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Diatoms from a native Iowa prairie

by

Judith Elizabeth Hunt Loescher

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Botany and Plant Pathology
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With one exception, no attempt to study intensively the diatom flora of prairie soils in the United States has been made. The major objective of this investigation was, therefore, to examine and report the diatom flora of an Iowa prairie soil which has been relatively unmodified by man's activities. A secondary objective of the study was to determine whether certain taxa are associated with particular prairie habitats. Sheeder Prairie, Guthrie County, Iowa, was selected as the study area because the diverse topography and soils and well-defined vegetational areas produce a variety of distinct habitats and because recent information was available on the ecology of the site with particular reference to higher plant vegetation.
Algae are generally regarded as inhabitants of bodies of water. However, numerous taxa are able to survive and reproduce in a variety of non-aquatic habitats. They are found in and on the soil; on bark, wood, mosses, and rocks; in caves; and on snow and ice. Various terms have been applied to such algae on the basis of the habitats in which they occur. Although these terms are intended to be descriptive, their use has sometimes resulted in confusion. In some cases a single term has been defined in several ways. Frequently in taxonomic and ecological papers, the terms are used without definition. For these reasons a summary of some of the terms applied to non-aquatic algae is presented.

Algae that are able to grow without being immersed in water and that do not form special resting stages during long periods of desiccation have been called "aerophilous" by Petersen (1915). However, in 1928 Petersen (1928a) noted that in many algae it is difficult to distinguish an ordinary vegetative cell from a special resting cell. He therefore abandoned the term "aerophilous" and replaced it with "aerial", using this term for those algae that are able to grow without being immersed in water and that may or may not form resting stages during prolonged periods of desiccation.

Smith (1950) defined the term "aerial" in essentially the same way as Petersen but added that aerial algae obtain their water mainly or entirely from moisture in the air. He listed as strictly aerial habitats the bark and leaves of trees, woodwork, stones, and rocky cliffs. Terrestrial algae are found on and in the soil. Smith (p. 17) stated
that "terrestrial algae are more nearly aerial than aquatic, but it is impossible to differentiate between aerial and terrestrial on the basis of the source of water."

Skvortzov (1937a, 1937b, 1938c) published several papers on subaerial diatoms — diatoms found living in the soil, on tree bark, on mosses growing on rocks, and in caves. He stated (1937b, p. 443), "Subaërial diatoms belong to the aerophilous algae, which are adapted to obtaining their water by absorption of atmospheric moisture and which survive the usually frequent dry periods, on which they are dependent because of their mode of living, without undergoing any particular resting stages."

Stoermer (1962) used the term "subaerial" to describe an undercut rock face of a waterfall which was supplied with considerable moisture as seepage and as spray from the falls.

Several authors have proposed classification systems for non-aquatic algae according to their habitats. Kolbe (1932) proposed the following system:

Aerial-aquatic habitats—which are at least occasionally moistened by water
1. hydropetric habitats—rills, especially on cliffs
2. caves
3. tidal zones and surf and spray zones
4. snow and ice

Aerial habitats—extremely dry habitats; inhabitants are the atmophytic algae
1. bryophytic forms—moss inhabitants
2. endolithic forms—rock inhabitants
3. epiphylllic forms—leaf inhabitants
4. edaphic forms—soil algae

In 1935 Petersen proposed the following classification system:

Aerial algae—such algae as grow out of water
1. Eu-aerial—occurring on prominent objects and drawing moisture exclusively from the atmosphere in the form of rain or dew
2. Terrestrial algae—growing on soil of all kinds
   a. Aero-terrestrial—such algae as often occur in aerial locations, but are found growing on the ground as well
   b. Eu-terrestrial—such as normally grow in or on soil only moistened by atmospheric water
      1. epiterranean—on the surface of the soil
      2. subterranean—occurring below the surface of the soil
   c. Hydroterrestrial—growing on soil which is always damp to wet
      1. freshwater
      2. saltwater
   3. Pseudo-aerial—grow on rocks and in other localities receiving a special supply of water (spray, springs, etc.)

Tiffany (1951) presented the following classification:

Edaphophytes—algae growing on or in soil
   1. Saphophytes—surface algae, completely or almost entirely exposed
   2. Cryptophytes—subterranean algae, not generally exposed

Aerophytes—algae growing on structures extending from or above the soil, not strictly soil forms
   1. Epiphyllophytes—algae growing on leaves
   2. Epiphloeophytes—algae growing on bark
   3. Epizoophytes—algae growing on animals
   4. Lithophytes—algae growing on or in rocks

Cryophytes—algae growing on ice or snow

Chapman (1964) classified terrestrial algae as follows:

Aerophytes
   1. Epiphyllophytes—algae growing on leaves
   2. Epiphloeophytes—algae growing on bark
   3. Epizoophytes—algae growing on animals
   4. Lithophytes—algae growing on rocks

Edaphophytes—algae that grow on or in soil
   1. True soil species
      a. Epiterranean—lying in the surface layers of the soil
      b. Subterranean—lying in the lower layers of the soil
   2. Casuals

Lund (1945) defined soil diatoms as those growing on soil moistened solely by direct atmospheric precipitation. According to Hustedt (1957), the terms "terrestrial" and "euterrestrial" tend to indicate that only the more or less moist soils are used as residences. Algae, however, are
not restricted to bare soils but are able to live in moss swards, on rocks, etc. Hustedt maintained that since the most essential characteristic of these habitats is better aeration, the terms used should relate to oxygen. He therefore proposed the classification given below:

- $O_2$-euryplastic (euryök)—all species which live both in water and in aerial habitats
- $O_2$-stenoplastic (stenök)
  - aerophilic—living by preference in aerial habitats
  - aerobiontic—limited to aerial biotopes

Algae have been recognized as components of the soil flora for several hundred years. Paracelsus mentioned the name *Nostoc* in the sixteenth century. Many references were made to soil algae in the literature of the following two centuries. In the nineteenth century considerable interest in cryptogams developed, resulting in the description of numerous new species of algae, including many that are found in or on soil. Petersen (1935) has summarized these early reports.

Algae have been found in soils of all types and at various depths. They are usually most abundant at or near the soil surface. Members of the Chlorophyceae, Cyanophyceae, Chrysophyceae, Xanthophyceae, Bacillariophyceae, Euglenophyceae, and Rhodophyceae have been reported from soils (Petersen, 1935; Fehér, 1936; Fritsch and John, 1942; Bold, 1970). Representatives of the Chlorophyceae and the Cyanophyceae are most common. Most of the genera found in soils are also represented in aquatic habitats. Some species are found in both aquatic and terrestrial habitats.

Of the several reviews of soil algae published in the last forty years, the best known and the most detailed is that of Petersen (1935). General discussions are presented by Fritsch (1922) and Lund (1962, 1967).
Recent reviews of the development and trends in soil algology in the USSR were written by Forest (1965) and Novichkova-Ivanova (1968). Forest (1962) summarized methods used in the analysis of soil algal communities and compared the results of four methods employed on two soils.

Two principal approaches to the floristic study of soil algae are direct examination and indirect examination. The former involves a microscopic examination of organisms in the materials collected. One of the techniques classified as indirect examination involves the culturing of the algae from soil and the study of them in cultures.

Both direct and indirect observation may lead to incomplete disclosure of the flora. Soil or other particles may obscure the algae in direct examination. The algae are generally present in relatively low numbers, so that large quantities of soil must be examined. The culture media used in indirect observation of the flora may favor the development of certain algae while inhibiting the development of others. Also, certain organisms may suppress the development of others by competition. A problem related to the use of indirect examination for determination of the algal flora is that results obtained by one investigator for a particular habitat may not be strictly comparable to those obtained by another worker for a similar habitat because different culture media or methods have been used.

Although numerous papers have been written on the soil algal flora of various localities, most of the effort has apparently been concentrated on identification of members of the Chlorophyceae, Cyanophyceae, and Xanthophyceae. Diatoms are frequently not identified to species — occasionally not even to genus — even though they are found in most
Fifty-nine infrageneric taxa of diatoms from 17 genera were reported. Direct examination supplemented by culture methods yielded 60 infrageneric taxa of diatoms from soils of a Danish preserve (Petersen, 1934). Soils stored, air-dry, for 36 months before culturing yielded five species and forms of diatoms; those stored for 30 months yielded nine (Petersen, 1935).

In a study of Australian soil algae, Phillipson (1935) reported very few diatoms in cultures developing from garden and virgin bush soil and was able to identify only two species. She observed that diatoms appeared in culture long after the other algae were well established.

The influence of pH on the soil algal flora has been of interest to several investigators. Diatoms were reported to be more characteristic of alkaline than acid soils (John, 1942; Fritsch and John, 1942). Fifteen diatom species, varieties, and forms were found in cultures developing from 24 British surface soils. Also studied were seasonal variations in taxa, differences in composition in cultures of soil from various depths, and algal succession in cultures maintained for several months. Brendemühl (1949) observed 114 forms of diatoms from enrichment cultures of 167 soil samples from various habitats in Germany. Floras developing from soils varying in moisture content and pH were compared. In a study of nine diverse German soils, Schelhorn (1936) found that the soils which had pH values in the neutral range produced the greatest number of diatom taxa in culture.

Diatoms living on bryophytes in various parts of the world have been the subjects of many studies. Carlson (1921) reported numerous diatom species from stones, soil, and mosses collected from Antarctic, South Georgia and the Falkland Islands. Mosses collected from a cave and from
trees and rocks in China also contained diatoms, among which were several new taxa (Skvortzov 1937a, 1937b, 1938c). Beger (1927) examined large numbers of mosses from trees, rocks, and soil from northern and central Germany. He observed that generally the number of diatom species living in aerial mosses is very low, usually less than 10, while the number of individuals is relatively high. Beger (1928) also compared the diatom floras of xerophytic and hydrophytic mosses from the alps. Krasske (1932) studied diatoms from the Austrian and German alps including those of dry mosses. He reported 67 species in 23 genera from 16 of the dry moss collections. Krasske (1948) also reported 29 infrageneric taxa of diatoms from mosses collected in South America, Java, Sumatra, and Ceylon. Hustedt (1942) exhaustively studied seven collections of liverworts and mosses from northwest Germany and reported 147 forms of diatoms from 22 genera. He also reported a number of aerophilic diatoms from the Sinai Peninsula and Lebanon (1949a). Brendemühl (1949) observed 35 forms of diatoms in cultures of five mosses from Germany.

