microns. Protoplast and method of reproduction unknown. Presumably an epiphyte.

This alga resembles *L. ampullaceum* (Stokes) Pascher but is nearly 10 microns taller than this living species despite its short neck (Pascher, 1913). It exceeds in size still more the other species of *Lagynion* described by Pascher.

CHRYSOPHYCEAE.

OCHROMONADACEAE? or CHROMULINACEAE?

Plate 4, Figs. 6-12.

These minute, feathery, bell-shaped silicified objects are inferred to be either the loricae of chrysophycean algae or a diminutive species of *Cyrtophora*. Each one of the smaller kind (Plate 4, Fig. 6) consists of a bell-shaped cup that is slightly constricted about midway between the apex and the open end. Inside the cup at this constricted zone is a ring of rounded nodes. From these nodes outward to the open end the

walls of the cup are cut into narrow stiff ribbons (or tentacles). The apex of the cup is attached to a stem or pedicel that is curved into a narrow U-shape and that has on its other end a smaller and apparently less fully developed cup. The whole organism is only about 9 microns long and the larger cup is about 4½ microns in diameter. A single unattached cup nearly twice the size of those having pedicels shows particularly well the inner ring of nodes (Plate 4, Fig. 7). Similar but even smaller cups not attached to pedicels are fairly numerous. Some of these are only about 2 microns in diameter. Neither the protoplast nor method of reproduction are known.

The general morphology of these fossils suggests that they are either the loricae of flagellate algae in the family Ochromonadaceae or an exceedingly small species of *Cyrtophora* in the Chromulinaceae. The fossils are, however, considerably more complex than any of the described living genera of the Ochromonadaceae and they differ from them and from such genera as *Cyrtophora* in having loricae at opposite ends of a recurved pedicel. The ring of bristles around the mouth of the lorica suggests the ring of setae or tentacles around the peristome of certain flagellate Protozoa.

The other group of slightly larger organisms found in the coprolite that also may be the loricae of flagellate algae are illustrated (Plate 4, Figs. 8-12). Although these individuals show a considerable variety of form they appear to constitute a developmental series. The simplest and therefore presumably the youngest form is that of a U tube 8 to 10 microns long whose open ends are flared like a trumpet (Plate 4, Fig. 8a). In the next two stages the walls of the flaring part of the U tube break up into narrow ribbon-like strips (Plate 4, Figs. 8b, 9). In the fourth stage the bottom of the U tube has apparently split and unrolled. Small nodes appear at the base of the bundles of strips (Plate 4, Fig. 10). Views of the objects inferred to be taken at about right angles to Fig. 9 of Plate 4 are shown in Fig. 11 of the same plate. Beyond this the sequential arrangement of the forms is not clear. Nevertheless, of exceptional interest is an individual that has another growing within it (Plate 4, Fig. 12). The smaller one is attached to the inner wall of the larger at a small but conspicuous node. This habit suggests certain colonial flagellate algae such as *Dinobryon*, whose loricae grow one based within the next below.

Although it is inferred that the objects in the series just

described are the loricae of minute flagellate algae their identity is not at all certain.

CHLOROPHYCEAE.

VOLVOCALES.

CHLAMYDOMONADACEAE.

CHLAMYDOMONAS sp. Ehrenberg.

Plate 4, Fig. 2.

Cell ovoid with one prominent anterior papilla. Length (including papilla) approximately 30 microns, width approximately 17 microns. Flagellae, internal structures, and mode of reproduction unknown.

Despite the unknown features of this fossil it bears a striking resemblance to *Chlamydomonas* Ehrenberg. Though perhaps somewhat smaller it is more like *C. gloeocystiformis* Dill than any of the other living species.

CHLOROCOCCALES.

OOCYSTACEAE.

Closteridium Reinsch.

CLOSTERIDIUM BULLIFORME, Bradley, n. sp.

Plate 4, Fig. 4.

Cellulae solitariae, pustuli- aut vesiculiformes, quarum latus alterum rectum, alterum alte arcuatum. Polus uterque habet spinam brevem, rectam, subtenuem, a superficie convexa deorsum directam. Membrana cellulae crassula atque levis, praeter illas spinas duas polares. Cellula sine spinis long. 60 micra, lat. 22 micra; spinae long. 8 micra. Chloroplastus, pyrenoidea, et modus reproductionis ignota. Una tantum cellula consociata cum multis desmidiis atque nonnullis aliis algis inventa est.