Important contributions to the taxonomy and ecology of soil diatoms were made by Lund, who studied the diatom flora of 66 British soils by direct examination and by culture. Among the soils sampled were woodland, moor, garden, field, path, and grassland soils. He reported 13 genera with 52 species, varieties, and forms (Lund, 1946). He discussed the ecology of soil diatoms, their small size as compared with aquatic forms, the effect of size on the form of diatoms, and size in relation to environmental conditions. Seasonal variation and microstratification in a garden soil were also studied (Lund, 1945).
Bunt (1954) studied the diatom flora of Macquarie Island soils. He observed 18 genera and over 40 species. Thirteen forms, including seven new records for India, were found by Gandhi (1956) in a study of wet surface soils from Kolhapur, India, during the rainy season. Rosa and Lhotsky (1971) reported 14 species and forms of diatoms from high moor and humus-podzol soils from the Iser Mountains in northern Bohemia. Hantzschia amphioxys and Pinnularia borealis, considered to be the most ubiquitous soil diatoms, were the most frequent of all diatoms found.

Bock (1963) carefully examined the diatom flora of thin layers of soil and incrustations of rocks and seams of walls, all of which lacked a protective cover of mosses. Although these are considered to be extremely dry habitats, 107 infrageneric taxa were observed. Of these, 33 were considered indigenous. In another study (Bock, 1970), 45 collections of thin layers of soil from European rocks and walls yielded 107 species, varieties and forms of diatoms, all regarded as more or less regular residents of the habitats. An additional 60 species and varieties were considered as accidentals and not reproducing in the environment.

Flint (1958) determined the frequency of algae on the surfaces of three New Zealand tussock grassland soils by direct observation. Samples were taken at least once a season over the course of a year. In six out of 13 samples diatoms were observed to be the dominant group of algae. Flint concluded that seasonal periodicity is not a definite characteristic of soil algae. Potul'nikskii (1962) studied by direct examination 80 samples of soil from the Ukrainian SSR to determine biomass and the seasonal changes in numbers of cells per gram of soil. The diatom genera
observed were not listed, although one report of 20-50 thousand diatoms per gram of soil was given.

Esmarch (1911, cited by Petersen, 1935) and Robbins (1912) were the first investigators to report living algae from deeper layers of soil. Since the publication of their reports, the ability of algae to live deep in the soil has been questioned by several investigators. Culture methods have been used because relatively small numbers of algae are usually found below the soil surface. James (1935) observed several diatom taxa in cultures of four British soils collected at two and eight inch depths. Moore and Karrer (1919) found two diatom taxa in cultures of Missouri Botanical Garden soil from a depth of 100 cm. A culture of Missouri Botanical Garden soil obtained at a depth of 65 inches yielded one diatom species; yet diatoms were not found in cultures from the top 18 inches (Moore and Carter, 1926). Petersen (1935) reported only a few diatom species from several cultures of Danish soil from 20-30 cm depths.

Celecia and Morris (1966) studied the algal flora of seven Georgia Piedmont soils, each sampled at three depths. Four diatom genera were observed but the species were not identified. In a similar study of virgin and cultivated Venezuelan soils, Balloni and Matarassi (1968) also observed diatoms but did not identify them to species. However, they reported that the algal flora of the soils studied is composed primarily of Chlorophyceae and Bacillariophyceae.

Many investigations of soil algae have been undertaken in the United States. Coyle (1935) cultured soils from all seven major soil areas in Ohio and reported that diatoms were practically the sole algal
soils examined. The papers mentioned below represent a portion of the literature on aerial algae involving discussions of diatoms.

Diatoms were first reported from soils by Ehrenberg (1843), who examined soil adhering to plants collected in South America and Alaska. Among the many new taxa he described were Hantzschia amphioxys (Ehr.) Grun. and Pinnularia borealis Ehr., now recognized as two of the most common soil diatoms. Various authors described diatoms from aerial habitats in the latter part of the nineteenth century, but it was in the twentieth century that great interest in the soil algal flora developed. The investigations of Bristol and of Petersen discussed below were particularly important in stimulating research on soil diatoms.

Bristol (1919) reported one diatom, Nitzschia palea, among the algae appearing in a liquid culture of an English soil which previously had been stored, air-dry, for 48 years. She reported the development of numerous diatom taxa in cultures of cultivated soils which had been dry from four to 26 weeks (Bristol, 1920). She later studied the algal flora of some freshly collected arable English soils. The six diatom species found were present in cultures of both manured and unmanured wheat field soil. The same six taxa were found among other algae in cultures of soil from an adjacent manure plot (Bristol Roach, 1927).

Using culture methods and direct observation, Petersen (1915) reported 36 species of diatoms from 11 genera from Danish soils. In a study of the aerial algae of Iceland, he observed 25 diatom genera with over 100 species by direct examination of collections from soil, woodwork, stones, cliffs, caves, and trees (Petersen, 1928a). In another study, the soil algae were examined in culture (Petersen, 1928b).
constituents of acid soils. She identified 40 species and varieties of
diatoms from soils, from woods and cultivated and uncultivated fields.
Using a different culture medium and 12 Tennessee soils, Hofstetter (1968)
observed that diatoms were absent from the acid soils of azalea beds but
were present in most other soils. The disparity of these two reports
illustrates a serious problem associated with the use of culture methods in
defining the algal flora of soils or other habitats.

Willson (1958) studied comparatively the algal flora of oak forests
and tall grass prairies in central Oklahoma. Twenty-three species of
diatoms were reported from cultures. Six algae classed as "predominants"
(those algae occurring in 45-100 per cent of the soil samples per season)
were common to both vegetation types; three of these were diatoms
(Hantzschia amphioxys, Navicula mutica, and Pinnularia borealis).

Four diatom taxa (not identified to species) were observed among
algae which developed from cultures of 60 soil samples of neutral loamy
sand and alkaline sandy loam from Washington (Fairchild and Willson,
1967). One diatom species was reported from cultures of algae started
from soil particles adhering to herbarium specimens from the Missouri
Botanical Garden (Parker, Schanen and Renner, 1969).

Seasonal collections of virgin arid soils from Utah yielded diatoms
in addition to green, yellow-green, and blue-green algae. No clear
seasonal variation in the algal flora was observed. Diatoms were among
those algae predominating in eight of the nine samples collected over a
two-year period (Martin, 1939). Direct examination of soils of the
Sonoran Desert of Arizona yielded unidentified diatoms in addition to
numerous blue-green algae (Cameron, 1960). VanLandingham (1966) observed
61 infrageneric diatom taxa from three samples of dry lake beds in Nevada. Most of the taxa found are characteristic of dry habitats. From a similar area in takyrs in the Turansk Plain (USSR), Sdobnikova (1958) reported eight infrageneric taxa of diatoms. Cyanophyta and Chlorophyta were most numerous in the clayey soils.

Forest, Willson and England (1959) autoclaved soil from a tall grass prairie, then replaced the soil in the prairie. The algal floras of sterilized and unsterilized soil were examined after 1, 3, and 5-1/2 months of exposure. Twelve diatom species and varieties were observed.

The first of several studies on aerophilic diatoms in Iowa was done by Hayek and Hulbary (1956). The authors examined six Iowa City soil samples and observed 18 species, eight of which had not been reported previously from soils. Stoermer (1962) found 40 species of diatoms on the moist undercut rock face of South Falls near Pella. About half of those taxa are well represented in the aquatic flora of Iowa. The rest have been regarded by various authors as being characteristic of alpine, northern or aerial environments. Lichen and moss collections from Ledges State Park in Boone County yielded 10 species that were common in the collections (Dodd and Stoermer, 1962). Reimer (1970) took six samples from Cayler Prairie, a tall grass prairie in northwest Iowa. He found 70 diatom species, varieties, and forms in six samples. Two samples were collections of plankton from intermittent standing water. Only four of the collections were of duff and soil. However, results of the study indicate that the upland soil diatom flora is much less diverse than that of the swale.
MATERIALS AND METHODS

Description of Study Area

Sheeder Prairie is one of four prairie remnants in the Iowa preserve system. It is located in the SW 1/4, Section 33, Seely Township, Guthrie County, Iowa. The preserved area totals 10.1 HA, of which 9.3 HA are native prairie. The remaining 0.8 HA is composed of areas around the edges of the plot that were formerly under cultivation but are now reverting to prairie vegetation.

Sheeder Prairie is diverse physically as well as in its vegetation. It is located in the Shelby-Sharpsburg-Macksburg soil association area. The soils have developed under prairie vegetation from five types of parent material — loess, glacial till, alluvium, till-derived sediments over till, and paleosol. The topography includes ridges, slopes varying in degree from steep to slight, drainage ways, and relatively flat alluvial areas. The combination of slope position, aspect, and soil parent material provides a range of moisture conditions.

A detailed analysis of the higher plant vegetation as it is related to slope position was presented by Kennedy (1969). He characterized the prairie as a mesic, tall-grass dominated upland prairie. Two belt transects with a common origin were positioned to encompass the maximum variations in altitude and parent materials. On the basis of slope position and parent material he established 18 stands along the two transects. According to the prairie continuum analysis performed, the continuum index values of the stands ranged from 347.3 (dry-mesic) to 265.5 (wet-mesic).
For the study of the diatoms of Sheeder Prairie, nineteen collection sites were chosen to represent a number of habitats present in the prairie (Fig. 1). Wooden stakes were used to mark the sites. No attempt was made to quantify the vascular plant vegetation at the sampling sites.

Brief descriptions of the collection sites are given below. Plant species occurring at the sampling sites are listed, together with the soil parent material when it is known. Each of the ten sites corresponding to locations on Kennedy's transects is identified by a hyphenated number. The first part of the number designates transect 1 or 2; the second is the distance in meters from the common origin of the transects.

Station 1—*Ambrosia trifida* L., *Helianthus laetiflorus* Pers., *Verbena hastata* L.


Fig. 1. Topographic map of Sheeder Prairie. Locations of the nineteen collection stations are indicated. Contour intervals are 2.5 feet with all elevations relative to the lowest point on the prairie.
Station 9 (1-0)—*Phlox pilosa* L., *Panicum scribnerianum* Nash, *Poa pratensis* L.
Parent material: loess

Station 10—*Prunus americana* Marsh., *Rhus radicans* L.


Parent material: alluvium

Parent material: Kansan till

Station 15 (2-240)—*Ceanothus ovatus* Desf., *Elymus canadensis* L., *Stipa spartea* Trin., *Poa pratensis* L.
Parent material: Kansan till


Station 17—*Cannabis sativa* L., *Ambrosia trifida* L., *Chenopodium album* L.

Station 18—*Acer negundo* L.

Station 19—*Acer negundo* L., *Amblystegium varium* (Hedw.) Lindb.

Collecting and Preserving Techniques

Collections from the 19 sites described above were made on the following dates:

- September 21, 1969
- January 25, 1970
- April 11, 1970
- June 6, 1970
- September 23, 1970
- October 28, 1970
- December 6, 1970
Supplementary collections, studied less intensively, were made on the following dates:

May 19, 1969
June 15, 1969
July 20, 1969
October 11, 1970
November 15, 1970

The May collections were made at various locations on the prairie. In June and July samples were taken at 10-m intervals along Kennedy's transects. On the last two dates collections were made at the 19 sites described above.

All of the collections made except those from stations 18 and 19 were of litter from the surface of the soil. The following procedure was followed in collecting litter samples. Decaying vegetation on the surface of the soil from an area about 25 cm$^2$ and no further than about 30 cm from the marker stake was removed and placed in labeled plastic sandwich bags. Localized areas where the soil was obviously disturbed were avoided. At station 18 the soil surface from an area of about 25 cm$^2$ was scraped up or chipped out and placed in a bottle or a plastic bag. On May 19, 1969, when water was standing at this site, the bottom sediments were collected with a small pipette. Mosses growing on soil at station 19 were removed with as little soil as possible and placed in a bottle or plastic bag. All samples were transferred to labeled vials and preservative (formalin or Transeau's solution) was added.

Preparation of Samples for Light and Electron Microscopy

Because the taxonomy of diatoms is based almost exclusively on the sculpturing of the siliceous cell walls, it is necessary to remove the protoplasts before identification of taxa can be attempted. After
"cleaning" the valves must be mounted in a medium having a high index of refraction. Although all identifications were made from prepared slides, freshly collected or preserved material was examined occasionally in wet mounts to determine which taxa were living at the time collections were made.

The cleaning technique used is a modification of the nitric acid-potassium dichromate method described by Hohn and Hellerman (1963). After cleaning, the diatoms were allowed to settle for at least 8 hours before the supernatant was decanted. The dilution process was repeated until the supernatant was colorless and its pH was 4 or higher. Occasionally large amounts of higher plant cell wall material remained after cleaning. In such cases the sample was flooded with 72% \( \text{H}_2\text{SO}_4 \) (w/v) and allowed to stand overnight. Dilution was carried out as described above.

Permanent slides were made in the following manner. A suspension of the cleaned material in water was placed on a clean coverslip and allowed to dry slowly. The coverslip was then heated to evaporate any remaining water. A drop of Hyrax mounting medium (Index of Refraction 1.71 — Ruedrich, personal communication, 1971) was placed on the microscope slide. The coverslip was inverted and placed on the medium; then the preparation was heated to evaporate the solvent.

Light microscopic observations were made with a Leitz Laborlux microscope. Photographs were made using a Nikon F camera and either Kodak Pantomic-X or High Contrast Copy film.

Because many soil diatoms are extremely small and their wall markings are difficult to discern with a light microscope, it was
thought that useful information might be obtained from transmission electron microscopy. Techniques developed by Begres (1971) for studying the same specimen with both the transmission electron microscope and the light microscope were employed. The samples were first cleaned by the standard hydrogen peroxide-potassium dichromate method (Werff, 1955). After removal of the reagents by dilution and decantation, the samples were boiled gently in concentrated nitric acid until the sediment was almost white. The acid was removed by successive decantations; the diatoms, suspended in distilled water, were placed on copper grids (3 mm diam., 150-200 mesh, coated with a 0.5% Formvar film), and the water was allowed to evaporate slowly. The grids were inspected with the aid of a compound microscope to locate particular taxa for study. Dr. Begres operated the electron microscope (RCA Model EMU-3F). Photomicrographs were taken using Cronar film.
RESULTS

A total of 74 taxa from 15 genera were observed during the course of this study. All taxa encountered are listed alphabetically in Table 1 with the occurrence of each indicated for each sampling site. Table 2 shows the total number of taxa and the number of accidentals — taxa represented by only one specimen in all of the prairie collections examined — found at each station. In the section following the tables the treatment of each taxon includes a reference, information on occurrence, and a voucher slide number. Voucher slides, which will be added to the Iowa State University diatom collection, are identified by a two-part numbering system. The first part is the date of collection of the sample. The second part consists of the station number (preceding the colon) and the slide number. An "S" preceding the station number indicates that the collection was made at a supplementary collection site which is described on the slide label. The reference is the description and illustration used in making the identification. The sites on the prairie at which each taxon occurred are indicated. In addition ecological comments of other investigators and their reports of occurrence in non-aquatic habitats are summarized. Descriptions of morphological variability and taxonomic problems are presented where appropriate. The plate and figure numbers of each taxon illustrated in this section are given below the name of the taxon.

Achnanthes Bory

_Achnanthes lanceolata_ (Bréb.) Grun. var. _lanceolata_

Slide: 6-6-70 18:5
Table 1. Occurrence of taxa at sampling stations (+ indicates presence, - indicates absence)

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*Descriptions of the sampling stations are found in Materials and Methods
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Reference: Patrick and Reimer 1966, p. 269, Pl. 18, Fig. 1-10.

Found in collections from stations 18 and 19.

Considered by Petersen (1935) to be primarily a hydrophytic species although it appears in the hydroterrestrial community. Regarded by Beger (1928) as a bryophilous species of the xeric type. Found by Krasske (1932) to be especially abundant on irrigated rocks and mosses. Observed by Reimer (1970) in collections from a prairie swale.

Achnanthes lanceolata var. dubia Grun.

Slide: 1-25-70 19:1

Reference: Patrick and Reimer 1966, p. 271, Pl. 18, Fig. 11-15.

Found in collections from stations 18 and 19.


Amphora Ehrenberg

Amphora montana Krasske var. montana

Slide: 4-11-70 18EMd:4

Reference: Krasske 1932, p. 119, Pl. 2, Fig. 27.

Found in collections from stations 18 and 19.

Considered to be an aerophil by Krasske (1938) and Hustedt (1957). Reported from moist mosses under a waterfall by Krasske (1932) and from soils by Lund (1946). Occasionally observed in collections from extremely dry rocks and walls by Bock (1963, 1970). Reported by Reimer (1970) from soil and duff of a prairie swale and hilltop.

Amphora submontana Hust. var. submontana

Slide: 4-11-70 18EM:3

Reference: Hustedt 1949b, p. 112, Pl. 11, Fig. 4.
Only one specimen found in a single collection from station 18. Apparently an accidental. No reports of occurrence in aerial habitats found.

**Caloneis P. T. Cleve**

*Caloneis amphipropaena* (Bory) P. T. Cleve var. *amphipropaena*

Slide: 6-15-69 9:1

Reference: Patrick and Reimer 1966, p. 579, Pl. 53, Fig. 2.

Only one valve found in a single collection from station 9. Apparently an accidental. No reports of occurrence in aerial habitats found. Apparently a hydrophytic species.

*Caloneis bacillum* (Grun.) P. T. Cleve var. *bacillum*

Slide: 6-6-70 19:4

Reference: Patrick and Reimer 1966, p. 586, Pl. 54, Fig. 8.

Found in samples from stations 1, 18, and 19. According to Patrick and Reimer (1966), often found in standing alkaline waters. Reported from moist terrestrial habitats by several workers (Krasske, 1932, abundant on irrigated mosses; Hustedt, 1942, in mosses on a post above water; Stoermer, 1962, on the moist undercut rock face of a waterfall). Found by Dodd and Stoermer (1962) among mosses and lichens and by VanLandingham (1966) in samples from three dry lakes. Reported by Reimer (1970) in duff of a prairie swale. Petersen (1935) considered it not distinctly terrestrial; he reported it as a eutrestrial, hydro-terrestrial and pseudoaerial species from various localities in northern Europe.
Cymbella Agardh

*Cymbella triangulum* (Ehr.) P. T. Cleve var. *triangulum*

Slide: 1-25-70 18:4

Reference: P. T. Cleve 1894, p. 168 (no illustration); Stoermer 1964, Pl. 4, Fig. 10 [as *C. triangulatum* (Ehr.) P. T. Cleve].

Only one specimen found in a single collection from station 18. Apparently an aquatic species; no reports of occurrence in aerial habitats found.

*Cymbella ventricosa* Kutz. var. *ventricosa*

Slide: 1-25-70 19:2

Reference: Cleve-Euler 1955, p. 124, Fig. 1177a (as *C. ventricosa a genuina* Mayer).

Found in collections from stations 18 and 19.

Considered by Petersen (1928a) to be a pronounced hydrophil. According to VanLandingham (1966), not common in non-aquatic environments. Found by Hustedt in mosses on posts in a river (1957) and on liverworts above water (1942). Reported by Krasske (1932) in nearly every sample from irrigated cliffs and mosses.

Fragilaria Lyngbye

*Fragilaria brevistriata* Grun. var. *brevistriata*

Slide: 4-11-70 18ab:6

Reference: Patrick and Reimer 1966, p. 128, Pl. 4, Fig. 14.

Only one specimen found. Probably an accidental.

Infrequently observed in aerial habitats. Although VanLandingham (1966) reported it from three dry lake beds, he found it to be rare.
Reported by Bock (1970) as an accidental in collections from dry rocks and walls.

**Fragilaria construens** var. *venter* (Ehr.) Grun.

Slide: 1-25-70 4:4

Reference: Patrick and Reimer 1966, p. 126, Pl. 4, Fig. 8-9.

Only one specimen found in a single collection from station 4.

Probably an accidental.

Considered by Petersen (1928a) to be "hardly an aerial form".

Reported by VanLandingham (1966) as being uncommon in non-aquatic areas.

Found by Hustedt (1942) on liverworts above water. Found by Krasske (1932) on moist rocks and mosses.

**Fragilaria vaucheriae** (Kütz.) Petersen var. *vaucheriae*

Slide: 9-21-69 6:1

Reference: Patrick and Reimer 1966, p. 120, Pl. 3, Fig. 14-15.

Only one frustule found in a single collection from station 6.

Probably an accidental.

Apparently an aquatic species; no reports of occurrence in aerial habitats found.

**Fragilaria virescens** Ralfs var. *virescens*

Slide: 6-6-70 1:5

Reference: Patrick and Reimer 1966, p. 119, Pl. 3, Fig. 7-9.

Only one specimen found in a single collection from station 1.

Probably an accidental.

Reported by Reimer (1970) from Cayler prairie in three collections from a swale and in plankton samples from intermittent standing water.

Krasske (1932) found this species on moist rocks and mosses but stated
that it was entirely lacking in the xeric and mesic habitats. Petersen (1928a) found it especially abundant in places where water is plentiful at least occasionally. He stated that the species would hardly withstand very intense desiccation.

**Frustulia Rabenhorst nom. cons., non C. Agardh**

*Frustulia vulgaris* (Thwaites) DeT. var. *vulgaris*

Slide: 4-11-70 18ab:1

Reference: Patrick and Reimer 1966, p. 309, Pl. 22, Fig. 3.

Found only in collections from station 18.