Cells solitary, blister- or bladder-shaped, one side straight and the other highly arched. At each pole is a short, straight, and rather fine spine that is directed downward from the convex surface. The cell wall is rather thick and is smooth except for the two polar spines. Length of cell without spines 60 microns, width 22; spines 8. Chloroplast, pyrenoids, and method of reproduction unknown. Only one cell was found associated with many desmids and a few other algae.

C. bulliforme resembles *C. siamensis* (W. and G. S. West) Smith in having one side straight and the other strongly curved. In cell size *C. bulliforme* is more nearly comparable to *C. siamensis*, which is 77 microns long without the spines and 28 microns wide. In the shape and orientation of the spines, however, *C. bulliforme* is more nearly like *C. crassispinum* Reinsch, though the spines are much more delicate.

ZYGNEMATALES.

DESMIDIACEAE.

Cosmarium Corda.

COSMARIUM sp. cf. *C. pachydermum* Lund.

Plate 3, Figs. 10-11.

Hoc desmidium satis persimile est illi *C. pachydermo* vivo per formam rotundatam, isthmum maxime latum atque membranam specie crassam. Paucis exemplis inventis, impossibile dici utrum similitudo ad membranam punctatam pertineat. Forma a latere visa ignota.

Longa 52 micra; isthmus lat. 26 micra.

This desmid resembles rather closely the living *C. pachydermum* in its rounded outline, exceptionally wide isthmus, and apparently thick cell wall. Whether the similarity extends to the punctate wall or not is impossible to say from the few specimens available. The shape in side view is unknown.

Length 42 microns; breadth of isthmus 26 microns.

Staurastrum Meyen.

STAURASTRUM ENTEROXENUM, Bradley n. sp.

Plate 2, Figs. 5-10; Plate 3, Figs. 1-9.

Cellulae parvae, longiores quam latae, ad isthmum tortae per 180°; a latere visae profunde constrictae, non autem a fronte, sinus apertus, a latere visus acutus, a fronte autem obtusus; semicellulae satis late ellipticae ad paene obovatas, angulis lateralibus rotundatis. A vertice visae triangulares, angulis rotundatis, lateribus convexis aut paene rectis, angulis semicellulae superioris cum illis semicellulae inferioris alternantibus. Superficie membranarum cellularum non bene preservata; aliae suggerunt membranam levem, aliae subiliter granulatam esse. Chloroplasti axiales, parvi (?), specie duo corpora pocu-

liformia, tergum contra tergum habentia, in isthmo juncta; pyrenoidea magna, singulum (?) in semicellula.

Cellula 30-33 micra long., isthmus lat. (a fronte visus) 15-20 micra, (a latere visus) 6-9 micra.

Cells small, longer than broad, twisted at the isthmus through 180°, deeply constricted in side view but not in front view, sinus open and acute-angled in side view but obtuse-angled in front view; semicells rather broadly elliptic to almost obovate, lateral angles rounded. Vertical view triangular, angles rounded, sides convex or nearly straight, angles of upper semicell alternating with those of the lower semicell. Surface of cell walls not well preserved; some individuals suggest that the wall is smooth, others that it is finely granulate. Chloroplasts axile, small (?), apparently two cup-shaped bodies back to back with the junction in the isthmus; pyrenoids large, one (?) in each semicell.

Length 30 to 33 microns; breadth of isthmus (front view) 15 to 20, (side view) 6 to 9 microns.

Zygospores found with the desmids, though by no means certainly belonging to this species, are large (68 microns in diameter) globose and ornamented with closely spaced rather coarse conical verrucae, each of which bears a short spine at its apex (Plate 2, Fig. 10). The few zygospores found resemble those figured by the Wests (1911, pl. 125) for *Staurastrum orbiculare* W. and G. S. West.

The form and size of these fossil desmid cells are very nearly like the living *S. alternans* Brebisson which, according to the Wests (1911), has a world-wide distribution. The fossil desmid differs from *S. alternans* in being longer than wide, in having a convex or more rounded triangular outline in vertical view, and in having a much broader isthmus in front view.

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U. S. Department of the Interior,
Geological Survey,
Washington, D. C.