Thought by Petersen (1928a) not to be a terrestrial species. Reported by Hustedt (1942) from mosses and liverworts from above water and by Stoermer (1962) from the undercut rock face at the base of a waterfall. Found by Hustedt (1957) on mosses and *Vaucheria* at and above the water surface.

**Gomphonema Ehrenberg nom. cons., non C. Agardh**

*Gomphonema angustatum* (Kütz.) Rabh. var. *angustatum*

Slide: 5-19-69 18:5

Reference: Hustedt 1930, p. 373, Text Fig. 690.

Found in collections from stations 1, 18, and 19.

Reported by VanLandingham (1966) as generally uncommon in non-aquatic habitats. When reported from aerial collections it is usually found in low numbers (Bock, 1963 and 1970, from extremely dry habitats; Reimer, 1970, in soil and duff from a prairie upland). Found in soil and duff of a prairie swale (Reimer, 1970) and in mosses and liverworts above water (Hustedt, 1942).
Gomphonema angustatum var. sarcophagus (Greg.) Grun.

Slide: 1-25-70 18:6

Reference: Hustedt 1930, p. 373, Text Fig. 691.

Found in collections from stations 1, 18, and 19.

Apparently infrequently reported from aerial habitats. Reimer (1970) found a few specimens in duff from a prairie swale. Reported by Hustedt (1942) from mosses and liverworts above water level.

Hantzschia Grunow nom. cons., non Auerswald

Hantzschia amphioxys (Ehr.) Grun. var. amphioxys

Plate I, Fig. 1, 2, 4, 6, 7; Plate II, Fig. 1, 2, 4-6; Plate III, Fig. 1-6; Plates IV, Fig. 1-5.

Slides: 5-19-69 18:5; 1-25-70 5EM:4; 4-11-70 5:1; 4-11-70 18:5; 6-6-70 19:4

Reference: Hustedt 1930, p. 394, Text Fig. 747.

Found in collections from all stations.

Generally regarded as one of the most ubiquitous soil diatoms. Considered by Hustedt (1957) to be an extraordinarily eurytopic species, but abundant only in aerial habitats. Called euterrestrial by Petersen (1935), a bryophilous species of the xeric type by Beger (1928), and a characteristic form of dry mosses by Krasske (1932). Reported to be abundant in mosses near springs by Hustedt (1949a). Found by Bock (1963, 1970) in collections from dry rocks, walls and soil. Found by Lund (1946) on 51 of 66 soils examined; by Hustedt (1942) on mosses and liverworts above water; by Skvortzov (1937b, 1938c) among mosses on tree bark and
rocks; by Hayek and Hulbary (1956) on soils; and by Reimer (1970) in soil, duff, and plankton collections from a prairie.

The specimens observed varied greatly in form and structure (Plate I, Fig. 1, 2, 4, 6, 7; Plate II, Fig. 1, 2, 4, 6). The cells measured ranged from about 27.5-89.5 microns in length and from about 4.5-9 microns in breadth. The striae were coarsely punctate in some specimens and indistinctly punctate in others. The striae count ranged from 13-28 in 10 microns. There were 6-9 keel puncta in 10 microns.

Several valves with abnormal striae and two with abnormal keels were observed (Plate III, Fig. 5, 6; Plate IV, Fig. 2). Also found were valves that had two dissimilar ends. Generally one end of such a valve was more protracted than the other.

Numerous frustules of *H. amphioxys* bearing spines were found in collections from stations 1, 11, 18, and 19 (Plate III, Fig. 4; Plate IV, Fig. 1, 3-5). These spiny frustules were almost always found in linear colonies (Plate III, Fig. 1-4), even in prepared slides of cleaned material. In most colonies a frustule appearing to be normal occupied the central position, and on either side of the central cell there were one to two spiny cells. The central cell of a colony was wider in the pervalvar direction than the adjacent spiny cells. Although the central cells were approximately rectangular in girdle view, many had distinct protuberances in the region of the girdles (Plate III, Fig. 1). The length of the cells measured ranged from 23-66 microns. In girdle view the external valves of the spiny frustules appeared to have normal keels and striae. The innermost valves, however, bore the spines on their internal surfaces and apparently lacked normal keels. Two such valves,
seen in valve view, had abnormal striae patterns and were thinly 
silicified (Plate IV, Fig. 3, 5). The spines projected several microns 
into the cell cavity, often nearly reaching the apposing valve. The 
spines were frequently hooked and in some cases the tips of adjacent 
spines were united. In a few cells the spiny valves appeared to be 
hypothecae. However, in most cells it was impossible to determine which 
valves were hypothecae. Many cells with poorly developed spiny valves 
were found. In one case, two valves, facing the same direction as the 
adjacent valve of the central cell, were observed on one side of a central 
cell. In neither valve was there evidence of formation of an apposing 
valve or plate.

Although several authors (Peragallo, 1920; Krasske, 1949; Dodd and 
Stoermer, 1962; Bock, 1963, 1970) have reported finding cells of 
\textit{H. amphioxys} with spiny valves, neither the descriptions nor the 
illustrations given indicate whether the spines project into the cell 
or outward from the valve surface. I am, therefore, not certain that I 
have observed the same kind of anomalous structures.


Plate I, Fig. 3, 5.

Slide: 1-25-70 5EM:4

Reference: Hustedt 1930, p. 394, Text Fig. 748.

Found in collections from stations 4, 5, 6, 7, 12, and 18.

The specimens found varied less in form and structure than those of 
\textit{H. amphioxys} var. \textit{amphioxys}. The cells ranged from 25-52.5 microns in 
length and from 5-8 microns in breadth. The striae count varied from 
15-22 in 10 microns; the keel puncta were 6-8 in 10 microns.
According to Bock (1970), this taxon is one of the most widespread diatoms of extreme habitats, although he found that it was not especially abundant in a single biotype. Krasske (1932) noted that it was rarer than *H. amphioxys* var. *amphioxys*.

**Meridion Agardh**

*Meridion circulare* (Grev.) Ag. var. *circulare*

Slide: 5-19-69 18:1

Reference: Patrick and Reimer 1966, p. 113, Pl. 2, Fig. 15.

Found in collections from stations 1, 18, and 19.

Numerous cells of *M. circulare* containing internal valves were observed. These were especially common in collections from station 18 made on September 21, 1969, and January 25, 1970.

Found by Krasske (1932) among irrigated mosses of cliffs but not in dry moss. In a report of a culture study, Brendemühl (1949) included this species among those that are found only or predominantly on moist habitats near a body of water. Reported by Hustedt (1942) on mosses and liverworts above water. Considered an accidental in collections of Bock (1970) and Petersen (1928a). Present in soil and duff of a prairie swale (Reimer, 1970).

**Navicula Bory**

*Navicula americana* Ehr. var. *americana*

Slide: 6-15-69 9:1

Reference: Patrick and Reimer 1966, p. 493, Pl. 47, Fig. 3.

One valve found in a single collection from station 9.
Apparently an aquatic species. No reports of occurrence in aerial habitats found.

**Navicula atomus** (Kütz.) Grun. var. atomus

Slide: 1-25-70 19A soil

Reference: Hustedt 1962, p. 169, Text Fig. 1303.

Found in collections from stations 1 and 19.

Considered by Petersen (1935) to be a terrestrial species. Reported to prefer calcareous to non-calcareous substrates (Bock, 1963; Fritsch and John, 1942). Thought to thrive in neutral or alkaline soil containing much organic matter (Petersen, 1928a). A pronouncedly nitrophilous species (Petersen, 1934). Found in a collection of mosses by Skvortzov (1937a) who called it a common subaerial diatom.

**Navicula charlatii** var. charlatii f. simplex Hust.

Plate II, Fig. 3.

Slide: 1-21-69 6:1

Reference: Hustedt 1966, p. 603, Text Fig. 1607b,c.

Found in collections from stations 5, 6, and 7.

No reports of this form occurring in aerial habitats have been found.

**Navicula cincta** var. rostrata Reimer

Slide: 1-25-70 18:7

Reference: Reimer 1961, p. 314, Pl. 1, Fig. 1.

Found in collections from stations 1, 18, and 19.

No reports of this variety in aerial habitats were found.

**Navicula contenta** var. biceps (Arnott) van Heurck

Plate XI, Fig. 1.
Navicula contenta var. parallela Petersen

Slide: 6-15-69 S2-100:3

Reference: Hustedt 1930, p. 277, Text Fig. 458b.

Found in only one sample (from a supplementary collection).

Regarded by Hustedt (1957) as an aerobiontic form. Krasske (1932) stated that although it is one of the most abundant forms of the xeric type, it is also abundant on moist rocks and mosses.

Navicula cryptocephala var. cryptocephala f. terrestris Lund

Slide: 5-19-69 S5:5

Reference: Lund 1946, p. 86; Text Fig. 9H-W.
Found only one specimen (in a supplementary collection).

Reported by Lund (1946) from cultures from 11 soils.

**Navicula cuspidata** (Kütz.) Kütz. var. *cuspidata*

*Slide: 6-15-69 18:2*

*Reference: Hustedt 1961a, p. 59, Text Fig. 1206a.*

Found in collections from station 18.


**Navicula cuspidata** var. *ambigua* (Ehr.) P. T. Cleve

*Slide: 1-25-70 18:4*

*Reference: Hustedt 1961a, p. 62, Text Fig. 1206b.*

Found in collections from station 18.

Regarded by Hustedt (1957) as similar to the species ecologically.

No reports of occurrence on soils were found. This taxon is not recognized by some diatomists.

**Navicula cuspidata** var. *heribaudi* M. Peragallo in Héribaud

*Slide: 1-25-70 18:6*

*Reference: Hustedt 1961a, p. 60, Text Fig. 1207.*

Found in collections from station 18.

No reports of occurrence on soils were found.

**Navicula decussis** Østrup var. *decussis*

*Slide: 5-19-69 S5:1*

*Reference: Patrick and Reimer 1966, p. 518, Pl. 49, Fig. 15.*

Only one specimen found in a supplementary collection.

Apparently an aquatic form. No reports of occurrence in aerial habitats were found.
Navicula dismutica Hust. var. dismutica

Plate VIII, Fig. 2.

Slide: 4-11-70 18:6

Reference: Hustedt 1966, p. 595, Text Fig. 1600.

Only one valve found in a collection from station 18.

Reported by Hustedt (1966) to be very abundant in mosses from the alps.

Navicula minuscula Grun. var. minuscula

Slide: 5-19-69 18:5

Reference: Hustedt 1962, p. 254, Text Fig. 1381.

Found in collections from station 18.

Apparently not usually found in collections from dry aerial habitats.

One cell found by Stoermer (1962) in a collection from an undercut rock face of a waterfall. Reported by Bock (1963) as an accidental from a dry habitat.

Navicula mutica Kütz. var. mutica

Plate V, Fig. 1-19; Plate VI, Fig. 1-21; Plate VII, Fig. 1-7; Plate VIII, Fig. 3; Plate X, Fig. 1-9; Plate XI, Fig. 3-5.


Reference: Bock, 1963, p. 229, Plate 1, Fig. 8-11, 14-17, 35-38, 54-65.

Found in collections from all stations.

Considered to be euterrestrial by Petersen (1935); often aerophilous by Hustedt (1957) and Patrick and Reimer (1966). Found in prairie soil and duff collections by Reimer (1970). Generally regarded as one of the
most common of all soil diatoms. Found on mosses by Krasske (1932, 1938, 1948), Beger (1927, 1928), and Skvortzov (1938c); on mosses and liverworts by Hustedt (1942, 1949a); on mosses and lichens by Dodd and Stoermer (1962). Called a bryophilous species of the xeric type by Beger (1928). Reported to be common to abundant in three dry lakes studied by VanLandingham (1966). Reported from soils by Lund (1946), Brendemühl (1949), Bunt (1954), Hayek and Hulbary (1956), Forest, et al. (1959), and Forest (1962).

Because unsolved taxonomic problems exist in the *Navicula mutica* complex, several of the forms observed will not be assigned to infra-specific categories. For the present time these specimens are placed in categories based on valve outline since in this species this is the main criterion used in the separation of infraspecific taxa. The four groups appear to me to consist of:

1. rhombic forms
2. elliptical forms
3. narrowly lanceolate forms
4. forms not belonging to the above three groups.

Descriptions of morphological variations found among the cells in each category are presented below.

Most of the cells of *N. mutica* observed are members of the first group. These cells are basically rhombic in outline and have broadly rounded ends (Plate V, Fig. 1-19; Plate X, Fig. 1-8). The valve margins are frequently very weakly sinuate. The isolated punctum in the central area is, with few exceptions, a submarginal pore that penetrates the cell wall at an oblique angle with the external opening near the valve margin.
The cells observed varied from about 6-33 microns in length and from about 4.5-9.5 microns in breadth. Striae counts ranged from 18-25 in 10 microns.

Some understanding of the morphological changes associated with a decrease in the size of cells of the rhombic type was gained from examination of a large number of cells, including auxospores, found in the litter samples and in agar cultures established during the course of this study. The morphological variations occurring with changes in size appear to be the same whether the immediate origin of the cells was a culture or a litter sample.

The observed auxospores of the rhombic forms varied in length from about 26-32 microns. The valves were distinctly tumid in the middle and the valve faces were convex (Plate VII, Fig. 4, 5). In most cells the striae were radial throughout, although several cells were seen in which the striae abruptly changed direction from radial to convergent. The puncta were more variable in size and were less regularly placed than in smaller cells. The polar nodules were located entirely on the valve face and one or more rows of puncta could usually be seen between the polar nodules and the valve margins. The distal raphe ends were comma shaped. The proximal raphe ends were usually turned at about right angles to the apical axis. The canal connecting the proximal raphe ends was either entirely visible or only partially visible, the two ends then appearing as "hooks." The isolated punctum was a submarginal pore penetrating the cell wall obliquely with the external opening near the valve margin.

Changes in form and structure accompany the decrease in the size of cells formed by division of auxospores and their derivatives (Plate V, Fig. 1-19). With the decrease in cell length, the polar nodules become
located progressively closer to the poles of the cell, thus becoming less visible (Plate VII, Fig. 7). The position of the oblique submarginal isolated punctum and the striae count and angle change little. In the larger cells portions of the canal connecting the proximal raphe ends were frequently visible as "hooks" (Plate V, Fig. 6, 8). With successive cell divisions the rhombic outline of the larger cells graded into the rhombic-elliptical outline of the smaller cells.

The members of the elliptical group vary in outline from narrowly elliptical (in the largest members) to elliptical (in the smallest members) (Plate VI, Fig. 1-15). The isolated punctum is, with few exceptions, a perpendicular pore located about midway between the valve center and the valve margin. The specimens measured ranged from about 9.5-27.5 microns in length and from about 4.5-7 microns in breadth. The striae count in most individuals was from 18-24 in 10 microns. One specimen with 28 striae in 10 microns was observed.

The third group is composed of a few cells that are narrowly lanceolate with acute ends (Plate VI, Fig. 16-21; Plate XI, Fig. 3-6). The cells vary in length from about 14-19 microns, in breadth from about 4.5-6 microns. "Ghost" puncta are usually present in the central area (Plate VI, Fig. 21) and the isolated punctum is discernible with difficulty or not at all. The striae count ranged from 20-25 in 10 microns.

The fourth group is composed of a small number of cells — some of which may be abnormal forms — that cannot be assigned to the above three form groups. One of these cells is illustrated in Plate VIII, Fig. 3.
Auxospores apparently not belonging to the rhombic form group are illustrated in Plate VII, Fig. 1, 3, and 6.

Abnormal valves of *N. mutica* were found several times and were observed with both the light microscope and the transmission electron microscope. In addition, several cells were found that had one normal and one abnormal valve. Although the form of the abnormal valves was typical in all examples, the striae were composed of puncta that varied considerably in size and shape and that were somewhat irregularly placed (Plate VII, Fig. 2; Plate X, Fig. 9).

*Navicula mutica* var. *mutica* f. *intermedia* (Hust.) Hust.

Plate VIII, Fig. 11-16; Plate XI, Fig. 8, 9.

Slide: 6-15-69 6:1

Reference: Hustedt 1966, p. 585, Text Fig. 1593a, b.

Found in collections from stations 1, 3, 5, 10, 11, 12, 13, and 18.

Reported by Krasske (1948) as an aerophilic moss form of the tropics. Reported from a prairie swale by Reimer (1970) and from a layer of soil on a wall by Bock (1970). Stated by Hustedt (1937) to be abundant only in aerated habitats in springs and brooks and on wet mosses.

The specimens found were from 8-20 microns long, 7.5-9 microns broad, and had about 21-26 striae in 10 microns. Every cell observed differed from the illustrations cited above in that the isolated punctum was formed by an oblique instead of a perpendicular pore.

*Navicula mutica* var. *undulata* (Hilse) Grun.

Plate VIII, Fig. 1.

Slide: 1-25-70 4:4

One specimen found in a collection from station 4.

No reports of occurrence in aerial habitats found.

**Navicula neoventricosa** Hust. var. *neoventricosa*

Plate VIII, Fig. 6-10; Plate XI, Fig. 2.

Slide: 4-11-70 18EM:3

Reference: Hustedt 1966, p. 612, Text Fig. 1612.

Found in collections from stations 5, 15, 18, and 19.


**Navicula nigrii** De Notaris var. *nigrii* sensu Granetti

Slide: 6-6-70 18:4

Reference: Granetti 1968, p. 428, Text Fig. 1, 2.

Found in collections from stations 1, 18, and 19.

*N. minima* Grun., which is included in Granetti's concept of *N. nigrii*, was reported by Hustedt (1942, 1957) from collections of bryophytes and by Hayek and Hulbary (1956) from soils.

**Navicula pseudatomus** Lund var. *pseudatomus*

Slide: 1-25-70 18:7

Reference: Lund 1946, p. 74, Text Fig. 6K-W.

Only one specimen found in a collection from station 18.

Reported by Lund (1946) to be the most ubiquitous soil diatom next to *Hantzschia amphioxys* in his cultures from soils. Found in great abundance on well-cultivated soils (Lund, 1946). Reported by Forest, et al. (1959) in a study of algal colonization of prairie soils. Found by Bock (1963) in a collection from dry rocks.
Navicula taatula Hust. var. taatula

Slide: 1-25-70 18:3

Reference: Hustedt 1962, p. 250, Text Fig. 1375.

Found in collections from stations 1, 18, and 19.

Reported from liverworts above water by Hustedt (1949a), from soil by Bock (1963, 1970), and from prairie swale collections by Reimer (1970).

Navicula tenelloides Eust. var. tenelloides

Slide: 1-25-70 18:5

Reference: Patrick and Reimer 1966, p. 534; Hustedt 1957, Text Fig. 38-39.

Several specimens found in collections from station 18.

Considered by Hustedt (1942, 1957) to be an aerophil of rather genera distribution, an aerophil by Krasske (1948) and Patrick and Reimer (1966). Found in soil by Lund (1946). Found among mosses and algae at the water surface by Hustedt (1957), among mosses and liverworts by Hustedt (1942), and on an undercut rock fact of a waterfall by Stoermer (1962).

Navicula viridula var. argunensis Skvortzov

Slide: 1-25-70 18:2

Reference: Skvortzov 1938a, p. 408, Pl. 1, Fig. 9, 33.

Two specimens found in collections from station 18.

No reports of occurrence in aerial habitats found.

Navicula sp. 1

Slide: 1-25-70 18:6

Found in collections from station 18.
Navicula sp. 4
Slide: 5-19-69 18:5
Found four specimens in collections from stations 1, 18, and 19.

Navicula sp. 6
Slide: 4-11-70 19:4
Found only one specimen in a collection from station 19.

Navicula sp. 7
Slide: 9-21-69 1:1
Found in collections from stations 1 and 19.

Navicula sp. 9
Slide: 9-21-69 11:1
Found only one specimen in a collection from station 11.

Neidium Pfitzer

Neidium affine (Ehr.) Pfitzer var. affine
Slide: 1-25-70 18:6
Reference: Reimer 1959, p. 7, Pl. 1, Fig. 1.
Found in collections from station 18.
Apparently infrequently found in aerial habitats. Reported by Bunt (1954) to be very rare in two samples of Macquarie Island soils.

Neidium affine var. capitata Wälder
Slide: 4-11-70 18ab:2
Reference: Foged 1960, p. 14, Text Fig. 11.
Several frustules found in one collection from station 18.
No reports of occurrence in aerial habitats found.
Neidium bisulcatum (Lagerst.) P. T. Cleve var. bisulcatum

Slide: 6-6-70 18:6

Reference: Patrick and Reimer 1966, p. 397, Pl. 36, Fig. 5.

Found in only one collection from station 18.

Found in an enriched culture of soil algae by Lund (1946), who stated that it is probably not a soil diatom. Found (with N. bisulcatum f. undulata O. Müll.) by Krasske (1932) in samples from cliffs and mosses.

Reported from wet mosses by Hustedt (1934).

Neidium bisulcatum var. baicalense (Skv. & Meyer) Reimer

Slide: 5-19-69 18:3

Reference: Patrick and Reimer 1966, p. 397, Pl. 36, Fig. 6.

Found in collections from station 18.

No reports of occurrence in aerial habitats found.

Neidium sp. 1

Slide: 4-11-70 18EMd:5

Found in collections from stations 1 and 18.

Neidium sp. 2

Slide: 1-25-70 18:1

Only one specimen found in a collection from station 18.

Nitzschia Hassall nom. cons.

Nitzschia amphibia Grun. var. amphibia

Slide: 9-21-69 1:1

Reference: Hustedt 1930, p. 414, Text Fig. 793.

Found in collections from stations 1, 2, 3, 11, 18, and 19.
Reported by Beger (1928) on mosses from a waterfall, by Petersen (1928a) from moist rocks and soil, and by Krasske (1932) from moist mosses. Found in soil by Fritsch and John (1942), and in dry lake beds by VanLandingham (1966). Found by Reimer (1970) in prairie swale collections as well as in samples of plankton from intermittent standing water. Thought by Petersen (1928a) to be unable to withstand much desiccation.

**Nitzschia apiculata** (Greg.) Grun. var. *apiculata*

Slide: 6-6-70 6:3

Reference: Hustedt 1930, p. 401, Text Fig. 765.

Only one frustule found in a collection from station 6. Probably an accidental.

No reports of occurrence in aerial habitats found.

**Nitzschia communis** var. *hyalina* Lund

Slide: 5-19-69 18:3

Reference: Lund 1946, p. 104, Text Fig. 13G-K.

Found in collections from stations 18 and 19.


**Nitzschia denticula** Grun. var. *denticula*

Slide: 6-15-69 Sl-20:6

Reference: Hustedt 1930, p. 407, Text Fig. 780.

Only one frustule found in a supplementary collection. Probably an accidental.

Reported by Krasske (1932) from dry mosses. Found by Hustedt (1949a) among mosses from granite cliffs.
Nitzschia linearis (Ag.) W. Smith var. linearis

Slide: 4-11-70 18EMd:1
Reference: Hustedt 1930, p. 409, Text Fig. 784.
Found in one collection from station 18.
Reported by Krasske (1932) to be abundant among moist mosses.
Found by Stoermer (1962) on the undercut rock face of a waterfall.

Nitzschia parvula var. terricola Lund

Slide: 9-21-69 11:1
Reference: Lund 1946, p. 97, Text Fig. 14A-I.
Found in collections from stations 1, 11, 12, and 18.
Originally found in moderate numbers in a soil plate culture by Lund (1946). Found by Reimer (1970) in soil and duff from a prairie swale.

Nitzschia sp. 1

Slide: 9-21-69 1:1
Found in collections from stations 1, 12, 13, 16, 18, and 19.

Nitzschia sp. 2

Slide: 5-19-69 18:3
Found in collections from station 18.

Pinnularia Ehrenberg nom. cons., non Lindley et Hutton

Pinnularia borealis Ehr. var. borealis

Plate IX, Fig. 1-13; Plate XI, Fig. 6, 7.
Slides: 9-21-69 14:4; 1-25-70 6:1; 6-6-70 14:2.
Reference: Cleve-Euler 1955, p. 32, Fig. 1037a,b,d,h.
Found in collections from all stations except station 16.
Generally regarded as one of the most common soil diatoms. Considered to be eutererestrial by Petersen (1935), a bryophilous species of the xeric type by Beger (1928), a typical moss inhabitant by Krasske (1938). Found among bryophytes by Krasske (1932), Skvortzov (1937a, 1938c), Petersen (1934) and Beger (1927). Reported from soils by Lund (1946), Petersen (1928a), Bunt (1954), Forest (1962), and Rosa and Lhotský (1971). Found by Bock (1963, 1970) in numerous collections from extremely dry habitats.

Great variation in shape, striae length and angle, and central areas was found in the cells observed. Assignment of specimens to infra-specific categories will not be made at this time because of the great variability and possible intergradations between some of the described varieties and forms. The cells measured ranged from 20-45 microns in length, from 5-9 microns in breadth, and had 4-6 striae in 10 microns. The valve ends varied from rounded and slightly tapered to rectangular. The striae ranged from marginal (very short) to long (nearly reaching the raphe). The longer striae were usually radiate at the center of the valve and convergent at the ends. Cells with long striae had central areas formed by either the shortening or the absence of central striae. Central areas were lacking in cells with short marginal striae.

Pinnularia borealis var. congolensis Zanon

Plate VIII, Fig. 4, 5.

Slide: 6-6-70 6:5

Reference: Zanon 1938, p. 641, Plate 1, Fig. 27.

Found in collections from stations 5 and 6.
Pinnularia brebissonii (Kütz.) Rabh. var. brebissonii

Slide: 5-19-69 18:4

Reference: Patrick and Reimer 1966, p. 614, Pl. 58, Fig. 6.

Found in collections from stations 1 and 18.

This taxon is often cited as P. microstauron var. brebissonii (Kütz.) Hust. Reported from mosses by Beger (1928) and from damp rocks by Petersen (1928a). Found in soil by Lund (1946) and Bunt (1954). Considered by Petersen (1935) to be hydrophytic and hydroterrestrial.

Pinnularia brebissonii var. diminuta (Grun.) P. T. Cleve

Slide: 1-25-70 18:4

Reference: Patrick and Reimer 1966, p. 616, Pl. 58, Fig. 7.

Found in collections from stations 18 and 19.

This taxon is often cited as P. microstauron var. brebissonii f. diminuta Grun. Reported by Reimer (1970) from a collection of soil and duff from a prairie swale. Considered by Bock (1970) to be an accidental in collections from dry rocks and walls.

Pinnularia obscura Krasske var. obscura

Slide: 4-11-70 13:2

Reference: Patrick and Reimer 1966, p. 617, Pl. 58, Fig. 9.

Three specimens found, two in a collection from station 5 and one in a collection from station 13.

Pinnularia viridis var. intermedia P. T. Cleve

Slide: 6-6-70 13:1

Reference: Cleve-Euler 1955, p. 74, Fig. 1103c, d.

Found in collections from stations 18 and 19.

No reports of occurrence in aerial habitats found.

Pinnularia sp. 1

Slide: 4-11-70 18ab:6

Found in collections from stations 18 and 19.

Stauroneis Ehrenberg

Stauroneis anceps Ehr. var. anceps

Slide: 4-11-70 18ab:8

Reference: Patrick and Reimer 1966, p. 361, Pl. 30, Fig. 1.

Found in collections from station 18.


Stauroneis borrichii (Petersen) Lund var. borrichii

Slide: 4-11-70 18EMd:4

Reference: Hustedt 1959, p. 803, Text Fig. 1151a.

Found in collections from stations 17 and 18.

**Stauroneis phoenicenteron** (Hatzsch) Ehr. var. phoenicenteron

Slide: 6-6-70 18b:1

Reference: Hustedt 1959, p. 766, Text Fig. 1118a.

Found in collections from stations 18 and 19.

Apparently not common in dry habitats. According to Krasske (1932), rather abundant in brooks, ditches, and puddles. Occurred on mosses and liverworts above the water surface (Hustedt, 1942). Reported as an accidental by Bock (1970) in collections from dry rocks and walls.

**Stauroneis sp. 1**

Slide: 4-11-70 19:4

Found in collections from stations 18 and 19.

**Stauroneis sp. 2**

Slide: 6-6-70 18:3

Found in collections from stations 18 and 19.

This taxon is similar to *S. ignorata* var. *rupestris* (Skv.) Reimer in striae count, the shape of the central fascia and the presence of thickenings at the margins of the fascia. However, the proximal raphe ends are more distant, and the valve margins of all specimens found are distinctly convex like those of *S. smithii* var. *incisa* Pantocsek. Because one of the critical characteristics of *S. ignorata* var. *rupestris* is parallel valve margins, *Stauroneis* sp. 2 will remain unnamed until additional specimens including type material are examined.
Surirella Turpin

**Surirella angusta** Kütz. var. angusta

Slide: 6-6-70 1:1

Reference: Hustedt 1930, p. 435, Text Fig. 844-845 (as *S. angustata* Kütz.)

Found in collections from stations 1, 18, and 19.

Apparently uncommon in dry habitats. Found by Hustedt (1942) on mosses and liverworts above water level, by Bunt (1954) on one Macquarie Island soil, and by Bock (1963, 1970), who regarded it as an accidental in collections from dry rocks and walls.

**Surirella ovata** Kütz. var. ovata

Slide: 6-6-70 1:1

Reference: Hustedt 1930, p. 442, Text Fig. 864.

Found in collections from stations 1, 18, and 19.

Apparently uncommon in aerial habitats. Found by Hustedt (1942) on mosses and liverworts above water level. Lund (1946) reported it as occurring in 24 soil collections but rarely in large numbers. Reported from soils by Hayek and Hulbary (1956). Regarded by Bock (1963, 1970) as an accidental in collections from rocks and walls.

**Surirella ovata** var. pinnata W. Smith

Slide: 6-6-70 18:4

Reference: Hustedt 1930, Text Fig. 865.

Found in collections from station 18.

Found by Hustedt (1942) on mosses growing on a post above water. Two specimens reported by Stoermer (1962) from moist rocks near the base of a waterfall.
Plate I

Fig. 1-2. Hantzschia amphioxys var. amphioxys X 2000
Fig. 3. Hantzschia amphioxys f. capitata X 2000
Fig. 4. Hantzschia amphioxys var. amphioxys X 2000
Fig. 5. Hantzschia amphioxys f. capitata X 2000
Fig. 6-7. Hantzschia amphioxys var. amphioxys X 2000
Plate II

Fig. 1-2. *Hantzschia amphioxys* var. *amphioxys* X 2000
Fig. 3. *Navicula charlatii* f. *simplex* X 2000
Fig. 4-5. *Hantzschia amphioxys* var. *amphioxys* X 2000
Fig. 6a-b. *Hantzschia amphioxys* var. *amphioxys* at two levels of focus X 2000
Plate III

Fig. 1a-b. Colony of *Hantzschia amphioxys* var. *amphioxys* with two spiny cells on either side of the central cell (two levels of focus) X 1000

Fig. 2. Colony of *Hantzschia amphioxys* var. *amphioxys* with one spiny cell on each side of the central cell X 1000

Fig. 3a-b. Colony of *Hantzschia amphioxys* var. *amphioxys* with one spiny cell on either side of the central cell (two levels of focus) X 1000

Fig. 4a-b. Colony of *Hantzschia amphioxys* var. *amphioxys* containing three spiny cells (two levels of focus) X 1000

Fig. 5. Valve of *Hantzschia amphioxys* var. *amphioxys* with abnormal striae X 2000

Fig. 6a-b. Cell of *Hantzschia amphioxys* var. *amphioxys* with a normal valve (a) and an abnormal valve (b) X 2000
Plate IV

Fig. 1. Surface of a normal valve of *Hantzschia amphioxys* var. *amphioxys* (spines from plate below are visible) X 2000

Fig. 2. Abnormal valve of *Hantzschia amphioxys* var. *amphioxys* X 2000

Fig. 3a-c. Spine-bearing plate of *Hantzschia amphioxys* var. *amphioxys* at three levels of focus X 2000

Fig. 4. Surface of a normal valve of *Hantzschia amphioxys* var. *amphioxys* (spines from the plate below are visible) X 2000

Fig. 5a-d. Spine-bearing plate of *Hantzschia amphioxys* var. *amphioxys* at four levels of focus (the tips of the plate have been broken off) X 2000
Plate V

Fig. 1-19. *Navicula mutica* var. *mutica* X 2000
Plate VI

Fig. 1-21. *Navicula mutica* var. *mutica* X 2000
Plate VII

Fig. 1a-c. *Navicula mutica* var. *mutica*? auxospore at three levels of focus X 2000

Fig. 2. Abnormal valve of *Navicula mutica* var. *mutica* X 2000

Fig. 3. *Navicula mutica* var. *mutica*? auxospore X 2000

Fig. 4. *Navicula mutica* var. *mutica* auxospore X 2000

Fig. 5a-b. *Navicula mutica* var. *mutica* auxospore at two levels of focus X 2000

Fig. 6. *Navicula mutica* var. *mutica*? auxospore X 2000

Fig. 7. Nearly typical valve of a daughter cell of a *Navicula mutica* var. *mutica* auxospore X 2000
Plate VIII

Fig. 1. *Navicula mutica* f. *undulata* X 2000
Fig. 2. *Navicula dismutica* var. *dismutica* X 2000
Fig. 3. *Navicula mutica* var. ? X 2000
Fig. 4-5. *Pinnularia borealis* var. *congolensis* X 2000
Fig. 6-10. *Navicula neoventricosa* var. *neoventricosa* X 2000
Fig. 11-16. *Navicula mutica* f. *intermedia* X 2000
Plate IX

Fig. 1-13. *Pinnularia borealis* var. *borealis* X 2000
Plate X

**Fig. 1-8.** *Navicula mutica var. mutica* (electron micrographs) X 4000

**Fig. 9.** *Navicula mutica var. mutica* abnormal valve. Soil particles have obscured some of the puncta (electron micrograph) X 4000
Plate XI

Fig. 1. Navicula contenta var. biceps (electron micrograph) X 4000
Fig. 2. Navicula neoventricosa var. neoventricosa (electron micrograph) X 4000
Fig. 3-5. Navicula mutica var. mutica (electron micrographs) X 4000
Fig. 6-7. Pinnularia borealis var. borealis (electron micrographs) X 4000
Fig. 8-9. Navicula mutica f. intermedia (electron micrographs) X 4000
DISCUSSION

The Diatom Flora of Prairies—Observations of Diversity

During the course of this study 74 diatom species, varieties, and forms belonging to 15 genera were encountered. Of these, four taxa have not, to my knowledge, been previously reported from Iowa. They are *Navicula charlatii* f. *simplex*, *Navicula contenta* var. *parallela*, *Navicula dismutica*, and *Pinnularia borealis* var. *congolensis*. Seventeen of the 74 taxa encountered were represented by only a single specimen in all the material examined and were therefore considered to be accidentals.

Several investigators (Brown, Larson, and Bold, 1964; Luty and Hoshaw, 1967; Schlichting, 1961, 1964; Loescher, unpublished data) have found viable diatoms in the atmosphere. The diatoms I have regarded as accidentals may have been transported in various ways as empty frustules or as living cells incapable of reproducing on the prairie.

In a study of the diatoms of another Iowa prairie, Cayler Prairie, Reimer (1970) reported 70 species, varieties, and forms belonging to 14 genera. Reimer examined six collections, two of which were plankton net samples from standing water. Three were collections from a swale, and one was from a drier upland site. Of the 70 taxa encountered in Cayler Prairie, only three taxa were restricted to the plankton collections.

A comparison of the diatom floras of Sheeder and Cayler prairies shows that the two areas have 11 genera in common. They are *Achnanthes*, *Amphora*, *Caloneis*, *Fragilaria*, *Gomphonema*, *Hantzschia*, *Meridion*, *Navicula*, *Nitzschia*, *Pinnularia*, and *Stauroneis*. Of those genera not represented in both floras, *Diploneis*, *Rumotia*, and *Rhopalodia* were found only in
Cayler Prairie; Cymbella, Frustulia, Neidium, and Surirella were found only in the Sheeder flora. Although at least 70 species, varieties, and forms were encountered in each study, only 19 were found in both prairies. The dissimilarity of the floras is not surprising when the differences in water availability at the collections sites are considered. Only one of the Cayler collections was made from a relatively dry habitat, whereas most of the Sheeder Prairie collection sites are considered relatively dry. Of the 19 taxa common to the two prairies, seven were found only at the wettest of the Sheeder collection sites (stations 18 and 19) and four were found at the wettest sites as well as at a station down the drainage way from them (station 1). Two of the taxa were considered to be accidentals. Thus 13 of the 19 taxa found in both prairies were encountered at fewer than four collection sites on Sheeder Prairie. Differences in taxonomic philosophy probably account for a few taxa not being reported in both studies.

Many factors—the availability of light, water, and nutrients; temperature; interactions with other organisms; etc.—affect the survival and reproduction of diatom species and, as a result, influence the composition of the flora of a particular habitat. Because little is known of the requirements of individual taxa, the presence of particular taxa at certain sites on Sheeder Prairie cannot, for the most part, be explained. The availability of water in aerial habitats, however, apparently has a marked effect on the diversity of the flora. The difference between the number of taxa observed at upland and lowland sites on Sheeder Prairie is particularly striking. Collections from three upland sites, stations 9, 14, and 15, all of which were located in
stands regarded by Kennedy (1969) are relatively dry, yielded five, three, and four taxa, respectively. In contrast, 56 and 31 taxa were found at stations 18 and 19, respectively, the only stations where standing water was observed. A similar difference in diversity was noted by Reimer (1970), who found eight taxa in a collection from a Cayler Prairie upland and 47 taxa in a collection made the same day from a prairie swale.

Two collections from station 1 (those made on September 21, 1969, and June 6, 1970) contained many taxa which were otherwise encountered only in collections from stations 18 and 19. Because other collections from station 1 contained few specimens, and because station 1 is located below stations 18 and 19 in the same drainage way, it is probable that the additional taxa were carried downslope by run-off water.

No more than a few diatom cells were found in any collection from station 17, the site of a haystack ca. 1965. No explanation for the depauperate flora can be given. Collections from stations 2 and 3, which were located in similar low alluvial areas but which had not been recent haystack sites, yielded four and five taxa, respectively, and these were present in moderate numbers.

The three diatom taxa that are generally considered to be the most common in non-aquatic habitats all were found in collections from Sheeder Prairie. Hantzschia amphioxys var. amphioxys and Navicula mutica var. mutica were found in collections from all sampling stations, while Pinnularia borealis var. borealis was found in collections from all stations except station 16. Navicula contenta var. biceps and Navicula mutica f. intermedia were each found in eight stations; Hantzschia amphioxys f. capitata and Nitzschia amphibia var. amphibia were found in
collections from six sampling sites. The latter four taxa have been found in non-aquatic collections by several investigators.

Apparent Selection Against Rapheless Species

It is recognized that most terrestrial diatoms belong to the order Pennales and that most of these also have a true raphe (Petersen, 1915, 1928a; Patrick and Reimer, 1966). Because the diatoms that possess a raphe are motile, it is thought that they are able to move into moister areas as the soil dries and to return to the soil surface after being washed into deeper layers by rain (Petersen, 1928a, 1935; Lund, 1945; Patrick and Reimer, 1966). Lund (1945) observed that when water films were no longer seen around soil particles, diatom movement ceased; when water was then added, many of the cells began to move again.

Only two of the 15 genera represented in the Sheeder Prairie flora, Fragilaria and Meridion, are rapheless. Each of the four Fragilaria taxa observed was represented by only a single cell or valve and was therefore considered to be an accidental. Meridion circulare, which was found, often abundantly, in all collections from station 18, is considered to have been growing at this site. This taxon was also found at station 19, where, as at the adjacent station 18, standing water was observed on two occasions. The specimens of M. circulare observed in collections from station 1 were probably carried down the drainage way by run-off water.

The five rapheless taxa found by Reimer (1970) in the Cayler Prairie flora also belong to Fragilaria (three species) and Meridion (two varieties). Of these only Fragilaria crotonensis Kitton was not found in soil and duff collections. Other studies of non-aquatic diatom
diatom floras in Iowa have yielded similar results. Stoermer (1962) observed one species of centric diatom (*Melosira roeseana* Rabh.) and no pennate diatom taxa that lack raphes in a collection from the base of a waterfall. Among diatoms associated with lichens and mosses, Dodd and Stoermer (1962) found one centric species (*Melosira roeseana*) and no pennate diatoms lacking raphes. Hayek and Hulbary (1956) found, with the exception of one frustule of *Cyclotella kuntzingiana* Thwaites, no diatom species not possessing at least one raphe in the soils they studied. Bock (1963, 1970) found a number of rapheless taxa in two studies of diatoms from extremely dry habitats in Europe. However, many were apparently accidentals as they were represented only by broken specimens or single valves. In one study, nine of the 107 taxa encountered were rapheless; of these, seven were considered accidentals (Bock, 1963). In collections from dry rocks and walls, 22 taxa of 119 encountered were rapheless; of these 12 were considered accidentals (Bock, 1970).

**Variation in *Navicula mutica***

*Navicula mutica*, long recognized as an extremely variable taxon, presents several taxonomic problems to diatomists, especially to those investigating aerial habitats where numerous morphological expressions are commonly found. Over 60 varieties and forms have been described. The multitude of names is probably due to a number of factors, including the world-wide distribution and the morphological variability of the species. It is likely that extreme forms of a variation series have been given different names because the extent of variability was unknown. To my knowledge, the degree to which the environment influences form in
Navicula mutica has not been investigated. Other sources of confusion exist in the literature. For example, Grunow (in Heurck, 1880) illustrated Kützing's type specimen of *N. mutica* and labeled it *N. mutica* var. göppertiana (Bleisch) Grunow. Grunow also listed Stauroneis cohnii Hilse as a synonym for *N. mutica* var. cohnii (Hilse) Grunow in Heurck's atlas (Heurck, 1880), but in the text of Heurck's synopsis (Heurck, 1885) he listed *S. cohnii* Hilse as a synonym for *N. mutica* Kütz.

Yet another source of confusion is the number of different concepts of *Navicula mutica* held by various authors. The main disagreement between investigators concerns the shape of the valve. Cleve (1894) said that the valves of *N. mutica* are elliptical-lanceolate and of variable shape. Meister (1913) stated that the valves are elliptical to lanceolate. Both Cleve and Meister said that the valve margins often are undulate. Skvortzov (1936) illustrated an elliptical specimen and described the shape of *N. mutica* as elliptic-lanceolate. Patrick and Reimer (1966), Bock (1963), and Hustedt (1930) stated that the valves are lanceolate with rounded ends that are sometimes slightly protracted. Later Hustedt (1966) amended his statement, saying that the valves are elliptical to elliptical-lanceolate with bluntly rounded, not protracted ends. The descriptions in the literature differ somewhat in the size ranges and striae counts given but generally agree on the shape and width of the central area, the shape of the axial area, the angle of the striae, and, in the more recent descriptions, the bends in the proximal raphe ends (Bock, 1963; Hustedt, 1966).

Bock (1963) stated that valve form is the most variable character of *N. mutica* and that, with few exceptions, it represents the single
criterion for the separation of varieties and forms. According to Bock, the change in valve form in the species proceeds in two directions. There may be continuous variation producing weakly lanceolate forms, or producing elliptical-lanceolate to lanceolate or weakly lanceolate forms that lack protracted ends. Hustedt (1937) and Bock (1963) both observed that undulate margins are found in all form groups. Hustedt (1937) stated that a combination of the varieties and forms of *N. mutica* for the purpose of nomenclatural simplification is impossible, because the variations frequently have striking characteristics and have only a limited local occurrence. Bock (1963) came to a different conclusion and stated that the variation in shape of valves within the species is so great that only a few extreme forms can be distinguished in a systematic arrangement. He further stated that since many forms have been found to be much more widely distributed than initially assumed, a combination of taxa should no longer be completely rejected (Bock, 1963, 1970).

The angle at which the isolated punctum penetrates the cell wall may not be as reliable a diagnostic character as formerly thought. Hustedt (1955, 1966) emphatically stated that the isolated punctum in the central area of *N. mutica* is a pore penetrating the cell wall perpendicularly. Two varieties having stigmas (oblique pores with heavily silicified areas around the inner apertures), *N. mutica* var. *tropica* Hust. and *N. mutica* var. *stigma* Patr., are recognized. Bock (1963) observed considerable variation in the position of the isolated punctum in various expressions of *N. mutica*. In his specimens the punctum was usually found about midway between the valve center and the valve margin, but in some cases it was near the proximal ends of the raphe. When the punctum
was located at the valve margin the pore appeared to penetrate the cell wall diagonally instead of perpendicularly. With very few exceptions, similar marginal puncta were observed in the rhombic specimens of *N. mutica* from Sheeder Prairie. I found no specimens having stigmas in the collections from the prairie.

With two exceptions (*N. mutica* f. *intermedia* and *N. mutica* f. *undulata*), the specimens of *N. mutica* found in the Sheeder Prairie collections were not assigned to infraspecific taxa because of the problems mentioned above. Three distinct forms of *N. mutica* were observed which deviated from published descriptions of similar taxa. The assignment of these forms to new infraspecific taxa should not be undertaken until specimens from other collections, including type material, have been examined. Support for the extensive foreign travel entailed in such examinations was not available.

Bock (1963) summarized his conclusions by stating that the abundance of forms in *N. mutica* cannot be completely accounted for by the changes that occur with a decrease in cell size. He suggested that the species may have a broad ecological valence and that the strikingly different habitats which it occupies might have influenced the development of many ecotypes. Although Bock (1970) recognized the need for a revision of *N. mutica*, he gave several reasons for not attempting one. One was that stunted forms, present in the material collected from habitats under extreme environmental conditions, could lead to false taxonomic interpretations. In addition, little material from aquatic habitats was available for comparison with the specimens from aerial habitats.
It seems evident that a revision of *N. mutica* and related species should encompass not only a study of type material housed in herbaria throughout the world, but also specimens and clonal cultures of specimens obtained from a variety of habitats representing the ranges of the taxa. The latter approach (clonal cultures) is particularly appealing since I have determined that the organism grows well in laboratory culture. However, the physical facilities and time required to accomplish the total evaluation are beyond the normal limits of one doctoral program.

**Internal Valves and Craticula**

Internal valves and craticula are siliceous structures produced by certain taxa. Internal valves are additional cell walls formed within the original walls and may resemble the original valves in structure. Craticula are usually described as strongly silicified plates having the same shape as the valves but having a prominent median rib and several transverse ribs. In collections from Sheeder Prairie internal valves were observed in *Meridion circulare*, *Hantzschia amphioxys*, and in species of *Neidium* and *Pinnularia* which could not be identified. Craticula were found in *Navicula cuspidata var. heribaudi*. The presence of such structures is considered significant because the formation of internal valves and craticula is regarded as a response to some unfavorable environmental condition (Geitler, 1953, 1963; Petersen, 1935; Hustedt, 1961b). Among the causes cited are desiccation (Grunow, 1882, cited by Müller, 1899), fluctuating salt content in the water (Beger, 1927; Asske, 1927), nutritional deficiency (Geitler, 1927, 1932), variation
in the concentration of the medium (Liebisch, 1929; Hustedt, 1939), and a more or less sudden increase in external osmotic pressure (Cholnoky, 1968).

Internal valves are formed by certain species of diatoms when their cells are plasmolyzed. A new valve is formed on the surface of the protoplast which has been drawn away from the cell wall (Cholnoky, 1954). At least in some species internal valves can be formed repeatedly; up to eight internal valves were observed by Hustedt (1927) in cells of *Eunotia serpentina* Ehr. and up to seven valves were seen by Beger (1927) in *Melosira dickiei* (Thwaites) Kütz. Cells which have formed internal valves apparently retain the ability to undergo cell division (Geitler, 1927; Liebisch, 1929; Cholnoky, 1954).

It has not been established whether nuclear division is always involved in internal valve formation. Hustedt (1961b) stated that internal valves originate by incomplete cell division. Geitler reported that mitosis and cytokinesis are involved in the formation of internal valves in *Eunotia pectinalis* (Kütz.) Rabh. (Geitler, 1953, 1963) and *Meridion circulare* (Grev.) Ag. (Geitler, 1963). In these species the two daughter protoplasts produced by cell division under unfavorable environmental conditions are very unequal in size. The smaller protoplast is incapable of forming a new valve and degenerates, but the larger, normal-sized protoplast produces an internal valve that is typically curved inward at the ends and that lies within the epitheca of the mother cell. Cholnoky (1968) was not convinced that abortive nuclear division always precedes internal valve formation in *E. pectinalis*. He suggested that, following cell division, cell extension is inhibited by excess osmotic pressure in the environment.
and internal valve formation results. He postulated that weak increases in environmental osmotic pressure do not produce plasmolysis in non-dividing cells but they decrease the turgor pressure in dividing cells so abnormal cell division results.

The observed cells of *Meridion circulare* having internal valves were identical in structure to those described by Geitler (1963). A few frustules of *Neidium* sp. with internal valves were found in girdle view. Because of the position of the specimens the species could not be identified and the internal valves could not be described. The arrangement of the extra valves, however, was like that described for *Navicula (Anomoeoneis) sphaerophora* (Geitler, 1927) and *Eunotia serpentina* Ehr. (Hustedt, 1927). Because the three specimens of *Pinnularia* found with extra valves were in girdle view, no description of their structure is given.

The spiny plates I have observed in *Hantzschia amphioxys* are similar in most respects to those illustrated and described as internal valves by Krasske (1949). The examples Krasske observed, however, possessed spines but lacked striae; those I found had both spines and striae. The colonial structure I observed in the spiny clusters of *H. amphioxys* is similar to that illustrated by Bock (1970) for *H. fenestrata* Hustedt., which, he stated, apparently forms internal valves in the same manner as *H. amphioxys*.

In most species in which internal valve formation has been described, the internal valves are produced within the original valves of the cell and are consequently smaller. If additional internal valves are produced, they form within the innermost internal valves (Geitler, 1927, 1953;
Hustedt, 1927; Cholnoky, 1954). Although extra valves can be formed repeatedly in *H. amphioxys*, the resulting structure is unlike that described for most taxa. The outer, presumably older valves are not necessarily longer than the inner valves; in some cases they are markedly shorter than the inner valves (Plate III, Fig. 1, 4). It is possible that the larger original cell walls had been shed, but it is unlikely that this would have occurred in all of the many colonies studied. In addition, a spine-bearing plate is frequently found associated with an extra valve. The relationship of the outer valve to the spine-bearing plate is similar to that of epitheca to hypotheca. Although I have found no description in the literature of production of a similar structure by another taxon, the *H. amphioxys* colonies might originate in a manner similar to the internal valve formation in *Eunotia pectinalis* and *Meridion circulare*. If so, colonies with several spiny frustules would originate by repeated unequal cell division, and the few specimens in which no spiny plates were produced could be explained either by degeneration of the smaller protoplast before the plate was formed or by a lack of cell division with the plasmolyzed protoplast simply producing an internal valve. The case of the central protrusion often visible in the middle of the central cell of a colony when seen in girdle view (Plate III, Fig. 1, 3) might be explained by a cell, formerly under water stress, producing intercalary bands under conditions of increased water availability. Whatever the explanation, these hypotheses for the development of internal valves in *H. amphioxys* presented above must be tested by study of the formation of these structures under laboratory-induced stress. Further morphological
examinations of the spine-bearing plates and other components of the colonies should also be undertaken.

It has been questioned whether craticula can be compared with internal valves. Cholnoky (1968) stated that the two structures cannot be compared directly, even though they evidently are formed under the same environmental influences. He suggested that craticula decrease cell volume and thus elevate the osmotic pressure within the cell, but he had no evidence to support his hypothesis. He further stated that, unlike internal valves, craticula are not formed on the plasmolyzed surfaces of the protoplast. Craticula and internal valves thus differ developmentally as well as structurally.

The survival value of internal valves has been disputed for many years. Pfitzer (1871) considered cells having internal valves to be resting stages that enable cells to withstand unfavorable conditions. Petersen (1928a, 1935) regarded them as teratologic formations produced under unfavorable conditions, rather than a kind of resting cell. Hustedt (1939) thought that the protection of the cell against desiccation was only a secondary attribute of the structure. Cholnoky (1968) suggested that the diatom species capable of forming internal valves or craticula have a significant ecological advantage over other taxa in habitats with fluctuating osmotic pressure, since the development of unadapted species is apparently inhibited by sudden increases in osmotic pressure. He characterized biotopes favoring the formation of internal valves as freshwater habitats in which the osmotic pressure is increased by strong evaporation during a portion of the year.


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